Perceived Timing of Auditory and Inertial Cues During a Postural Perturbation in Younger and Older Adults

by Julian Lupo

A thesis

presented to the University of Waterloo

in fulfilment of the

thesis requirement for the degree of

Master of Science

in

Kinesiology

Waterloo, Ontario, Canada, 2015 ©Julian Lupo 2015 I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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

ABSTRACT

How the perceived timing of sensory events changes during a fall is relatively unknown.

Common anecdotal reports suggest that people often report distortions in their perception of time with very little recollection of what occurred during the fall. Previous research has found that the vestibular system is perceptually slow compared to the other senses (45-160ms delay), indicating that vestibular stimuli must occur prior to other sensory stimuli in order for it to be perceived as synchronous. The purpose of Study 1 examined links between falling and delays in inertial perception. In study 1, young healthy adults were recruited to establish whether temporally unpredictable postural perturbations are perceptually delayed relative to an auditory stimulus. In study 2, a second group of young healthy adults and a group of older adults are compared. Motion capture was used in study 2 to determine whether the perceived timing of a fall relative to a sound is related to behavioural reflexes generated in response to falling. Participants made temporal order judgments (TOJ) identifying whether the onset of their fall or sound came first to measure the point of subjective simultaneity (PSS) between sensory cues, with certainty measured by the just noticeable difference (JND). Study 1 results show that the onset of a perturbation has to precede an auditory stimulus by ~44 ms to appear coincident with the fall. Results from younger adults in Study 2 closely replicated those from Study 1, where a fall has to precede an auditory stimulus by ~44ms in order for the stimulus pair to be perceived as simultaneous. The results also clearly demonstrate that older adults require a fall to occur even earlier before an auditory stimulus than was required for younger adults (~88ms). The only significant relationship between perceptual responses and behavioural reflexes was a positive correlation between stride length and JND for younger adults. The additional lead times for detecting perturbation onset that are found in older adults may help explain the increased likelihood for fall incidence in older adult populations.

Acknowledgments

First and foremost, I would like to express my sincere gratitude to my supervisor Dr.

Michael Barnett-Cowan for his time spent, as well as his mentorship and guidance throughout my academic career. I would also like to acknowledge the help I received from all of my lab mates as well as other students in the program.

Contents

ABSTRACT	ii
Acknowledgments	iv
List of Figures	vi
1.1 Background	1
2.1 Perceived timing of sensory events	7
2.1.1.1 Reaction time	
2.1.1.2 Simultaneity judgments	9
2.1.1.3 Temporal order judgments	10
2.2 Factors influencing time perception	12
2.2.1 Physiological variables	12
2.2.2 Stimulus intensity	13
2.2.3 Attention and spatial location	14
2.3.1 Visual, auditory, and tactile	15
2.3.2 Vestibular system	16
2.3.2.1 Vestibular physiology	17
2.3.2.2 Vestibular perception is slow	18
2.4 Postural stability and balance control	20
2.5 Rationale	21
2.6 Research objectives	22
Study 1 - Developing and evaluating a novel approach to examine the perceived timing of large unexpected perturbations	24
3.1 Method	24
3.1.1 Participants	24
3.1.2 Protocol and materials	24
3.1.3 Data analysis	28
3.1.4 Statistical analysis	30
3.2 Study 1 results	
4.1 Introduction to Study 2	
4.2 Materials and method	
4.2.1 Participants	
4.2.2 Protocol and materials	
4.2.3 Data acquisition and analyses	
4.2.4 Statistical analysis	50

4.3 Results	51
5.1 General discussion	58
Appendix A	65
References	68

List of Figures

- 1. Summary of recent experiments highlighting a delay of vestibular perception.
- 2. Reaction time data from Barnett-Cowan and Harris, 2009.
- 3. Temporal order and simultaneity judgment data from Barnett-Cowan and Harris, 2009.
- 4. Lean and release cable set-up.
- 5. Trial design schematic.
- 6. Distribution of SOAs for Study 1.
- 7. Single participant TOJ data from Study 1.
- 8. Perceived timing of unpredictable falls.
- 9. Study 1 PSS and JND.
- 10. Lean and release cable set-up for younger and older adults.
- 11. Distribution of SOAs for Study 2.
- 12. Stride leading foot on a single trial.
- 13. Stride peak velocity.
- 14. Trunk onset.
- 15. Trunk peak velocity.
- 16. Perceived timing of unpredictable falls for Study 2.
- 17. Study 2 PSS and JND.
- 18. Motion capture Study 2 results.

1.1 Background

Optimal perception of the world around us requires the central nervous system (CNS) to use multiple sources of sensory information derived from different sensory modalities. Utilizing several sources of sensory information is important because sensory redundancy can improve the ability to extract meaningful signal from noise (Ernst & Bülthoff, 2004). For example, as sensory signals that share common information in space and in time are most likely to have been generated from a common event, detecting sensory redundancy is a critical way that the CNS determines which stimuli are bound together. Synchrony often characterizes whether stimuli from different modalities should be perceived as belonging together or originating from separate and independent events or objects (Spence et al., 2003). Maintaining a perception of simultaneity, however, remains difficult due to the propagation of different energies (King & Palmer, 1985). For example, we see lightning before hearing thunder due to the differences in the physical arrival time of the stimuli at the eye and ear (Spence & Squire, 2003), making it increasingly difficult for our perceptual systems to consistently and accurately perceive simultaneous events. Resultant transmission time for the information to reach the CNS (Békésy, 1963), as well as different stimulus parameters characteristic of each event (Harris, Harrar, Jaekl, & Kopinska 2010) can affect the perceived timing of sensory events. Furthermore, one's attention can influence the processing speed of incoming stimuli (Spence, Shore, & Klein, 2001), yielding delays between sensory events that do not necessarily correspond with the physical timing of phenomena.

While for over one hundred years researchers have been measuring the perceived timing of sensory events, only recently has considerable focus been directed towards the perceived timing of self-motion, and in particular from the vestibular system, which is crucial for self-

motion perception and balance control. The transduction of and physiological responses to vestibular stimulation are incredibly fast (Corey & Hudspeth, 1979; Lorente de No, 1933), however, recent work has found that the vestibular system is perceptually slow compared the other senses (45-160 ms delay; Figure 1 (Barnett-Cowan & Harris, 2009, 2011; Barnett-Cowan, Raeder, & Bülthoff, 2012; Barnett-Cowan, 2013; Sanders, Chang, Hiss, Uchanski, & Hullar, 2011; Soyka, Bülthoff, & Barnett-Cowan, 2013)). Thus, in order for vestibular stimuli to be perceived synchronously, vestibular stimulation surprisingly needs to be presented prior to other sensory stimuli (Barnett-Cowan & Harris, 2011).

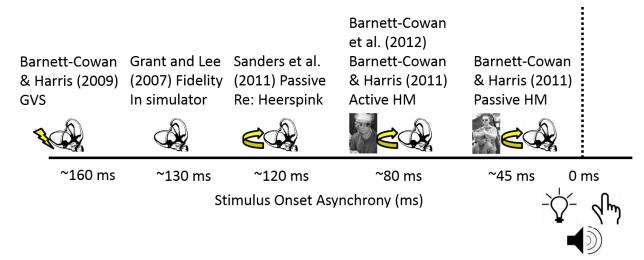


Figure 1. Summary of recently reviewed experiments highlighting the degree to which vestibular stimuli need to be presented first compared to stimuli of a different modality in order to be perceived as occurring simultaneously (from Barnett-Cowan, 2013). Head movement is represented as HM, and galvanic vestibular stimulation is represented as GVS.

A number of factors are thought to affect delays in vestibular perception. Firstly, different experimental methods produce different lead times of vestibular stimulation required for perceived synchrony. The relatively large delay of 160 ms found using galvanic vestibular stimulation (GVS; Barnett-Cowan & Harris, 2009) could be attributable to the unnaturalness of

the stimulus (Barnett-Cowan & Harris, 2009, 2011; Sanders et al., 2011). However, a similar delay of 120 ms was found using low-amplitude whole-body rotations (Sanders et al., 2011), and while high amplitude passive head-on-body rotations can yield delays as low as 45 ms (Barnett-Cowan & Harris, 2011), inertial stimulation is consistently perceived slower than other stimuli.

Differences also arise depending on whether an individual's head is passively or actively moved, since efferent information is more readily available during rapid head movements, faster head movements could be perceived quicker because they are anticipated. When the head is actively moved however, a perceptual delay of ~80 ms, as opposed to 45 ms, persists. Slow vestibular perception has also been thought to arise from unequal stimulus characteristics between the vestibular stimulus and of a comparison stimulus. When pairing active head movements with an equivalent comparison auditory stimulus matched for duration and temporal envelope, a perceptual delay still persists with the lead time required for perceived synchrony being approximately 73 ms (Barnett-Cowan et al., 2012).

What can explain these perceptual responses that are strikingly slower than reflexive behaviours arising from vestibular stimulation? Slow vestibular perception could arise from the additional time required to integrate information from velocity to position in order to perceive and react to an event or object. Generating reflexive movements such as the vestibulo-ocular reflex (VOR) and vestibulo-spinal reflex can be computationally faster than the time required to integrate and determine position and velocity from acceleration (Fernandez & Goldberg, 1976). For example, latency of the angular VOR and the translational VOR takes approximately 10 ms and 30 ms, respectively, not including the additional time required for information to reach the cortex and generate subsequent temporal order or simultaneity judgments (see Barnett-Cowan, 2013 for review). Finally, another explanation for delayed vestibular perception is that the brain

may prioritize physiological responses over perceptual awareness as the VOR and vestibulospinal reflex are paramount in maintaining perceptual and postural stability as observers interact
with the world, while perception about the timing of vestibular information is less critical. This
latter hypothesis, suggesting that we do not have direct conscious awareness of vestibular
stimulation, predicts that perceptual responses to vestibular stimulation and physiological
reflexes may be independent.

Despite physiological and non-physiological factors involved in modulating perception (e.g., stimulus intensity), the CNS is remarkably efficient in reconstructing the actual timing of a multisensory event (Vroomen & Keetels, 2010). It has been argued that a neural mechanism called 'simultaneity constancy' resynchronizes incoming asynchronous multisensory signals representing an event by combining signals from different senses that have varying processing times (Engel & Dougherty, 1971; Kopinska & Harris, 2004) and is at least partially responsible for the ability to accurately perceive simultaneity of vestibular events (Barnett-Cowan, 2009) despite sensory and perceptual delays. Harris and colleagues (2010) propose a three-stage model responsible for maintaining perceptual constancy. Here, average processing speeds of the different sensory systems are resynchronized to match the incoming stimuli and stimuli that fall within temporal and spatial windows are identified as belonging to the same event. Furthermore, previous experience involving calibration among particular pairings of stimuli are adjusted and applied according to the present situation. As such, the neural mechanisms underlying simultaneity constancy are thought to be an integral component in shaping how people construct a coherent representation of the world as it unfolds in time.

Much remains unexplained regarding delayed vestibular perception and self-motion in general and further research can provide insight into the mechanisms involved and their effect on

perception and action. For instance, the fact that vestibular stimulation onset is perceived slower compared to other sensory stimuli remains difficult to understand as people are not directly aware of this perceptual delay. The CNS does a remarkable job at binding stimuli together as to provide a coherent world to interact with. Nevertheless, this relatively new finding of perceptual delays for vestibular perception is changing the way that researchers assess vestibular function and it may have implications for aspects of sensory motor control such as balance and fall recovery (see Barnett-Cowan, 2013). However, to date no research has examined whether perceptual lags exist in response to temporally unpredictable falls and it remains unknown whether a perceptual delay in the perceived onset of a fall would affect an individual's motor control since they are not directly aware of it. Common anecdotal reports suggest that people often demonstrate distortions in their subjective perception of time with little to no recollection of what occurred during the fall, or experience prolonged sensation of the fall (Stetson, Fiesta, & Eagleman, 2007). In addition, the prevalence of falling steadily increases with age (Sattin et al., 1990) and in disease states (e.g., Parkinson's disease), highlighting the need to identify and alert individuals who are more likely to fall (e.g., older adults), of imminent lapses in balance. Furthermore, it is relatively unclear how perception of sensory processing changes during a fall and how this process changes across the lifespan. In general, knowledge on how multisensory processes are affected as people age is sparse (Diederich, Colonius, & Schomburg, 2008; Laurienti, Burdette, Maldjian, & Wallace, 2006). However, previous work has found that older adults are physically and perceptually slower than younger adults (Diederich et al., 2008; Laurienti et al, 2006; Poliakoff, Shore, Lowe, & Spence, 2006; Setti, Burke, Kenny, & Newell, 2011). Therefore, it is important to establish whether the timing of a fall event is perceptually delayed, how perceptual delays relate to physiological reflexes generated in response to a fall to

maintain balance control, and whether these perceptual and behavioural effects change with aging.

The present thesis was comprised of two studies. Study 1 examined the links between falling and delays in inertial perception (using a sample of young, healthy adults). In study 1, young healthy adults were recruited to establish whether an unexpected postural perturbation is perceptually delayed relative to an auditory stimulus. In study 2, the perceived timing of a postural perturbation is compared between a second group of young healthy adults and a group of older adults. Motion capture was also used in study 2 to determine whether the perceived timing of a postural perturbation and the certainty with which participants make their judgements are related at all with assessment measures for balance control and behavioural reflexes generated in response to falling. What follows is a review of the literature on the perceived timing of sensory events, factors that affect time perception, and further rational and specific hypotheses of the present study.

2.1 Perceived timing of sensory events

Perception involves the processing of higher order information that allows for online cognition of stimuli and subsequent goal-directed action. Perception of the world around us requires the CNS to integrate multiple sources of sensory information originating from both the self and the environment. However, maintaining a perception of simultaneity remains difficult given that the CNS has to mediate several differences between multiple sensory modalities (Fujisaki, Shimojo, Kashino, & Nishida, 2004). Discriminating between temporal characteristics of multiple events is important given that synchrony provides a beneficial cue in identifying whether stimuli belong to the same or a different event (Spence et al., 2003). Furthermore, multisensory integration affects how observers interact with the world by improving their perception and motor control. By measuring the perceived timing of events one can infer how the CNS processes sensory information generated under different circumstances such as a fall. Here, there are three primary methods by which perceptual latency is measured; Reaction time (RT) tasks, simultaneity judgments (SJ), and temporal order judgments (TOJ).

