Age-related changes in multisensory self-motion perception

by

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A thesis submitted in conformity with the requirements for the degree of Doctor of Philosophy

Department of Psychology
University of Toronto

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Abstract
To derive the precise estimates of self-motion necessary to perform mobility-related tasks like walking and driving, humans integrate information about their movement from across their sensory systems (e.g. visual, auditory, proprioceptive, vestibular). However, recent evidence suggests that the way in which multiple sensory inputs are integrated by the adult brain changes with age. The objective of this thesis was to consider, for the first time, whether age-related changes in multisensory integration are observed in the context of self-motion perception. Two research approaches were used. First, I used a simple, simulated driving task to provide visual cues to self-motion and to manipulate the availability of auditory and/or vestibular cues to self-motion (i.e., unisensory versus multisensory conditions). The results revealed that relative to younger adults, older adults generally demonstrate greater differences in performance between multisensory and unisensory conditions. However, the driving task could not disentangle the effects of age-related differences in real-world driving experience from age-related differences in sensory integrative mechanisms. Second, I used an established and highly controlled psychophysical heading perception task to evaluate whether, like younger adults, older adults integrate visual and vestibular cues to self-motion in a statistically optimal fashion. I considered conditions where each of the two cues was presented alone, in combination and congruent, or in combination but indicating conflicting heading angles. Results showed that while older adults
did demonstrate optimal integration during congruent conditions, they were comparatively less tolerant to spatial conflicts between the visual and vestibular inputs. Overall, these results may have important implications for the way that older adults perform mobility-related tasks under various perceptual and environmental conditions.
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List of Abbreviations

2IFC  Two Interval Forced Choice
ANOVA  Analysis of Variance
ARHL  Age-Related Hearing Loss
CI-MA  Causal Inference – Model Averaging
cm  Centimeters
CoM  Center of Mass
CoP  Center of Pressure
dB  Decibels
EP  Endocochlear Potential
ETDRS  Early Treatment Diabetic Retinopathy Study
fMRI  Functional Magnetic Resonance Imaging
FMS  Fast Motion Sickness
FOE  Focus of Expansion
HMD  Head-Mounted Display
HRTF  Head-Related Transfer Function
Hz  Hertz
ILD  Interaural Level Difference
ITD  Interaural Time Difference
JND  Just Noticeable Difference
m  Meters
MLE  Maximum Likelihood Estimation
MoCA  Montreal Cognitive Assessment
MSSQ  Motion Sickness Susceptibility Questionnaire
MSTd  Dorsal Medial Superior Temporal
mV  Millivolts
OHC  Outer Hair Cells
PASA  Posterior-Anterior Shift of Attention
PET  Positron Emissions Tomography
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<td>PIE</td>
<td>Principle of Inverse Effectiveness</td>
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<tr>
<td>PPC</td>
<td>Population Probability Coding</td>
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<tr>
<td>PSE</td>
<td>Point of Subjective Equality</td>
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<td>PT</td>
<td>Planum Temporale</td>
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<td>RMSE</td>
<td>Root Mean Squared Error</td>
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<tr>
<td>RT</td>
<td>Response Time</td>
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<tr>
<td>s</td>
<td>Seconds</td>
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<tr>
<td>SC</td>
<td>Superior Colliculus</td>
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<tr>
<td>SNR</td>
<td>Signal to Noise Ratio</td>
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<tr>
<td>SNST</td>
<td>Stroop Neuropsychological Screening Test</td>
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<tr>
<td>SSQ</td>
<td>Simulator Sickness Questionnaire</td>
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<tr>
<td>TPJ</td>
<td>Temporo-Parietal Junction</td>
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<tr>
<td>TUG</td>
<td>Timed Up &amp; Go</td>
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<tr>
<td>UFOV</td>
<td>Useful Field of View</td>
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<td>VOR</td>
<td>Vestibulo-Ocular Reflex</td>
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Chapter 1
General Introduction

1 Introduction

Everyday mobility-related tasks like walking and driving are contingent upon reliable self-motion perception. In other words, they require the observer to precisely estimate the parameters of their movement including their speed, heading, and the distance that they have traveled. No single sensory system is entirely reliable across all behavioural and environmental conditions but self-motion typically stimulates multiple sensory systems simultaneously (e.g., visual, proprioceptive, vestibular, and auditory). Younger adults and non-human primates have been shown to integrate redundant estimates of self-motion from across their sensory systems (Butler, Campos, Bültthoff, & Smith, 2011; Butler, Smith, Campos, & Bültthoff, 2010; Fetsch, Turner, DeAngelis, & Angelaki, 2009). This process enables them to derive a multisensory self-motion percept that is more precise than that afforded by any single sensory estimate in isolation.

