

HEAD ACCELERATION DURING BALANCE

by

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Abstract

The overall purpose of this thesis was to study the angular and linear accelerations that occur at the head during quiet standing in healthy humans. To date, there were few descriptions of linear head accelerations in quiet standing, and no focus on angular head accelerations. The contribution of the vestibular system to standing balance can be better understood from recognizing these, the stimuli that the system experiences during the task.

Head accelerations were measured under four manipulations of sensory condition, and RMS and median frequency values were reported for linear and angular head accelerations in Reid's planes. Coherence was also calculated between force plate forces and head accelerations, and between lower leg EMG and angular head accelerations in the directions of the semi-circular canals. This study considered two factors in the manipulation of quiet standing sway: vision (eyes open/closed) and surface (hard/compliant foam).

The results show that angular head accelerations are repeatable under full sensory conditions, and that angular head acceleration RMS is above known vestibular thresholds in all tested sensory conditions. Linear head acceleration absolute maximum and RMS values matched previous reports under similar conditions. Significant coherence was found below 7Hz in both coherence analyses, likely due to the mechanical linkage. This coherence also showed defined troughs in varying regions, which were attributed to the interference of active systems (visual, somatosensory and vestibular) on the mechanical propagation of forces. The results also reinforced that the inverted pendulum model is valid in quiet standing on a hard surface in the sagittal and frontal planes.

This study shows that the vestibular system is able to detect sway at the head during quiet standing under all four sensory conditions tested. Consequently, the vestibular system may play a range of roles in quiet standing, which may change as its relative importance in

balance increases. The measurement of head accelerations is confirmed as a useful technique in studying balance in quietly standing humans.

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Literature review

Balance and sway

Balance is the critical task of preserving equilibrium of the body segments with respect to gravity. This task requires maintenance of the body's center of mass within the base of support, although stabilization of the trunk and head in space may take priority during balance (Horak & MacPherson, 1996; Latt et al., 2008). Muscle stiffness and tonic activity, including paradoxical muscle contractions, can account for a proportion of the successful execution of balance, as can passive joint stiffness and long-latency functional stretch reflexes (Horak & MacPherson, 1996; Nashner, 1976). Balance is no simple task, however, and it requires the convergence of many types of sensory information to achieve. The everyday posture of quiet standing uses input from three main sensory systems: somatosensory, visual and vestibular. The many channels of available sensory information lead to redundancies, which help in the interpretation and disambiguation of each sense's output. Exactly how this information is used to accomplish balance is not fully understood, but it is known to be dependent on task and context (Horak & MacPherson, 1996).

It is well known that people sway while standing quietly, and that the amount and quality of information available from these three sensory systems affects that sway (as do other factors). Sway during quiet standing in healthy humans is usually described as an inverted pendulum, with responses to regular sway controlled by rotations around the ankles (Horak & MacPherson, 1996; Winter, 1995). Within this inverted pendulum model, healthy humans with all sensory information available sway maximally at about 0.3 Hz as measured at the center of mass (CoM, displacement in both mediolateral and anteroposterior directions). In power spectral density

estimates, studies have found most CoM sway power below 1Hz (Jeka et al., 2004), although some power up to 5Hz has been reported (summarized in Winter, 1995). Power spectral density estimates of center of pressure (CoP) data have similar results: 90% of power is below 2Hz, with maximums between 0.30-1.20 Hz in the anteroposterior direction, and 0.30-0.90 Hz in the mediolateral direction (Soames & Atha, 1982). These results were based on sampling durations of 4 minutes, and therefore were long enough to catch low-frequency components of sway according to Carpenter et al. (2001).

Factors affecting sway

Sway during quiet stance is greatly affected by a number of factors, and thus can be affected by eliminating or producing errors in the signals from the three sensory systems that maintain standing balance: somatosensory, visual and vestibular.

Somatosensory contributions to balance (including skin touch, pressure and proprioception) is often measured with patients with peripheral neuropathy (Lafond et al., 2004; Simoneau et al., 1994), or in healthy subjects by providing erroneous somatosensory information. This erroneous signal can be achieved by having the subject stand on a sway-referenced platform (as in Nashner, 1971) or a block of thick foam (Horak & MacPherson, 1996; Jeka et al., 2004). Both of these methods limit the usefulness of the somatosensory afference, mostly from the feet and ankles. These methods have shown that sway amplitude as measured from the center of pressure or center of mass increases when subjects have less somatosensory information available to them (Dietz, 1992; Horak & MacPherson, 1996; Jeka et al., 2004). Sway can be reduced by introducing further somatosensory information, for example, by touching something stationary and external with another part of the body. This extra information decreases

sway even when vision is present (Jeka & Lackner, 1994). Touching one's own body can also decrease sway (Nagano et al., 2006).

Visual information is also used to stabilize sway in standing. People with their eyes closed sway 30% more than they do with their eyes open in a feet-apart stance (as reported by Romberg, reviewed in Horak & MacPherson, 1996). It has also been shown that the variability of postural sway is decreased when the eyes are engaged in a tracking task (Stoffregen et al., 2007). Vision is thought to contribute most to standing balance in frequencies below 1Hz (Diener & Dichgans, 1988).

The vestibular system is likely the least understood of the sensory systems that contribute to balance. Patients with vestibular lesions are often tested to try to decipher the importance of vestibular input to the maintenance of quiet stance, although erroneous signals can also be introduced to a healthy population by electrical stimulation. Patients with bilateral vestibular loss can exhibit sway within the range of normals when under full sensory conditions (Dietz, 1992; Yoneda & Tokumasu, 1986). They are usually able to stand without one of the two remaining balance systems (somatosensory and vision), but without both they will fall when attempting to stand quietly (Nashner et al., 1982). This is strong evidence for some role for vestibular input during quiet standing, yet Fitzpatrick and McCloskey (1994) found that healthy people cannot consciously perceive vestibular inputs while standing quietly, while somatosensory (proprioceptive) and visual inputs were consciously perceived during normal sway. The authors noted that subconscious processing of vestibular inputs is likely. Indeed, in 1982 Nashner, Black and Wall (Nashner et al., 1982) suggested that vestibular information was not used consciously as an indicator of instability. They proposed that vestibular input was processed subconsciously at a high level, and used as an internal reference by which to resolve conflicts in visual and

somatosensory information. This view of the vestibular system as more of a 'quiet partner' in standing balance is also supported by Day and Fitzpatrick, who call the vestibular system the "silent sense" in balance (Day & Fitzpatrick, 2005). It also may be supported by the presence of a whole-body balance response to selective electrical stimulation of the vestibular organs (Fitzpatrick & Day, 2004), for if the vestibular system created responses without other sensory input, one might expect the response to be confined to the head.

It may appear that the vestibular system is a prime candidate for an internal reference of the vertical (the direction of the gravity vector). This hypothesis is further supported by studies that show illusory sway in supported subjects presented with artificial vestibular signals (Horak & Macpherson, 1996). However, experiments conducted in an environment lacking much useful somatosensory information (in this case, immersion in a tank of water) found that estimates of the direction of the vertical under these vestibular-dependent conditions were highly erroneous compared to a land-based condition with intact somatosensory sense (± 20 degrees vs. $\pm 1-2$ degrees; Nelson, 1968; Horak & Macpherson, 1996). It appears, therefore, that the vestibular system alone does not account for an internal reference to the vertical.

Another proposed main use for vestibular contributions in standing is active stabilization of the head in space (Horak & Macpherson, 1996). It has been shown that patients with complete vestibular loss refrain from using a hip strategy when perturbed (which is the situation in which a control subject would likely use a hip strategy; recall that the ankle strategy is principal in quiet standing). The hip strategy requires a counterrotation of the head and trunk, and tends to stabilize the head to the environment. The reluctance of vestibular patients to adopt this strategy seems to show that they have difficulty with active head stabilization (Horak & Macpherson, 1996; Black et al., 1988), perhaps due to their vestibular lesion. As reviewed in the following sections, the

vestibular system is designed to detect head motion, and therefore seems a most suitable candidate for the active stabilization of the head in space.

The vestibular system may also contribute to standing balance through the execution of the vestibulospinal reflex. This reflex as evoked by electrical stimulation of the vestibular nerve has been shown to increase in magnitude in the lower leg muscles under ‘vestibular dependent’ standing conditions (for example, eyes closed on a compliant surface; Welgampola & Colebatch, 2001). Welgampola and Colebatch (2001) thought that this might point to the vestibular system as a “backup” sensory system, intended to maintain balance when vision and somatosensory senses have “failed”.

It may be that the vestibular system in quiet standing is used for all or none of: resolving alternative sensory conflict; an internal reference of the vertical; active head stabilization; or the amplitude modulation and release of the vestibulospinal reflex. There are of course other possibilities, as much remains unknown about the normal uses of this system in quiet stance. One of the reasons for this may be the way that this system has mainly been studied in the past.

As previously mentioned, the vestibular contributions to standing in humans have mostly been inferred from studies using vestibular lesion patients. However, these patients have almost certainly been afflicted with their condition for long periods of time and may have already adapted to their deficit, using other sensory systems in compensatory strategies that are not well understood. Indeed, studies in cats show that otherwise healthy animals who have been bilaterally lesioned have substantial deficits in balance (including an inability to stand at all) immediately following the lesion (Macpherson & Inglis, 1993). These animals appeared to adapt rapidly and by the end of the first month had regained the ability to stand and walk stably. Studies using vestibular lesion patients, then, include a confounding factor in regards to the

compensation strategies that adapted lesion patients develop over time. Therefore, it remains unclear how vestibular information is used during standing sway in healthy humans under different sensory conditions. A closer look at the vestibular system's location, anatomy and neurophysiology may aid in deciding how this could best be explored.

Anatomy and neurophysiology of the vestibular system

The human vestibular system is located in the inner ear on both sides of the head, rigidly embedded in the skull. It is a continuous bony structure lined with membrane and filled with fluid. The system consists of two different types of structures: the three semi-circular canals and the two otolith organs.

Semi-circular canals

Location and orientation

The semi-circular canals (SCCs) are three ducts located within bony loop-shaped cavities embedded in the inner ear, within the petrous part of the temporal bone (Drake et al., 2005). These canals are approximately mutually orthogonal and are called the horizontal (or lateral), posterior, and anterior (or superior) canals. The SCCs are generally considered responsible for the detection of angular acceleration of the head in their respective planes.

A recent study involving CT scans of human skulls revealed detailed information on the orientations of the SCCs within the skull (Della Santina et al., 2005). The researchers used reference planes that are commonly used to landmark skull locations, called Reid's planes. To define these planes, the interaural axis was first located. This is the axis connecting the points at the center of each bony external auditory canal. Z_{REID} was thus defined as the plane that contained the interaural axis and the points on the edge of the most inferior part of each

infraorbital rim (this is also known as the Frankfort plane; Drake et al., 2005). The plane was over defined, but the study found all points to lie within 0.5mm of it. Y_{REID} was defined as the plane bisecting and perpendicular to the interaural axis, and X_{REID} was the plane perpendicular to Z_{REID} and containing the interaural axis. The origin was located at the center of the left external auditory canal. The orientations of the canals were found in relation to these reference planes. The horizontal canal was angled upwards towards the eyes at approximately 20 degrees to Z_{REID} . The posterior and anterior canals were both perpendicular to the horizontal canal, and were at approximately 48.5 (+/- 5.1) degrees and 38.4 (+/- 5.1) degrees to the Y_{REID} plane, in opposing directions. The SCCs were found to be very close to being mutually orthogonal, but were not. This means that rotation about any axis would inevitably stimulate more than one SCC at a time.

Reid's axes are used in this thesis, yet it is important to note that the direction convention has been changed. In the Reid's axes used in this document, X_{REID} remains positive forward but Y_{REID} is now positive right, and Z_{REID} is positive down. All reported results use this new definition of Reid's axes.

Each of the canals has a mirrored twin in the vestibular apparatus on the opposite side of the head. The orientation difference between these is negligible (Della Santina et al., 2005), meaning that the twin canal provides an inverse duplicate signal. This makes one set of canals effectively redundant. This arrangement may decrease error in vestibular conclusions by improving amplitude and directional sensitivity (Fitzpatrick & Day, 2004).

The SCCs in most mammals are approximately equal in size and are proportionally related to the size of the mammal. In humans, however, the horizontal canal is smaller than the other two (Spoor et al., 1994). This may be because the anterior and posterior canals together code for angular acceleration in the sagittal and frontal planes, which are most important for the

maintenance of balance (Fitzpatrick et al., 2006). Evolution may have therefore favoured larger anterior and posterior canals for bipedal stance (Day & Fitzpatrick, 2005). Larger canals are more sensitive to smaller perturbations, meaning that the horizontal SCC may be physiologically less sensitive than the other two. It appears, however, that rotation in its axis is perceived better (see section “Sensitivity”, page 10).

Physiology

The bony canals are filled with perilymph fluid and lined with a membrane which is itself filled with endolymph fluid. Each SCC contains a bulging area near its base called the ampulla, which contains the sensory transducer called the cupula. The cupula consists of many hairs, the stereocilia, and one large hair on the outer edge called the kinocilium. Head acceleration causes the bony canals to move with the head, and the endolymph fluid lags due to inertia and the viscous properties of the fluid. This lag causes a pressure differential which pushes the cupula in the ampullae, causing the hairs inside to bend either towards or away from the kinocilium. This causes an increase or a decrease (respectively) in the firing rate of the vestibular nerve ending attached to the cupula (Fitzpatrick & Day, 2004).

Although the SCCs are generally considered to be responsible for detecting angular acceleration, the viscous properties of the endolymph fluid in the ducts actually causes the SCCs to act as angular velocity transducers under a certain band of frequencies (Highstein et al., 2005; Lysakowski & Goldberg, 2004). Mathematically, this band is approximately 0.025 – 30 Hz. At frequencies below 0.025Hz, the stiffness of the cupula and mass of the endolymph fluid cause the SCCs to act as acceleration transducers directly. At frequencies over 30Hz, the same factors cause the canals to act as displacement transducers. This temporal filtering is a characteristic of the fluid movement in the canals, occurring before mechanotransduction from the hair cells

(Rabbitt et al., 2004). Some collateral nerve fibres between hair cells tend to act as differentiators between the hair cells and the vestibular nuclei (Ross, 2003), meaning that at least some acceleration information is still conveyed to those nuclei even when in the velocity-transducing frequency range.

Otolith organs

Location and orientation

There are two otolith organs in the inner ear. They are called the utricle and saccule, and they are responsible for detecting linear acceleration in the approximate horizontal and vertical planes, respectively. The otoliths are membranous sacs located in a cavity called the vestibule, inferior to the SCCs. The utricle is attached to all three of the SCCs, and they drain endolymph fluid into it on the side opposite to the ampullae. The saccule also shares endolymph fluids through a small passage called the utricosaccular duct (Drake et al., 2005). In this way, all of the vestibular organs share common endolymph fluids.

Physiology

The otoliths each contain a sensory section of membrane called the macula (or macule). The macula is approximately flat, and is covered in 20,000-30,000 stereocilia (Fitzpatrick & Day, 2004). There are also many kinocilia, spread across the surface of the maculae with their associated stereocilia. All of the hair receptors on the macula are embedded in a gel-like fibrous substance, which is topped with otoconia. The otoconia are crystals of calcium carbonate attached to the top of the gel, and they provide inertia to the system. When the head is accelerated the otoconia lag behind, bending the gel and embedded hairs in the direction opposite the acceleration (Blumenfeld, 2002). This action bends the stereocilia towards or away from their kinocilia, and changes the firing rate of the attached nerve rootlets.

The directional sensitivity of each bundle of hair receptors varies across the macula, forming a curved line of maximal sensitivity near the middle of the macula. This line is called the striola, and it is the movement of the stereocilia towards or away from the striola which causes an increase or decrease in the firing rate of the attached nerves. The striola is curved in order to provide information in many directions in the plane. The hair cells in the saccular macula are arranged to have a directional sensitivity away from the striola, whereas the utricular macula's polarity is towards the striola (Fitzpatrick & Day, 2004).

The morphology of the otolith organs makes them sensitive to linear accelerations, which includes gravity according to Einstein's equivalence principle. Unfortunately this leads to an ambiguity in otolith output, which becomes problematic mostly at high frequencies (Nashner, 1971). This ambiguity may be solved by input from the SCCs, as shown from vestibular nucleus recordings in monkeys (Angelaki et al., 2004) and cats (Uchino et al., 2005).

Sensitivity

The vestibular organs certainly seem ideal for detecting sway at the head during quiet stance. Meiry (1966) found otolith sensitivity to be approximately 0.059 m/s^2 (6 milli-g). However, Nashner reasoned that the otolith organs likely play no role in detecting body sway (1971). According to mathematical models, otolith sensitivity is highest at a very low frequency of body sway and therefore its function is most likely relegated to encoding a static vertical reference. However the SCCs, in the pitch axis at least, have a calculated threshold of approximately 0.05 deg/sec^2 and are sensitive enough to detect the small accelerations that occur at the head during sway in quiet stance (according to Nashner, 1971). They are likely most effective in coding information at head sway frequencies above 0.1Hz (Nashner et al., 1989),

which is in the lower range of the head sway power reported by Easton et al. (0.15Hz; Easton et al., 1998).