2.1.1.1 Reaction time

Reaction time is described as the interval between the presentation of a stimulus and the initiation of a motor response to that particular stimulus. RT can be defined in three different ways as it can pertain to i) muscle activity onset, ii) initial movement onset (Gage, Zabjek, Hill, & McIlroy, 2007), and iii) the time of a button press or end of a movement response (Jaśkowski, Jaroszyk, & Hojan-jezierska, 1990), depending on the specific response collected in a particular study. Detection of initial muscle activity through the use of electromyography (EMG), an experimental technique used to evaluate and record electrical activity produced by the muscles, is best suited for reliable RTs when kinematic data is required (Tomberg, Levarlet-Joye, &

Desmedt, 1991). For perceptual experiments where muscle activity is not desired, response to a presented stimulus via button press is sufficient in identifying perceptual delays (Hirsh & Sherrick, 1961; Roufs, 1963). In relation to the present study, it has been previously found that the perceived timing of vestibular stimuli relative to light, touch, and sound using button press RTs is delayed by approximately 200-250 ms (see Figure 2 for review of RT data). The present study will not be using RTs because a startling event (e.g., a fall) may yield erroneous button presses through anticipation of an upcoming perturbation. Furthermore, if muscle activation onset was being measured, it would be difficult to determine whether control of movement onset was volitional or reflexive.

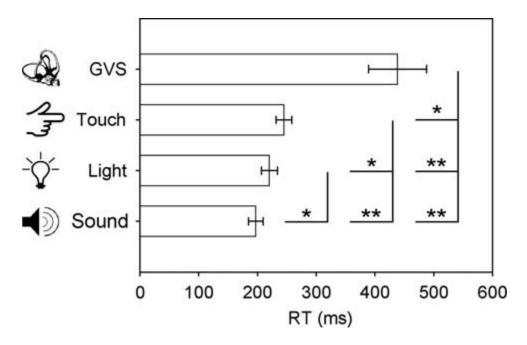


Figure 2. Reaction time data found in Barnett-Cowan and Harris, 2009. Reaction time to vestibular stimulation via GVS is significantly delayed in relation to touch (200 ms), light (220 ms), and sound (250 ms). *=p < 0.05, **=p < 0.01.

2.1.1.2 Simultaneity judgments

Simultaneity judgments (SJ) are used to determine the simultaneity of two or more stimuli presented at different stimulus onset asynchronies (SOA). Participant responses to a wide range of SOAs are used to calculate the point of subjective simultaneity (PSS) by fitting a Gaussian function to the data (see section 3.1.3). The PSS is the greatest likelihood of a participant reporting two stimuli as occurring simultaneously. A PSS of 0 ms would represent that the two events are truly simultaneous. For SJs, the PSS is calculated using the midpoint of the range of participant responses (Eijk, Kohlrausch, Juola, & van de Par, 2008); see Figure 3 bottom row for an example), and the just noticeable difference (JND) is calculated as one standard deviation from the PSS (Harris et al., 2010). The JND typically indicates the time a combination of stimuli need to be separated by in order to be perceived as asynchronous, where smaller JNDs generally indicate higher participant accuracy (Spence et al., 2003).

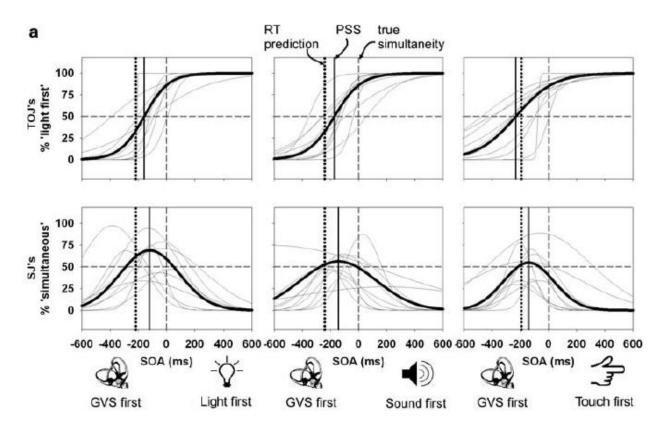


Figure 3. Temporal order judgment (top row) and simultaneity judgment (bottom row) data found in Barnett-Cowan and Harris, 2009. Positive and negative SOA values represent which stimulus was perceived to be first. Negative SOAs represent that GVS occurred first, where positive SOAs indicate the comparison stimulus (light, sound, or touch) occurred first, as illustrated by the cartoons. The gray lines represent the individual participants' data fit. The black curve represent the average data fit of all participants. The black dotted vertical line represents the RT prediction for each stimulus pair. The solid vertical line indicates the average PSS value. The dashed vertical line signifies the point of true simultaneity (SOA = 0ms).

2.1.1.3 Temporal order judgments

Unlike simultaneity judgments, temporal order judgments (TOJ) primarily are used to determine which stimulus occurred first; an indirect measure of simultaneity (Spence et al., 2001). For TOJs, the PSS is calculated by fitting a cumulative Gaussian (see section 3.1.3) and

taking the point at which the proportion of one stimulus judgment equals the other, typically identified as the 50% point (Eijk et al., 2008; Harris et al., 2010; see Figure 3 top row for an example). JNDs are estimated by taking the slope between the 25% and 75% mark of the psychometric function.

While these methods are all widely used, the literature has yielded inconsistent results regarding SJs and TOJs as they are prone to differing estimates of the PSS (Eijk et al., 2008). Specifically, Eijk and colleagues (2008) investigated the relative influence of both methods on the outcome of audio-visual perception. Since visual cues will usually reach the eye faster than sound will reach the ear due to different propagation speeds of light and sound (e.g., see lightening and hear thunder moments later), one would assume that the visual cue must precede the auditory component to achieve simultaneity. While overwhelming research supports this (Hirsh & Sherrick, 1961; Jaskowski et al., 1990; Spence et al., 2001, 2003), some research has shown the opposite, with sound preceding the visual cue (Vroomen, Keetels, de Gelder, & Bertelson, 2004). Furthermore, it was found that SJs provided a more stable PSS value with respect to audio-visual discrimination tasks, suggesting that when the primary interest is perceived audio-visual synchrony, SJs should be preferred over TOJs (Eijk et al., 2008). Additionally, differences in the PSS may be reflected in the perceptual demands of the task, as SJs and TOJs measure different things (i.e., simultaneity vs. successiveness). Increased lead time for TOJs may be a by-product of having to sort through more incoming information before a correct response can be made (Shore, Gray, Spry, & Spence, 2005). As research involving vestibular perception has shown that both TOJs and SJs reveal similar delays relative to a comparison stimulus (Barnett-Cowan & Harris, 2009; Sanders et al., 2011; Barnett-Cowan et al., 2012), but with TOJ JNDs being lower (i.e., more precise) than SJ JNDs (Barnett-Cowan et al.,

2011), the present study will employ the use of TOJs to identify perceptual latencies in vestibular stimulation.

2.2 Factors influencing time perception

2.2.1 Physiological variables

There are multiple factors that can provide a challenge for the CNS to accurately observe the temporal relationship of incoming stimuli and its influence on perception (Harrar & Harris, 2008). While some variables can be directly altered (e.g., stimulus intensity and attention), more naturally occurring differences cannot. For instance, a simple action involving the touching of a computer key elicits a multisensory event that evokes visual, auditory, and tactile information. While observers perceive this event as occurring at the same time, physiologically processing the information depends on the specific sensory modality the event activated due to different transduction latencies (King & Palmer, 1985; Pöppel, Schill, & Steinbüchel, 1990). Visual reaction time is proportional to stimulus intensity, with higher intensities being perceived quicker (Pöppel et al., 1990). Additionally, subjective experience of external events such as the keyboard press is dependent on the different conduction velocities within the ascending pathways innervating different cortical areas (Von Békésy, 1963; Corey & Hudspeth, 1979; Bergenheim et al., 1996). For example, tactile stimuli delivered to two different skin areas will arrive at different times in the somatosensory cortex, with the proximal stimulus being perceived first (Bergenheim et al., 1996). How these neurons affect cross-modal interaction makes it increasingly difficult for the CNS to consistently and accurately perceive simultaneous events (King & Palmer, 1985). For the present experiment, it should be noted that perturbations evoking compensatory reactions are not a direct measure of vestibular contribution. As such, participant

responses may be hindered or potentiated due to the addition of processing somatosensory information.

2.2.2 Stimulus intensity

Depending on the tasks and stimuli involved, the processing of multiple stimuli is modulated by a multitude of different stimulus parameters. Research has found that an intense stimulus is easier to attend to than a weak stimulus (Roufs, 1963). Stimulus intensity has an overwhelming influence on modulating perception, as lower intensities are reflected as longer latencies and slower reaction times (Craig & Baihua, 1990; Pöppel et al., 1990; Roufs, 1963; Wilson & Anstis, 1969). For example, with respect to visual stimuli, dimly lit lights are perceived later than brighter lights by up to 100 ms (Wilson & Anstis, 1969). Furthermore, Roufs (1963), who studied stimulus luminance measured over a large range of intensities, found that perception is logarithmically related to the intensity of a stimulus. As stimulus luminance increases, observers are quicker at detecting the onset of stimuli. The same theory of stimulus intensity holds true across most modalities. Craig and Baihua (1990) investigated an observer's ability to detect the temporal order of tactile patterns using TOJs. When presenting bilateral tactile patterns, observers were more accurate at judging which occurred first when the stimuli were more intense and presented to bilateral sites. On the other hand, less intense stimuli were judged first during same-site stimulation. Furthermore, performance improved in detecting which stimulus came first when both the intensity and stimulated site provided redundant information. Additionally, psychological evidence suggests that the existence of multiple stimuli can improve or worsen an observer's perception (Diederich, 1995). Diederich (1995) argues that compared to single stimuli, inter-sensory interaction can facilitate processing of incoming stimuli and improve perceptibility, as evidenced by shorter reaction times to double, and triple stimulation. The

summation effect of multiple stimulation increases the intensity of a stimulus and lowers sensory thresholds, thus allowing for earlier detection. With regards to study 1, it should be noted that while the auditory stimulus duration remains constant across observers and is well above threshold, the amplitude of the fall approximately standardized by the lean angle of the ankle is not constant. Since the amplitude of the stimulus is partially related to the height of the observer, participants may have experienced stronger or weaker falls, which may affect the PSS.

2.2.3 Attention and spatial location

Focusing our attention on incoming sensory stimuli allows us to suppress or ignore irrelevant information resulting from a particular event, while focusing and processing relevant sensory cues to better interact with the environment (Herrmann & Knight, 2001). If an observer directs their attentional resources to a particular sensory modality (e.g., audition), the resultant PSS may be closer to true simultaneity (i.e., 0 ms) than when their attention is directed towards a different modality (e.g., tactile; Spence et al., 2001). Early research on attentional manipulation suggests that attention does not speed up perception in the attended modality (Hamlin, 1895; Spence et al., 2001). However, recent research has shown evidence of modulating the PSS due to prior entry regardless of modality (Spence et al., 2001). Spence and colleagues' (2001) found that when participants were told to attend to a particular modality, (there was a shorter PSS present). However, their results differed from past research in that lower JNDs only occurred when presenting stimuli from different spatial locations (Harrar & Harris, 2008; Spence et al., 2003; Zampini, Guest, Shore, & Spence, 2005). Previous studies on attentional manipulation consistently presented stimuli from the same location, suggesting that stimuli are more likely to be perceived as simultaneous when they originate from the same location (Spence et al., 2003; Zampini et al., 2005; Harrar & Harris, 2008). Consequently, observers are more likely to bind

spatially related information together and judge simultaneity based on location and not perception of the stimulated modality (Zampini et al., 2005). While observers may choose to attend to either stimulus (e.g., the fall or sound), this thesis does not focus on the particular effects of attention on perception. However, it should be noted that this may influence participant responses if they were to preferentially focus on either the fall or auditory stimulus.

2.3 Relative timing of sensory events

As previously noted, maintaining a perception of simultaneity is difficult given multiple modulating factors between the sensory modalities (Fujisaki et al., 2004). However, a form of perceptual constancy helps facilitate multisensory integration (Kopinska & Harris, 2004). Multisensory integration is important because it affects how observers interact with the world by mediating perception and motor control. Given the significance of accurate perception and fluid motor control, it is important to understand how these variables affect the perceived order of stimuli in different sense modalities. The majority of research uses SJs, TOJs, and RT tasks, or a combination of them, to determine perceived simultaneity and temporal order. Determining temporal lags within, or between different sensory modalities is accomplished by identifying the PSS between the stimuli. The following section will describe the individual perceptual latencies of each modality by highlighting that these mechanisms are fast physiologically, but they are much slower, perceptually.

2.3.1 Visual, auditory, and tactile

In addition to a multitude of stimulus parameters, conduction latencies can affect the perception of synchrony. Due to different propagation speeds of light, sound, and touch, the CNS needs to be aware of stimulus lag (Eijk et al., 2008). The auditory system, in relation to the visual and somatosensory systems, has the fastest processing of information once it reaches the sensory

receptors (Von Békésy, 1963; Eijk et al., 2008) due to the short conduction latencies of the hair cells within the cochlea (40 µs; Corey & Hudspeth, 1979). This is significantly faster than the transduction of tactile stimuli (500 µs to 2.6 ms; Alvarez-Buylla & Ramirez de Arellano, 1952) and the photoreceptors (15-93 ms; Kuffler, 1953). Using TOJ experiments, it has been found that a visual stimulus often needs to precede a sound (within a few meters) by about 20 ms in order for the pair to be perceived as synchronous (Hirsh & Sherrick, 1961; Engel & Dougherty, 1971; Jaskowski et al., 1990; Kopinska & Harris, 2004; Jaekl & Harris, 2007; Harrar & Harris, 2008; Eijk et al., 2008). Hirsh and Sherrick (1961) also expanded their research to determine the relative lead time a stimulus would need to be perceived as synchronous in relation to other sensory modalities. It was found that a touch stimulus often needs to precede a light in order to achieve perceptual synchrony (Hirsh & Sherrick, 1961; Spence et al., 2001, 2003; Harrar & Harris, 2008) and that a touch must also lead the presentation of a sound stimulus (Hirsh & Sherrick, 1961; Zampini et al., 2005; Harrar & Harris, 2008). Given what is known about the transduction latencies of each modality and the seminal work conducted by Hirsh and Sherrick (1961), it is likely that when it comes to determining successiveness of multiple stimuli, the auditory system is fastest, followed by the somatosensory system, while the visual system is the most sluggish. However, up until recently, very little has been known about the perceived timing of vestibular stimulation in relation to the other senses.