However, comparatively little research has considered how multisensory self-motion perception differs between older and younger adults.

It is well established that there are age-related changes in the individual sensory systems and that, in the context of self-motion perception, older adults are generally less precise than younger adults when using their individual sensory systems to estimate self-motion parameters (Atchley & Andersen, 1998; Lich & Bremmer, 2014; Roditi & Crane, 2012; Warren, Blackwell, & Morris, 1989). There is also evidence to suggest that there may be important developmental changes in terms of cue integration strategies. Notably, among older adults (65+ years of age), the global changes in cue reliability associated with age-related changes in the sensory systems at both the peripheral and central levels, coupled with changes in the capacity to inhibit cross-modal sensory inputs, are thought to cultivate heightened sensory integration (see Mozolic, Hugenschmidt, Peiffer, & Laurienti, 2012). This phenomenon has predominantly been observed in the context of simple stimulus detection and stimulus discrimination tasks where the available sensory inputs have a differential effect on the performance of older and younger adults (e.g., Laurienti, Burdette, Maldjian, & Wallace, 2006; Peiffer, Mozolic, Hugenschmidt, & Laurienti,
2007). Specifically, it has been shown that while both younger and older adults demonstrate faster stimulus detection during bimodal sensory presentations compared to unimodal sensory presentations, older adults demonstrate a greater bimodal performance advantage. Given that precise self-motion perception is contingent upon multisensory integration, age-related changes in the way that older adults integrate information from across their sensory systems could impact the precision with which older adults perceive and thereby control their movement. At present, the question remains as to whether age-related changes in multisensory integration generalize to multisensory self-motion perception.

From a theoretical standpoint, this represents an important gap in current knowledge. Although there is some indication that there are age-related changes in multisensory integration, these changes have largely been examined under highly constrained and oversimplified task and stimulus conditions, such as how quickly a stationary observer responds to the onset of a stationary flash of light, a stationary tone, or both cues presented simultaneously (e.g., Molholm et al., 2002). Thus, it is not clear whether the purported age-related changes in multisensory integration generalize to the more dynamic and complex sensory inputs that older adults encounter in their daily lives, including those elicited by self-motion. From a practical standpoint, considering age-related changes in multisensory self-motion perception is an important pursuit because older adults are at a much higher risk for injurious and fatal accidents, including falling while walking (e.g., Hausdorff, Rios, & Edelberg, 2001) and they are second only to young, novice drivers in their involvement in collisions with other motor vehicles (Hakamies-Blomqvist, 1993; Langford & Koppel, 2006). Thus, there is a clear need to understand and to mitigate the factors that place older adults at risk of injury. Much emphasis has been placed on the cardiopulmonary, musculoskeletal, neurophysiological, and cognitive factors involved in age-related declines in performance on mobility-related tasks, but it is also important understand the antecedents from a perceptual perspective. Most research on age-related changes in self-motion perception has emphasized how older adults estimate specific self-motion parameters using the individual sensory systems in isolation of one another. Because self-motion perception is fundamentally a multisensory task, age-related changes in multisensory integration may represent an important contributor to age-related changes in the ability to perceive and to control self-motion that has been relatively overlooked. The purpose of the current thesis was to
examine whether age-related differences in multisensory integration can be observed in the context of multisensory self-motion perception, where they could in turn contribute to changes in the way that older adults perform everyday mobility-related tasks.

Figure 1.1 depicts a conceptual model of the gaps in current knowledge pertaining to aging and multisensory self-motion perception that the current thesis was attempting to fill. The arrow at the top of Figure 1.1 represents the developmental trajectory of multisensory integration. The performance gains associated with multisensory integration (e.g., reductions in perceptual variability) first emerge at 6-8 years of age (Gori, Del Viva, Sandini, & Burr, 2008; Nardini, Jones, Bedford, & Braddick, 2008) and approach mature levels in adolescence (12-14 years; Nardini, Bedford, & Mareschal, 2010) but may continue to develop well into adulthood. Certain aspects of multisensory integration (e.g., the temporal binding window) may not reach full maturity until 50 years of age (e.g., Noel, De Near, Van der Burg, & Wallace, 2016). However, there is growing evidence to suggest that important changes in multisensory integration emerge again in late adulthood (age 65+). The callout box focuses on age-related changes in multisensory self-motion perception specifically and the core domains of interest to this thesis.