In 1989, a group led by Nashner plotted theoretical SCC and otolith thresholds, along with theoretical limits on the use of a pure ankle strategy, to discover whether the vestibular organs could detect the accelerations that occur at the head during quiet standing sway. Two areas were labeled to represent typical values of sway for vestibular-only and full sensory conditions. It appeared that the vestibular organs were theoretically able to detect head accelerations in quiet stance under vestibular-dependent sensory conditions. This was a theoretical model, however, and its conclusions under full sensory conditions were uncertain (see Nashner et al., 1989).

The perceptual threshold of the SCCs has been experimentally measured, and in velocity terms is about 1.5 deg/s about the vertical axis (stimulating the horizontal canal; Benson et al., 1989). Thresholds about the two axes in the horizontal plane were discovered to be higher, at 2.04 deg/s in roll and 2.07 deg/s in pitch. A previous study using acceleration as the stimulus found no significant difference between the SCC thresholds (Clark & Stewart, 1970). These studies were completed using turning tables or seats, however. It is still unclear whether these theoretical and measured thresholds are exceeded by the motions of the head (to which the vestibular apparatus is rigidly attached) during normal standing sway.

Head acceleration during quiet stance

Most of the balance studies mentioned in the preceding sections used CoP as measured from a force plate to infer stability of the participants. Since my thesis is focused on stability at the head, it is important to note that a comparison of CoP and head sway measures found that they infer stability in a similar manner (Sakaguchi et al., 1995). A correlation analysis using

linear acceleration data found a very strong (“almost one”) correlation between head sway and center of gravity sway in equivalent directions (i.e. both head and center of gravity in mediolateral direction; Matsubara et al., 1983; Miyoshi et al., 1983). Therefore, it may not be unreasonable to expect head acceleration results to follow similar trends to those discussed in the preceding sections (which are mostly CoP results). There are some studies, however, that have measured head acceleration directly, although not so thoroughly as the CoP studies.

There is little reporting of angular head accelerations during quiet stance in the literature, but a technique called “acceleration registrography” has been used to record linear head accelerations along one axis (Kitahara, 1965; Tsujikawa, 1966). One study using this technique to measure mediolateral sway showed head accelerations of approximately 20.8 milli-g (in the 10-second period with the highest accelerations) during quiet standing in a normal stance, with no difference when vision was excluded (Tsujikawa, 1966). In a tandem stance, these accelerations increased to a maximum of 25.5 milli-g with the eyes open, and 45.5 milli-g with the eyes closed. In both stances, brief periods of acceleration up to 250 milli-g were observed. A more recent study by Winter et al. (1998) calculated linear head acceleration from head displacement data during quiet standing trials, with the eyes open in a comfortable stance. They found mean linear head accelerations from 0.016 - 0.018 m/s² (~1.7 milli-g) in the anteroposterior direction, and 0.01 – 0.012 m/s² (~1.1 milli-g) mediolaterally.

In even more recent work, head movement information is sporadically mentioned as a control condition, usually in comparison to head movement profiles from platform translation or moving visual fields (Easton et al., 1998; Kelly et al., 2005; Keshner & Dhaher, 2008). Frequency analyses on head sway data during quiet stance are scarce. One study, focused on the effectiveness of sound as a balance aid, reported as a control condition a maximum mean power

of 0.15Hz for the displacement of the head in the mediolateral direction during quiet stance in healthy subjects with eyes closed (Easton et al., 1998). Power was reported from 0.05Hz to 0.58Hz overall.

Information on linear head accelerations during quiet stance are limited in current literature; those on angular accelerations even more so. A description of the acceleration behaviour of the head during quiet stance did not exist prior to this thesis. This description is of particular interest because the vestibular system is rigidly connected to the head, and is therefore directly affected by accelerations there. The vestibular system is theoretically sensitive enough to detect head accelerations, yet these accelerations had not been characterized. This may be due to only recent developments in instrumentation sensitivity and computing power making this kind of description accurate. A complete description of linear and angular head accelerations in relation to Reid's axes of the head was the first objective of this thesis study.

Measuring head acceleration

Accurate measurement of the acceleration of the head was a fundamental part of the success of this thesis. For years, it has been common practice in automobile crash testing to calculate angular acceleration by using an array of nine linear accelerometers (Padgaonkar et al., 1975; King, 1993; Blouin et al., 2007; Yoganandan et al., 2006). The most common arrangement used is called a 3-2-2-2, and consists of the 9 accelerometers rigidly mounted on a triangular-pyramidal metal frame. Three accelerometers are orthogonally arranged at the peak of the pyramid, and the other 6 are in right-angle pairs at each of the triangular base points. Theoretically, only 5 linear accelerometers are necessary to resolve the 3 angular acceleration equations; a 6th is required for concurrent linear acceleration calculations. In reality, the inherent noisiness of each accelerometer may lead to an accumulation of errors, resulting in an overall

inaccurate calculation. Adding 3 more accelerometers introduces redundancy into the system, removing the opportunity for multiplication of errors and ensuring a more accurate and stable result (Padgaonkar et al., 1975).

Vestibular innervation

Once accelerations at the head during standing sway have been accurately measured and described, the accelerations that the SCCs experience can also be described (since they are rigidly embedded in the skull in known planes). What effect can these stimulated vestibular organs have on the body? A closer look at the innervation of the vestibular system and the associated nervous connections is appropriate.

Afferent innervation

The nerve that conveys all information from the vestibular organs to the brain is the eighth cranial nerve, known as the vestibulocochlear nerve. This nerve begins as either calyx or bouton endings attached to receptor hair cells in the crista of the SCCs, and the maculae of the otolith organs (Lysakowski et al., 1995; Ross, 2003). These nerve rootlets are involved in very early parallel processing (likely differentiation; Ross, 2003) by way of collateral inputs between hair cells. The rootlets, or primary vestibular afferents, then synapse in nearby ganglia before converging with nerves from the neighbouring cochlea to form the aptly named vestibulocochlear nerve. This nerve passes through the internal acoustic meatus and into the skull (Drake et al., 2005), traveling to the vestibular nuclei in the brainstem (Blumenfeld, 2002). The secondary vestibular nuclei reside in the brainstem, specifically in the pons and medulla (see “Reticulo- and vestibulo-spinal pathways”, page 16, for further information on the vestibular nuclei).

An important feature of the primary vestibular afferents is that they have a resting firing rate, which varies between species. It has not been directly measured in humans, but is known to be ~90-115 Hz in macaque monkeys (Cullen & Minor, 2002). This spontaneous discharge requires no stimulus and is hypothesized to contribute to muscle tone (Lysakowski & Goldberg, 2004). Its main advantage is that it allows bidirectional signals to emerge from the vestibular organs as either an increase or a decrease in the base firing rate. The change in rate is not linear, however, as the afferents appear to be more sensitive to excitatory rather than inhibitory inputs (Ross, 2003).

The type of base firing rate splits the primary vestibular afferents into two main groups: regularly and irregularly firing. Regular primary afferents make up about 75% of the total number of primary afferents, with irregular making up the last 25%. There are no exact criteria for classification, however, and sometimes “intermediate” afferents are mentioned in literature (Plotnik et al., 2005). Irregular units are associated with larger diameter primary afferents, and generally have a lower tonic rate, higher sensitivity and lower refractory period than regular afferents (Fitzpatrick & Day, 2004; Goldberg et al., 1984; Lysakowski & Goldberg, 2004). They are also more sensitive to electrical stimulation (see “Galvanic vestibular stimulation”). The irregularity of these afferents does not appear to help code information for velocity any better than regularly firing afferents (Highstein et al., 2005).

Efferent innervation

The vestibular system is also equipped with an efferent nervous system, although its function is still under discussion. The efferent nerves start in the brain stem, predominantly in the lateral vestibular nucleus, and innervate the vestibular system both ipsi- and contra-laterally (Klinke & Galley, 1974). In mammals, it appears that vestibular efferent excitation excites

vestibular afferents (both SCC and otolith; Plotnik et al., 2005). The efferents can be excited by rotations in any direction, but require large angular velocities for this effect to be seen. Even then, the excitation from efferents is much smaller than usual afferent responses. Vestibular efferents can be stimulated in other ways, as well, including direct manipulation of the otoliths and passive limb movement (as seen in rabbits and frogs, reviewed in Klinke & Galley, 1974). It has been noted that, in animals given a muscle-relaxant, electrical stimulation of ascending spinal cord routes has no effect on vestibular efferents. Contrastingly, stimulation of the descending motor axons from the reticular formation causes vestibular efferent activity shortly after (15ms; Klinke & Galley, 1974). Both a feedback and a feed-forward mechanism have been proposed for the efferent system. Plotnik et al. (2005), using decerebrate chinchillas, put forward one model that includes positive and negative feedback, and another that included a feed-forward excitation loop, monitored by descending inhibition. Currently, all models are highly theoretical and the behaviour and purpose of the vestibular efferent system in conscious, intact animals (and humans) is unknown.

Reticulo- and vestibulo-spinal pathways

Afferent information from the vestibulocochlear nerve is integrated with other information in the vestibular nuclei, located in the medulla and pons in the brainstem. There are four vestibular nuclei; superior, lateral, medial and inferior, on each side of the brainstem. As a group, they accept input from 4 sources: the vestibular afferents (via the vestibulocochlear nerve), the vestibular cerebellum, the reticular formation and the contralateral vestibular afferents (via commissural fibres; Ruckenstein, 2004).

The four vestibular nuclei are responsible for different aspects of vestibular control. The lateral nucleus controls vestibulospinal reflexes throughout the body via the lateral

vestibulospinal tract (LVST). These reflexes are important for balance and ipsilateral extensor tone. The medial and inferior nuclei together influence more proximal vestibulospinal reflexes, acting on the vestibulocollic reflex and general head and neck coordination through the medial vestibulospinal tract (MVST, also called the descending medial longitudinal fasciculus or descending MLF). Lastly, the superior and medial nuclei coordinate the vestibuloocular reflex through the ascending MLF (Blumenfeld, 2002).

The vestibular nuclei also communicate with the brain. The nuclei output to the bulbar reticular formation and the vestibular cerebellum in particular, inhibiting flexors and extensors throughout all levels of the spinal cord via the reticulospinal tract (RST; Ruckenstein, 2004), which is known to be involved in automatic balance control (Blumenfeld, 2002). There are many more vestibular connections within the brain, which are not the focus of this project and therefore will not be reviewed here (see Carpenter, 1988, for further detail on these).

Recent work by Cathers et al. (2005) used electrical vestibular stimulation to determine that the otolith organs and SCCs can be considered as separate sensory systems, which cause muscular reflexes via independent reflex pathways. These pathways were previously postulated to be the reticulospinal and lateral vestibulospinal tracts (Britton et al., 1993), based on an assessment of their vestibular connections and conduction speeds. A later study (Dakin et al., 2007) suggested that the otolith signal traveled through the reticulospinal tract, and the SCC signal traveled through the vestibulospinal pathways, based on frequency characteristics of the reflex response. However, work on cats (Uchino et al., 2005) has shown that 15-43% (perhaps more) of the neurons in the vestibular nuclei responded to convergent input from more than one vestibular organ source. Of these, convergent inputs between otoliths and SCCs were common. Evidently, it is still unclear how vestibular inputs converge and are weighted to evoke muscular

reflexes. What is clear is that there are connections from the vestibular organs, through the vestibular nuclei (where other information may be integrated) to the muscles of the lower limbs.

Vestibulomotor reflex

Muscular reflexes in the limbs or trunk evoked by vestibular inputs are termed vestibulomotor or vestibulospinal reflexes, as they begin in the vestibular organs and are communicated to the muscles via the spinal cord. Most information on these reflexes has been collected using artificial vestibular stimulation (see “Galvanic vestibular stimulation” and “Stochastic vestibular stimulation” sections).

Vestibulomotor reflex responses aren't always present in all muscles. They are found only in those that are posturally active, whether they are upper or lower limb (Britton et al., 1993). Muscles that are active but not involved in maintaining balance do not exhibit this reflex, although motor neuron pool excitability may still be affected by the vestibular system (Kennedy et al., 2004).

The vestibulomotor reflex response can be broken down into two parts, the short latency (SL) and medium latency (ML) waves. These waves are of opposing polarity, with the ML response in the direction of resultant postural sway (Fitzpatrick & Day, 2004). In electrical stimulation studies, muscle facilitation is ipsilateral to the anode, and inhibition is ipsilateral to the cathode. The SL wave has an onset of 55-65ms in the leg, and is smaller than the ML response. The ML response latency is about 110-120ms in the lower limb (earlier in the paraspinals at ~61-75ms; Ali et al., 2003; Ardic et al., 2000; Britton et al., 1993).

Balance is dependent on many sensory systems (as reviewed above), and it follows that changes in sensory conditions may change the size or latency of the responses originating in the vestibular system. Head position, for example, changes the meaning of vestibular information in

relation to the body. The polarity of the vestibulomotor reflex is therefore dependent on head position (Britton et al., 1993; Dakin et al., 2007; Lund & Broberg, 1983), with resulting sway responses directed along the interaural axis (Fitzpatrick & Day, 2004). Both SL and ML responses increase in magnitude when vision is removed, external support is removed, the surface is sway-referenced (or compliant), and when stance width decreases (Welgampola & Colebatch, 2001). These changes are all reflective of the relative importance of vestibular information under such sensory conditions. An increase in background muscle activity can also increase reflex size (Lee Son et al., 2005).

The ML response seems to be more susceptible to changes in sensory input than the SL, and more useful to maintenance of balance because of its direction (Fitzpatrick & Day, 2004). It is not clear what purpose the SL response serves. Indeed, some researchers have gone so far as to call it an evolutionary dead end (Britton et al., 1993) and many studies looking at vestibular-origin reflexes report only ML information. This view is not unanimous, however: one study proposed that the origins of the SL and ML are separate, attributing the ML to the SCCs and concluding that the SL was of utricular origin (Cathers et al., 2005). Neither viewpoint has conclusive evidence to endorse it. The exact origin(s), pathway(s) and purpose(s) of the vestibulomotor reflexes are still uncertain. Results found using artificial vestibular stimulation, however, have contributed towards the further understanding of the behaviour of this reflex. Although this thesis does not use this technique, is worthwhile to present it in this review as it is useful to understand the origin of the reflexes presented above.

Galvanic vestibular stimulation

Galvanic vestibular stimulation, or GVS, is a research method commonly used to investigate the vestibular system; vestibulomotor reflexes in particular. It consists of an

electrical current applied trans-cutaneously at the mastoid process(es), which transiently stimulates the vestibular system at the discharge site (where the nerve rootlets accept neurotransmitters from the transducing hair cells; Goldberg et al., 1984). The firing rate in the nerve is increased or decreased, depending on whether the current is cathodal or anodal, respectively. The overall result in standing is sway towards the anode (Lund & Broberg, 1983).

An important feature of GVS is that it is non-selective in its effect. That is, it will change the firing rate of all vestibular afferents, no matter their origin. It has been found, however, that irregular vestibular afferents are most sensitive to GVS, and its effect on these afferents far outweighs its effect on regular and intermediate afferents (Goldberg, 2000). The cumulative effect of GVS on the vestibular organs is proposed in Fitzpatrick and Day's 2004 review (Fitzpatrick & Day, 2004). It is believed that GVS is interpreted by the brain as a real vestibular signal, and that its effects are compensatory to this (erroneous) signal. Sway, changes in walking trajectory and vestibulomotor reflexes can be all elicited using GVS in this way.

Stochastic vestibular stimulation

Following the success of pulsed GVS experiments, research groups began to use pseudo-random band-limited GVS (termed stochastic vestibular stimulation, or SVS) in order to evoke sway and reflex responses in humans. Different research groups have used a form of frequency analysis (see the "Data Analysis" section for a more detailed look at this analysis) to investigate the relationship between the SVS input and resultant EMG or CoP. In this way, it has been found that humans can act much like a "responder" to low-frequency bipolar SVS (0-2Hz) in the mediolateral direction (CoP; Pavlik et al., 1999), and to low-frequency monopolar SVS in the anteroposterior direction (Scinicariello et al., 2002). SVS appears to have the same effect on postural stability as profound bilateral vestibular loss (MacDougall et al., 2006).

Another group recently tested lower limb vestibulomotor reflexes elicited by SVS in standing. A 0-50Hz stimulus bandwidth was tested, and statistically significant coherence with lower limb EMG was found in the 0-20Hz range, maximally in the 5-7Hz and 11-16Hz bandwidths, for bilateral soleus and medial and lateral gastrocnemii (Dakin et al., 2007). Reflex peaks and polarities corresponded to those elicited with GVS.

It is apparent that electrical vestibular stimulation can elicit reflexes in posturally engaged muscles, and that these reflexes originate in the vestibular organs and are frequency-dependent. It is unknown whether vestibular reflexes can be evoked by naturally-occurring vestibular stimuli; that is, accelerations at the head during quiet standing sway. The investigation of this question was the basis for the second part of this thesis.

Research motivation

Prior to this study, there was no complete description of the acceleration profile of the head during quiet standing. Linear accelerations had been studied to an extent (Kitahara, 1965; Tsujikawa, 1966), but detailed analysis was lacking. There were no studies reporting angular head acceleration behaviour during quiet standing at all. The complete description of linear and angular acceleration at the head during quiet stance under different visual and somatosensory sensory conditions was the first aim of this thesis.

In his early experiments regarding body sway, Nashner (1971) calculated that the vestibular organs are sensitive enough to detect these small accelerations at the head during body sway (which will be characterized in the first part of this thesis). Studies on vestibular-loss patients show that they cannot stand without somatosensory and visual inputs (Nashner et al., 1982). It is apparent that the vestibular system has some role in standing sway, but what role it may play is unknown. Studying the relationship between accelerations at the head (what the vestibular system transduces) and forces at the feet may help to decipher what role the vestibular system plays in standing balance, and also uncover balance mechanisms that include the head.