2.3.2 Vestibular system

Self-motion perception in everyday life is heavily dependent on the integration of visual, somatosensory, and vestibular cues (Roy & Cullen, 2004). The vestibular system is important for perception and action, as it provides both fast compensatory reflexes and it facilitates reference frame coordination in higher cortical levels of processing perceptual information and generating

coordinated motor control (Angelaki & Cullen, 2008). To date, extensive research has demonstrated varying temporal delays related to the perceived timing of visual, auditory, and somatosensory stimuli. Surprisingly, comparing the perceived timing of vestibular stimulation relative to other sensory events has not garnered the same amount of attention (Barnett-Cowan, 2013). However, recent research that has directly assessed the temporal perception of vestibular input relative to other stimuli has yielded counter-intuitive and important insight regarding how the CNS temporally processes multisensory events and how it represents sensory information in space, time, and in motion. There is also evidence to suggest that perceptual mechanisms involved in regulating time perception are distorted during a fall (Stetson, Fiesta, & Eagleman, 2007).

2.3.2.1 Vestibular physiology

The vestibular system, a system crucial for self-motion and balance, is comprised of two interconnected structures, containing three semicircular canals (anterior, posterior, and horizontal) and two otolith organs (utricle and saccule; Angelaki & Cullen, 2008). Described as being the inner ear balance organs, the semicircular canals and otolith organs are important for providing online input to the CNS regarding the orientation of the head relative to gravity, as well as detecting angular and linear head motion (Agrawal et al., 2009). Vestibular organ information and its central projections into the brainstem and cerebellum is then used to maintain gaze and postural stability through both the vestibulo-ocular reflex (VOR) and vestibulo-spinal reflex, respectively (Angelaki & Cullen, 2008; Agrawal, 2009). The VOR moves the eyes in the opposite direction of head movement (Lorente De Nó, 1933), while vestibular-proprioceptive afferents control posture through signals from the skin, joints, and muscles (Angelaki & Cullen, 2008). The uniqueness of the vestibular system and its ability to maintain perceptual and postural

extremely short physiological latencies (Lorente De Nó, 1933). For example, the VOR possesses a 5-6 ms latency in response to vestibular nerve stimulation (Huterer & Cullen, 2002). In addition to simple connectivity, the speed of the vestibular and auditory system is made possible due to the short conduction latencies (i.e., 40 µs; Von Békésy, 1963) of the hair cells within the semi-circular canals and otoliths (Corey & Hudspeth, 1979). Given such rapid processing, it would appear that vestibular and auditory stimuli are perceived as equally fast. However, recent work suggests that perception of vestibular stimulation is slow compared to all other senses (Barnett-Cowan & Harris, 2009; 2011).

2.3.2.2 Vestibular perception is slow

Vestibular perception is essential because quickly detecting when your head has moved relative to other events assists in maintaining perceptual and postural stability. Early investigations that directly examined the perceived timing of vestibular perception involved the assessment of reaction time to angular and linear acceleration changes (Mulder, 1908; Clark & Stewart, 1962; Guedry, 1974; Jones & Young, 1978). Unexpectedly, vestibular perception exhibited significantly large reaction time delays to rotational and linear vestibular stimulation ranging from 500-600 ms (see Barnett-Cowan, 2013 for review). In comparison to other senses, Baxter and Travis (1938) reported that it took approximately three times longer for observers to discriminate between rotation and vision, and twice as long for audition. More recently, direct stimulation of the vestibular system by way of galvanic vestibular stimulation (GVS) was measured relative to light, sound and touch using RT, SJs and TOJs (Barnett-Cowan & Harris, 2009; see Figure 1 for review). Similar to previous research, GVS elicited a reaction time delay using button presses of 438 ms. In addition, perceived simultaneity when GVS is paired with

light, sound, or touch, only occurred when the vestibular stimulus preceded the other senses by 160 ms. Due to the unnaturalness of the GVS, it was thought that the temporal delay was attributable to how GVS stimulates all receptors in the otolith organs and semi-circular canals as opposed to simulating real movement. However, Sanders and colleagues (2011) found a similar delay (120 ms) when pairing low-amplitude whole body rotations with an auditory stimulus. Similarly, Grant and Lee (2007) studied vestibular phase error thresholds for motion simulation and found that the vestibular cues had to lead visual cues by 133ms in order to preserve optimal simulator fidelity. These studies are similar in that they both attempt to isolate kinematic and proprioception influence on detecting perception of rotation (Barnett-Cowan, 2013). Given passive low-amplitude stimulation resulted in slow vestibular perception, faster head-movements should result in shorter lead times due to additional proprioceptive information. However, when comparing rapid active and passive head movements in relation to touch, light, and sound, a vestibular delay still existed with the active head movement leading by 80 ms, and 45 ms for passive (Barnett-Cowan & Harris, 2011). It should be noted that perceptual judgments pertaining to the perceived order of events may be biased in the present study as sensory events usually happen following every time the head moves (Barnett-Cowan, 2013). As the vestibular system tends to rarely work in isolation and has no distinct conscious sensation (as in touch), the CNS may prioritize physiological responses over perceptual awareness by relying on other sensory modalities to confirm sensory onset, and thus delaying perception. Nevertheless, it is far less important to contemplate the onset of a fall than to react and regain balance from an unexpected fall (Barnett-Cowan, 2013), highlighting the importance of the vestibular reflex system which is crucial for how people interact with the environment.

2.4 Postural stability and balance control

The ability to predict whether someone is likely to fall is important for mitigating fall incidence and improving the quality of life for older adults who are at an increased risk of falling and whose quality and duration of life is likely to rapidly deteriorate following a fall (Tinetti, Liu, & Clause, 1993). Setti and colleagues (2011) presented a sound-induced flash illusion to younger adults, older adult non-fallers, and older adult fallers to identify a potential relationship between a history of falling and multisensory processes. The sound induced flash illusion occurs when two beeps are presented together with one flash, however, the double beep influences the participant to perceive the flash as occurring twice. They found that the older adult fallers performed significantly worse than both the younger and older adult non-fallers at longer SOAs, where performance should be easier. These results suggest that disruptions in the ability to integrate multisensory information may be associated with an increased likelihood of falling, and hint at a relationship between the perceived timing of multisensory events and fall behaviour.

The standard Romberg test is an effective way of testing an individual's postural imbalance. It is one of the most commonly performed tests during neurological examinations (Khasnis & Gokula, 2003). It requires an individual to stand erect with their feet together, hands at their side, and their eyes-open (EO) or eyes-closed (EC) for 30-seconds to one minute. This position requires sensory integration between the somatosensory, visual, and vestibular pathways in order to maintain upright balance. In Study 2 of the present study, participants will be required to complete both an EO and EC Romberg test. By conducting an eyes-closed test, it may reveal any sensory deficiences that are masked by vision. As the present experiment is novel and reliationships between the PSS and JND to behavioural measures are unknown, the ability to identify whether individuals with larger balance impairments, as measured by the Romberg test,

also exhibit a slower rate of processing and worse accuracy (i.e., higher PSS and JND) will be assessed. A positive relationship between these measures would potentially suggest that a slower rate of processing of incoming stimuli may contribute to worse overall balance control, however, no relationship between the two would suggest that the two are separate processes.

2.5 Rationale

It is unclear as to how the perceived timing of sensory events changes during a fall.

Common anecdotal reports suggest that people often report distortions in their perception of time with little to no recollection of what occurred during the fall. Approximately 15% of the Canadian population is 65 and older and the alarming rate at which older adults experience falls each year leads to lengthy hospitals stays (WHO, ageing & life course unit, 2008; Sattin et al., 1990). Therefore, research highlighting potential mechanisms involved in balance control is of growing concern. As previously discussed, the vestibular system is perceptually slow compared to the other senses (45-160ms delay), indicating that vestibular stimuli must be presented prior to other sensory stimuli in order for it to be perceived as synchronous. Previous work on vestibular perception has not been extended to assess the perceiving timing of a fall, nor does it address differences between young and older populations and possible relationships with balance control. The unique approach presented in the present experiments may help to establish a link between delayed perception of inertial stimulation with falling behaviour.

To date, no study has examined whether a similar perceptual lag exists while indirectly stimulating the vestibular system through a temporally unpredictable fall. Therefore, the purpose of the present study is to directly assess the perceived timing of two multisensory events during a fall in order to provide a better understanding of how the CNS represents sensory information, as it is thought maybe an inability to adequately integrate incoming stimuli may have a detrimental

effect on balance control. TOJs between the occurrence of the fall and auditory stimulus will be measured to determine perceived simultaneity, as TOJs have shown to be a reliable method in eliciting simultaneity in past research (Barnett-Cowan & Harris, 2009, 2011; Sanders et al., 2011).

It is hypothesized that the onset of a fall will be perceptually delayed relative to an auditory stimulus due to slow inertial perception as found in previously conducted studies. Alternatively, the onset of a fall may elicit no lead time relative to an auditory stimulus, suggesting that slow vestibular perception reported in the literature is restricted to direct vestibular stimulation and movements of the head, as recent evidence suggests that vestibular input can distort the perception of time itself (Barnett-Cowan & Harris, 2009).

2.6 Research objectives

This thesis is comprised of two studies designed to address the following research objectives:

Study 1: Developing and evaluating a novel approach to stimulate and examine the perceived timing of a fall using large temporally unpredictable perturbations.

- Evaluate a novel mechanism to illicit the feel of falling and measure temporal characteristics of the event in relation to an auditory stimulus.
- Measure the perceived timing of a postural perturbation relative to an auditory stimulus as well as the precision with which participants make their judgments.

Study 2: Determining age-related differences of the PSS and JND using temporally unpredictable in older populations.

• Compare the perceived timing of a postural perturbation between young and older adults.

Assess the relationship between the PSS and JND for the perceived timing of a postural
perturbation with outcome measures of balance and posture control using the Romberg
test and behavioural kinematics measured using motion capture.

Study 1 - Developing and evaluating a novel approach to examine the perceived timing of large unexpected perturbations

3.1 Method

3.1.1 Participants

The sample consisted of 8 healthy adults (4 female), free of musculoskeletal, auditory, visual, vestibular or other neurological disorders. Participants ranged in age from 17-25 (M = 22.12 years, SD = 2.42 years). All participants gave their informed written consent to participate in the study, which was approved through a University of Waterloo Research Ethics Committee, which complies with The Code of Ethics of the World Medical Association (Declaration of Helsinki).

3.1.2 Protocol and materials

Using a lean-and-release perturbation system (Lakhani, Mansfield, Inness, & McIlroy, 2011), participants made TOJs to determine the perceived timing of a fall paired with an auditory stimulus. Participants were instructed to stand in a standardized foot position (heel centers 0.17m apart, 14° between the long axes of the feet (McIlroy & Maki, 1997)), using a marked piece of wood as a guide. Using a standardized foot position ensured that the foot orientation and width of the base of support for each participant was identical (Mansfield, Inness, Lakhani, & McIlroy, 2012). Participants wore a harness with a cable attached posteriorly at the height of the 2nd and 3rd thoracic vertebrae, along with a safety harness fixed to the ceiling to prevent injury in the event of failed balance recovery. Participants were given a button in each hand, the left button to indicate that the sound came first and the right button to indicate the fall came first (identified as a red button).

Participants, while blindfolded, were instructed to lean forward (indicated by tapping on their shoulder) from the ankle at a neutral position such that their body weight was supported by the cable (129.5 cm in Length; see Figure 4). The experimenter applied a perturbation following a "go signal" identified on a monitor by releasing a pin attaching the cable to a rigid support, causing the participant to fall in a forward direction and evoking a compensatory reaction (e.g., a step). The timing of the perturbations was randomized in relation to an auditory stimulus that was administered through headphones (Sennheiser S1 Digital), once the participant was relaxed in the forward lean position. The perturbations were temporally unpredictable to the participant. Also, prior to the start of testing, two practice trials were completed in order to become acquainted with the physical demands of the task (i.e., making a judgment post fall). There were 110 judgments at varying stimulus onset asynchronies (SOA). There were 15-30 seconds between each perturbation, while each trial lasted approximately 15 seconds. A short rest break at the 60th trial was given for a total experiment time of one hour.

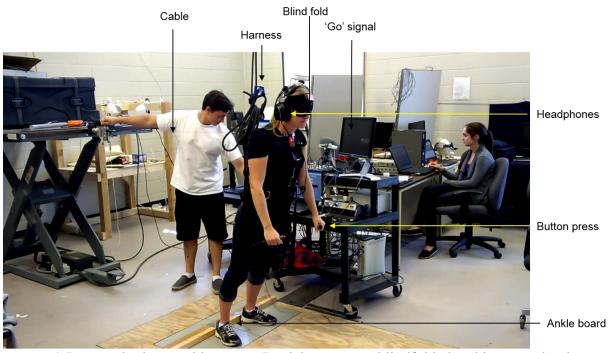


Figure 4. Lean and release cable set-up. Participants were blindfolded and instructed to lean forward such that their body weight was supported by the cable from neutral stance. Perturbation

onset time was calculated by a mounted load cell attached to the mechanical lift that was used to account for height differences among participants.

Temporal order judgment task

The TOJ task involved the presentation of a supra threshold sound (250 ms; 500 Hz) while listening to white noise, which masked all externally generated sound, before or after the onset of a postural perturbation. After each perturbation the participants were instructed to perform the TOJ task by indicating whether they thought their fall or the auditory stimulus occurred first via button press (i.e., right button = fall), then they were asked to return to their standardized foot position (marked on a stable block of wood). The participants were instructed to respond as quickly and accurately as possible but were not judged on their reaction time. The sound stimulus was presented relative to cable release at varying SOAs between 0 and 650 ms, representing the width of trial onset.

Sound generation and stimulus onset

The sound stimulus was generated using a LabVIEW[™] (National Instruments, Austin, Texas, USA) program, consisting of a 250 ms square wave burst at 500Hz, and was administered through noise cancelling headphones (Sennheiser S1 Digital). Participants listened to white noise (downloaded from commercially available software) during all trials at a level that was loud enough to mask any external noise capable of alerting them of the upcoming perturbation, while still being able to distinctly detect the sound stimulus. Figure 5 represents a schematic of the onset of the stimuli presented on each trial. The trial begins with either the perturbation or auditory stimulus occurring immediately following a "go signal," with the 2nd stimulus following the first anywhere from 0 to 650ms thereafter. Figure 6 represents the trial SOA distribution for

Study 1. Note that because the timing of the fall was controlled by an experimenter, the distribution of SOAs is not tightly controlled. Indeed, on average, the perturbation occurred first 66% of the time.

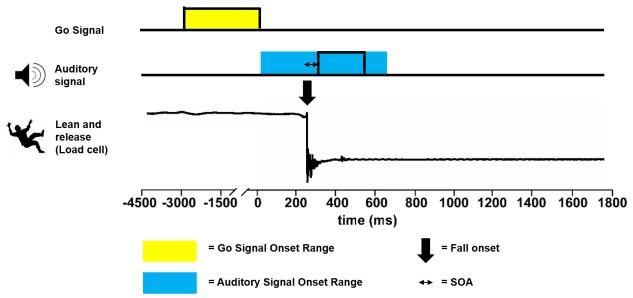


Figure 5. Trial design schematic. The trial begins with the onset of a go signal (yellow) followed by the perturbation or sound. The onset of the sound (blue) and fall occurs anywhere from 0 to 650 ms after the offset of the go signal.