At a functional level, there are broad age-related changes in the way that older adults perform tasks that involve self-motion, such as walking and driving (far right). Previous investigations have considered how age-related changes in the way that the individual sensory systems convey self-motion in isolation of one another (far left) and how this may contribute to age-related changes in performance on mobility-related tasks. Reliable self-motion perception is contingent upon multisensory integration and there is evidence of age-related changes in terms of multisensory integrative mechanisms (middle left). However, this evidence is largely based on visual-auditory stimulus detection tasks. Thus, an important gap in current knowledge is whether age-related differences in multisensory integration extend to the more dynamic cues and specific cue combinations involved in self-motion perception (middle right) where they may then contribute to age-related differences in performance on mobility-related tasks like walking and driving. The purpose of the current thesis was to fill this gap by examining whether the age-related differences in multisensory integration observed in the context of simple stimulus detection generalize to multisensory self-motion perception.
Figure 1.1 Conceptual framework representing gaps in current knowledge pertaining to age-related changes in multisensory self-motion perception.
To examine age-related changes in multisensory self-motion perception, I utilized two distinct experimental methods. The first set of experiments involved developing and implementing a novel, multisensory driving task. This basic driving task was designed to provide visual cues to self-motion, and also allow me to manipulate the presence or absence of redundant auditory cues (Chapter 3; Ramkhalawansingh et al., 2016a), vestibular cues (Chapter 4; Ramkhalawansingh et al., 2016b), or auditory plus vestibular cues combined (Chapter 5). Driving performance measures (speed variability, lane keeping) enabled inferences about whether the combination of available cues had a differential effect on how older and younger adults perceived and thereby controlled their own movement. The purpose of this series of experiments was to extend current knowledge by considering whether previously observed age-related changes in multisensory integration generalize to more complex and dynamic cues, to different sensory cue combinations, and to performance under more realistic task constraints. Because age-related differences in driving performance may have also been influenced by age-related differences in driving experience, in my second experimental approach I utilized a more highly controlled and well-established psychophysical heading perception task (e.g., Butler et al., 2010; Fetsch et al., 2009; Gu, Angelaki, & DeAngelis, 2008; Gu, DeAngelis, & Angelaki, 2007) to hone in on age-related differences in visual-vestibular integration (Chapter 6).

The heading perception task consisted of visual cues (optic flow) and vestibular cues (passive translation) and required observers to discern the direction of self-motion on the basis of either visual, vestibular, or both sensory inputs combined. This paradigm has previously been used to demonstrate that younger adults and non-human primates employ an optimal cue integration strategy to reduce perceptual variance and to weight more reliable sensory inputs higher (Butler et al., 2010; Fetsch et al., 2009). This phenomenon has predominantly been demonstrated by artificially manipulating the relative reliability of the available sensory inputs (e.g., adding random motion noise to the optic flow). The heading perception task has also been used to elucidate the neural correlates of optimal visual-vestibular sensory integration (Fetsch, Pouget, DeAngelis, & Angelaki, 2012; Gu, DeAngelis, & Angelaki, 2012; Morgan, Deangelis, & Angelaki, 2008). Given that Chapter 4 revealed that older and younger adults were differentially affected by the availability of vestibular cues, the aim of the work reported in Chapter 6 was to compare older and younger adults to determine whether the naturally occurring, global age-
related changes in terms of the reliability of the available sensory inputs affect the integration strategies that older adults utilize, and whether these differences could, in turn, contribute to age-related differences in multisensory self-motion perception.