In 1994, Horak et al. eliminated vision and most somatosensory inputs and translated the head of both healthy subjects and vestibular patients. They found direction-specific responses in the lower legs that most likely stemmed from vestibular inputs, as these responses were not present in patients with adult-onset vestibular loss. This experiment showed that the vestibular organs are coupled to the lower legs in absence of electrical stimulation. More recently, SVS has been used to show that vestibulomotor reflexes can be elicited in the lower legs using stochastic electrical vestibular stimuli. Dakin et al. used a correlation analysis to show a weak coupling between the artificial vestibular inputs and muscular responses in lower leg muscles in standing

(Dakin et al., 2007). It is reasonable to consider, then, that the vestibular system is able to be actively involved in the modulation of lower leg activity in quiet standing sway, and that it may be activated by the head motions present during standing sway. The last part of this thesis was designed to examine the relationship between lower leg muscle activity and angular head accelerations in the direction of the semicircular canals during natural sway in quiet standing under 4 sensory conditions.

Aims

The aims of this thesis study were as follows:

- A. To describe the angular and linear head acceleration behaviour in normal human subjects during quiet standing sway under 4 sensory conditions.

Hypothesis

1: Head accelerations characteristics will differ when measured under different sensory conditions. RMS will increase and median frequency will decrease as the standing condition becomes more unstable.

- B. To determine the relationship between angular and linear head accelerations and forces and moments at the feet, and to establish how this relationship changes with eye closure.

Hypotheses

- 1: Head accelerations and force plate forces will be coupled in-phase.
- 2: Eye closure will most effect coherence below 1Hz.

- C. To determine the relationship between angular head accelerations and lower leg muscular activity, and to establish how this relationship changes with changing sensory conditions.

Hypotheses

- 1: Angular head accelerations and EMG recordings from the lower legs will be coupled.
- 2: This coupling will be strongest under the most vestibular-dependent sensory condition.

Methods

Participants

Eleven participants (7 female, 4 male) were recruited for the study. They were of good health, with no past or current neurological conditions and no sensory or motor dysfunctions of the lower extremities. Height ranged from 154 - 191 cm (mean 172 cm), and mass ranged from 58-86 kg (mean 70.7kg). All subjects had intact vestibular systems and were between the ages of 21 and 33 (mean 26.2 years old). This age range was chosen to exclude people over the age of 40 because it is known that despite sensory conditions, focus or instructions, balance tends to degrade with age. Studies have shown that seniors (>65 years old) show an increase in COP excursion over young subjects, and are more dependent on a hip strategy (normally reserved for large perturbations) than their younger controls (Amiridis et al., 2003). Vestibular function also tends to degrade as people age, leading to longer vestibulomotor reflex latencies and smaller reflex responses (Welgampola & Colebatch, 2002). These responses appear to remain intact below the age of 60 (Welgampola & Colebatch, 2002), however to err on the side of caution, no subjects older than 40 years were recruited to participate in the study.

All participants gave informed written consent, and the study was conducted in accordance with the ethical guidelines established by the University of British Columbia.

Apparatus

Acceleration of the head was measured using a custom-made 9-accelerometer array. A rigid, lightweight, pyramidal array was attached to an adjustable plastic headband which was fitted snugly to the participant's head. All nine accelerometers were from Kistler Instrument Corp. (Amherst, NY), model 8330A3. These accelerometers were linear and had a working

range of $\pm 3g$ and a sensitivity of $1.2V/g$ ($\pm 10\%$). They were recommended by Kistler for low-acceleration, low-frequency applications, and they thus had a resolution of less than $1.3\mu g$, from 0-10Hz. The accelerometer output was DC and analog.

Force plate data (forces in 3 directions and moments around 3 axes) was recorded using an AMTI force plate (5571), in the same manner as the accelerometry data.

Surface EMG was recorded from three different muscles, bilaterally. Soleus (SO), medial gastrocnemius (MG) and tibialis anterior (TA) were recorded from the lower leg. Signals were recorded using self-adhesive Ag/AgCl surface electrodes (Soft-ETTM H59P: Kendall-LTP, Chicopee, MA, USA). They were placed over the specified muscle belly in landmarked areas, with an inter-electrode distance of ~ 10 mm.

The accelerometer and force plate data were recorded using a National Instruments PXI-4495 DAQ, with 24-bit precision. Concurrent EMG data were collected from a National Instruments PXI-6289 DAQ, with 16-bit precision. Data were recorded simultaneously on the same computer using a custom LabVIEW data acquisition program. A $\sim 1V$ square pulse from a signal generator was sent to both DAQ boards at the beginning of every trial to allow offline elimination of computer lag between the boards. All data were recorded at 2kHz and saved in a text file to be analyzed offline; this analysis was completed using Matlab 7 software (Mathworks Inc., Natick, MA).

The frame of the accelerometer array also supported a small plastic structure with reflectors mounted on it. This 'head reference tool' was part of the Polaris Vicra optical tracking system (NDI – Northern Digital Inc., Waterloo, ON). The tool, along with a reference wand and infrared LEDs and detectors, allowed the accelerometry data to be transformed to head-space coordinates. All acceleration data was therefore able to be described in terms of Reid's axes of

the head and, from there, could be further transformed to relate to the directional sensitivities of the SCCs.

Experimental procedure

Two sensory conditions were manipulated in this experiment. They were the surface condition (hard or compliant) and visual condition (eyes open or eyes closed). Repeatability was also a concern, given the descriptive nature of the first aim. There were therefore 6 trials in total: 2 control trials (both the first and last trial) and 4 experimental trials in between that were randomized in order. Each trial was 4.5 uninterrupted minutes long (270 seconds). The trials are summarized in Table 1. A brief familiarization session was provided before the first trial, which acquainted the subjects to the task and all conditions (at approximately 30s per condition) before the accelerometer array was fitted. This allowed familiarization to occur without increasing the amount of time with the accelerometer array tightened (which tended to be uncomfortable after long periods). Seated breaks were offered after each trial, and a 10 minute break was observed after the third trial (halfway through the testing session). At this point, the accelerometer array was removed to relieve head pressure, and subjects sat and rested. The accelerometer array was replaced and all points were redigitized before continuing to the last 3 trials.

Trial	Name	Surface Condition	Visual Condition	
Control 1		Hard (force plate only)	Eyes open	← First trial
Exp 1	EOHS	Hard (force plate only)	Eyes open	} Random order
Exp 2	ECHS	Hard (force plate only)	Eyes closed	
Exp 3	EOSS	Compliant foam	Eyes open	
Exp 4	ECSS	Compliant foam	Eyes closed	} Random order
Control 2		Hard (force plate only)	Eyes open	← Last trial

Table 1: List of experimental conditions

When subjects arrived for testing, they were fitted with electrodes for EMG collection and stood on the appropriate surface for the short familiarization session. Thin metal washers (from 0 – 7 in number, as necessary) were added bilaterally between the hard frame of the accelerometer array and the adjustable headband in order to fit each subject more securely and comfortably. The accelerometer array, complete with head reference tool, was then tightened around the head, and the subject was seated with the Polaris Vicra system's cameras in place beside them. The reference wand was touched to 37 points to digitize them with respect to the head reference tool. On the subject, these points were: nasion; the center of each external auditory canal (to mark the location of the interaural axis); the points on the edge of the most inferior part of each infraorbital rim; the inferiormost point of each mastoid process; skull vertex; external occipital protuberance; and glabella. On the accelerometer array, two points on opposite corners of each accelerometer were digitized (18 points in all), as were 9 pre-marked points on the aluminum frame (three on each orthogonal side; see Figure 1). In this way, Reid's axes were defined in terms of the position of the accelerometer array, and the center of mass of the head was identified (National Aeronautics and Space Administration, 1978).

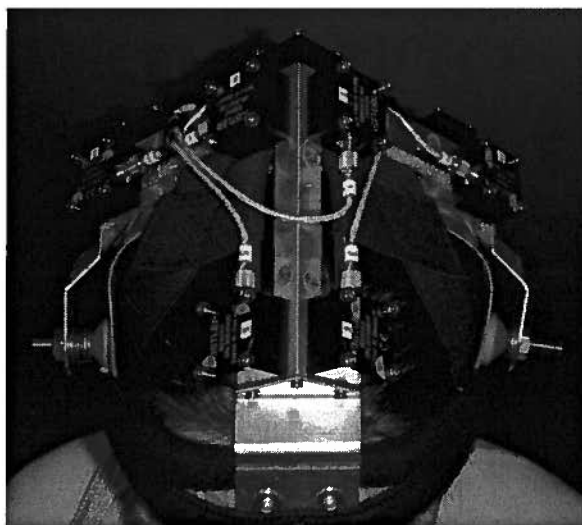


Figure 1: Setup of the accelerometer array on a subject's head. The head reference tool is not seen in this photograph. Washers are visible between the hard and soft frames of the apparatus.

According to recent studies, the exact nature of the instructions given to the participants affects their sway patterns (Ishizaki et al., 1991; Zok et al., 2008; Vuillerme & Nafati, 2007). For example, a person instructed to “stand relaxed” or “stand quietly” has a larger sway magnitude than someone told to “stand as still as possible”. Therefore, subjects were instructed to stand relaxed on the appropriate surface (in bare feet or socks) with their arms by their sides and their feet as close together as possible without touching. During all “eyes open” trials, subjects were asked to focus on a small, distant, stationary target at eye level.

Since focus of attention can change sway patterns, subjects were not given any more instructions, nor were they exposed to undue external stimuli (i.e. music, talking, moving objects, etc.). In a 2000 study, Shumway-Cook and Woollacott (2000) showed that during a cognitive auditory tone-recognition task, young people (<45 years old) had no detriment to postural stability due to the additional attention demands, no matter the sensory condition. However, another study in 2003 showed (in young, healthy subjects) decreases in mediolateral sway magnitude during a cognitive task (a multi-step arithmetic problem), and increases in the same value during a non-balance related motor task (a finger pinch at 10% MVC; Weeks et al., 2003). This study showed that directing a person’s attention internally (as in the finger pinch) may increase sway, while an external focus (the math problem, which was physically unrelated to the person) decreases sway in young healthy individuals (see also McNevin & Wulf, 2002; Vuillerme & Nafati, 2007). In this study, attention was not purposely directed.

Data analysis

Processing of the data involved rectifying all EMG channels and calculating linear and angular head accelerations for the axes of interest from the nine-channel accelerometry data. The spatial data from the Polaris Vicra system was used to create a transformation matrix from an

array-space reference frame to one centered about Reid's axes (modified as described in the literature review). The origin of Reid's axes was defined as the center of mass of the head. This is approximated to be in the midsagittal plane, rostral of the interaural axis by 17% of the distance measured between the vertex and the interaural axis (National Aeronautics and Space Administration, 1978; as in Blouin et al., 2007).

Angular accelerations of the head were computed using the following equation set:

$$\begin{aligned}\alpha_x &= \frac{A_{z1} - A_{z0}}{2d_{y1}} - \frac{A_{y3} - A_{y0}}{2d_{z3}} \\ \alpha_y &= \frac{A_{x3} - A_{x0}}{2d_{z3}} - \frac{A_{z2} - A_{z0}}{2d_{x2}} \\ \alpha_z &= \frac{A_{y2} - A_{y0}}{2d_{x2}} - \frac{A_{x1} - A_{x0}}{2d_{y1}}\end{aligned}$$

Equation 1: Angular acceleration equation for the head, where: a_i is angular acceleration about axis i , A_i is linear acceleration from accelerometer i , and d_i is the distance between accelerometers, from Blouin et al., 2007.

Once angular accelerations relative to the accelerometer array axes were calculated, they were transformed into accelerations about Reid's axes, and also to accelerations about the axis of each SCC (as measured in Della Santina et al., 2005). Angular accelerations were high-pass filtered at 0.2Hz in an attempt to remove drift due to temperature and tilt, which appeared to be concentrated below this limit. These data were also low-pass filtered at 100Hz. Linear acceleration data were transformed to the directions of Reid's axes, and the DC offset was removed for all calculations except absolute maximum linear acceleration (as the effect of gravity that it implies cannot be identified using this experimental setup).

These accelerometry data were used to complete the first aim of the thesis: describing the acceleration profile for the head. For both linear and angular accelerations in all 3 directions (in relation to Reid's axes) absolute maximum value, RMS, median frequency and the 95% confidence interval frequency were calculated. Of these, RMS and median frequency were compared between the control trials (see Table 1: Control 1, Control 2 and Exp 1), and also between sensory conditions 1 through 4 (see Table 1: Exp 1-4) as described in the Statistics section.

Following this description, a coherence analysis was completed between angular head accelerations in the Reid's planes and forces and moments collected from the force plate, in order to uncover a possible linear relationship between them. Linear head accelerations (ML and AP) were run against forces (in terms of what the body, not the plate, experiences) in equivalent axes. Angular head accelerations about all 3 Reid's axes were also run against angular force plate data (the moments). Finally, linear head accelerations were run against force plate moments in the direction that they were likely to affect (e.g. linear head acceleration in x may cause a force plate moment about y). It is important to note that these coherence analyses were not valid for experimental conditions 3 and 4 (those on the compliant surface), because it is unknown how the introduction of the soft foam affects the transmission of forces from the subject's feet to the force plate. Therefore, force plate data from conditions 3 and 4 were not analyzed. Also, 3 of 11 subjects had unusable force plate data. Their results are not included in any analyses using force plate data; therefore, the force plate coherence analysis is completed using 8 subjects.

A coherence analysis was also completed between angular head accelerations in the planes of the SCC's and all 6 muscle EMG recordings under each of the 4 sensory conditions, using data from all 11 subjects.

Coherence between the concurrent data sets in each analysis was computed over subjects using Equation 2 (below) on concatenated data sets of equal length from each subject. Coherence is an indicator of the linear relationship between two signals across frequencies. It is unit-less and bound between 0 and 1, 1 denoting a perfect linear relationship and 0 denoting independence (Halliday & Rosenberg, 1999; Rosenberg et al., 1989). The result can be interpreted as the percentage of the signal's variance that can be accounted for by the influence of the other signal. Coherence between the data sets was calculated using a publicly available Matlab script (available for download at <http://www.neurospec.org/welcome.html>), which is based on a methodology described by Rosenberg et al. (Rosenberg et al., 1989; used previously in Dakin et al., 2007 and Roskell et al., 2007). Final coherence plots were all subjected to a moving average filter using a Hanning window with weights of 0.25, 0.5, 0.25. This created a smoother plot and simplified the identification of the major areas of coherence, without requiring modification of the 95% confidence intervals (Farmer et al., 1993).

$$|R_{AB}(\lambda)|^2 = \frac{|f_{AB}(\lambda)|^2}{f_{AA}(\lambda)f_{BB}(\lambda)}$$

Equation 2: Coherence between signals A and B is calculated by dividing the cross-spectra's magnitude squared, by the product of the two autospectra.

Time-cumulant density (TCD) functions were also calculated for the concatenated data sets to provide a time domain representation of the relationship between the signals. TCD functions are inverse Fourier transforms of coherence and although they cannot be used to directly measure the amplitude of the relationship in millivolts, the timing of the function peaks and troughs (maximums and minimums, in this case) provides an estimate of the phase lag between the signals. The polarity of the response can also be interpreted from the plot. A positive

TCD indicates in-phase forces/accelerations between the force plate and head, or facilitation of the muscle in relation to head accelerations (in the EMG coherence analysis). A negative TCD of course implies the opposite. TCD plots were not subjected to a filter.

Statistics

Statistical comparisons on the acceleration results were made on two sets of data. Within these sets only RMS and median frequency were statistically tested. The first set, made of three control trials, were compared using a 2-way mixed intraclass correlation (yielding an intraclass correlation coefficient or ICC) to test the reliability of the head acceleration measures. The measures were deemed repeatable if the $ICC > 0.5$ (Weir, 2005). The second set, of the four sensory condition trials, were tested for statistically significant differences using a 2-way repeated measures ANOVA. This ANOVA tested for main effects of surface and vision and for an interaction between them. If an interaction was present, a post-hoc Tukey test was performed. All tests were completed to a p value of 0.004, which is equivalent to a p value of 0.05 with a Bonferonni correction factor for multiple comparisons of 12. The intraclass correlations were calculated using SPSS (version 14.0, SPSS Inc., Chicago, IL); the ANOVAs were done using Statistica (version 6.1, Statsoft, Tulsa, OK).

Coherence analyses between angular head accelerations and force plate forces were completed on concatenated data (8 subjects total), to a frequency resolution of ~ 0.015 Hz, using segments of 65.536s length. Analyses on angular accelerations used 33 of these segments, while analyses on linear accelerations used only 30 (due to the necessary shorter length of the linear accelerations data set; it was shortened in transformation into Reid's axes). Coherence between head accelerations and EMG were also done on concatenated data (11 subjects total), to a frequency resolution of ~ 0.06 Hz, using 169 segments each 16.384s in length.

Any coherence was deemed significant at a particular frequency when it surpassed a 95% confidence interval, which is calculated based on the number of disjoint sections (Halliday et al., 1995; Halliday & Rosenberg, 1999). Differences in coherence between conditions were compared using a Difference of Coherence (DOC) method from Amjad et al. (Amjad et al., 1997). Ninety-five percent confidence intervals for the DOC test were determined by a chi-squared distribution with $k-1$ degrees of freedom (k being the number of conditions being compared; $p=0.05$).