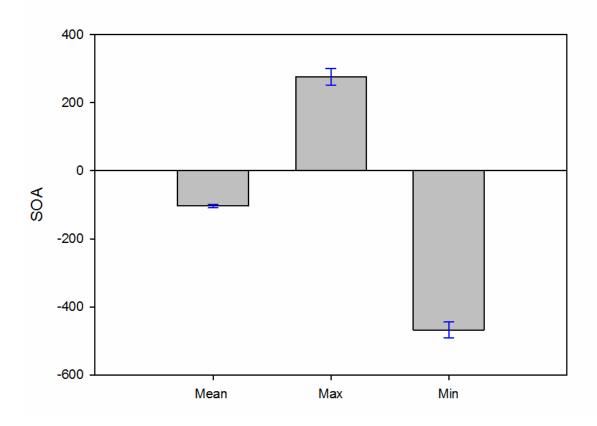


Figure 6. Distribution of SOAs for Study 1. The mean SOA was -103 ms where the maximum and minimum SOA were 276 and -467 ms, respectively. Error bars are \pm 1 SEM.

Load cell

A 200lb load cell was used to provide an indication of perturbation onset time and also maintain consistency of lean across trials by identifying the weight on the cable prior to the perturbation (Mansfield et al., 2012). The load cell data was sampled at 1000 Hz.

3.1.3 Data analysis

TOJ data acquired at various SOAs are plotted as a function of the percentage of trials in which either response was chosen. Negative SOAs indicate that a fall occurred prior to the auditory stimuli (Figure 7). A two-parameter logistic function (Equation 1) was fit to the TOJ

data using Sigma Plot 12.0, where *x0* refers to the PSS and *b* refers to the slope of the logistic curve that is proportional to the just noticeable difference (JND).

(1)
$$y = \frac{100}{1 + e^{-\frac{(x - x_0)}{b}}} \%$$

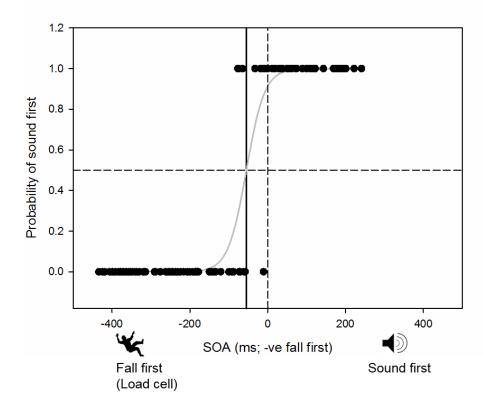


Figure 7. One participant's TOJ data (0s and 1s) acquired at different SOAs. The grey line is the logistic function fit to the data, where the PSS (solid vertical line) is the point at which the function crosses 0.5. The black circles represent the individual responses for each trial. The dashed vertical line signifies the point of true simultaneity (SOA = 0ms). Fall first and sound first on the x-axis are represented by two symbols (falling person and a speaker icon, respectively).

The PSS, the point at which a temporal asynchrony between two stimuli presented successively is perceived as simultaneous, was obtained from the logistic function. Recorded TOJs were analyzed for correct trials only. Trials were deemed as an error if there was a response prior to the end of the trial, or if no response was given. Trial errors occurred on fewer than 3% of all trials and these trials were not repeated later in the experiment.

3.1.4 Statistical analysis

To test the initial hypothesis that perceived simultaneity of the inertial and auditory stimuli will exhibit a similar perceptual lag during a sudden fall as found in previous multisensory processing experiments, a one-sample t-test will be conducted. A significance level of $\alpha = 0.05$ will be used for statistical analysis. In order to determine if the distribution of SOAs were influencing the resultant PSS due to having a high percentage of fall first trials, correlational analyses were performed between the PSS, JND and trial distribution descriptive statistics.

3.2 Study 1 results

The results show that the onset of a fall has to precede an auditory stimulus to appear coincident with the fall. Figure 8 shows the logistic fits for all 8-participants (grey lines), as well as an average logistic curve derived from the average PSS and JND values. The average PSS (-44.23 ms, s.e. 9.25) was significantly different from true simultaneity (one-sample *t*-test, $t_{(7)}$ = -4.78, p = 0.001; Figure 9A). The average JND (50.22 ms, s.e. 5.53) is shown in Figure 9B.

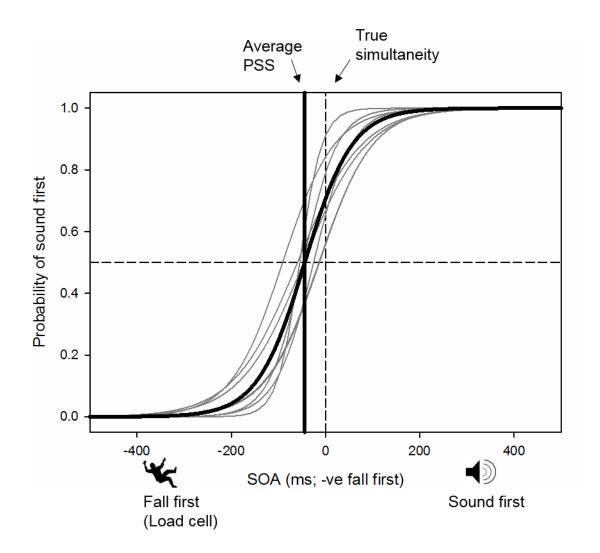


Figure 8. Perceived timing of unpredictable falls. Positive and negative SOA values represent which stimulus was perceived to be first. Negative SOAs represent the fall occurred first (load cell), where positive SOAs indicate the sound occurred first, as illustrated by the cartoons. The gray lines represent the individual participants' data fit. The black curve represent the average data fit of all participants. The solid vertical line indicates the average PSS value. The dashed vertical line signifies the point of true simultaneity (SOA = 0ms).

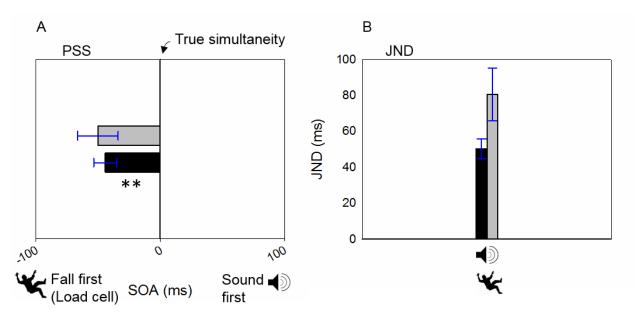


Figure 9. Study 1 results. (A) Average PSS (black) plotted relative to SOA for auditory stimulus. (B) Median JND data (black) for fall-sound pair. For reference only, the data also shows results from Barnett-Cowan & Harris (2011; grey) for passive head movements relative to an auditory stimulus (different subjects, n = 15). Error bars are ± 1 SEM. ** p = 0.001

Spearman correlations were analyzed with respect to the PSS, JND and SOA distribution descriptive statistics for the younger adults in Study 1 (see Table 1). Correlational analyses reveal that there is no significant statistical relationship between the resultant PSS and the high percentage of fall first trials.

YOUNGER ADULTS	PSS	JND
Mean	r = .07	r =10
(M = -103.58 ms, SD = 14.53 ms)	p = .839	p = .794
Standard deviation	r =10	r =36
(M = 191.42 ms, SD = 9.59 ms)	p = .794	p =.353
Standard error	r =12	r =26
(M = 18.28 ms, SD = 0.97 ms)	p = .749	p = .498
C.I. of mean	r =12	r =26
(M = 36.24 ms, SD = 1.92 ms)	p = .749	p =.498
Range	r =02	r = .02
(M = 743.88 ms, SD = 115.47 ms)	p = .931	p = .931
Max	r = .35	r =32
(M = 276.50 ms, SD = 68.09 ms)	p = .353	p = .387
Min	r = .53	r =23
(M - 467.29 mg, CD - 65.10 mg)	p = .160	p = .537
(M = -467.38 ms, SD = 65.10 ms) Median	r = .10	r = .00
(M 0650 CD 720)	p = .794	p = .977
(M = -96.50 ms, SD = 7.39 ms) 25%	r = .60	r =21
(14 AFI 14 AFI 10 66)	p = .102	p = .578
(M = -271.41 ms, SD = 18.66 ms) 75%	r =19	r =02
	p = .619	p = .931
(M = 59.16 ms, SD = 23.85 ms) Skewness	r = .33	r = .02
	p = .387	p = .931
(M = -0.004 ms, SD = 0.11 ms) Kurtosis	r = .57	r =02
	p = .120	p = .931
(M = -1.07 ms, SD = 0.17 ms) K-S distribution	p = .120 r =60	p = .031 r = .07
as o distribution	p = .102	
(M = 0.08 ms, SD = 0.01 ms) K-S probability	p = .102 r =60	p = .839 r =07
(M = 0.11 ms, SD = 0.10 ms)	p = .102 $r = .57$	p = .839 r =02
S Wilk		
(M = 0.96 ms, SD = 0.01 ms)	p = .102 $r = .20$	p = .931 r =26
S Wilk probability		
(M = 0.02 ms, SD = 0.04 ms)	p = .714	p = .658
Sum ($M = -11347.90 \text{ ms}, SD =$	r = .07	r =10
1530.96 ms)	p = .839	p = .794
Sum of squares (<i>M</i> =	r =31	26
5181959 ms, $SD = 465378$ ms)	p = .423	p = .498

Table 1. Spearman correlations of younger adults from Study 1. Perceptual (i.e., PSS and JND) and SOA (i.e., distribution statistics) correlations are presented.

3.3 Discussion

It was hypothesized that if an individual's perception of time was distorted due to a fall, it would be expected that there would be no lead time relative to an auditory stimulus, suggesting that slow vestibular perception reported in the literature is restricted to direct vestibular stimulation and movements of the head. It was also hypothesized that onset of a fall would be delayed relative to an auditory stimulus. Consistent with predictions, here it has been shown that young, healthy individuals are no more cognizant of indirect vestibular stimulation during onset of a postural perturbation than what has previously been reported for passive head movements (Barnett-Cowan, & Harris, 2011). While past research has shown that a similar perceptual delay exists across different experimental measures, it was not clear how this delay would be affected by unexpected perturbations.

Participant certainty (i.e., JND) for Study 1 was better than what was reported for passive head movement detection (Barnett-Cowan, & Harris, 2011). This suggests that participants may be more certain about whether they thought the sound or perturbation came first even in a more physically evoking situation (e.g., falling), however, this requires future work with a within-subjects design. As the vestibular system rarely works alone, this improved certainty may be a result of the influence of other sensory systems (i.e., somatosensory) aiding in detecting perceptual stimulation onset (see Barnett-Cowan, 2013). Furthermore, as previous literature demonstrates, the nature of a stimulus may have a substantial influence on perceptual detection (Roufs, 1963). As such, a fall, which is more physically arousing, may be easier to attend to than a simple head movement and may have aided participant certainty.

One limitation of Study 1 is that the perturbation stimulus was not standardized across participants. The amplitude of the perturbation was a consequence of a set cord length and not standardized by a percentage of the participant's body weight. As a result, participants

experienced smaller or larger perturbations depending on their height and weight. Given the novelty of the present experiment, it is difficult to determine how a standardized perturbation amplitude would influence individuals' rate of processing (PSS) and judgement certainty (JND). Another possible limitation to Study 1 is that the dB level for both the white noise and auditory tone was not standardized across participants. A consequence of this may have affected participant responses by making it easier or harder to process the sound stimulus.

Study 2 will establish whether similar perceptual processing delays exist for those susceptible to increased fall behaviour, particularly older adults. Participants will be affixed with a motion capture system to identify any age-related stepping behaviours. Given past research on perturbation induced stepping, older adults tend to exhibit more frequent and shorter step lengths than younger adults (Luchies, Alexander, Schultz, & Ashton-Miller, 1994; Judge, Davis, Õunpuu, 1996). Due to the novelty of testing perceptual responses in a dynamic setting, the addition of motion capture is exploratory as it is unknown as to whether older adults will elicit different perceptual delays and whether it will relate to different stepping behaviours.

Study 2 – Determining age-related differences of the PSS using unexpected perturbations in older populations

4.1 Introduction to Study 2

Optimal multisensory integration is important in everyday life because it combines information from multiple sensory modalities to allow people to have accurate perceptual sense of themselves and their environment. It also modulates their behaviours to perform better in an environment that is constantly changing. One such system that is integral to maintaining a healthy and active lifestyle throughout the lifespan is balance control. Balance control is affected by multiple systems, including visual, motor, somatosensory, musculoskeletal, and vestibular (Hu & Woollacott, 1994a). Recent evidence on the interaction between perception and kinematics has shown how both vestibular and proprioceptive information in conjunction with visual information jointly contribute to identify the amount of distance traveled while walking through virtual perceptual space (Campos, Butler, & Bülthoff, 2012). It was found that both proprioceptive and vestibular cues provide more coherent cues than visual alone, contributing to greater travelled distance estimates during walking. This suggests that body-based information (i.e., vestibular and proprioceptive) has a significant influence on how people interact with their environment, even during simple activities such as, stepping and walking. As such, a decline in integrating multiple sensory information would affect an individual's perception and subsequent action. The present study examines age-related differences involved in multisensory processing with respect to inertial and auditory cues to determine whether balance deficits are related to delays in temporally processing sensory information related to a fall. This research is important due to the growing number of falls experienced by older adults each year. A leading cause of death in the United States is a result from falling in older adults, as one in every three older

people fall each year (Sattin et al., 1990). Alarmingly, as people age there is an exponential increase in the number of falls they experience and that involve medical attention (Hu & Woollacott, 19941; Sattin et al., 1990). Furthermore, lengthy hospital stays averaging 11.6 days overall can have an unhealthy effect on your independence and attitude on life, including costly hospital bills (Sattin et al., 1990). As such, it is necessary to learn and develop measures that can aid in reducing the incidence of falls in older adults, as well as improving their way of life as they age.