The remainder of this thesis is divided into six main sections. Chapter 2 consists of a literature review, Chapters 3-5 consist of the simulated driving experiments, and Chapter 6 consists of the heading perception experiment. Specifically, Chapter 3 examines whether age-related differences in visual-auditory integration extend to more complex and dynamic visual and auditory cues. Chapter 4 examines whether age-related differences in multisensory integration extend to visual and vestibular interactions. Chapter 5 examines whether the effect of combining more than two sensory inputs is additive or sub-additive and whether these effects are different between younger and older adults. Chapter 6 examines more explicitly whether younger and older adults utilize the same cue integration strategies to derive their self-motion percept. Finally, Chapter 7 provides a description of the novel contributions that this thesis makes to knowledge pertaining to age-related differences in multisensory self-motion perception, and to multisensory integration more generally. I then reflect on the limitations associated with the current body of work and directions for future research.
Chapter 2

Literature Review

2 Literature Review

In the following literature review, my aim is to provide the context necessary to understand how age-related changes in multisensory integration may result in age-related differences in multisensory self-motion perception. Therefore, it is necessary to first establish how the individual sensory systems convey self-motion, why multisensory integration is necessary to derive a consistently reliable self-motion percept and to consider behavioural and neurophysiological evidence as to how multisensory integration yields a reliable self-motion percept. My focus will then shift toward describing age-related changes in self-motion perception. I will begin by briefly reviewing current knowledge pertaining to age-related changes in the capacity to detect self-motion using the individual sensory systems in isolation. I will then review current behavioural and neurophysiological knowledge pertaining to visual-auditory cue integration (the literature for which most of the existing knowledge in multisensory integration and aging has been generated) and evidence of age-related changes in multisensory integration more generally. Finally, I will outline my experiments designed to elucidate how age-related differences in multisensory integration may affect multisensory self-motion perception.

2.1 What is self-motion perception?

Many everyday tasks involve self-motion, which is to say that they elicit dynamic changes in one’s own position with respect to the environment (Warren & Wertheim, 1990). Self-motion can vary widely in terms of both the source of propulsion and the level of control that one exerts over their own movements. For instance, movement can be self-propelled (e.g., walking) or it can arise from different forms of conveyance including those that are actively controlled (e.g., driving a car) and those that are passive in nature (e.g., riding on a train) (see Britten, 2008; Campos & Bülthoff, 2012; Cullen, 2012). The magnitude of self-motion can also vary considerably, ranging from the gross displacements associated with traveling from one location to another (e.g. walking from home to work) to the minute movements necessary for maintaining a stable posture. Nearly all instances of self-motion are motivated by specific goals such as
acquiring resources or avoiding harm. Reliable self-motion perception is necessary to ensure that one’s own behaviour is consistent with their underlying goals. In other words, the observer undergoing self-motion must detect and update information about how their position is changing with respect to physical space and over time (e.g., direction, distance traveled, velocity).

The visual, vestibular, proprioceptive, and auditory systems are each capable of conveying information about self-motion. However, no single sensory system is equally reliable across all possible behavioural and environmental circumstances (Ernst & Bülthoff, 2004). Further, the neural encoding of sensory information is inherently noisy and this introduces a persistent level of error into one’s perceptual estimates (Faisal, Selen, & Wolpert, 2008; Knill & Pouget, 2004). Despite these sources of perceptual ambiguity, the observer undergoing self-motion typically retains their capacity to navigate their environment effectively. This capacity is due in part to the fact that self-motion typically innervates multiple sensory systems simultaneously such that each sensory system provides independent estimates of the parameters of one’s own movement. By integrating these redundant signals, it is possible for the observer to maximize the precision of their self-motion percept (Butler et al., 2010; Fetsch et al., 2012, 2009; Gu et al., 2008; Morgan et al., 2008). Thus, reliable self-motion perception is contingent upon integrating information about self-motion from across the sensory systems (Ernst & Bülthoff, 2004). To illustrate this point, I will first consider how the visual system conveys self-motion and how information from the vestibular, proprioceptive, and auditory systems can serve to augment self-motion perception at the behavioural level. I will then consider the mechanisms by which the nervous system is thought to integrate multiple sensory inputs to optimize the precision of self-motion perception.