Results

Linear and angular head accelerations about Reid's axes were analyzed for absolute maximum value, RMS, median frequency and 95% confidence interval frequency (95% CIF). Absolute maximum and 95% CIF are reported in the included tables but were not statistically tested.

Control trials

The three control trials revealed repeatability in angular RMS and median frequency ($ICC \geq 0.867$ in all directions for RMS; $ICC \geq 0.685$ in all directions for median frequency). The average RMS in roll, pitch and yaw was $2.02 \pm 1.38 \text{ rad/s}^2$, $2.38 \pm 1.08 \text{ rad/s}^2$ and $2.39 \pm 1.71 \text{ rad/s}^2$ (mean \pm SD), revealing a high standard deviation in every direction. Average median frequency for the 3 control trials in roll, pitch and yaw was $8.5 \pm 2.36 \text{ Hz}$, $3.94 \pm 0.80 \text{ Hz}$ and $4.66 \pm 0.62 \text{ Hz}$, respectively.

Linear acceleration results were not repeatable in some instances. RMS was repeatable in AP and IS directions ($ICC > 0.634$) but was not in ML ($ICC = 0.377$). Average RMS for AP was $0.21 \pm 0.09 \text{ m/s}^2$, and for IS was $0.06 \pm 0.04 \text{ m/s}^2$. Median frequency was repeatable in AP ($ICC=0.515$; average value $0.02 \pm 0.03 \text{ Hz}$), but not in ML or IS ($ICC \leq 0.382$).

Complete tables of control trial data can be found in Appendix 1.

Sensory condition trials

Four experimental trials tested head acceleration characteristics under different manipulations of two factors: vision and surface. To recall, these trials were eyes-open hard-surface (EOHS, Exp 1), eyes-closed hard-surface (ECHS, Exp2), eyes-open soft-surface (EOSS, Exp 3), and eyes-closed soft-surface (ECSS, Exp 4). The results from these conditions are

summarized in Table 2 (angular) and Table 3 (linear). Convention follows our modified Reid's axes: positive roll is right ear down, positive pitch is nose up, and positive yaw is nose right.

Angular acceleration

The angular acceleration RMS ANOVA showed an interaction effect between vision and surface factors for roll ($F(1,10)=14.781$), pitch ($F(1,10)=23.919$) and yaw ($F(1,10)=19.612$). A post-hoc Tukey test revealed that in all axes, the difference lay in ECSS RMS, it being significantly higher than RMS in all other conditions (roll all $p \leq 0.000393$; pitch all $p \leq 0.000213$; yaw all $p \leq 0.000276$; see Figure 2).

The ANOVA on median frequency of angular head accelerations showed main effects of surface in roll ($F(1,10)=24.135$; $p=0.00061$) and yaw ($F(1,10)=26.373$; $p=0.00044$), where median frequency under HS conditions was significantly higher than SS. No main effects in median frequency were observed about the pitch axis. Results can be seen in Figure 3.

	Exp 1 EOHS			Exp 2 ECHS			Exp 3 EOSS			Exp 4 ECSS			
ROLL (x)													
Absolute Max	1.88	+/-	1.09	2.14	+/-	0.92	2.29	+/-	1.04	3.57	+/-	2.11	rad/s ²
Overall RMS	0.27	+/-	0.06	0.29	+/-	0.06	0.31	+/-	0.05	0.39	+/-	0.07	rad/s ²
Median Freq	8.45	+/-	2.50	8.10	+/-	1.65	7.20	+/-	2.16	5.14	+/-	1.19	Hz
95% CIF	21.35	+/-	2.75	20.50	+/-	2.60	20.06	+/-	1.86	18.79	+/-	2.53	Hz
PITCH (y)													
Absolute Max	2.42	+/-	0.90	2.39	+/-	0.91	2.63	+/-	0.57	4.05	+/-	1.24	rad/s ²
Overall RMS	0.29	+/-	0.05	0.33	+/-	0.05	0.36	+/-	0.06	0.51	+/-	0.08	rad/s ²
Median Freq	3.95	+/-	0.80	3.69	+/-	0.57	3.69	+/-	0.61	3.69	+/-	0.48	Hz
95% CIF	17.66	+/-	3.31	16.73	+/-	3.42	14.09	+/-	2.14	11.88	+/-	1.19	Hz
YAW (z)													
Absolute Max	2.21	+/-	1.61	2.33	+/-	1.71	2.51	+/-	1.47	3.81	+/-	2.11	rad/s ²
Overall RMS	0.29	+/-	0.06	0.31	+/-	0.06	0.37	+/-	0.07	0.49	+/-	0.09	rad/s ²
Median Freq	4.62	+/-	0.50	4.41	+/-	0.47	3.96	+/-	0.42	3.60	+/-	0.45	Hz
95% CIF	15.56	+/-	2.39	15.38	+/-	2.22	14.11	+/-	2.25	12.49	+/-	2.19	Hz

**Table 2: Angular acceleration characteristics in roll, pitch and yaw under four sensory conditions.
Mean +/- standard deviation.**

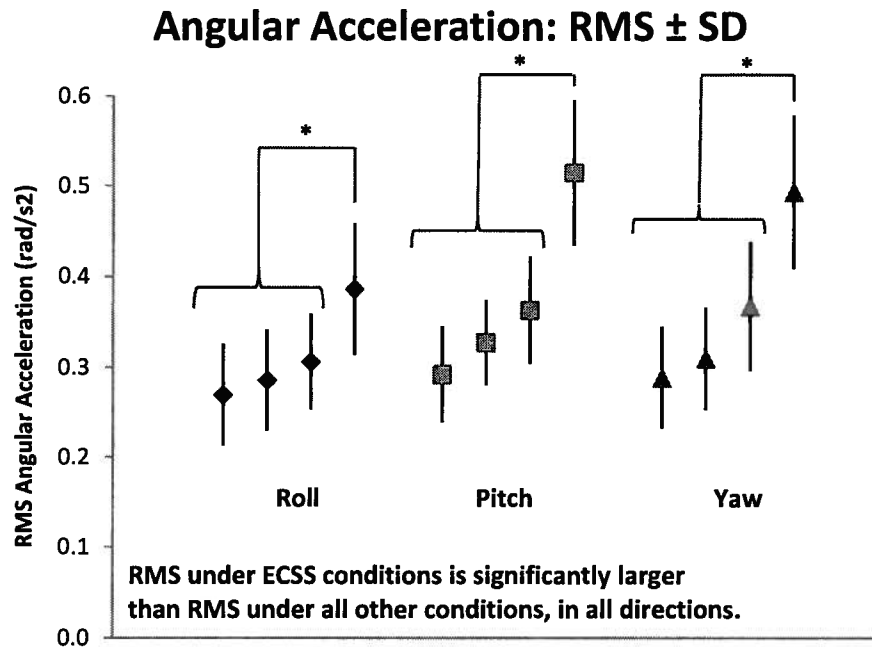


Figure 2: Angular acceleration RMS under four sensory conditions in three directions (mean \pm SD). Presented as same-shaped points in order, these are: EOHS, ECHS, EOSS and ECSS. The statistical analysis showed an interaction between vision and surface factors; a post-hoc Tukey test revealed that RMS under ECSS was significantly larger than RMS in all other conditions ($p \leq 0.000393$, denoted with an asterisk).

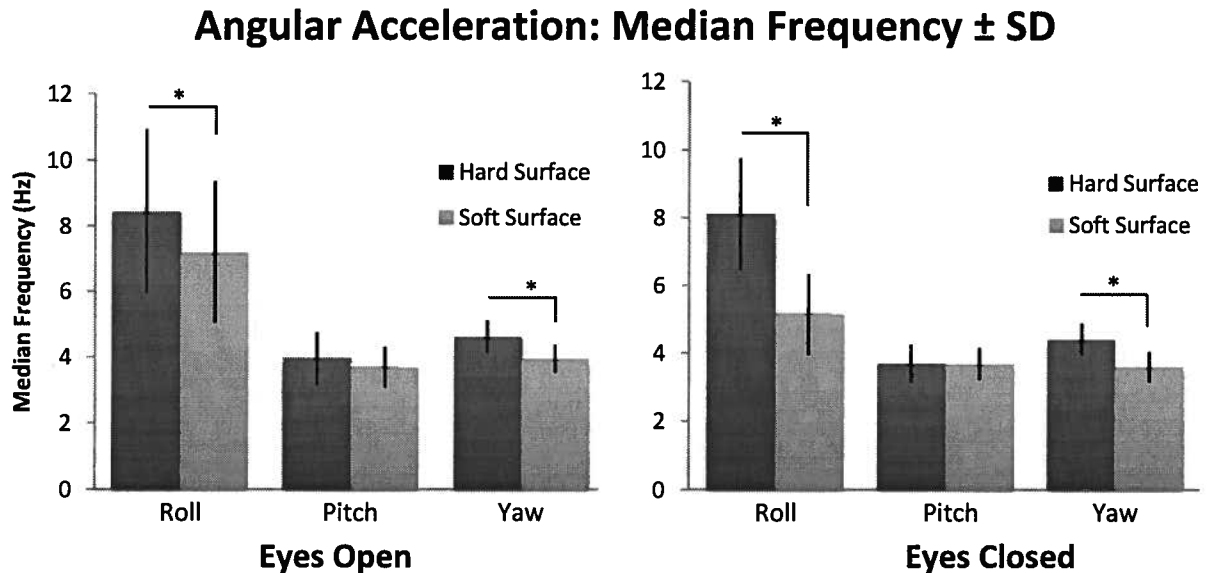


Figure 3: Angular acceleration median frequency in three directions (mean \pm SD). The statistical analysis showed main effects of surface condition in roll and yaw ($p \leq 0.00061$, denoted with an asterisk), but no main effects in pitch.

Linear acceleration

There were no significant main effects in the linear acceleration data, either in RMS or median frequency (all $p \geq 0.00756$). Table 3, below, shows the values of the linear acceleration measures under all sensory conditions.

	Exp 1 EOHS			Exp 2 ECHS			Exp 3 EOSS			Exp 4 ECSS			
AP (x)													
Absolute Max	2.57	+/-	1.07	2.91	+/-	1.16	2.50	+/-	1.12	2.60	+/-	1.15	m/s ²
Overall RMS	0.24	+/-	0.09	0.20	+/-	0.08	0.21	+/-	0.06	0.27	+/-	0.09	m/s ²
Median Freq	0.01	+/-	0.02	0.04	+/-	0.02	0.03	+/-	0.02	0.05	+/-	0.10	Hz
95% CIF	1.17	+/-	1.58	1.98	+/-	1.63	1.92	+/-	1.57	1.73	+/-	0.76	Hz
ML (y)													
Absolute Max	0.73	+/-	0.25	0.85	+/-	0.26	0.93	+/-	0.38	1.34	+/-	0.72	m/s ²
Overall RMS	0.11	+/-	0.05	0.12	+/-	0.04	0.13	+/-	0.03	0.19	+/-	0.08	m/s ²
Median Freq	0.05	+/-	0.06	0.06	+/-	0.05	0.07	+/-	0.04	0.15	+/-	0.12	Hz
95% CIF	9.93	+/-	5.74	9.29	+/-	5.46	7.67	+/-	5.71	4.52	+/-	4.11	Hz
IS (z)													
Absolute Max	9.79	+/-	0.18	9.76	+/-	0.20	9.85	+/-	0.19	9.97	+/-	0.23	m/s ²
Overall RMS	0.06	+/-	0.04	0.06	+/-	0.04	0.05	+/-	0.03	0.07	+/-	0.04	m/s ²
Median Freq	0.74	+/-	2.14	0.27	+/-	0.40	0.68	+/-	1.44	1.40	+/-	1.69	Hz
95% CIF	17.68	+/-	11.26	15.93	+/-	9.11	17.22	+/-	9.65	15.08	+/-	8.47	Hz

Table 3: Linear acceleration characteristics in anteroposterior (AP), mediolateral (ML) and inferosuperior (IS) direction under four sensory conditions. Mean \pm standard deviation.

Canal-transformed accelerations

Angular and linear head accelerations about Reid's axes were transformed to the directions of the right SCCs using transformation matrices from Della Santina et al. (2005). The values are reported in Table 4 on page 40 for discussion. The results are statistically compared between canals in Appendix 2.

	Exp 1			Exp 2			Exp 3			Exp 4			
	EOHS			ECHS			EOSS			ECSS			
Right Anterior Canal (x)													
Absolute Max	2.22	+/-	0.85	2.29	+/-	0.65	2.49	+/-	0.81	4.00	+/-	1.47	rad/s ²
Overall RMS	0.28	+/-	0.05	0.31	+/-	0.05	0.35	+/-	0.05	0.50	+/-	0.07	rad/s ²
Median Freq	4.94	+/-	0.90	4.55	+/-	0.60	4.46	+/-	0.82	4.00	+/-	0.50	Hz
95% CIF	20.04	+/-	2.55	19.48	+/-	3.11	17.64	+/-	2.77	14.85	+/-	2.10	Hz
Right Horizontal Canal (y)													
Absolute Max	2.20	+/-	1.51	2.44	+/-	1.79	2.60	+/-	1.29	3.81	+/-	1.87	rad/s ²
Overall RMS	0.30	+/-	0.06	0.32	+/-	0.06	0.37	+/-	0.07	0.49	+/-	0.08	rad/s ²
Median Freq	4.95	+/-	0.69	4.93	+/-	1.14	4.04	+/-	0.52	3.55	+/-	0.47	Hz
95% CIF	18.10	+/-	2.51	17.76	+/-	2.34	16.42	+/-	1.61	15.01	+/-	1.68	Hz
Right Posterior Canal (z)													
Absolute Max	1.76	+/-	0.79	2.03	+/-	0.98	2.34	+/-	0.83	3.48	+/-	1.92	rad/s ²
Overall RMS	0.27	+/-	0.06	0.29	+/-	0.05	0.32	+/-	0.05	0.43	+/-	0.08	rad/s ²
Median Freq	5.46	+/-	0.97	5.06	+/-	0.85	4.86	+/-	1.05	4.15	+/-	0.68	Hz
95% CIF	19.05	+/-	2.17	18.24	+/-	2.88	16.78	+/-	1.74	14.60	+/-	1.69	Hz

Table 4: Angular head acceleration characteristics in the directions of the canals under four sensory conditions. Mean +/- standard deviation. Statistical differences are not marked.

Coherence

Force plate

Coherence was first calculated to uncover possible linear relationships between certain combinations of head acceleration and force plate forces. The results can be seen in Figure 4. Linear head accelerations vs. linear force plate forces in equivalent axes were first examined, in anteroposterior and mediolateral directions. Coherence between linear head acceleration and linear force plate forces in the anteroposterior direction (“AP relationship”) reached significance under 7Hz, with three distinct peaks: one below 1Hz (maximum coherence 0.49), one at 1-3Hz (reaching a coherence of ~0.36) and a larger one at 4-7Hz (reaching a maximum coherence of

0.54). A Difference of Coherence (DOC) test revealed that coherence increased significantly when vision was removed, both under 1 Hz and in the peak around 5Hz. In the mediolateral direction (“ML relationship”), coherence peaked in the very low-frequency range (under 1 Hz; coherence 0.59) and again at 3.5 Hz. A DOC test showed that this 3.5 Hz peak was significantly larger in the EO condition (coherence of 0.46 vs. 0.35 in EC), and again showed significant differences in coherence under 1Hz (EC > EO).

Coherence between angular head accelerations and plate moments was calculated using axes in the same direction. In roll, small peaks (coherence ~0.12) around 3, 5 and 7Hz are observed under both conditions. The pitch direction also shows low coherence in similar regions (coherence ~0.15-0.20). The DOC test revealed that pitch coherence at 3 and 7Hz was higher when the eyes were open. Both pitch and roll also had significant coherence under 1Hz, which increased with eye closure.

Coherence in the yaw direction was seen in three distinct areas: under 2Hz (peak at a coherence of 0.69), at 3.5Hz (peak coherence ~0.35), and 5Hz (peaks coherence from 0.2-0.3). Small groups of peaks (coherence <0.2) were also seen at ~7Hz and ~12Hz, with significance found up to 20Hz (the upper frequency limit tested). A DOC test revealed differences under 2 Hz and that eye closure caused a lower 5Hz peak.

The last set of data analyzed for force plate coherence were linear head accelerations vs. the force plate moments that they would cause, given an inverted pendulum model about the ankles. Coherence between linear head accelerations and angular force plate data reached significance in certain bands in both directions. The linear acceleration of the head in the anteroposterior direction (x) was related to the force plate moments about the pitch axis (y) differently according to visual condition. Both visual conditions showed some significant

coherence from 0-20Hz, but areas of maximum coherence were concentrated below 2Hz and between 4-6Hz. The DOC test showed that eye closure increased coherence under 2Hz (coherence ~ 0.50 in EC vs. ~ 0.25 in EO), and in narrow-bandwidths at 4, 6 and 9Hz.

Differences between conditions also appeared in coherence between linear head accelerations in the mediolateral direction (y), and angular plate forces about the roll axis (x). The EO condition was coherent from 0-20Hz, with peaks under 1.5Hz (coherence ~ 0.57), and at around 6, 10, and 15Hz (all coherence ~ 0.25). In the EC condition, coherence reached 0.60 under 1.5Hz, and a distinct low-coherence peak was found between 5-6Hz. A DOC test showed once more that eye closure increased coherence below 1Hz, with other small differences showing that coherence decreases with eye closure in the higher frequencies.