There is little knowledge about how multisensory processes are affected as people age (Diederich et al., 2008; Laurienti et al., 2006) and may be a reason as to why older adults fall more than younger adults. Previous studies involving older populations have found that older adults are physically and perceptually slower than younger adults with respect to eye movements (Diederich et al., 2008), response time (Laurienti et al, 2006), TOJs (Poliakoff et al., 2006), and sound-induced flash illusions (Setti, Burke et al., 2011). Furthermore, multisensory research in older populations has yielded conflicting results, which is attributable to the use of different testing procedures and analyses (Laurienti et al., 2006). More recent work has found that relative to younger adults, older adults tend to have larger temporal binding windows (i.e., larger JNDs) (Poliakoff et al., 2006; Diederich, 2008; Setti, 2011). This allows for relevant and irrelevant stimuli to be processed and also reduces the probability of successfully integrating multiple stimuli (Laurienti et al., 2006). Setti and colleagues (2011) found that older adults were more susceptible to sound-induced flash illusions at longer SOAs, reflecting an inefficient processing of irrelevant stimuli in the CNS. Additionally, when older participants are presented with pairs of visual and vibrotactile stimuli to either hand and asked to make TOJs of which stimulus came first, older observers required more time and were less accurate than young observers to

correctly perceive the temporal order (Poliakoff et al., 2006). These results indicate that poor early perceptual processing may lead to less coherent multisensory perception. Further, Hu and Woollacott (1994a; 1994b) found that older adults are unable to ignore multiple ambiguous sensory cues as they fall or sway significantly more under sensory conflict situations, which may lead to a loss of balance and posture.

While some researchers claim that multisensory integration degrades as a function of age, others have not found this to be the case. Laurienti and colleagues (2006) found that as an individual gets older, their unisensory perception starts to deteriorate because they tend to rely more on integration of the senses. As such, it is possible that older adults can benefit from having larger temporal binding windows (i.e., larger JNDs) which will allow them to exploit redundant cues to form a reliable and coherent perception. Given that there may be a link between poor multisensory perception and balance control (Setti et al., 2011), more recent work has focused on improving multisensory integration among individuals who suffer from balance and posture deficits.

While muscle spindles do not diminish over time, the number of vestibular axons significantly decreases as a function of age (Strupp, Arbusow, & Pereira, 1999). Strupp and colleagues (1999) found a symmetrical increase in the sensory weighting of proprioception with age in determining body orientation, which suggests that other systems involved in balance and posture will compensate for those that start to deteriorate. This notion can be used to train older adults to exploit otherwise redundant cues from other sensory modalities to improve their balance (Spence et al., 2003). Spence and colleagues (2003) demonstrated that exploiting spatially redundant cues facilitated precision with which observers made speeded audio-visual and visuo-tactile TOJs. Hu and Woollacott (1994a) significantly improved the balance and

posture of older adults following a 10-hour multisensory balance-training program, as compared to the older control groups. They found that inter-sensory training was significantly more effective in reducing postural sway and falling immediately post-treatment and during a 4-week follow-up than training one sensory system to improve balance. Additionally, Hu and Woollacott (1994b) found that multisensory training can not only improve sensory perception to improve balance, but also aid in improving muscle activation and movement characteristics involved in maintaining posture. This research highlights the potential significance of training multisensory perception to improve an individual's balance and posture.

To date, there have been no studies that have explored the use of a lean and release perturbation system to indirectly elicit inertial cues in older adults in relation to an auditory stimulus. As a result, the main objective of Study 2 is to identify age-related differences of the PSS using temporally unpredictable perturbations with older adults. It is hypothesized that following unexpected perturbations, older adults will have a larger PSS and a shallower slope than younger adults. This is due in large part to having larger temporal binding windows (i.e., larger JNDs), allowing for a greater portion of time for multiple stimuli to be 'bound' together. Due to this perceptual widening, older adults may misattribute incoming stimuli and make them more susceptible to falling.

Additionally, it is hypothesized that those who exhibit balance impairments on the Romberg test will also elicit higher PSS and JND values. In addition to the Romberg, a motion capture system will also be affixed to participants to identify age-related differences in falling and stepping behaviours that may be related to the perceptual task. In particular, the peak velocity of the 'trunk', peak velocity of the stepping foot, the step length, and the difference in timing between initial trunk onset and ankle-off will be identified for both groups. While the

addition of the Romberg and motion capture equipment is purely exploratory in nature, it is predicted that those who exhibit higher PSS and JND values will also exhibit shorter step lengths, and reach higher peak velocities during the fall. This research has the potential to influence our understanding of the important link between delayed perception of inertial stimulation and unconscious processing during a fall, which may lead to further research on how the CNS temporally processes multisensory events.

4.2 Materials and method

4.2.1 Participants

A sample of 12 younger healthy adults (ages 19-25; M = 22.00 years, SD = 1.71 years; 7 female) and 11 older healthy adults (ages 61-72 years old; M = 67.00 years, SD = 4.38 years; 9 female) were recruited to participate in this study. The average heights of the younger adults (M = 168.25 cm, SD = 7.47 cm) and older adults (M = 165.36 cm, SD = 9.83 cm) were recorded as well as their weights (M = 140.83 lbs, SD = 28.77 lbs; M = 158.45 lbs, SD = 28.50 lbs) for younger and older adults, respectively. All older adults were recruited through the University of Waterloo's WRAP pool. All participants were free of musculoskeletal, auditory, visual, vestibular or other neurological disorders and gave their informed written consent to participate in the study, which was approved through a University of Waterloo Research Ethics Committee, which complies with The Code of Ethics of the World Medical Association (Declaration of Helsinki).

4.2.2 Protocol and materials

Procedure

The falling experiment procedure was the same as outlined in study 1 with only a few modifications. Participants were instructed to wear shorts and a t-shirt before arriving to the lab.

After giving informed consent and completing a brief health questionnaire (see Appendix A), participants were required to complete a randomized EO and EC Romberg balance task for a maximum of 30-seconds while standing on two force plates. In addition to wearing a harness with a cable attached posteriorly at the height of the 2nd and 3rd thoracic vertebrae, participants also wore 8-non-invasive passive reflective (Optotrak) clusters of 4-markers that tracked how the body was moving following the initial lean position. The clusters were placed on both feet, both thighs (above the knee), both forearms, and both upper arms (above the elbow). Two single markers were also affixed to the 3rd knuckle of each hand (see Figure 10 for reference).

Participants were required to cross their arms with each hand approximate to the opposite shoulder. A restrictive Velcro strap was used to secure their arms from moving throughout the experiment. Unlike Study 1, however, the buttons were taped together over the left shoulder and were situated in a comfortable position for each participant. Participants were also required to indicate whether they thought the fall or sound came first by pressing either the red button (indicated by their index finger) or the black button (indicated by their middle finger).

Participants, while blindfolded, were instructed to lean forward (indicated by tapping on their shoulder) from the ankle at a neutral position such that their body weight was supported by a cable. Perturbation amplitudes were standardized by a percentage of the participant's body weight corresponding to a particular lean angle that is sufficient in evoking compensatory stepping reactions (Lakhani, Mansfield, Inness, & McIlroy, 2011). Each perturbation consistently occurred at approximately 10% of the participant's body weight. The experimenter applied a perturbation following a "go signal" identified on a monitor by releasing a pin attaching the cable to a rigid support, causing the participant to fall in a forward direction and evoking a compensatory reaction (e.g., a step). For older adults, a volunteer was standing on each

side of the participant to reduce any potential falls from the perturbation. Also, prior to the start of testing, 10-practice trials were completed in order to become acquainted with the physical demands of the task (i.e., making a judgment post fall). There were 110 judgments at varying SOAs. There were 15-30 seconds between each perturbation, while each trial lasted approximately 15 seconds. A short rest break at the 60th trial was given for a total experiment time of approximately two hours.



Figure 10. Lean and release cable set-up for both younger and older adults. Participants were blindfolded and instructed to lean forward such that their body weight was supported by the cable from neutral stance. Perturbation onset time was calculated by a mounted load cell attached

to the mechanical lift. Participants were also affixed with a motion capture system (Optotrak).

Temporal order judgment task

Similar to Study 1, the TOJ task involved the presentation of a supra threshold sound (250 ms; 500 Hz) while listening to white noise, which masked all externally generated sound, before or after the onset of a perturbing fall. After each perturbation the participants were instructed to perform the TOJ task by indicating whether they thought their fall or the auditory stimulus occurred first via button press (i.e., index finger button = fall). They were subsequently asked to return to their standardized foot position, which was marked on a stable block of wood. The participants were instructed to respond as quickly and accurately as possible. The sound stimulus was presented relative to cable release at varying SOAs between 0 and 650 ms, representing the width of trial onset.

Sound generation and stimulus onset

The sound stimulus was identical to study 1 and was generated using a LabVIEW[™] (National Instruments, Austin, Texas, USA) program, consisting of a 250 ms square wave burst at 500Hz, and was administered through noise cancelling headphones (Sennheiser PXE 450; 77 dB). Participants listened to white noise (downloaded from commercially available software; 70 dB) during all trials at a level that was loud enough to mask any external noise capable of alerting them of the upcoming perturbation, while still being able to distinctly detect the sound stimulus. See Figure 5 for the study's trial design. Figure 11 represents the trial SOA distribution for Study 2. On average, the perturbation occurred first 70% of the time for the younger adults, and 69 % for the older adults.

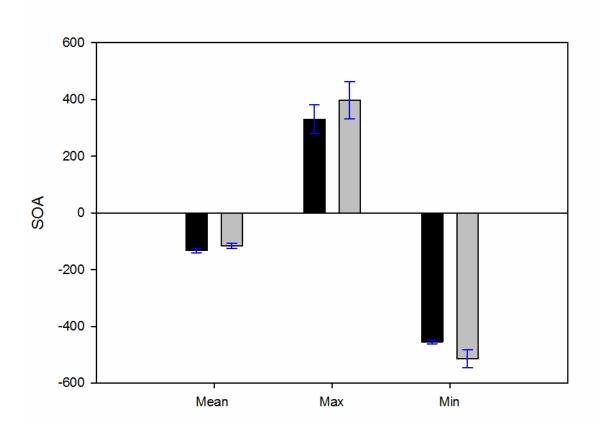


Figure 11. Distribution of SOAs for Study 2. The black bars represent the trial distribution data for the younger adults. The younger adult mean SOA was -132 ms where the maximum and minimum SOA were 329 and -455 ms, respectively. For the older adults (grey), the mean SOA was -116 ms where the maximum SOA was 398 ms and minimum was -514 ms. Error bars are \pm 1 SEM.

4.2.3 Data acquisition and analyses

Load cell

A 1000lb load cell sampled at 1000 Hz was used to provide an indication of perturbation onset time and also maintain consistency of lean across trials by identifying the percentage of body weight on the cable prior to the perturbation. TOJs for the lean and release experiments

were analyzed as a function of SOAs fit with a logistic curve (see Equation 1) to extract the PSS and JND using Sigma Plot 12.0. Recorded TOJs were analyzed for correct trials only. Trials will be deemed as an error if there is a response prior to the end of the trial, or if no response is given. *Motion tracking (Optotrak)*

Two Optotrak Certus Motion Capture Camera banks (Northern Digital Incorporated, Waterloo, Ontario), each consisting of three cameras (i.e., 6 total cameras) were placed in front of the participant and used to record the motion of the markers that were affixed to the participant. A digitizing cube was used to identify the capture volume in front of the two camera banks with a capture error of less than .5 mm. A 4-marker digitizing probe (Northern Digital Incorporated, Waterloo, Ontario) was also used to create imaginary markers with respect to each cluster by pointing to the anatomical landmark of interest (e.g., the ankles, knees, hips, wrists, elbows, shoulders, etc.). Motion was sampled at 32 Hz and used to record the stride length of the stepping foot, the peak velocity of the stepping foot from foot-off-to-foot-contact, the peak velocity of the "trunk" (i.e., the sum magnitude vector of the four upper body clusters), and the difference between trunk onset and ankle-off of each participant.

The global coordinate system defined by the point on the floor at the back of the right force plate, corresponds to a positive movement in x, represented as a forward motion in the anterioposterior (AP) direction. A positive movement in y-corresponds with upward motion, and a positive movement in z-corresponds with rightward motion in the mediolateral (ML) direction. All analyses of the current study were performed on the un-filtered raw collected data in the sagittal plane to identify motion in the AP direction. Average data loss ($M_{YA} = 20.67\%$, s.e. 7.28%; $M_{OA} = 14.51\%$, s.e. = 4.10%) was due to missed trials and noisy data (e.g., lost markers). Determining the leading foot for each trial was completed in MATLAB 2014a® by taking the

heel marker in the x-direction that created the earliest and largest change in position (see Figure 12). The mean and standard deviation of the leading heel movement in the x-direction during the standing still phase was then used to define step onset as the data point that exceeds the mean still movement plus ten times the standard deviation of the still movement. The stride length of each trial was then determined as the peak change in x minus the value of x at step onset. X position data is then differentiated to acquire peak velocity of the stepping foot (Figure 13).

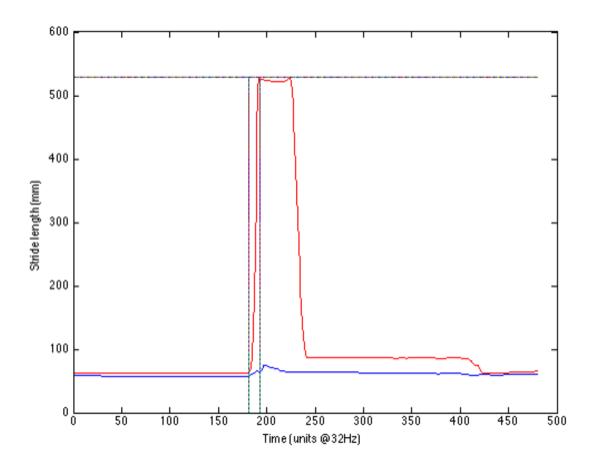


Figure 12. Stride leading foot for a single trial. The solid red line indicates movement of the right foot (here shows as the stepping response of the leading foot following a perturbation). The step is described as reaching peak stride distance followed by returning to the original upright position. The first vertical dotted line indicates heel onset. The second vertical line indicates the

peak step distance and the blue line indicates movement of the left foot (here shown as the stepping response of the non-leading stepping foot).

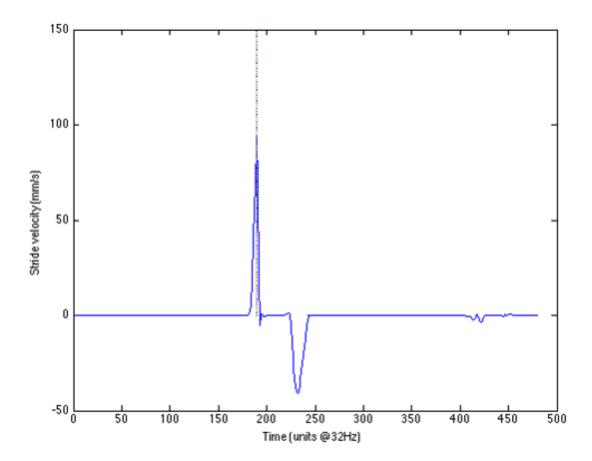


Figure 13. Stride peak velocity. The solid blue line represents the velocity of the stepping foot from a single trial following a perturbation (positive amplitude), followed by the stepping foot returning to the original upright position (negative amplitude). The dotted vertical line indicates the point of peak velocity of the stepping foot.