2.1.1 Unisensory contributions to self-motion perception

2.1.1.1 Visual self-motion perception

When moving through the environment, the visual scene appears to flow outward from a single point called the focus of expansion (FOE). The FOE corresponds to one’s destination and can thereby be used to discern heading angle (Gibson, 1950; Regan & Beverley, 1982; Warren & Hannon, 1988). The rate of optic flow can be used to judge speed (Larish & Flach, 1990) and to estimate the relative distance that one has traveled (Frenz & Lappe, 2005; Lappe, Bremmer, &
van den Berg, 1999). The medial superior temporal cortex (MST) is thought to play a crucial role in extracting estimates of self-motion parameters from visual information. While neurons within the primary visual cortex have very narrow spatial receptive fields that allow the observer to resolve specific features within the visual scene, the MST contains specialized neurons with very large spatial receptive fields that encompass up to an entire quadrant of the visual field (Komatsu & Wurtz, 1988; Tanaka & Saito, 1989, 1989). These broad receptive fields enable MST neurons to detect global motion patterns including the radial expansion of the visual scene created by self-motion (Tanaka & Saito, 1989). To extract estimates of the parameters of self-motion, individual MST neurons are tuned to respond selectively to specific features of the visual flow field. With respect to heading estimation, each MST neuron has a gradient of preferred foci of expansion, but they are each maximally sensitive to a focus of expansion at a specific location within the visual field (Duffy & Wurtz, 1991, 1995). There is an over-representation of neurons tuned to headings that are close to the center of the visual field but the majority of MST neurons are tuned to respond preferentially to optic flow with a shifted center of motion (Duffy & Wurtz, 1995). Across the entire population of MST neurons, all possible foci of expansion within the visual field are represented (Duffy & Wurtz, 1995). This selectivity is thought to allow MST neurons to encode the observer’s heading or direction of self-motion.

Optic flow is a very powerful cue to self-motion in that when it is presented to a physically stationary observer, it can elicit a strong illusory experience of self-motion (i.e., vection; Brandt, Dichgans, & Koenig, 1973). This phenomenon is perhaps best illustrated by the train illusion, in which an observer on a stationary train perceives the optic flow induced by the movement of an adjacent train as self-motion rather than object motion (Brandt, Bartenstein, Janek, & Dieterich, 1998). Despite optic flow’s strong influence on perceived self-motion, optic flow alone is not always sufficient for robust self-motion perception. Under many circumstances, visual motion cues are ambiguous. Large field visual motion always has two explanations, as it can represent either the observer’s own movement through the environment or the movement of external objects around the observer (Brandt et al., 1998). The train illusion also helps to illustrate the inherent ambiguity associated with discerning the cause of retinal image motion (Brandt et al., 1998, 1973; Kleinschmidt et al., 2002). Daily life routinely presents conditions that broadly diminish the reliability of visual cues to self-motion, such as moving through a darkened
environment (Shams & Kim, 2010). Nevertheless, the understanding of self-motion typically remains unambiguous and the observer retains the capacity to guide their behaviour effectively. Observers undergoing self-motion can overcome these ambiguities by combining optic flow cues with redundant information about movement derived from the vestibular, auditory, and proprioceptive systems as will be described below (Campos & Bülthoff, 2012; Ernst & Bülthoff, 2004).

### 2.1.1.2 Vestibular self-motion perception

The vestibular system is also a robust, independent source of information pertaining to self-motion. The vestibular system is comprised of the semicircular canals and the otolith organs which encode angular acceleration and linear acceleration, respectively (Angelaki & Cullen, 2008). Due to the force of their inertia, the fluid of the semicircular canals and the otolithic membranes lag behind the acceleration and deceleration of the head and body (Brodal, 2010). Their displacement deflects hair-like cellular structures called cilia that in turn transduce changes in velocity. Together, these systems enable the observer undergoing self-motion to detect the magnitude and direction of transient movements along any given vector (Cullen, 2012; Highstein, Fay, & Popper, 2004). Because the vestibular system detects physical acceleration, it is robust to some of the perceptual ambiguities that stem from the limitations associated with the visual system. For instance, unlike vision, the vestibular system is not affected by ambient lighting and can recover true heading when the observer is moving in a darkened environment (Page & Duffy, 2003). Similarly, one’s acceleration vector does not change when the head and/or eyes are oriented away from the direction of self-motion and therefore the vestibular system can recover true heading when one is looking in a different direction from the direction in which they are traveling (Liu & Angelaki, 2009). The vestibular system can also help to disambiguate the movement of the self from that of external objects, given that self-motion typically innervates both the visual and vestibular systems, whereas the movement of external objects does not elicit vestibular responses (Dokka, DeAngelis, & Angelaki, 2015; MacNeilage, Banks, Berger, & Bülthoff, 2007).