Time-cumulant density (TCD) plots revealed the timing and polarity of the relationships. When considering the implications of polarity it should be noted that, mechanically speaking, the forces at the feet must be proportional to the acceleration of the center of mass in the same direction. Since signal magnitude is not of importance to the coherence analysis (except when considering the signal-to-noise ratio), one can consider the coherence between foot forces (/moments) and head accelerations to also be representative of the coherence between center of mass linear (/angular) acceleration and head accelerations. TCD polarity signals the phase relationship: positive indicates in-phase (e.g. forward/forward), and negative indicates out-of-phase (e.g. forward/backward).

TCD plots from pooled data revealed that AP plate forces (forces on the feet) appeared to lag AP head accelerations by approximately 180 ms in the EO condition, and 145ms in the EC condition. In the ML direction, however, foot force preceded the head accelerations by 210ms in the EO condition and by 110ms in the EC condition. In both AP and ML directions the TCD was

positive, meaning that the forces on the feet are in phase with head accelerations (forward/forward, etc.).

TCD plots also showed that force plate moments in roll preceded angular head accelerations about the same axis by about 210ms EO, and 130ms EC. In pitch and in yaw, the force plate moments occurred after the angular head accelerations about the same axis. In pitch this lag was 100 – 110 ms (EC/EO, respectively). In yaw, the lag decreased to about 45ms in both conditions. The relationships were negative in polarity, indicating opposite phase. In this case, however, it is the moments on the force plate that we compared, not those on the foot.

AP head accelerations preceded pitch plate moments by 65ms in the EO condition, and by 5ms in the EC condition. The signals were in-phase. In contrast, ML head accelerations lagged angular plate moments in roll by about 80 – 90 ms (EC/EO, respectively), and the signals were out of phase. TCD plots can be seen in Figure 4.

Interestingly, the plane of sway seemed to dictate whether the relationship between forces/moments and linear/angular head accelerations was a leading or lagging one. In the sagittal plane, which includes AP forces and pitch moments, the head accelerations lead force plate forces. In contrast, in the frontal plane including ML forces and roll moments, head accelerations lagged force plate forces, in similar time frames.

The differences in EO/EC are not statistically significant according to dependent t-tests conducted on data from all subjects (8 subjects; all $p > 0.05$). Statistical tests could not be run on timings from pooled data between conditions as there were only two values to compare.

Head Accelerations vs. Force Plate Data: Coherence, DOC and TCD

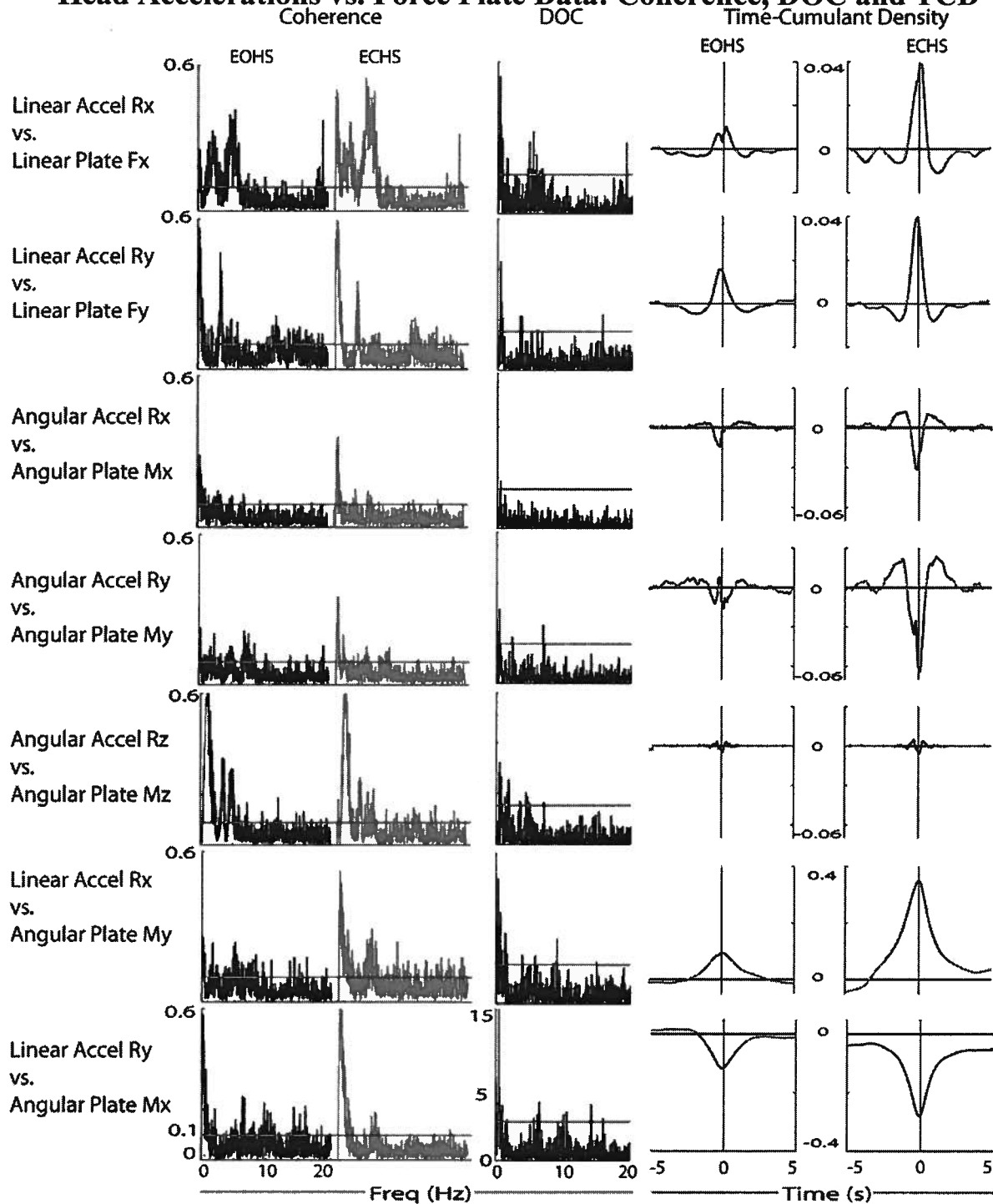


Figure 4: Coherence and TCD plots for Reid head accelerations vs. force plate forces. Red lines denote 95% confidence intervals for coherence (blue EO, green EC) and DOC. Black crosses represent zero in the TCD plots; blue lines represent parts of the plot that do not reach significance.

EMG

Coherence was calculated between angular head accelerations in the directions of all SCCs, and EMG from soleus (SO), medial gastrocnemius (MG) and tibialis anterior (TA) bilaterally. Select results are presented here, but caution is advised. The paper from which the canal transformation matrix was taken (Della Santina et al., 2005) explicitly warned against using the results to calculate prime directionality of the canals from anatomical landmarks, as they are poorly aligned. The assumption that these prime directionalities are reliable from landmarking is inherent in the interpretation of the coherence analysis. Results are therefore not likely to be robust. They are selectively presented in short-form (soleus only) in Figure 5, and can be found in their entirety in Appendix 3.

Plots of coherence between bilateral soleus and the 3 SCCs reveal a few interesting relationships. There are significant peaks in coherence between the horizontal canal acceleration and bilateral soleus under 6Hz (up to a coherence of 0.16 in ECSS). A DOC test revealed that coherence increases significantly in parts of this region from EOHS through ECHS and EOSS, to ECSS.

In the anterior and posterior (or together, vertical) canals, coherence differed by muscle side. A 4-way DOC test revealed no difference between conditions in right soleus/anterior canal coherence, or between conditions in left soleus/posterior canal coherence. Differences were seen in left soleus/anterior canal coherence and right soleus/posterior canal coherence, however, between all conditions. This may be due to signal strength. Forward-right accelerations, which the right anterior canal would pick up, would require excitation in right soleus to counteract in order to maintain stability. Forward-left accelerations would require excitation in left soleus to maintain stability and would be picked up by the left anterior canal, which is approximately

equivalent in direction to the right posterior canal. Active contraction would increase the signal to noise ratio, making a significantly coherent result more likely. This side will be termed the “leaning-affected side.”

In both vertical canals, the leaning affected side was highest in coherence under the ECSS condition but differed in areas between all conditions. In ECSS, significant coherence was found in two main peaks, from 0-2Hz and 3.5-7.5Hz, with coherence reaching only 0.17 at maximum. A less well-defined peak also is visible around 17-20Hz. The lower-frequency peak seems to correspond with SVS/EMG coherence results from Dakin et al. (2007), who reported peaks from 5-7Hz and 11-16Hz. Dakin’s higher-frequency coherence band was not observed.

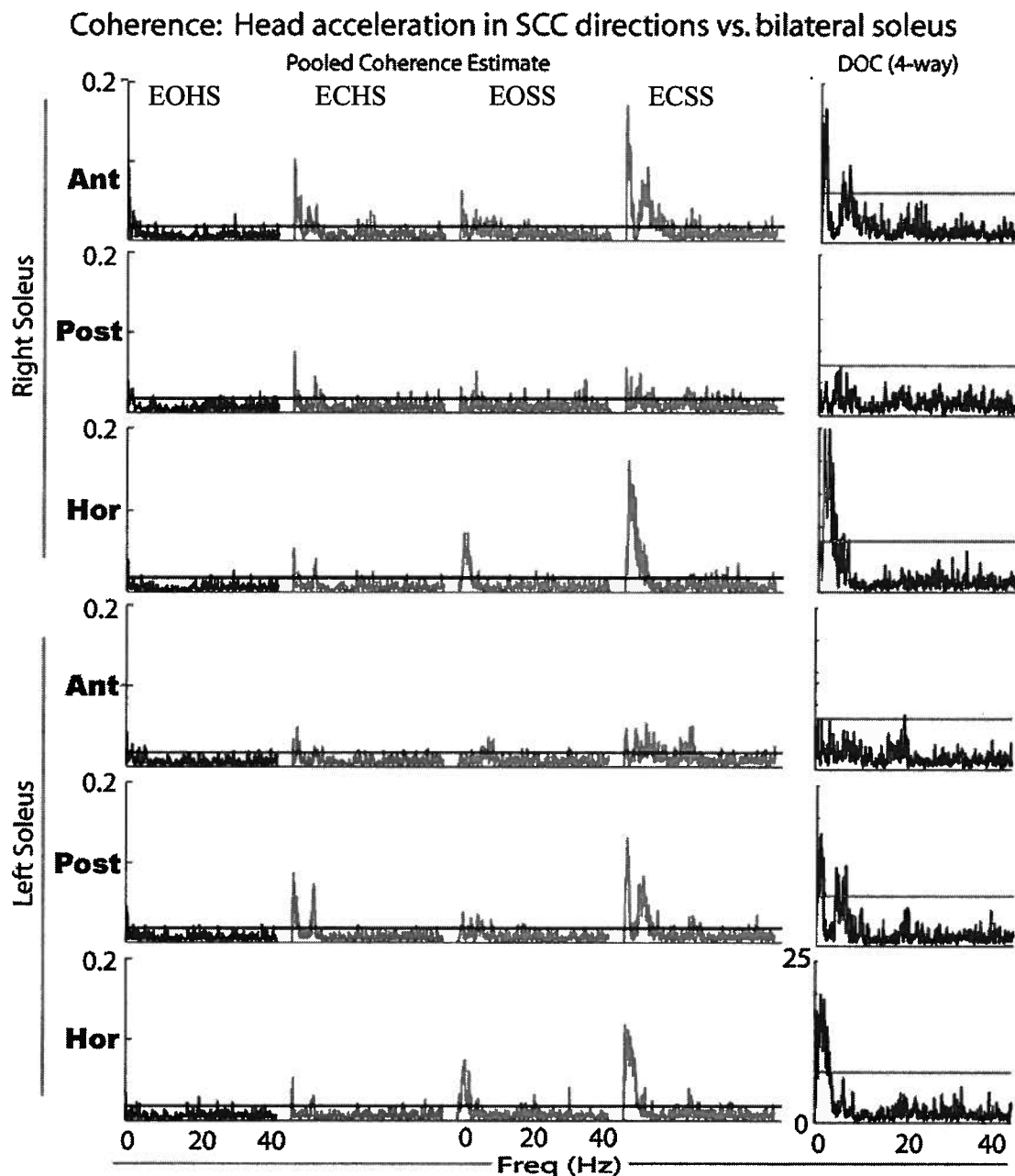


Figure 5: Head accelerations in the direction of the SCCs (anterior, posterior and horizontal canals as marked) vs. EMG from bilateral soleus. Horizontal lines denote 95% confidence intervals, sensory conditions are as labeled. The rightmost plot is the 4-way DOC test.

TCD plots revealed a lead of muscles over head accelerations in all canals (see Appendix 3). The relationship in soleus for all canals is shown in Figure 6. The muscle lead is seen

bilaterally, with an opposite polarity in opposing legs. In soleus, for the EOHS condition in the anterior canal, this lead is approximately 135ms for the first peak (the one furthest from time zero). The second peak (closer to time zero) is of opposite polarity and occurs before head accelerations by around 40ms. In the horizontal and posterior canals, EMG leads head accelerations by around 115-125ms, as calculated from the pooled TCD plots. These lead times change in the ECSS condition, as evidenced in Figure 6. Under these conditions, the first peak in right soleus EMG leads head accelerations in the anterior canal by 360ms, in the posterior canal by 200ms, and in the horizontal canal by 330ms.

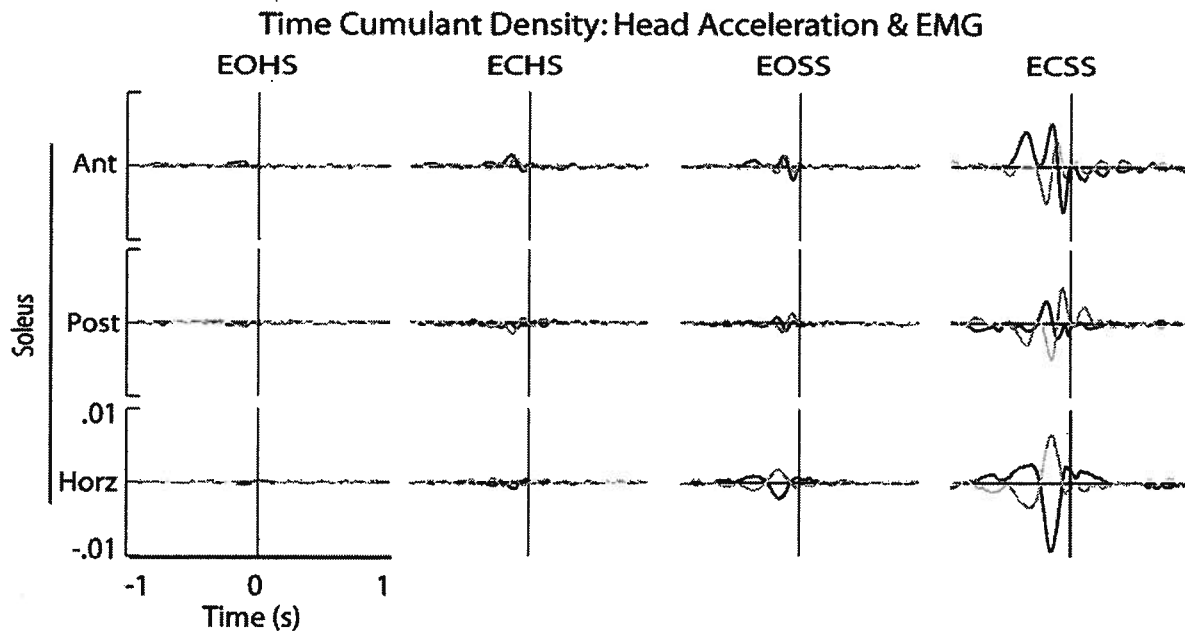


Figure 6: TCD plots between anterior, posterior and horizontal semi-circular canal accelerations and soleus EMG under four sensory conditions. Black lines are right muscles, grey are left. Crosses denote zero. Blue parts of the plots do not cross the boundaries of significance.

Discussion

Repeatability

The nature of this study is exploratory in that angular head accelerations have not been reported in literature to date. If this data is to be compared to other populations (patients, for example) in the future, then repeatability in healthy subjects is certainly of interest. According to this study, angular head acceleration RMS and median frequency were repeatable in all axes under the full sensory condition (EOHS; about Reid's axes). Linear head acceleration measures were repeatable in the anteroposterior direction but were not mediolaterally. This may be because movement in the anteroposterior direction has the advantage of a larger base of support, inevitably increasing RMS and median frequency standard deviations and therefore lowering the chances of finding a significant difference between trials. Having said this, it is not clear whether or not this non-repeatability is actually true for linear head acceleration measures, given some limitations in linear acceleration measurements (discussed in "Limitations").

Repeatability was not tested under differing sensory conditions, and therefore it cannot be commented on past EOHS.