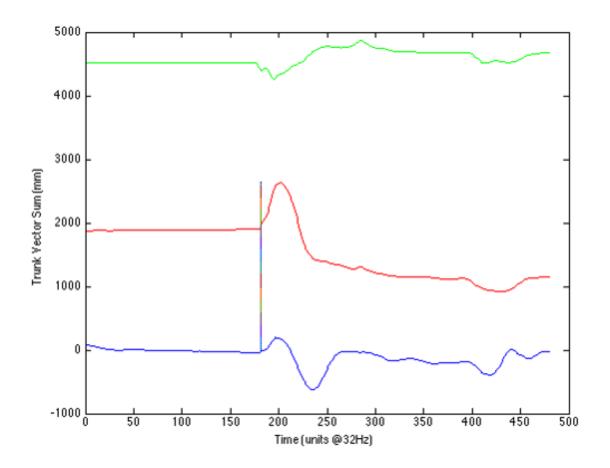


Figure 14. Trunk onset. The vector sum of 4 "trunk" markers (left lateral elbow, right lateral elbow, left lateral wrist, right lateral wrist) in the x, y, and z direction are represented as red, green, and blue, respectively. The red line indicates the position of the trunk following a perturbation represented as a positive amplitude. Following the perturbation, the participant returns to an upright position, indicated by immediate movement in the opposite direction elicited by the fall. The solid vertical line indicates trunk onset. The green line (movement in y; vertical) begins with the chest leaning forward, then falling down followed by an immediate return to an upright position. The blue line (movement in z; lateral) represents a rightward stepping motion, indicating that the participant stepped with their right foot, followed by a return to the initial position.

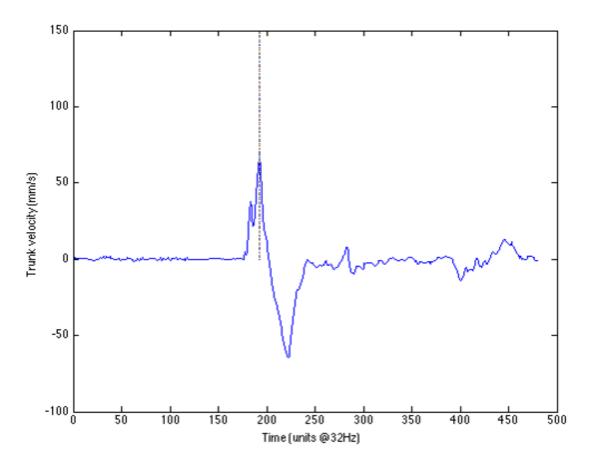


Figure 15. Trunk peak velocity. The solid blue line represents the velocity of the trunk from a single trial following a perturbation (positive amplitude), followed by the participant returning to the original upright position (negative amplitude). The vertical line indicates the point of peak velocity of the trunk.

In order to find the peak velocity of the trunk following a perturbation, 4 markers (left lateral elbow, right lateral elbow, left lateral wrist, right lateral wrist) were vector summed (i.e., all x positions are added together at each point in time) to determine a common point corresponding with the chest due to having the participants arms crossed across the chest and strapped down to prevent movement (Figure 14). The mean and standard deviation of the first 50

data points in the x-direction (i.e., standing still phase) was then used to define trunk movement onset, which corresponds to the data point that exceeds the mean still movement plus ten times the standard deviation of the still movement. X position data is then differentiated to acquire peak velocity of the trunk (Figure 15). To determine whether there are differences between the onset of the trunk and ankle-off, the trunk onset is subtracted from the stride onset, multiplied by 1000 and divided by 32.

Force plates

Two force plates (50.80 cm x 46.48 cm; Bertec, Columbus, Ohio; 1000 Hz) were used to measure the ground reaction forces on each foot during the EO and EC Romberg balance task. Specifically, force plate signals were used to determine AP and ML centre-of-pressure (CoP) excursions during the task. The variability was measured as the root-mean-square (RMS), and was used to determine the amount of bodily sway during the Romberg test prior to beginning the experiment.

4.2.4 Statistical analysis

In order to test the hypotheses of Study 2, a one-sample *t*-test comparing the average PSS value of the lean and release against true simultaneity (0 ms) was performed. Furthermore, an independent *t*-test was conducted to compare the average PSS values of the lean and release of the older adult subjects with the younger adults. Also, to assess differences in the certainty with which young and older adult participants made their judgements, another independent *t*-test between JND values was conducted. In instances where normality fails, Mann-Whitney *U* and Wilcoxon signed ranks tests were performed.

In order to determine if the distribution of SOAs were influencing the resultant PSS due to having a high percentage of fall first trials, correlational analyses were performed between the PSS, JND and trial distribution descriptive statistics.

Independent samples *t*-tests were used to determine any-age related differences between younger and older adults with respect to the Romberg test, stride length, defined as heel-off-to-heel contact, and peak-velocities of the stepping foot and trunk following a postural perturbation. An independent *t*-test was also used to determine the difference in timing onsets of the trunk and stepping foot.

Lastly, Spearman correlational analyses were conducted to account for unequal variance across variables and to identify any relationships between the stride length, peak velocities of the stepping foot and trunk, the trunk-stride onset, the Romberg test, the perceived rate of processing (i.e., PSS) and the JND separately for each age group.

4.3 Results

PSS

Figure 16A and B show the logistic fits for all participants (grey lines), as well as an average logistic curve derived from the average PSS and JND values. Comparable with Study 1 and previous research identifying delayed perceptual responses to vestibular stimulation, Study 2 results show that the onset of a fall has to precede an auditory stimulus to appear coincident with the fall for both groups. Here, the average younger adult PSS (-44.12 ms, s.e. 12.60) was significantly greater than true simultaneity (one-sample t-test, $t_{(11)}$ = -3.501, p = 0.002; Figure 17A). The average JND (52.54 ms, s.e. 8.36) is shown in Figure 17B. The average older adult PSS (-88.46 ms, s.e. 18.64) was also significantly greater than true simultaneity (Wilcoxon signed ranks, Z = -2.93, p < 0.001; Figure 17A). The average JND (57.73 ms, s.e. 12.40) is

shown in Figure 17B. Thus, both younger and older, healthy adults are no more cognisant of indirect inertial stimulation during fall onset than what has previously been reported for passive head movements (Barnett-Cowan & Harris, 2011). Additionally, the average PSS of the younger adults was significantly different from the average PSS of the older adults (Mann-Whitney rank sum test, U = 32, p = 0.039; Figure 17A). However, no significant difference of the slope was found between the younger and older adults (independent samples t-test, t(21) = -0.35, p = ns; Figure 17B).

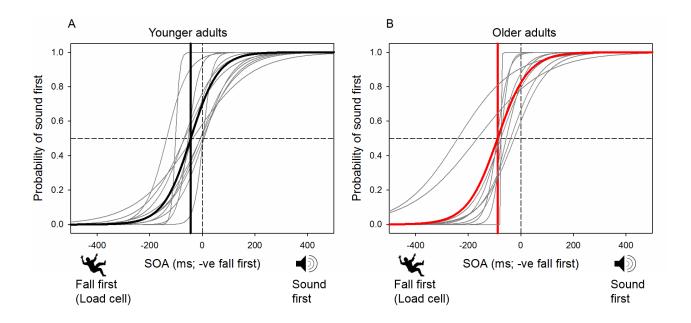


Figure 16. Perceived timing of unpredictable falls. Positive and negative SOA values represent which stimulus was perceived to be first. Negative SOAs represent the fall occurred first (load cell), where positive SOAs indicate the sound occurred first, as illustrated by the cartoons. The grey lines represent the individual participants' data fit. A) The black curve represents the average data fit of all younger adult participants. The solid black vertical line indicates the average PSS value. B) The red curve represents the average data fit of all older adult participants.

The solid red vertical line indicates the average PSS value. The dashed vertical line signifies the point of true simultaneity (SOA = 0ms).

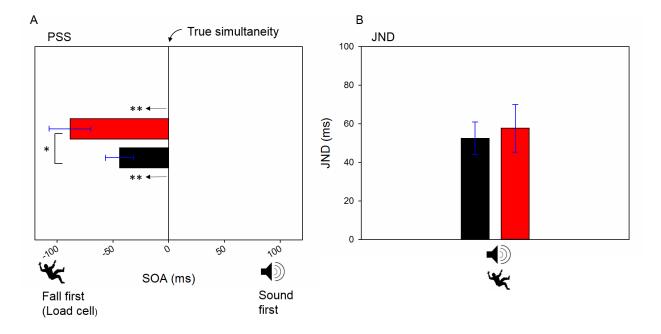


Figure 17. Study 2 results. (A) Average younger adult (black) and older adult (red) PSS plotted relative to SOA for auditory stimulus. (B) Median younger adult (black) and older adult (red) JND data for fall-sound pair. Error bars are \pm 1 SEM. * p = .05, ** p = 0.001. Double asterisks also refer to one way t-tests relative to an SOA of 0 ms, represented by black arrows.

SOA distribution

Spearman correlations were analyzed with respect to the PSS, JND and SOA distribution statistics for both the younger and older adults (see Table 2). Correlational analyses reveal that there is no significant statistical relationship between the resultant PSS and the high percentage of fall first trials in both the younger and older adult groups. However, the older adult PSS and mean SOA is very close to significance, r = .57, p = .060.

YOUNGER ADULTS	PSS	JND
Mean	r =06	r =06
(M = -132.88 ms, SD = 21.19 ms)	p = .852	p = .852
Standard deviation	r = .23	r = .13
(M = 195.98 ms, SD = 11.22 ms)	p = .456	p = .667
Standard error	r = .18	r = .14
(M = 19.68 ms, SD = 1.08 ms)	p = .572	p = .651
C.I. of mean	r = .18	r = .14
(M = 39.06 ms, SD = 2.13 ms)	p = .572	p = .651
Range	r =01	r = .02
(M = 785.0 ms, SD = 148.16 ms)	p = .974	p = .939
Max	r =13	r =11
(M = 329.63 ms, SD = 144.2 ms)	p = .683	p = .716
Min	r =45	r =15
(M = -455.38 ms, SD = 17.08 ms)	p = .136	p = .635
Median	r =18	r =04
(M = -136.38 ms, SD = 26.10 ms)	p = .572	p = .904
25%	r =22	r =20
(M = -301.31 ms, SD = 24.39 ms)	p = .484	p = .527
75%	r = .11	r = .03
(M = 36.94 ms, SD = 39.05 ms)	p = .733	p = .921
Skewness	r = .01	r = .13
(M = 0.17 ms, SD = 0.18 ms)	p = .956	p = .667
Kurtosis	r =22	r =15
(M = -0.89 ms, SD = 0.57 ms)	p = .484	p = .619
K-S distribution	r = .07	r = .49
(M = 0.09 ms, SD = 0.18 ms)	p = .817	p = .10
K-S probability	r =18	r =37
(M = 0.10 ms, SD = 0.12 ms)	p = .575	p = .245
S Wilk	r =19	r =56
(M = 0.95 ms, SD = 0.01 ms)	p = .542	p = .058
S Wilk probability	r = .02	r = .63
(M = 0.01 ms, SD = 0.004 ms)	p = .905	p = .096
Sum ($M = -13167.6 \text{ ms}$, $SD =$	r =10	r = .01
2074.39 ms)	p = .749	p = .974
Sum of squares (<i>M</i> =	r = .25	r = .22
5570005 ms, $SD = 457724.7$ ms)	p = .429	p = .484

OLDER ADULTS	PSS	JND
Mean	r = .57	r = .15
(M = -116.65 ms, SD = 24.67 ms) Standard deviation	p = .06 r =36	p = .653 r = .18
	p = .270	p = .575
(M = 198.02 ms, SD = 13.71 ms) Standard error	p = .270 r =41	p = .373 r = .21
Standard error	p = .119	p = .520
(M = 20.16 ms, SD = 1.70 ms) C.I. of mean	p = .199 r =41	p = .320 r = .21
(M - 40.02 ms, SD - 2.40 ms)	p = .199	p = .520
(M = 40.03 ms, SD = 3.40 ms) Range $(M = 913.14 \text{ ms}, SD =$	r =19	r = .27
246.66 ms)	p = .557	p = .40
Max ($M = 398.29 \text{ ms}, SD =$	r =02	r = .19
173.39 ms)	p = .946	p = .557
Min	r = .48	r =14
(M = -514.86 ms, SD = 84.30 ms)	p = .124	p = .673
Median	r = .44	r = .25
(M = -103.86 ms, SD = 35.01 ms)	p =.168	p = .450
25%	r = .49	r = .42
(M = -280.75 ms, SD = 31.64 ms)	p = .116 r = .01	p = .188 r = .19
75%	7 – .01	7 – .19
(M = 34.96 ms, SD = 30.22 ms)	p = .968 r =08	p = .557 r =26
Skewness		
(M = 0.07 ms, SD = 0.24 ms)	p = .797 $r = .07$	p = .416 r = .20
Kurtosis		
(M = -0.56 ms, SD = 0.71 ms) K-S distribution	p = .818 r =16	p = .538 r =37
	p = .633	p = .245
(M = 0.08 ms, SD = 0.01 ms) K-S probability	r = .14	r = .37
	p = .653	p = .245
(M = 0.14 ms, SD = 0.09 ms) S Wilk	r =11	r = .79
(M = 0.97 ms, SD = 0.01 ms)	p = .734	p = .002
S Wilk probability	r =18	r = .77
(M = 0.02 ms, SD = 0.03 ms)	p = .575	p = .004
Sum $(M = -11309.7 \text{ ms}, SD =$	r = .45	r = .24
2636.69 ms)	p = .159	p = .467
Sum of squares (<i>M</i> =	r =50	r =16
5131799 ms, <i>SD</i> = 710903.6 ms)	p = .109	p = .614

Table 2. Spearman correlations of both younger (left) and older (right) adults. Perceptual (i.e., PSS and JND) and SOA (i.e., distribution statistics) correlations are presented.

Romberg test

Of the 23-participants, only 9-younger adults and 10-older adults were analyzed with respect to the Romberg test for Study 2. Four participants were excluded due to signal connection failures during collection. The average RMS values for younger adult EO-ML (M = 4.428 mm, s.e. = .390 mm) and EO-AP (M = 5.203 mm, s.e. = .606 mm) were not significantly different than the older adult EO-ML (M = 4.180 mm, s.e. = .487 m) and EO-AP (M = 5.497 mm, s.e. = .484 mm). The average RMS values for younger adult EC-ML (M = 6.418 mm, s.e. = .864 mm) and EC-AP (M = 5.792 mm, s.e. = .496 mm) were also not significant when compared to the older adult EC-ML (M = 5.569 mm, s.e. = .554 mm) and EC-AP (M = 6.494 mm, s.e. = .772 mm).