Self-motion perception on the basis of inertial cues is also thought to be mediated in part by the MST cortex (Fetsch, Wang, Gu, Deangelis, & Angelaki, 2007; Gu, Watkins, Angelaki,
DeAngelis, 2006; Page & Duffy, 2003). In non-human primates, it has been demonstrated that the MST contains neurons that respond to passive movement (e.g., externally generated physical displacement via a swing, moveable chair, or motion platform) in the absence of any visual input (e.g., moving under conditions of total darkness) (Bremmer, Kubischik, Pekel, Lappe, & Hoffmann, 1999; Duffy, 1998; Page & Duffy, 2003). Although there is a much higher prevalence of MST neurons that are tuned selectively to distinct visual headings (~ 98%), there are also large numbers of MST neurons that are selective for vestibular input conveying self-motion along various headings (~ 64%) (Gu et al., 2006).

That said, much like the visual system, the vestibular system has limitations that preclude robust self-motion perception under all conditions when isolated from other sensory inputs. For instance, linear translation and the tilting of the head along the sagittal plane innervate the otolith organs in an identical manner and thereby cannot be differentiated by the brain using otolithic signals alone (Angelaki & Cullen, 2008; MacNeilage et al., 2007). Furthermore, once a constant velocity has been achieved, the otolithic membranes return to their resting position and can no longer provide cues to self-motion (DeAngelis & Angelaki, 2012; Highstein et al., 2004). To perceive constant-velocity motion, one must rely on input from their visual system instead (Brandt et al., 1998). This illustrates that a strong reciprocal relationship exists between the visual and vestibular systems wherein the observer undergoing self-motion can lever the strengths of each system in order to overcome their respective limitations. The synergy between the visual and vestibular systems helps the observer to retain a highly robust understanding of their own movement under many different behavioural and environmental circumstances. Below I discuss in greater detail the mechanisms that are thought to underlie optimal visual-vestibular integration and how this might change with older age.

2.1.1.3 Proprioceptive self-motion perception

Within the body, there are receptors to detect forces that are caused by the body itself. For instance, muscles and tendons both contain receptors that detect changes in their length (Goodwin, McCloskey, & Matthews, 1972; Schultz, Miller, Kerr, & Micheli, 1984). Similarly, the joints contain receptors that detect the deformation of the joint capsules that occurs over their range of motion (Ferrell, Gandevia, & McCloskey, 1987). Together these systems enable one to
detect the position and orientation of their own body segments (see Graziano & Botvinick, 2002; Proske & Gandevia, 2012). Humans are capable of using such cues to derive estimates of self-motion parameters. For instance, it has been demonstrated that a walking observer can use body-based cues such as cadence and stride length to estimate the distance that they have travelled (Durgin, Akagi, Gallistel, & Haiken, 2009; Mittelstaedt & Mittelstaedt, 2001) and the rate of travel (Durgin, Reed, & Tigue, 2007; Terrier & Schutz, 2003) in the absence of visual information when they are walking at a normal and consistent pace (Mittelstaedt & Mittelstaedt, 2001). During self-generated movements (e.g., walking), copies of the motor signals initiating movements (i.e., efference copies; see Holst & Mittelstaedt, 1950), which reflect the expected motor output, are sent to the cerebellar nuclei (see Cullen & Brooks, 2015; Rondi-Reig, Paradis, Lefort, Babayan, & Tobin, 2014 for reviews). Proprioceptive input from joints, muscles, and tendons arising from the actual motor output (i.e., reafference; see Cullen, Brooks, & Sadeghi, 2009) then return to the cerebellar nuclei, allowing for the two signals to be compared. This process plays an important role in helping the observer to maintain a robust self-motion percept as a mismatch between the expected and the actual motor output can be used to estimate movement that is generated by external forces (i.e., exafference; see Cullen & Brooks, 2015). For example, tripping while walking would lead to unexpected proprioceptive inputs and the recognition that this input conflicts with the expected motor output helps the observer to initiate the appropriate corrective motor response (see Cullen, 2012). That said, the proprioceptive system is limited in that it cannot differentiate changes in the tilt of the support surface from changes in body orientation (Allison & Jeka, 2004). Such differentiation requires additional information about body position and orientation from the visual system (Assländer, Hettich, & Mergner, 2015). Moreover, different modes of propulsion alter the relationship between proprioceptive input and the parameters of self-motion. For instance, during walking, stride length and cadence may provide specific estimates pertaining to the speed and the relative distance that the observer has traveled but during other tasks like cycling, the relationship between leg movement and the rate and magnitude of self-motion is altered. Thus, the interpretation of proprioceptive input is context-dependent (Harris et al., 2002; Sun, Campos, & Chan, 2004).
2.1.1.4 Auditory self-motion perception