Comparison of data to previous accelerometry work

There have been no prior studies against which to compare angular head acceleration measurements, but linear head acceleration reports are available. Previous studies report mean mediolateral head accelerations in the EOHS condition from 0.011m/s^2 (Winter et al., 1998) to 0.2m/s^2 (Tsujikawa, 1966). The values from this study more closely resemble Tsujikawa's results, with linear head acceleration RMS around $0.11\text{--}0.19\text{m/s}^2$. This is possibly due to Tsujikawa's direct measurement technique. His group used accelerometers, while Winter et al.

used displacement data to calculate accelerations. Tsujikawa also measured brief periods of maximum acceleration in the mediolateral direction (with the eyes closed in a tandem stance) of approximately 2.45m/s^2 . In the roughly equivalent stance in this study (ECSS), maximum accelerations reached 1.34m/s^2 in ML and nearly 3m/s^2 in AP. Of course, linear accelerometer placement may contribute to this difference, and these directional discrepancies might be partially owed to Tsujikawa's methods, specifically the use of a tandem stance and one linear accelerometer atop a helmet. The conclusion is that linear acceleration measurements seem to replicate those previously found.

Comparison of acceleration data to reported vestibular thresholds

The most important message obtained from analyzing the sensory condition trials was that both absolute maximum and RMS angular head acceleration measured in this study exceeded reported thresholds for the vestibular SCCs. Subjective thresholds are reported from $0.06\text{-}3\text{ deg/s}^2$, depending on the study, while thresholds established by oculogyral illusion measurement found smaller values, around $0.04\text{-}0.28\text{ deg/s}^2$ (reviewed in Nashner, 1971). Nashner (1971) argued that these values varied because of differing response modalities, and endeavoured to discover the SCC threshold for the postural response modality. He calculated this threshold to be 0.05deg/s^2 , using an accelerated platform with a nulled ankle angle and no vision. Evidently, this setup is not equivalent to quiet standing, but does yield an interestingly low vestibular threshold 'in a postural response modality'. In any case, the smallest angular head acceleration RMS found in this study (that in the EOHS condition in the right posterior canal direction) was 0.27 rad/s^2 ; approximately 14.9 deg/s^2 . This is much larger than any reported vestibular threshold in any of the response modalities, and values become increasingly larger as vision and surface factors are manipulated. It is apparent that the vestibular system is

physiologically able to detect most of the angular acceleration behaviour at the head during quiet standing.

Angular head acceleration median frequency (in SCC directions) varied from around 3.5-5.5 Hz, over all conditions and directions. Head acceleration frequency measures to compare to are not reported in the literature to date. Displacement frequency values are more common but were not accurately calculable from this study's data. They would, however, certainly not be higher in frequency, so it is likely that these frequency values still fall into the range at which Highstein (2005) and Lysakowski & Goldberg (2004) argue that the SCCs are velocity transducers (0.025Hz – 30Hz). Ross (2003), however, has found collateral inputs between hair cells in the SCCs that likely lead to on-line differentiation. Acceleration data may still be transduced in the SCCs in quiet standing.

Linearly, the smallest head acceleration RMS occurred in the inferiosuperior direction, and was around the threshold for the otolith organs as reported by Meiry (1966). RMS in AP and ML directions greatly exceeded this threshold (0.20 and 0.11 m/s², respectively, vs. Meiry's threshold of 0.059m/s²), therefore it is likely that the otolith organs are able to detect linear head accelerations, in the transverse plane at least, that occur during quiet standing. It is thought that the otolith organs are most sensitive at a low frequency, and therefore act as a static and low-frequency vertical reference during quiet standing (Nashner, 1971). This argument may be supported by the results of this thesis, given the low median frequency found in the linear head acceleration data, which likely reflects a gravitational position effect.

The inverted pendulum

It is recalled from the literature review that the postural strategies used in standing balance are the ankle and hip strategy. The ankle strategy results in inverted-pendulum-type

sway and is normally used under full sensory conditions (Winter, 1995). Subjects resort to the hip strategy, which involves counterrotation of the head and hips, under unstable or shortened base of support conditions. The use of these strategies during the trials can be alluded to from the force plate/head acceleration TCD data. The positive polarity of both the AP and ML relationships reveals that the CoM and the head accelerate in-phase linearly, which seems to point to the use of an inverted pendulum ankle-strategy. In addition, the plate moment/angular head acceleration relationships also suggest an inverted pendulum. Although the polarities were negative, they were calculated using forces with respect to the force plate. When using the moments the foot (and consequentially the CoM) experiences instead, these polarities would be positive, pointing to an in-phase angular relationship as well. These findings are supported by a study by Winter et al. (2003), in which the applicability of the inverted pendulum model was investigated in each plane. The group found that the height and horizontal displacement RMS of body markers were correlated with a linear regression through the points at an R^2 of 0.966 in AP and 0.944 in ML (Winter et al., 2003). They concluded that the inverted pendulum model was valid in both planes, as we do.

The hip strategy involves counterrotation of the head and hip (Horak & Macpherson, 1996). If it was dominant, the polarity expected from the force plate relationships would be opposite to that found in the EOHS and ECHS conditions. Unfortunately force-plate relationships could not be investigated under soft surface conditions (see Limitations), so the expected negative polarity could not be established. However, a decrease in angular head acceleration median frequency on soft surfaces suggests a hip strategy and it was observationally apparent in the subjects during the soft surface conditions.

Although the relationships in the force plate TCD data suggested inverted pendulum sway on the hard surface in AP and ML, the analysis revealed that the timing differed between sagittal and frontal planes. Head angular accelerations lead moments on the feet in pitch (sagittal plane) by around 100ms, but lagged them in roll (the frontal plane) by 130-210ms. This finding points to differing balance mechanisms in the AP and ML directions, which was originally suggested by Winter et al. (1996) in a CoP study. They alleged that the balance mechanisms were independent in the different planes (owing to biomechanical differences). This thesis shows that the difference between these independent mechanisms lies in the timing of control in each plane. A “top-down” mechanism is indicated in the sagittal plane, where the head appears to accelerate just prior to moments appearing at the feet. A “bottom-up” mechanism describes the frontal plane, where moments at the feet precede head accelerations in roll. Further, this implies passive head control in the frontal plane, as the head accelerates after moments appear at the feet. Sagittal head control, being opposite in timing, is suggested to be active in a quietly standing person.

These conclusions are, of course, based on the relative behaviour at only two points and are valid only on a hard surface. Further study on the timing of the accelerations of more body segments would aid in strengthening or refuting this idea.

Purposeful sway

There are many ways in which quiet standing sway could be composed of both reactive and proactive contributions. Reactively, external (gravity, environmental interactions) and internal (respiration, heartbeat, articulation) perturbations may ‘knock’ the body, moving the center of gravity and requiring correctional sway back to the middle of the base of support. Indeed, contributions from heartbeat have been seen in linear head acceleration plots (Kitahara,

1965; Tsujikawa, 1966). Conversely, from a proactive viewpoint sway can be considered not as a consequence of constant corrections, but instead as a useful tool for creating a robust sensory environment. If possible, a completely static standing posture would seem ideal in regards to energy conservation and neural simplicity, but such a posture would deprive the body of a stream of constantly changing afferent information from different sensory systems. If these systems respond best to change (and velocity information has been reckoned as crucial for balance; Jeka et al., 2004), then static posture would be a barren sensory condition. The argument for proactive, or purposeful, control of sway reasons that the body introduces sway to reap the benefit of rich afferent information from a constantly changing sensory environment.

The work of Gatev et al. (1999) supports the notion of purposeful sway. They showed that lateral gastrocnemius activity was positively correlated with motion of the center of mass and center of pressure during quiet standing, and that the muscle activity lead the motion, rather than reacting to it. This lead was longest in a full sensory condition, and shortest in an eyes-closed, Romberg-stance condition. In short, their study showed a feedforward balance mechanism at work, where the body predicted the upcoming anteroposterior sway (upcoming load on the muscle) and activated the muscle to counter it. It was as if the body had planned to sway all along: Gatev called this 'exploratory behaviour of quiet stance'. Such behaviour is also seen by Loram and Lakie (2002a&b), and is further supported by the results of this thesis.

As found by Gatev, this study found a lower-leg EMG lead over upper-body behaviour. In Gatev's experiment it was CoM displacement; in this case, it is head accelerations. This leading relationship was true in all muscles and conditions for which timing of maximums and minimums could be determined. Gatev et al. found that EMG in lateral gastrocnemius lead CoM displacement by 260-350ms overall. In this study, the anterior and posterior canal lead times for

the first-occurring peak on a hard surface were estimated at ~115-135ms in soleus, supporting Gatev's results but showing a shorter lead. This difference may be due to the measures used in the coherence analysis: Gatev used displacement, whereas we used acceleration. The muscles are also different.

Active systems in standing balance

Either reactive or proactive, coherence in CoM-head acceleration and EMG-head acceleration are mostly confined below 7Hz. Having established that the mechanical strategy in standing under both HS conditions is likely the ankle strategy, we know that the inverted pendulum model dominates in this region. If the inverted pendulum were entirely true, however, the AP and ML force plate/head acceleration coherence would be perfectly coherent (at 1) within the frequency bands of quiet stance. This is evidently not the case. Overall lowering of coherence can be caused by slop in the mechanical linkage through joint flexibility and elasticity, but there are also defined troughs in the coherence plots. The force-plate/head acceleration coherence found is probably the result of the mechanical linkage from the foot (where the forces occur) to the head in the system, all below 7Hz. It is hypothesized that the troughs in coherence are carved out by active systems interfering in the propagation of forces through the mechanical linkage. This active input functions to reduce coherence in certain frequency bands. This hypothesis is supported by the finding that, in all force/head and EMG/head coherence analyses, conditions including vision had significantly lower coherence under 1Hz (as found by DOC tests). This suggests that vision is an active system in standing balance in this region, which aligns with reports that vision contributes most to standing balance at frequencies below 1Hz (Diener & Dichgans, 1988).

The higher-frequency gaps in coherence could be the result of other active systems. It is difficult to pinpoint exactly where these gaps lie, as their locations differ in each of the investigated relationships (although they appear similar in similar planes, AP vs. ML). Fitzpatrick et al. (1992) argued that ankle proprioceptive reflexes act to stabilize the body between 1 and 5Hz, which could cause some of the observed gaps in coherence, perhaps the ones around 2-3Hz and 4Hz. Fitzpatrick's experiments used 1-10Hz continuous random perturbations, so his results transfer to reactive control of quiet standing balance, which may be part but not all of the story as previously discussed.

Another gap is likely caused by active stabilization of the head in stance, as head and body are thought to be controlled independently during both ankle and hip strategies (Nashner et al., 1988). This active system would decrease coherence in both the EMG-head acceleration and CoM-head acceleration relationships, reflecting the decoupling of EMG and CoM from the head at certain frequencies. The main frequency trough in the EMG-head acceleration coherence is between 2-3.5Hz, and parts of that frequency range appear in coherence gaps in the CoM-head acceleration data, as well, leading to the consideration of this region for active head stabilization. This coherence gap is proposed to be of vestibular origin, for two reasons. Firstly, the gap is apparent in the ECSS condition when visual and somatosensory inputs are not reliable and therefore may not cause a gap. Secondly, head stabilization is one of the proposed main roles of the vestibular system in standing balance.

The role of the vestibular system in standing balance

In the beginning of this thesis, four potential purposes of the vestibular system in quiet standing balance were laid out. The results of this thesis do not point to one in particular, as caution must be taken when interpreting head acceleration results as a direct indication of the

role or importance of the vestibular system. The safest of these interpretations is likely in angular head acceleration RMS, which alludes to how much acceleration the canals are experiencing. The only difference in angular head acceleration RMS between conditions was in ECSS, the most vestibular-dependent sensory condition, when RMS increased significantly in all directions. There were no main effects of visual or somatosensory (surface) condition; therefore it could be that angular head acceleration RMS is dependent on the relative importance of the vestibular system in the sensory condition.

It has been determined that the SCCs are physiologically able to detect the smaller head accelerations occurring during the other sensory conditions (EOHS, ECHS and EOSS). In the most vestibular-dependent condition, however, head accelerations are allowed to increase significantly even though they are detectable when smaller. This could suggest that the vestibular system requires more stimulation through higher accelerations in order to participate directly in balance. This, in turn, seems to support two views. The first is of the vestibular system as “backup” system, which does not create balance responses of its own unless a ‘failsafe’ threshold is exceeded (which is higher than the perceptual threshold, and according to absolute maximum estimates could be around $3.5\text{-}4.0 \text{ rad/s}^2$). The second is that the vestibular system is always involved in balance through the vestibulospinal reflex, but requires a large input (acceleration) to create a large output (reflex). Studies using electrical vestibular stimulation would support this view, as responses increase with increasing stimulus intensity (Fitzpatrick & Day, 2004; Fitzpatrick et al., 1994). At least small areas of significant coherence were found in this study between lower leg EMG and head accelerations in the direction of the SCCs, under all conditions. If those accelerations are proportional to vestibular inputs, then this would suggest that the vestibular system is involved in balance to different degrees under all conditions,

possibly through the vestibulospinal reflex. The DOC tests show that coherence increases from EOHS through ECHS and EOSS, and is highest in ECSS as hypothesized. This confirms that the vestibular contribution to balance increases as other sensory information becomes less reliable, although its role cannot be distinguished.

These views do not exclude the possibility that the vestibular system acts as a ‘quiet partner’ comparator in lower-acceleration situations, as supposed by Nashner et al. (1982). In unstable ECSS conditions, it could be that head accelerations are allowed to become significantly higher as the limits of balance are reached and the CNS waits for visual and somatosensory information to yield a conclusion against which to compare vestibular information. If they are inconclusive, the vestibular backup response can be executed. If some sway is proactive, as hypothesized previously, then this could add another level to the vestibular comparisons. The balance system could use an efferent copy of the proactive AP drive to the ankle muscles to predict what will happen at the head, where the vestibular system resides. This would help the vestibular system in its possible role as a comparator, as comparing predicted to actual inputs would reinforce the verdict. This comparison would become more important as visual and somatosensory information becomes less reliable (as in ECSS condition), lending another explanation as to why the EMG-head acceleration coherence increases in more vestibular-dependent conditions.

It is still possible that the vestibular system is responsible for any or all of these roles and performs head stabilization in space as well. In this way, the vestibular system could be responsible for a gap in EMG-head acceleration and CoM-head acceleration coherence, as previously discussed.

Limitations of the study

Ideally, investigations involving the vestibular system would be completed using recordings directly from afferent and efferent nerves in the vestibular apparatus rootlets or the eighth cranial nerve. Not surprisingly these methods cannot be used in studies involving human subjects, so vestibular outputs must be inferred (and inferences must be recognized and treated with caution). In this study, inputs to the vestibular system were estimated to be proportional to angular head accelerations in the direction of each SCC; in turn, vestibular outputs were assumed to be proportional to these stimuli.

The novel nature of this study and its equipment goes hand in hand with many inherent limitations. The first involves drift in linear acceleration measurements. During the long, 4.5 min trials it is likely that gradual head or head and body tilt occurred as part of continual postural adjustments. The position-related effects of gravity on the linear accelerations cannot be accurately removed from the data in this experimental setup; therefore, very low-frequency components are present in the linear acceleration data (Figure 7). These components introduce more low-frequency power into the signal's power spectrum, artificially reducing the median frequency of the linear accelerations. The same low-frequency component may skew linear head acceleration RMS, as well, giving an artificially high RMS to the linear head accelerations despite a removal of the mean prior to processing. Kinematic data were not recorded during the trials, so this effect (caused by gravity) cannot be accurately removed nor can it be correctly estimated without further information. The exact frequency content of this position-related component is unknown. This is an interesting question for an additional study.

It is also probable that there is a low-frequency, position-related component in the force plate data. Carroll and Freedman (1993) found that quiet standing CoP was not a stationary

stochastic process, as had been previously assumed. Instead, average value and sway variance were time dependent, indicating travel in the center of CoP over time. The combination of position-related drift in both CoP and linear head acceleration data may cause a low-frequency spike in coherence between the signals that is misleading.

Other equipment limitations include intrinsic off-axis sensitivity in the accelerometers, possible drift due to temperature over the long trial time and, of course, potential head gear movement on the subject. Although the head apparatus was tightened and subjectively felt secure on each subject, parts of the apparatus were non-rigid plastic. This allowed for better adjustability and fit, but may have permitted some equipment shift during trials. Hair and skin shift over the skull was unavoidable using this experimental setup. By inspection, it appears that the accelerometer array was able to pick up very small angular and linear head accelerations, as seen in a sample second of angular and linear acceleration data (Figure 8).

When force plate data were recorded, efforts were made to ensure that the subject's head was aligned with equivalent force plate axes. The recording of natural head movement was paramount, however, and instructions needed to be limited. It is inevitable that these axes fell out of alignment during the trials, indeed in some subjects the inferiosuperior (z) axes never lined up at all. The coherence analyses on data collected in equivalent axes must therefore be treated with care, as these axes may be approximate but not equivalent, per se.