Motion capture

Only 10-younger adults and 10-older adults of the 23 participants were affixed with motion capture equipment in Study 2. Motion capture was being used as a collaboration effort across labs and only required 10-younger and 10-older adults. Figure 18 shows the group averages for each parameter of interest with younger and older adults represented as black and grey, respectively. Independent samples *t*-tests revealed that there are no significant group differences between stride length, stride peak velocity, trunk peak velocity, and difference in trunk-stride onset. Individual group Spearman correlations are also shown (see Table 3) which were conducted to identify any relationships between both the perceptual and behavioural variables (i.e., Romberg test and motion capture).

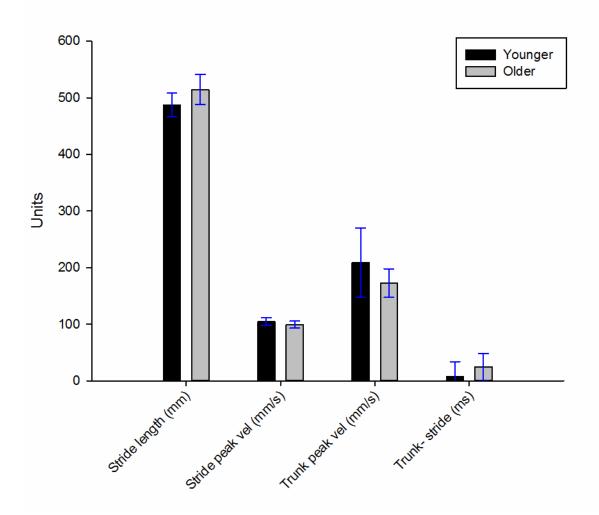


Figure 18. Motion capture Study 2 results. Average younger adult (black) and older adult (grey) motion capture raw data with respect to stride length, stride peak velocity, trunk peak velocity, and trunk-stride onset. Error bars are \pm 1 SEM.

YOUNGER ADULTS	PSS	JND	Stride length	Stride peak vel	Trunk peak vel	Trunk-stride	EO-ML	EO-AP	EC-ML	EC-AP
1 PSS	-	.21	04	58	15	16	.58	.80	.40	.61
2 JND		-	.67	06	.33	04	12	.20	10	13
3 Stride length			-	.41	.70	.49	13	.12	40	07
4 Stride peak vel				-	.73	.30	40	32	48	30
5 Trunk peak vel					-	.14	03	07	22	20
6 Trunk-stride						-	12	.05	53	.05
7 EO-ML							-	.45	.80	.55
8 EO-AP								-	.08	.69
9 EC-ML									-	.44
10 EC-AP										-
OLDER ADULTS	PSS	JND	Stride length	Stride peak vel	Trunk peak vel	Trunk-stri de	EO-ML	EO-AP	EC-ML	EC-AP
1 PSS	-	25	.32	.29	41	44	06	.04	08	60
2 JND		_	.24	29	.09	26	.31	31	03	03
			.2.	.27	.07	.20	.51			
3 Stride length			-	42	03	42	39	36	43	44
										44
3 Stride length				42	03	42	39	36	43	
3 Stride length 4 Stride peak vel				42	03 09	42	39	36	43	13
3 Stride length 4 Stride peak vel 5 Trunk peak vel				42	03 09	42 .53	39 .40	36 .60	43 .02	13 <u>.84</u>
3 Stride length 4 Stride peak vel 5 Trunk peak vel 6 Trunk-stride				42	03 09	42 .53	39 .40 .19	36 .60 .43	43 .02 .66 15	13 <u>.84</u> .08
3 Stride length 4 Stride peak vel 5 Trunk peak vel 6 Trunk-stride 7 EO-ML				42	03 09	42 .53	39 .40 .19	36 .60 .43 .33	43 .02 .66 15	13 <u>.84</u> .08 .13

Table 3. Spearman correlations of both younger (top) and older (bottom) adults. Perceptual (i.e., PSS and JND) and behavioural (i.e., motion capture and Romberg test) correlations are presented. r values in bold are significant at p < .05, r values that are underlined are significant at p < .01.

5.1 General discussion

The results in Study 2 provide further evidence that the perceived timing of a fall is slow relative to a comparison auditory stimulus. Indeed, results from younger adults in Study 2 closely replicated those from Study 1, where a fall has to precede an auditory stimulus by ~44ms in order for the stimulus pair to be perceived as simultaneous. The results from Study 2 also clearly demonstrate that older adults require a fall to occur twice as early before an auditory stimulus (~88 ms) than was required for younger adults, despite the fact that young and older adults were equally certain when judging the perceived timing of a fall. That older adults perceive fall onset with a delay that is two times slower than younger adults, represents an important insight into potential reasons why older adults are more likely to fall than younger adults. Further, differences in the lean angle used in Study 1 (~14°) and Study 2 (10°) yielded similar PSS (-44.23 ms vs -44.12 ms) and JND (50.22 ms vs 52.54 ms) values suggesting that although fall onset is perceived with a delay, the delay may not be attributable to differences in lean-angle, however future research could assess the effect of more extreme (e.g., 30°) lean angles.

Both studies of this thesis resulted in a higher percentage of fall first trials compared to sound first trials. A concern here is that the negative PSS values found could be a consequence of the distribution of SOAs, where the majority of fall first trials influence the PSS. To assess this concern, analyses compared the descriptive statistics of the SOAs with the PSS and JND from both studies. If the PSS or JND is being driven by the overall negative mean SOA in either study, then the resultant PSS and JND should be interpreted with caution as there may not be a perceived delay. However, both Study 1 and Study 2 showed no significant influence on the perceptual responses in relation to the distribution of trial SOAs, but the older adult PSS in Study 2 was trending towards significance. This suggests that the PSS and JND are not likely being

influenced by the percentage of fall first trials, but future research should utilize a defined set of SOAs between the two stimuli with an equal number of fall or sound first trials. Since the release of the cable is prone to experimenter delays, future experiments should also configure a mechanism that evokes the perturbation at a specific time to elicit a specific SOA between the two events.

How might these perceptual responses relate to balance control and reflexive fall recovery behaviour? Study 2 compared the Romberg test results between the younger and older adult groups where previously it has been shown that performance on a 30-second Romberg test significantly declines with age (Hain, 1997). Inconsistent with this previous work, there were no significant differences between younger and older adult performance on a 30-second EO or EC Romberg test, albeit a smaller sample was used in the present study. Spearman correlations were also conducted to identify whether individuals with larger balance impairments also exhibit a higher PSS and JND, where a relationship between perceptual and behavioural data would potentially suggest that a slower rate of processing of incoming stimuli may contribute to worse overall balance performance. With respect to younger adults, results from this analysis yielded a significant positive correlation between the PSS and EO-AP, indicating that as the perception of an event gets closer to true simultaneity (0 ms), younger adults exhibit more postural sway in the AP direction. Importantly, this relationship between perception and behaviour is not present in the older adult group. Significant positive correlations in the younger adult group were aslo found for EO-ML and EO-AP, EO-AP and EC-AP, indicating that as balance performance degrades, postural sway tends to increase in both the ML and AP directions. Also, balance performance tends to be exhibited across conditions of EO and EC with respect to the AP direction. In contrast, older adults elicited a significant positive relationship between EC-ML and EC-AP, showing that as performance in one direction decreases, performance in the other also tends to decrease. In contrast to predictions, there is no statistical evidence to suggest that those who exhibit greater balance impairments on the Romberg test, also tend to have higher PSS and JND values. However, all correlation results should be taken with caution as the sample size on the Romberg test was limited to one trial for each condition, and only 9 and 10 subjects for each group were available.

In addition to the Romberg test, motion capture equipment was also used to identify agerelated differences in behavioural responses resulting from a postural perturbation (e.g., a step) that may be relatable to the perceptual task. While previous literature has found that older adults tend to exhibit shorter stride lengths accompanied by more frequent steps than younger adults (Luchies et al., 1994; Judge et al., 1996), Study 2 found no significant difference between the younger and older adults with respect to stride length, peak velocities of the step and trunk, as well as the difference in onset of the trunk-stride (see Figure 16). It was predicted that those who exhibited a higher PSS and JND would also exhibit shorter stride lengths, and reach higher peak velocities of the stepping foot and trunk. With respect to the younger adults, results from this analysis yielded only one significant positive correlation between the JND and stride length, indicating that as participants elicit greater strides, the less certain they are at judging simultaniety. In contrast, it was originally thought that those who experience shorter steps would accompany higher PSS and JND values. However, no correlations support this hypothesis. While the number of trials per participant remains high, this result should also be taken with caution as the small sample size of 10 participants each may not have enough power to tease apart any underlining perceptual-behavioural relationships that may be present. It should be noted however, that due to finding no differences in both stepping and balance behaviours across

groups, it is possible that these two processes of perception and behavioural reflexes are not inextricably linked as was once thought. A possible explanation for this disociation is that inertial stimulation may not be directly accessible to our perception in that while this delay exists, it has no effect on the outcome of an individuals behaviour.

Further analyses between the behavioural data yield significant positive correlations in the younger adult group for stride length and trunk peak velocity, and stride peak velocity and trunk peak velocity, indicating that as an individual's stride length and stride peak velocity increases, their trunk peak velocity tends to increase as well. For the older adults, trunk peak velocity and EC-ML, as well as, trunk peak velocity and EC-AP, were also significantly positively correlated. This relationship suggests that balance performance on the Romberg test is related to how fast an individual falls following a postural pertubation. This confirms an already existing discovery that older adults with worse balance performance also tend to exhibit significantly shorter step lengths and heights resulting in faster trunk movement to maintain upright posture (Luchies et al., 1994).

Given these findings, it would be interesting to see whether this misattribution of incoming stimuli is also further expressed in those who exhibit a history of fall behaviour. It is possible that this greater perceptual latency might be a bi-product of degrading vestibular axons as people age. Strupp and colleagues (1999) reported an increase in age-related proprioceptive sensory weighting to aid in maintaining balance and posture, suggesting that other sensory systems will compensate for those that are deteriorating. While vestibular and hearing deficits were generally controlled for through the selection process of the University WRAP pool, no additional vestibular function test was administered prior to beginning the experiment which, if vestibular loss is actually present in the sampled populations, could explain this perceptual

phenomenon. For future research, the Fukuda Stepping Test (FST), or the Four Square Step Test (FSST) could be administered to identify any potential sensory re-weighting that may affect the outcome of the experiment as they are commonly used measures to reliably assess balance instability and peripheral vestibular dysfunction (Bonanni & Newton, 1998; Whitney, Marchetti, Morris, & Sparto, 2007).

The observed perceptual latency for fall onset may also be a result of anxiety from undergoing the experiment which may have inadvertently focused the participant's attention towards the fall rather than focusing on which stimulus came first. Young and Williams (2015) suggest that those who report a higher fear-of-falling (FOF) have a limited range of balance reflexes and a higher increase in autonomic activity with a profound attentional bias towards the threatening stimulus. Their research suggests that through FOF adoption strategies, participants compromise their balance by neglecting important sensory information necessary to execute dynamic movements (e.g., a step). Given that older adults are generally more susceptible to falling than their younger counterparts, this may affect their outlook on the experiment which may bias the resultant PSS. Unfortunately, no FOF questionnaire was administered, making it difficult to determine whether anxiety of the fall influenced the results. However, recent research on prior entry has shown evidence of modulating the PSS due to directing attentional resources towards a particular sensory modality with the resultant PSS being closer to true simultaneity (i.e., 0 ms; Spence et al., 2001). This suggests that if older participants were focusing primarily on the perturbation due to their anxiety, participants may not have delays in the perceived onset of a fall. However, one anecdote from testing participants in this study, older adults expressed no difference in their fear of undergoing the experiment compared to younger adults.

One theory that has yet to be discussed is the possibility that detection of delayed perceived simultaneity (i.e., negative PSS) can either indicate slow inertial detection, as indicated in this thesis, or a suppression in auditory detection, as the PSS is a relative measure of simultaneity. However, previous studies utilizing this particular experimental method have shown that similar perceptual delays exist in vestibular perception with respect to light, touch, and sound (Barnett-Cowan, & Harris, 2009; 2011), with the assumption that perception of head movement is delayed relative to another stimulus, and not suppression of the comparison stimulus. While response time was not collected for the present study, having participants respond immediately may have been a way of detecting whether inertial perception is delayed or whether auditory perception is supressed during a fall. Given what is known about sensory memory, the initial memory store that lasts a very short period of time and represents a high resolution of detailed information (Coltheart, 1980). Having participants respond immediately following the fall would facilitate performance by not relying on their short-term memory to determine which of two stimuli came first. Future analyses will look at the response times relative to the load cell to identify whether longer delays result in poorer recall. It is also possible that the comparison sound stimulus may have had a detrimental effect on the behavioural reflexes following a perturbation. For example, a loud stimulus may hinder detection of the comparison fall stimulus, or evoke a startle reflex. Consequently, future analyses should look to identify whether behavioural responses are different when the sound stimulus occurs between the participants PSS and true simultaneity. Future work should also utilize larger sample sizes and continue to examine differences between younger and older adult non-fallers, with older adult fallers, as further insights into this perceptual delay may yield important evidence as to why adults are more susceptible to falling as they age.

This thesis work helps inform our understanding for how the CNS temporally processes sensory information during a fall. The results from the present study provide evidence that the perceived timing of a fall is slow relative to a comparison auditory stimulus and that older adults require a fall to occur twice as early than what was required for younger adults. The observation that older adults perceive fall onset with a delay that is two times slower than younger adults, represents an important discovery which could guide current and future falls preventative strategies in the older adult population. This research also has the potential to change the way in which researchers study falling behaviours. While this particular method of testing (i.e., fall-sound comparison) is not an effective way of training older adults to prevent future fall occurrences in itself, future research can now integrate perceptual tasks such as the ones used here to further assess the role of the perceived timing of a fall with balance control and potentially detect and monitor those more likely to fall. As such, this thesis work may guide future research to identify effective methods of reducing falls in not only aging populations, but those who suffer from balance impairments at any age.

Appendix A HEALTH STATUS FORM

Perceived Timing of Auditory and Inertial Cues During a Postural Perturbation In Young and Older Adults

This questionnaire asks some questions about your health status. This information is used to guide us with your entry into the study. Contraindications to participation in this study include any neurological or musculoskeletal conditions, or any loss of hearing.