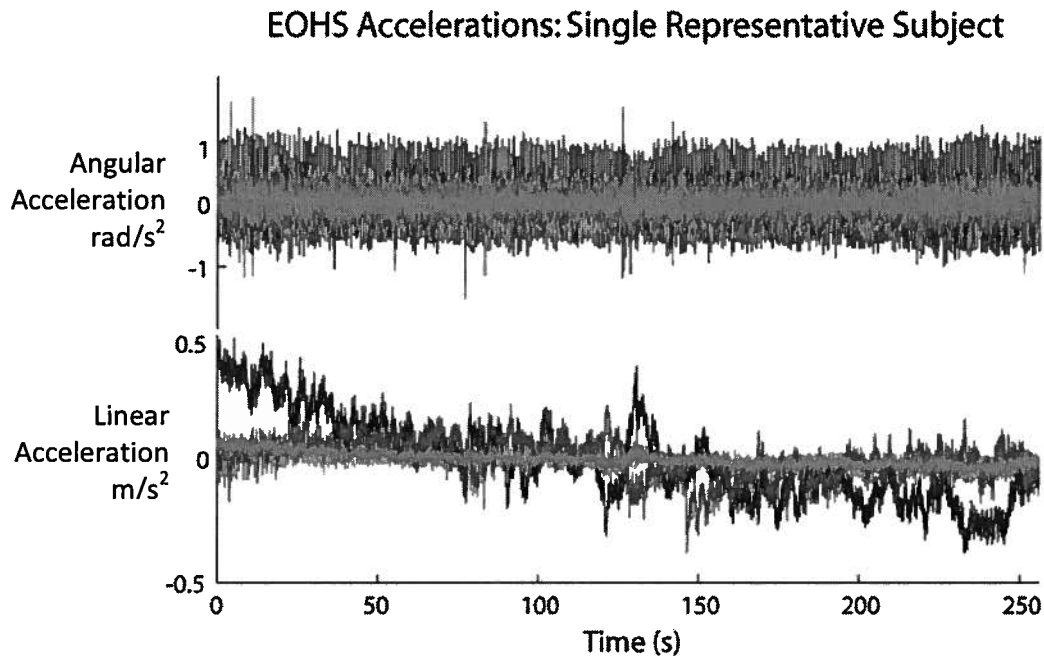


Figure 7: Angular and linear accelerations about Reid's axes for one EOHS trial in a representative subject over 4.5 minutes. Blue represents x (roll & AP), green is y (pitch & ML), red is z (yaw & IS). Means have been removed. Concurrent bursting in angular and linear accelerations can be seen around 135s. The low-frequency position-related component of linear acceleration can be clearly seen here, especially in ML and AP directions.

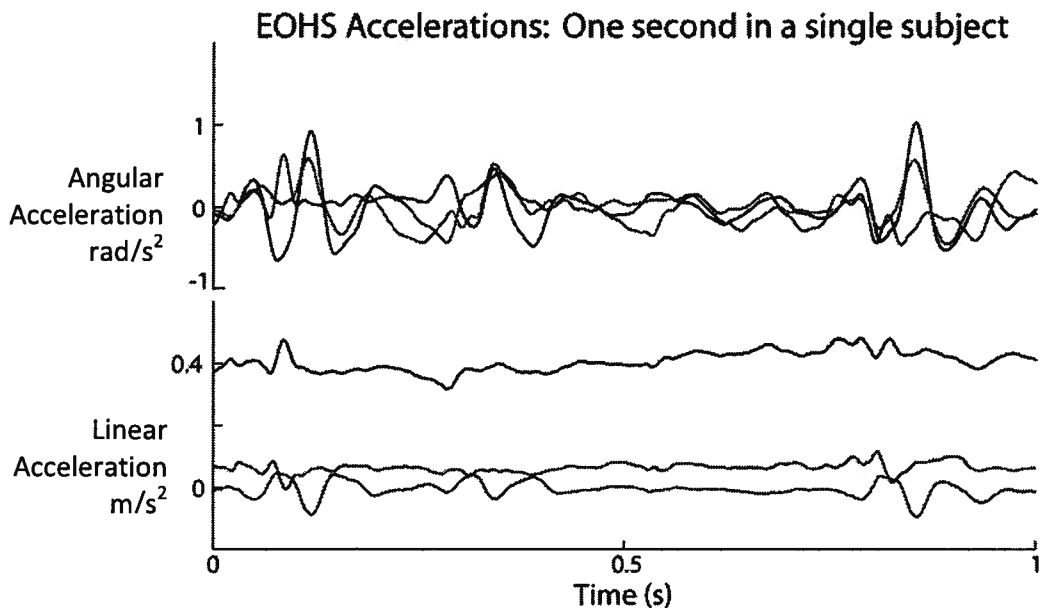


Figure 8: Processed accelerometer data from one second in the middle of one EOHS trial in a representative subject. Blue represents x (roll & AP), green is y (pitch & ML), red is z (yaw & IS). Overall means have been removed; reference frame is Reid's axes.

The transformation of head acceleration data from Reid's axes to the directions of the SCCs was an appealing and challenging direction to this study. Recent work has mapped the orientations of the individual canals in the human skull to a tenth of a degree (Della Santina et al., 2005). However, the authors warn against using this data to infer prime directionality of the canals, as anatomic planes align poorly with these prime directions, and the high inter-subject variability of these planes and the canals makes the estimates even worse. Accelerations in the directions of the SCCs have been calculated here, but are certainly estimates only. Additionally, it should be mentioned that the linear accelerations experienced by the vestibular apparatus cannot be discerned from this study. This is due not only to the previously mentioned limitations of the linear measurements, but also because no orientation information exists for human otolith organs, so no transformation could be completed.

The use of EMG in our coherence analysis also comes with limitations. Overall low muscle activity could lead to a low signal-to-noise ratio, and cross-talk in any of the signals could create misleading results. Care was taken to prevent cross-talk by appropriate landmarking, but the possibility is recognized. In terms of muscle specificity, it is evident from the coherence plots that medial gastrocnemius and soleus show higher vestibular connectivity than tibialis anterior. As expected, coherence in tibialis anterior rarely reached significance, even in the most vestibular-dependent conditions. This suggests a lack of vestibular coupling in TA, yet this conclusion is not supported by GVS studies (Fitzpatrick et al., 1994; Cathers et al., 2005). It is possible that coherence was not found in TA because the level of activation of this muscle under the conditions studied is small relative to its antagonists. This lowers the signal-to-noise ratio and makes it more difficult to identify a real relationship between the data.

There are a few data sets that would have added to this study. For example, accelerations were recorded from the head only, which fulfilled the aims of the study but brought up many other questions. Concurrent relative behaviour of the torso may have answered some of them but was estimated, not recorded. Concurrent center of pressure under soft surface conditions would also add to the data set. Unfortunately the validity of CoP when measured under foam is questionable, and therefore CoP data could only be analyzed for EO and EC conditions on the hard surface, limiting its usefulness. Hard surface CoP measures are available in Appendix 4.

Conclusions

The results of this study have provided a reference for angular and linear head acceleration behaviour during quiet standing sway in healthy humans under different visual and somatosensory conditions. It has been shown that angular head accelerations are repeatable under full sensory conditions, and that angular head acceleration RMS is above quoted vestibular thresholds in all tested sensory conditions. Linear head acceleration absolute maximum and RMS values tended to match previous reports under similar conditions.

The results reinforce that the inverted pendulum model is valid in quiet standing on a hard surface in the sagittal and frontal planes. Independent mechanisms of balance in these planes are maintained. The mechanical linkage in both planes confines the CoM-head acceleration and EMG-head acceleration coherence to below 7Hz, under which active systems are hypothesized to carve out frequency bands of influence. The visual system is suggested to operate below 1Hz, whereas the somatosensory and vestibular systems are proposed to have impact in the 2-4 Hz range.

The study also indicates that the vestibular system may play different roles in quiet standing balance as its importance in the maintenance of balance increases, but best supports the theory of the vestibular system as a head stabilizer and comparator. A third comparable variable (besides vision and somatosensory feedback) is proposed to be a vestibular input prediction, created from an efferent copy of the proactive drive to the ankle flexors and extensors.

This thesis study successfully measured the small accelerations occurring at the head in quiet stance. It uncovered limitations that afflicted the methods both in equipment and in analysis, and thus helped to ascertain the improvements that can be made to future studies in the

area. It is hoped that the achievements of this thesis will promote the use of head accelerography in quiet stance, a technique that has not yet been fully exploited in humans.

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Appendix 1: Tables of control trial data

	Control 1			Exp 1			Control 2			Mean			
ROLL (x)													
Absolute Max	1.96	+/-	1.68	1.88	+/-	1.09	2.23	+/-	1.42				rad/s ²
Overall RMS	0.27	+/-	0.06	0.27	+/-	0.06	0.28	+/-	0.06	0.27	+/-	0.06	rad/s ²
Median Freq	9.04	+/-	2.41	8.45	+/-	2.50	8.01	+/-	2.28	8.50	+/-	2.36	Hz
95% CIF	21.45	+/-	2.66	21.35	+/-	2.75	20.21	+/-	1.86				Hz
PITCH (y)													
Absolute Max	2.09	+/-	1.39	2.42	+/-	0.90	2.64	+/-	0.92				rad/s ²
Overall RMS	0.28	+/-	0.05	0.29	+/-	0.05	0.32	+/-	0.06	0.30	+/-	0.06	rad/s ²
Median Freq	4.05	+/-	0.90	3.95	+/-	0.80	3.82	+/-	0.73	3.94	+/-	0.80	Hz
95% CIF	18.68	+/-	3.79	17.66	+/-	3.31	16.49	+/-	2.20				Hz
YAW (z)													
Absolute Max	2.28	+/-	2.21	2.21	+/-	1.61	2.68	+/-	1.32				rad/s ²
Overall RMS	0.28	+/-	0.06	0.29	+/-	0.06	0.32	+/-	0.07	0.29	+/-	0.06	rad/s ²
Median Freq	4.84	+/-	0.68	4.62	+/-	0.50	4.53	+/-	0.69	4.66	+/-	0.62	Hz
95% CIF	15.54	+/-	2.21	15.56	+/-	2.39	15.61	+/-	2.40				Hz

Table 5: Results for angular acceleration of the head in roll, pitch and yaw during three control trials in the eyes-open, hard-surface condition. Mean +/- standard deviation between subjects. Final column shows overall means and standard deviations across all trials, if an ICC was performed and showed reliability.

	Control 1			Exp 1			Control 2			Mean			
AP (x)													
Absolute Max	2.37	+/-	1.17	2.57	+/-	1.07	2.79	+/-	1.28				m/s ²
Overall RMS	0.19	+/-	0.11	0.24	+/-	0.09	0.20	+/-	0.08	0.21	+/-	0.09	m/s ²
Median Freq	0.03	+/-	0.04	0.01	+/-	0.02	0.01	+/-	0.01	0.02	+/-	0.03	Hz
95% CIF	2.09	+/-	1.98	1.17	+/-	1.58	2.20	+/-	2.37				Hz
ML (y)													
Absolute Max	0.66	+/-	0.19	0.73	+/-	0.25	0.90	+/-	0.31				m/s ²
Overall RMS	0.09	+/-	0.03	0.11	+/-	0.05	0.11	+/-	0.04				m/s ²
Median Freq	0.02	+/-	0.02	0.05	+/-	0.06	0.06	+/-	0.07				Hz
95% CIF	12.56	+/-	3.03	9.93	+/-	5.74	10.08	+/-	5.28				Hz
IS (z)													
Absolute Max	9.79	+/-	0.14	9.79	+/-	0.18	9.78	+/-	0.21				m/s ²
Overall RMS	0.05	+/-	0.05	0.06	+/-	0.04	0.06	+/-	0.04	0.06	+/-	0.04	m/s ²
Median Freq	1.08	+/-	2.92	0.74	+/-	2.14	0.42	+/-	1.05				Hz
95% CIF	23.82	+/-	11.12	17.68	+/-	11.26	17.71	+/-	11.53				Hz

Table 6: Results for linear acceleration of the head in the anteroposterior (AP), mediolateral (ML) and inferosuperior (IS) directions during three control trials in the eyes-open, hard-surface condition. Mean +/- standard deviation between subjects. Final column shows overall means and standard deviations across all trials, unless the ICC was performed and did not show consistency between data sets.

Appendix 2: Differences in acceleration input to each SCC

A series of 1-way, 3-level ANOVAs were run on angular acceleration RMS and median frequency in the directions of the 3 SCCs, in order to identify any differences in angular acceleration felt by each canal. A summary of the information received by all canals can be found in Table 4 on page 40. The tests were completed to a p-value of 0.00625, representing a p-value of 0.05 with a Bonferroni correction factor for multiple comparisons of 8. If significant, post-hoc Tukey tests were performed to the same significance value to discover where differences lay. Statistically significant differences appeared in RMS in the ECSS condition only, showing the horizontal canal angular acceleration RMS to be smaller than the posterior canal values ($F(2,20)=8.56$, $p=0.0022$). There was one difference in median frequency: in the ECHS condition, horizontal canal median frequency was significantly higher than the anterior's ($F(2,20)=11.416$, $p=0.000542$).

Linear head accelerations in the directions of the semicircular canals were not analyzed.

Appendix 3: Coherence between head accelerations and EMG data

Coherence analysis was run between angular head accelerations in the planes of the right semi-circular canals and EMG data from 3 muscles bilaterally: medial gastrocnemius, soleus, and TA. Results can be seen in Figure 9 for the anterior canal, Figure 10 for the horizontal canal, and Figure 11 for the posterior canal. TCD plots are shown in Figure 12.

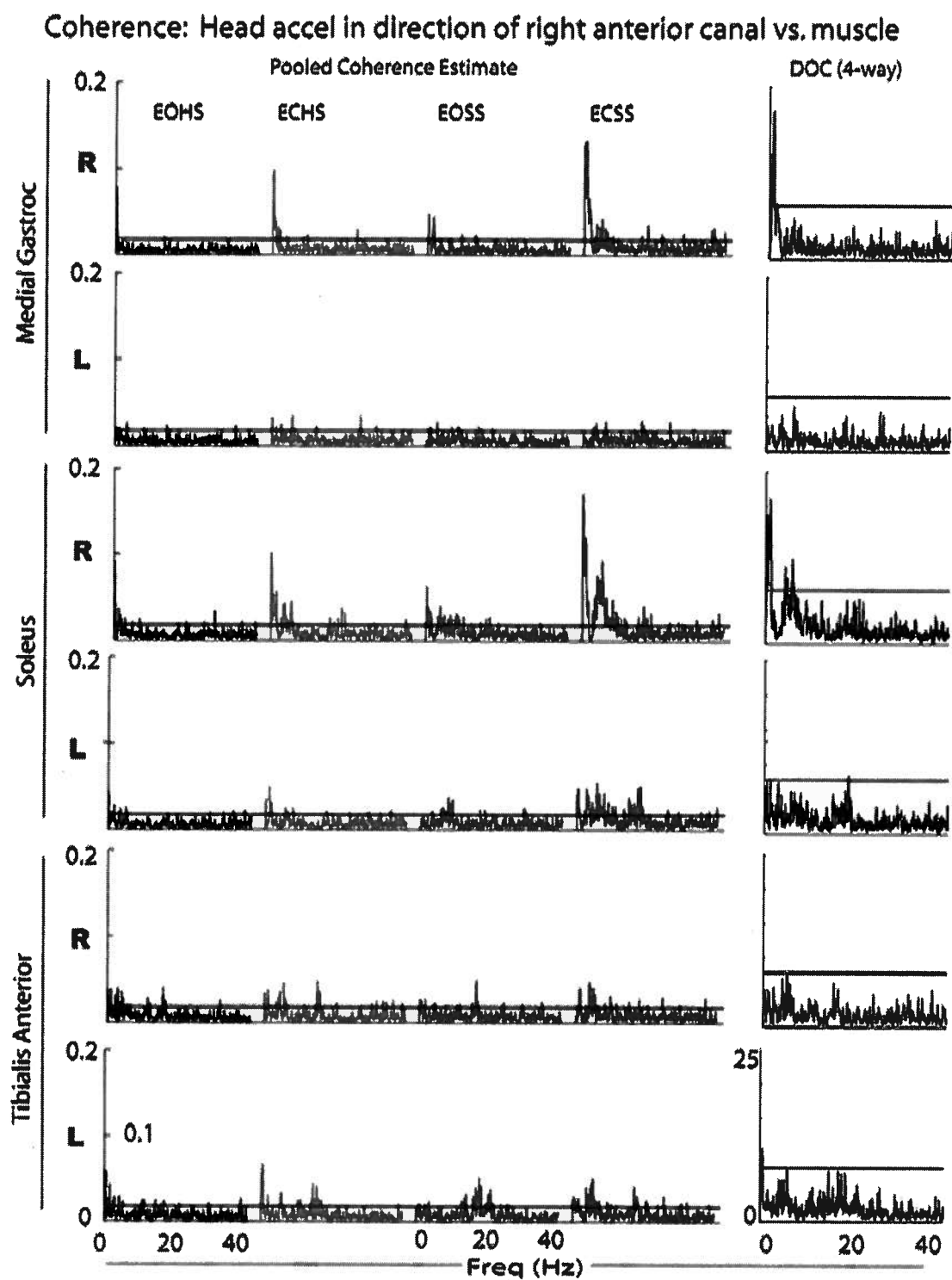


Figure 9: Coherence between anterior canal accelerations and EMG. Horizontal lines denote 95% CI. The first plots are coherence: EOHS, ECHS, EOSS, and ECSS in columns as labeled. The second plot shows a 4-way DOC test between all conditions.

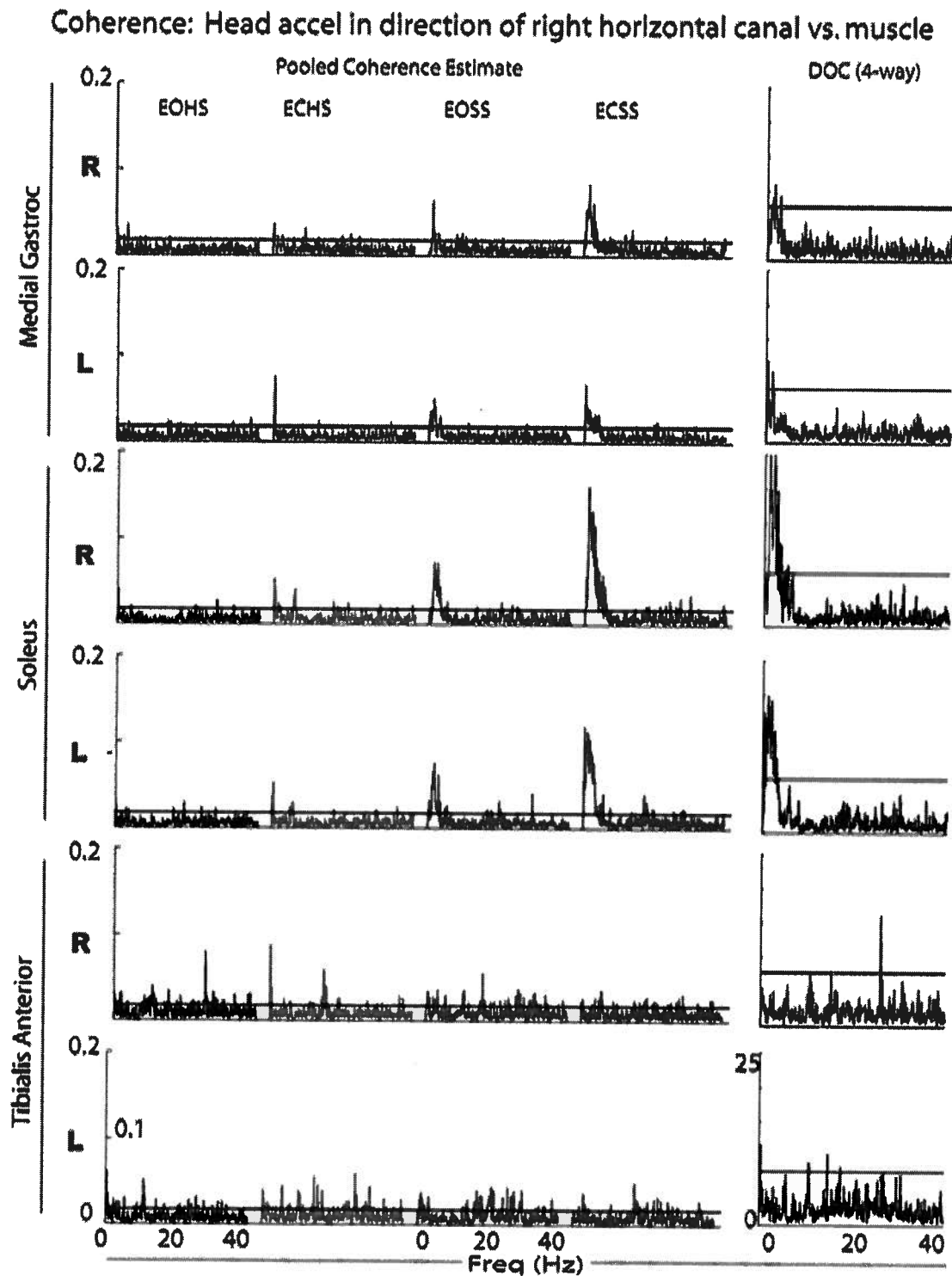


Figure 10: Coherence between right horizontal canal accelerations and EMG. Horizontal lines denote 95% CI. The first column is coherence: EOHS, ECHS, EOSS, and ECSS in columns as labeled. The second column shows the results of a 4-way DOC test between all conditions.

02- Pooled Coherence Estimate DOC (4-way)

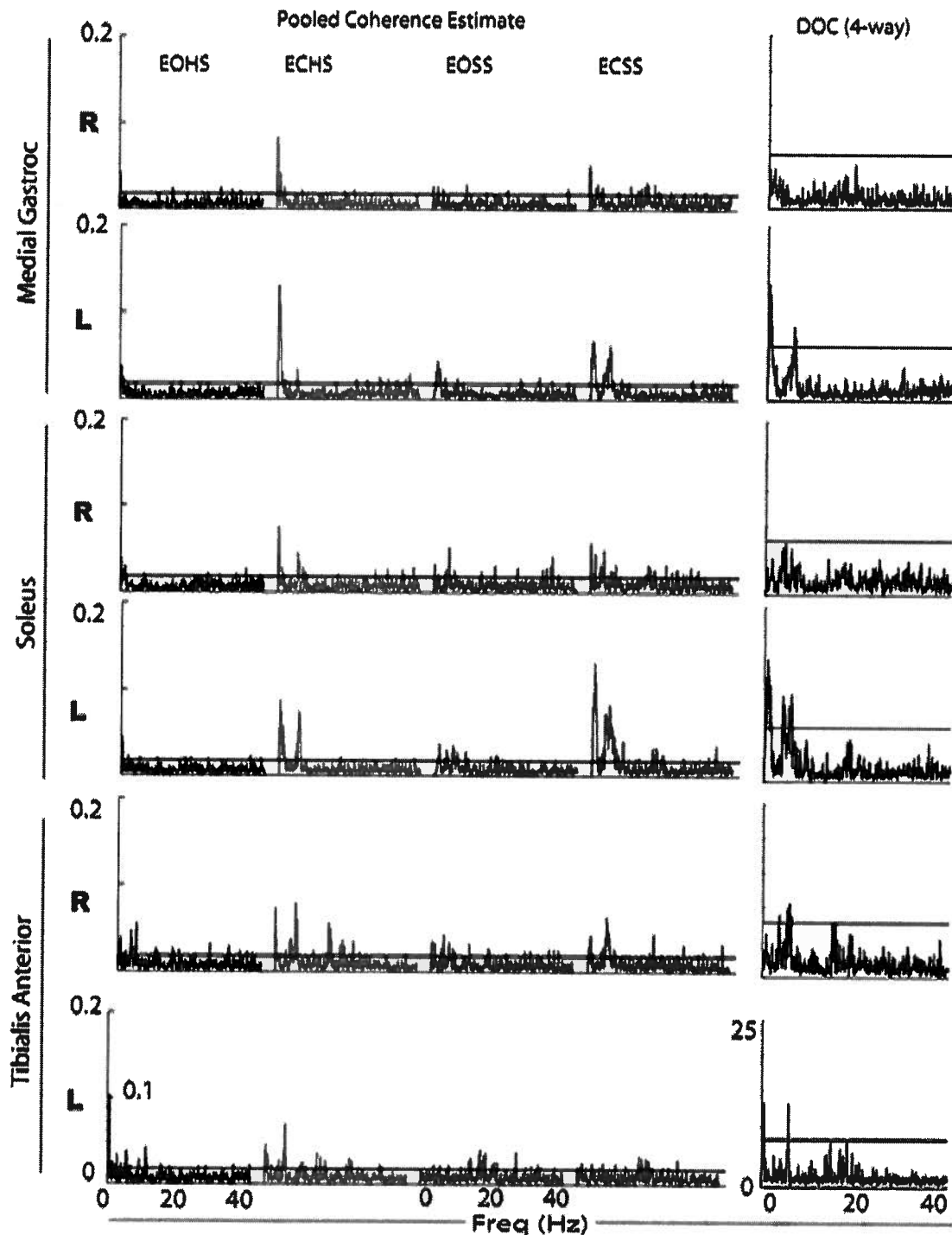


Figure 11: Coherence between posterior canal accelerations and EMG. Horizontal lines denote 95% CI. The first column is coherence: EOHS, ECHS, EOSS, and ECSS in columns as labeled. The second column shows the results of a 4-way DOC test between all conditions.

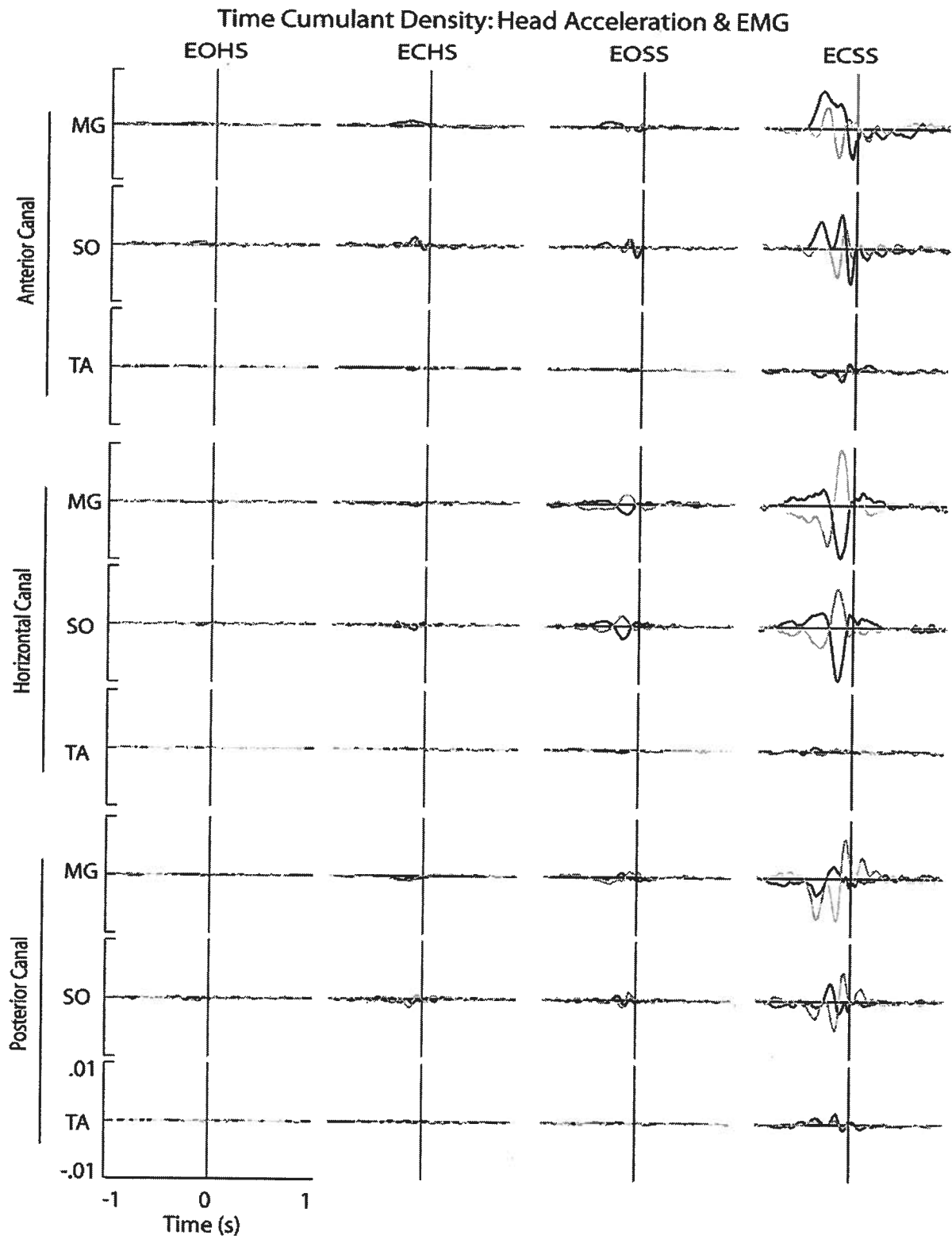


Figure 12: TCD plots between canal accelerations and EMG under four sensory conditions. Black lines are right muscles; grey, left. Blue parts of the plot do not cross the boundaries of significance.

Appendix 4: Center of pressure measures

COP RMS was repeatable in both AP and ML (ICC > 0.653), but was not at all in median frequency (ICC < 0.379 for AP and ML).

	Control 1			Exp 1			Control 2			Mean			
	Anteroposterior (x)												
Absolute Max	23.62	+/-	12.71	24.41	+/-	9.57	31.19	+/-	13.64				mm
Overall RMS	6.68	+/-	1.99	6.78	+/-	1.82	7.04	+/-	2.51	6.83	+/-	2.89	mm
Median Freq	0.04	+/-	0.02	0.03	+/-	0.02	0.05	+/-	0.03				Hz
95% CIF	0.54	+/-	0.21	0.58	+/-	0.23	0.53	+/-	0.21				Hz
	Mediolateral (y)												
Absolute Max	15.23	+/-	6.41	20.09	+/-	11.09	20.11	+/-	9.43				mm
Overall RMS	4.55	+/-	1.58	5.34	+/-	1.52	4.91	+/-	1.77	4.93	+/-	3.23	mm
Median Freq	0.05	+/-	0.02	0.06	+/-	0.05	0.10	+/-	0.06				Hz
95% CIF	0.69	+/-	0.26	0.60	+/-	0.17	0.72	+/-	0.23				Hz

Table 7: Results for COP displacement of in the anteroposterior (AP) and mediolateral (ML) directions during three control trials in the EOHS condition. Mean +/- standard deviation between subjects. Final column shows overall means and standard deviations across all trials if the ICC was performed and showed consistency between data sets.

	Exp 1			Exp 2			
	EOHS			ECHS			
	Anteroposterior (x)						
Absolute Max	24.41	+/-	9.57	28.51	+/-	13.37	mm
Overall RMS	6.78	+/-	1.82	8.57	+/-	1.97	mm
Median Freq	0.03	+/-	0.02	0.06	+/-	0.05	Hz
95% CIF	0.58	+/-	0.23	0.63	+/-	0.18	Hz
	Mediolateral (y)						
Absolute Max	20.09	+/-	11.09	23.76	+/-	6.74	mm
Overall RMS	5.34	+/-	1.52	5.96	+/-	1.40	mm
Median Freq	0.06	+/-	0.05	0.15	+/-	0.08	Hz
95% CIF	0.60	+/-	0.17	0.86	+/-	0.31	Hz

Table 8: Results for COP displacement of in the anteroposterior (AP) and mediolateral (ML) directions during two trials: EOHS and ECHS. Mean +/- standard deviation between subjects.


Appendix 5: Research Ethics Board Certificate of Approval



The University of British Columbia
Office of Research Services
Clinical Research Ethics Board – Room 210, 828 West 10th Avenue, Vancouver, BC V5Z 1L8

ETHICS CERTIFICATE OF FULL BOARD APPROVAL

PRINCIPAL INVESTIGATOR: Jean-Sebastien Blouin	INSTITUTION / DEPARTMENT: UBC/Education/Human Kinetics	UBC CREB NUMBER: H07-03119
INSTITUTION(S) WHERE RESEARCH WILL BE CARRIED OUT:		
Institution UBC		Site Vancouver (excludes UBC Hospital)
Other locations where the research will be conducted: N/A		
CO-INVESTIGATOR(S): Martin E. Héroux J. Timothy Inglis Chris Dain Daniel Mang Romeo Chua Melanie G. Roskell		
SPONSORING AGENCIES: Natural Sciences and Engineering Research Council of Canada (NSERC) - "Neurophysiology of human neck and lower limb motoneurons"		
PROJECT TITLE: Neurophysiology of human neck and lower limbs motoneurons		
THE CURRENT UBC CREB APPROVAL FOR THIS STUDY EXPIRES: April 22, 2009		
The full UBC Clinical Research Ethics Board has reviewed the above described research project, including associated documentation noted below, and finds the research project acceptable on ethical grounds for research involving human subjects and hereby grants approval.		

REB FULL BOARD MEETING REVIEW DATE: April 22, 2008																													
DOCUMENTS INCLUDED IN THIS APPROVAL:	DATE DOCUMENTS APPROVED:																												
<table border="1"> <thead> <tr> <th>Document Name</th> <th>Version</th> <th>Date</th> </tr> </thead> <tbody> <tr> <td>Protocol:</td> <td></td> <td></td> </tr> <tr> <td>Research Protocol</td> <td>Version 2</td> <td>May 13, 2008</td> </tr> <tr> <td>Consent Forms:</td> <td></td> <td></td> </tr> <tr> <td>Consent form</td> <td>Version 2</td> <td>May 13, 2008</td> </tr> <tr> <td>Advertisements:</td> <td></td> <td></td> </tr> <tr> <td>Advertisement</td> <td>Version 2</td> <td>May 13, 2008</td> </tr> <tr> <td>Questionnaire, Questionnaire Cover Letter, Tests:</td> <td></td> <td></td> </tr> <tr> <td>Epilepsy questionnaire</td> <td>Version 1</td> <td>May 13, 2008</td> </tr> </tbody> </table>	Document Name	Version	Date	Protocol:			Research Protocol	Version 2	May 13, 2008	Consent Forms:			Consent form	Version 2	May 13, 2008	Advertisements:			Advertisement	Version 2	May 13, 2008	Questionnaire, Questionnaire Cover Letter, Tests:			Epilepsy questionnaire	Version 1	May 13, 2008	May 21, 2008	
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CERTIFICATION: In respect of clinical trials: 1. The membership of this Research Ethics Board complies with the membership requirements for Research Ethics Boards defined in Division 5 of the Food and Drug Regulations. 2. The Research Ethics Board carries out its functions in a manner consistent with Good Clinical Practices. 3. This Research Ethics Board has reviewed and approved the clinical trial protocol and informed consent form for the trial which is to be conducted by the qualified investigator named above at the specified clinical trial site. This approval and the views of this Research Ethics Board have been documented in writing.																													
The documentation included for the above-named project has been reviewed by the UBC CREB, and the research study, as presented in the documentation, was found to be acceptable on ethical grounds for research involving human subjects and was approved by the UBC CREB.																													
Approval of the Clinical Research Ethics Board by one of:  Dr. Gail Bellward, Chair																													