Ρ	articipant ID:
Α	ge:
S	ELF REPORT CHECKLIST:
Ρ	ast Health Problems:
[] Stroke
[] Traumatic Brain Injury
[] Concussion
[] Brain Tumor
[] Amyotrophic Lateral Sclerosis
[] Cerebral Palsy
[] Multiple Sclerosis
[] Parkinson's Disease
[] Peripheral Nerve Injuries
[] Spina Bifida
[] Spinal Cord Injuries
[] Loss of Consciousness
[] Migraine/Severe/Frequent Headaches
[] Seizures or Epilepsy
[] Chronic Joint Pain
[] Chronic Muscle Pain
[] Back Injuries
[] Low Back Pain
[] Swollen/Stiff Joints
[] Bone Disease

[] Osteoarthritis
[] Rheumatoid Arthritis
[] Repetitive Strain Injury
[] Fibromyalgia
[] Heart Attack
[] Heart Murmur
[] High/Low Blood Pressure
[] High Cholesterol
[] Congenital Heart Disease
[] Disease of the Arteries
[] Rheumatic Fever
[] Emphysema, Pneumonia, Asthma, Bronchitis
[] Diabetes
[] Ulcers
[] Kidney or Liver Disease
[] Bleeding Disorders
[] Vestibular (balance) Disorders
[] Auditory Disorders
P	resent Health:
L	st current problems: List medications taken now or in last 2 weeks:
1.	1.
2	2.
3.	3.
4	4.
F	or Females: Pregnant Nursing
L	st Symptoms: In the last 2 weeks
[] Fatigue
[] Numbness/tingling of arms/legs/face
[] Loss of / trouble understanding speech

[] Loss of / double vision
[] Dizziness
[] Loss of coordination/balance
[] Severe/unusual headache
[] Memory problems
[] Vertigo
[] Shortness of breath
[] Joint/muscle pain
[] Back pain/injury
[] Leg pain/injury
[] Irregular heart beat
[] Chest pain/pressure
[] Persistent cough
[] Wheezing
Current Physical Training Status:
I consider my physical training status to be: High [], Average [], Low []
List the types of physical activities that you do on a regular basis:
Habits:
Smoking: Never [] Ex-smoker [] Regular [] Average # cigarettes/day []
Signature of Participant:

References

- Agrawal, Y., Carey, J., Charles, C., Santina, D., Schubert, M., & Minor, L. (2009). Disorders of balance and vestibular function in US adults: data from the National Health and Nutrition Examination Survey, 2001-2004. *Archives of ..., 169*(10), 938–944.
- Angelaki, D. E., & Cullen, K. E. (2008). Vestibular system: the many facets of a multimodal sense. *Annual review of neuroscience*, *31*, 125–50. doi:10.1146/annurev.neuro.31.060407.125555
- Barnett-Cowan, M. (2013). Vestibular Perception is Slow: A Review. *Multisensory Research*, 26, 1–17. doi:10.1163/22134808-00002421
- Barnett-Cowan, M., & Harris, L. R. (2009). Perceived timing of vestibular stimulation relative to touch, light and sound. *Experimental brain research*, 198(2-3), 221–31. doi:10.1007/s00221-009-1779-4
- Barnett-Cowan, M., & Harris, L. R. (2011). Temporal processing of active and passive head movement. *Experimental brain research*, 214(1), 27–35. doi:10.1007/s00221-011-2802-0
- Barnett-Cowan, M., Raeder, S. M., & Bülthoff, H. H. (2012). Persistent perceptual delay for head movement onset relative to auditory stimuli of different durations and rise times. *Experimental brain research*, 220(1), 41–50. doi:10.1007/s00221-012-3112-x
- Békésy, G. Von. (1963). Interaction of paired sensory stimuli and conduction in peripheral nerves. *Journal of Applied Physiology*, *18*(6), 1276–1284.
- Campos, J. L., Butler, J. S., & Bülthoff, H. H. (2012). Multisensory integration in the estimation of walked distances. *Experimental brain research*, 218(4), 551-565.
- Coltheart, M. (1980). Iconic memory and visible persistence. *Perception & psychophysics*, 27(3), 183-228.

- Corey, D. P., & Hudspeth, A. J. (1979). Ionic basis of the receptor potential in a vertebrate hair cell. *Nature*, 281(5733), 675–677.
- Bonanni, M., & Newton, R. A. (1998). Test–retest reliability of the Fukuda Stepping Test.

 Physiotherapy Research International, 3(1), 58-68.
- Craig, J., & Baihua, X. (1990). Temporal order and tactile patterns. *Perception & psychophysics*, 47(1), 22–34.
- Diederich, A. (1995). Intersensory facilitation of reaction time: Evaluation of counter and diffusion coactivation models. *Journal of Mathematical Psychology*, *39*, 197–215.
- Diederich, Adele, Colonius, H., & Schomburg, A. (2008). Assessing age-related multisensory enhancement with the time-window-of-integration model. *Neuropsychologia*, 46(10), 2556–62. doi:10.1016/j.neuropsychologia.2008.03.026
- Engel, G., & Dougherty, W. (1971). Visual-auditory distance constancy. *Nature*, 234, 308.
- Ernst, M. O., & Bülthoff, H. H. (2004). Merging the senses into a robust percept. Trends in cognitive sciences, 8(4), 162-169.
- Fernandez, C., & Goldberg, J. M. (1976). Physiology of peripheral neurons innervating otolith organs of the squirrel monkey. I. Response to static tilts and to long-duration centrifugal force Physiology of Peripheral Neurons Innervating Otolith Organs of the Squirrel Monkey. I. Response to S. *Neurophysiology*, *39*(5), 970–984.
- Fujisaki, W., Shimojo, S., Kashino, M., & Nishida, S. (2004). Recalibration of audiovisual simultaneity. *Nature neuroscience*, 7(7), 773–8. doi:10.1038/nn1268
- Grant, P. R., & Lee, P. T. S. (2007). Motion-Visual Phase-Error Detection in a Flight Simulator. *Journal of Aircraft*, 44(3), 927–935. doi:10.2514/1.25807
- Hain, T. C. (1997). Approach to the Dizzy patient in Practical Neurology (Ed. J. Biller).

- Hamlin, A. (1895). On the least observable interval between stimuli addressed to disparate senses and to different organs of the same sense. *The American Journal of Psychology*, *6*(4), 564–575.
- Harrar, V., & Harris, L. R. (2008). The effect of exposure to asynchronous audio, visual, and tactile stimulus combinations on the perception of simultaneity. *Experimental brain* research, 186(4), 517–24. doi:10.1007/s00221-007-1253-0
- Harris, L., Harrar, V., Jaekl, P., & Kopinska, A. (2010). Mechanisms of simultaneity constancy.

 Space and Time in Perception and Action, 232–253.
- Herrmann, C., & Knight, R. (2001). Mechanisms of human attention: event-related potentials and oscillations. *Neuroscience & Biobehavioral Reviews*, 25(6), 465–476.
- Hirsh, I. R. A. J., & Sherrick, C. E. (1961). Perceived order in different sense modalities. *Experimental Psychology*, 62(5), 423–432.
- Hu, M., & Woollacott, M. (1994a). Multisensory training of standing balance in older adults: I. Postural stability and one-leg stance balance. *Journal of gerontology*, 49(2), M52–M61.
- Hu, M., & Woollacott, M. (1994b). Multisensory training of standing balance in older adults: II.
 Kinematic and electromyographic postural responses. *Journal of gerontology*, 49(2), M62–M71.
- Huterer, M., & Cullen, K. (2002). Vestibuloocular reflex dynamics during high-frequency and high-acceleration rotations of the head on body in rhesus monkey. *Journal of neurophysiology*, 88, 13–28.
- Jaekl, P. M., & Harris, L. R. (2007). Auditory-visual temporal integration measured by shifts in perceived temporal location. *Neuroscience letters*, 417(3), 219–24. doi:10.1016/j.neulet.2007.02.029

- Jaskowski, P., Jaroszyk, F., & Hojan-jezierska, D. (1990). Temporal-order judgments and reaction time for stimuli of different modalities. *Psychological Research*, 52, 35–38.
- Judge, J. O., Davis, B., & Õunpuu, S. (1996). Step length reductions in advanced age: the role of ankle and hip kinetics. The Journals of Gerontology Series A: Biological Sciences and Medical Sciences, 51(6), 303-312.
- Khasnis, A., & Gokula, R. M. (2003). Romberg's test. Journal of postgraduate medicine, 49(2), 169-172.
- King, A., & Palmer, A. (1985). Integration of visual and auditory information in bimodal neurones in the guinea-pig superior colliculus. *Experimental Brain Research*, 60, 492–500.
- Kopinska, A., & Harris, L. R. (2004). Simultaneity constancy. *Perception*, *33*(9), 1049–1060. doi:10.1068/p5169
- Kuffler, S. (1953). Discharge patterns and functional organization of mammalian retina. *J Neurophysiol*, 16(1), 37–68.
- Lakhani, B., Mansfield, A., Inness, E. L., & McIlroy, W. E. (2011). Characterizing the determinants of limb preference for compensatory stepping in healthy young adults. *Gait & posture*, *33*(2), 200–4. doi:10.1016/j.gaitpost.2010.11.005
- Laurienti, P. J., Burdette, J. H., Maldjian, J. a, & Wallace, M. T. (2006). Enhanced multisensory integration in older adults. *Neurobiology of aging*, 27(8), 1155–63. doi:10.1016/j.neurobiologing.2005.05.024
- Luchies, C. W., Alexander, N. B., Schultz, A. B., & Ashton-Miller, J. (1994). Stepping responses of young and old adults to postural disturbances: kinematics. *Journal of the American Geriatrics Society*, 42(5), 506-512.

- Mansfield, A., Inness, E. L., Lakhani, B., & McIlroy, W. E. (2012). Determinants of limb preference for initiating compensatory stepping poststroke. *Archives of physical medicine* and rehabilitation, 93(7), 1179–84. doi:10.1016/j.apmr.2012.02.006
- McIlroy, W. E., & Maki, B. E. (1997). Preferred placement of the feet during quiet stance: development of a standardized foot placement for balance testing. *Clinical biomechanics* (*Bristol, Avon*), 12(1), 66–70.
- Poliakoff, E., Shore, D. I., Lowe, C., & Spence, C. (2006). Visuotactile temporal order judgments in ageing. *Neuroscience letters*, *396*(3), 207–11. doi:10.1016/j.neulet.2005.11.034
- Pöppel, E., Schill, K., & Steinbüchel, N. Von. (1990). Sensory integration within temporally neutral systems states: a hypothesis. *Naturwissenschaften*, 77, 89–91.
- Roufs, J. (1963). Perception lag as a function luminance. Vision Research, 3, 81–91.
- Roy, J. E., & Cullen, K. E. (2004). Dissociating self-generated from passively applied head motion: neural mechanisms in the vestibular nuclei. *The Journal of neuroscience : the official journal of the Society for Neuroscience*, 24(9), 2102–11. doi:10.1523/JNEUROSCI.3988-03.2004
- Sanders, M. C., Chang, N.-Y. N., Hiss, M. M., Uchanski, R. M., & Hullar, T. E. (2011).

 Temporal binding of auditory and rotational stimuli. *Experimental brain research*, 210(3-4), 539–47. doi:10.1007/s00221-011-2554-x
- Sattin, R. W., Lambert Huber, D. A., Devito, C. A., Rodriguez, J. G., Ros, A., Bacchelli, S., ... Waxweiler, R. J. (1990). The incidence of fall injury events among the elderly in a defined population. *American Journal of Epidemiology*, *131*(6), 1028–1037.

- Setti, A., Burke, K. E., Kenny, R. A., & Newell, F. N. (2011). Is inefficient multisensory processing associated with falls in older people? *Experimental brain research*, 209(3), 375–84. doi:10.1007/s00221-011-2560-z
- Shore, D. I., Gray, K., Spry, E., & Spence, C. (2005). Spatial modulation of tactile temporal-order judgments. *Perception*, *34*(10), 1251–1262. doi:10.1068/p3313
- Soyka, F., Bülthoff, H. H., & Barnett-Cowan, M. (2013). Temporal processing of self-motion: modeling reaction times for rotations and translations. *Experimental brain research*, 228(1), 51–62. doi:10.1007/s00221-013-3536-y
- Spence, C., Baddeley, R., Zampini, M., James, R., & Shore, D. (2003). Multisensory temporal order judgments: When two locations are better than one. *Perception & Psychophysics*, 65(2), 318–328.
- Spence, C., Shore, D. I., & Klein, R. M. (2001). Multisensory prior entry. *Journal of Experimental Psychology: General*, *130*(4), 799–832. doi:10.1037//0096-3445.130.4.799
- Spence, C., & Squire, S. (2003). Multisensory Integration: Maintaining the Perception of Synchrony. *Current Biology*, *13*(13), R519–R521. doi:10.1016/S0960-9822(03)00445-7
- Stetson, C., Fiesta, M. P., & Eagleman, D. M. (2007). Does time really slow down during a frightening event? *PloS one*, 2(12), e1295. doi:10.1371/journal.pone.0001295
- Strupp, M., Arbusow, C. A. V., & Pereira, C. B. (1999). Subjective straight-ahead during neck muscle vibration: effects of ageing, *10*(15), 3191–3194.
- Tinetti, M. E., Liu, W. L., & Claus, E. B. (1993). Predictors and prognosis of inability to get up after falls among elderly persons. *Jama*, 269(1), 65-70.

- Van Eijk, R. L. J., Kohlrausch, A., Juola, J. F., & van de Par, S. (2008). Audiovisual synchrony and temporal order judgments: Effects of experimental method and stimulus type.

 *Perception & Psychophysics, 70(6), 955–968. doi:10.3758/PP.70.6.955
- Vroomen, J., & Keetels, M. (2010). Perception of intersensory synchrony: A tutorial review.

 *Attention, perception & psychophysics, 72(4), 871–884. doi:10.3758/APP
- Vroomen, J., Keetels, M., de Gelder, B., & Bertelson, P. (2004). Recalibration of temporal order perception by exposure to audio-visual asynchrony. *Brain research. Cognitive brain research*, 22(1), 32–5. doi:10.1016/j.cogbrainres.2004.07.003
- Whitney, S. L., Marchetti, G. F., Morris, L. O., & Sparto, P. J. (2007). The reliability and validity of the Four Square Step Test for people with balance deficits secondary to a vestibular disorder. *Archives of physical medicine and rehabilitation*, 88(1), 99-104.
- Wilson, J., & Anstis, S. (1969). Visual delay as a function of luminance. *American journal of psychology*, 82(3), 350–358.
- Zampini, M., Guest, S., Shore, D., & Spence, C. (2005). Audio-visual simultaneity judgments. *Perception & psychophysics*, 67(3), 531–544.