In order to conceptualize how auditory cues contribute to the perception of self-motion, it is first necessary to consider how the auditory system detects the position of specific sound sources within the environment. The auditory system uses several major cues to localize sound sources within the environment, including frequency-dependent interaural level differences (ILD) and interaural time differences (ITD).

Depending on the orientation of the head relative to the sound source, as sound reaches the observer’s head, the head itself can differentially occlude (or ‘shadow’) either ear to produce ILDs (see Hartmann, 1999 for review). High-frequency sounds (>3 kHz) have wavelengths that are physically shorter than the diameter of the head and are thereby diffracted by the head, causing them to lose energy and to arrive at the more occluded ear with a discernably lower amplitude (see Gelfand, 2016; Hartmann, 1999 for reviews). Humans can detect ILDs that are as small as 1 dB (see Blauert, 1997); however, the magnitude of the ILD is also contingent upon the spectral content of the incoming sound. Low-frequency sounds (<0.5 kHz) have wavelengths that are larger than the distance between the ears and therefore they are not scattered by the head to the extent that high-frequency sounds are and they do not lose enough energy to yield a detectable ILD (see Feddersen, Sandel, Teas, & Jeffress, 1957; Hartmann, 1999).

Due to the spatial separation of the ears, sounds will take longer to arrive at the ear more distant from the sound source. Consequently, the different features of an incoming waveform (e.g., onsets) will arrive at each ear at different times. However, in instances where the features of the incoming waveforms happen to align at both ears, ITD is no longer a reliable spatial cue. A limitation associated with both the ITD and the ILD is that when auditory cues are located along the median plane, both the ITD and ILD are near zero (see Feddersen et al., 1957).

The head-related transfer function (HRTF) consists of the entire set of ITD and ILD cues that could be used to localize sounds originating from any location. Approaching soundwaves are scattered by the listener’s body, head, and the pinna (i.e., the external ear; see Hartmann, 1999). Insofar as the size of listeners’ bodies, heads and pinnae differ, each person has an individualized HRTF. Depending on the location of a sound source, the differential patterns of diffraction
change the spectral composition (frequency response) of the sound. For example, the pinna imposes a notch filter or a very narrow frequency band filter on incoming sounds. The precise frequency that is filtered changes as a function of the elevation of a sound source relative to the observer, shifting from between 5 kHz to 11 kHz as the elevation of the source increases (see Gelfand, 2016). Thus, variations in the spectral content of the auditory information arriving at each ear can also indicate the position of sound sources in space.

The observer undergoing self-motion experiences dynamic changes in the distance and azimuth to sound sources in the environment and this will in turn cultivate dynamic changes in the associated ITDs, ILDs, and interaural differences in the frequency response of the sound arriving at the ears (McKerrow, 2008; Speigle & Loomis, 1993). Additionally, as the observer moves toward or away from specific sound sources, they will experience changes in the associated amplitude (e.g., looming) and they may also experience characteristic changes in the frequency of the sounds as they approach and/or pass the source of emission (e.g., the Doppler effect) (Speigle & Loomis, 1993). Thus, movement through the environment is thought to create a field of dynamically changing binaural and monaural cues to object position that forms a pattern of information known as acoustic flow (McKerrow, 2008; Müller & Schnitzler, 2000). Acoustic flow is a term that was first coined to describe how bats use the continual changes in the spatio-temporal characteristics of the sounds reflected back to them to navigate their environment in a manner that is analogous to the way that other mammals use the global radial expansion of the various elements of a given visual scene to derive estimates of self-motion (Müller & Schnitzler, 2000).

There is behavioural evidence to suggest that humans may be able to exploit acoustic flow to help detect self-motion. For instance, it has been demonstrated that, when standing in a tandem Romberg stance, both sighted and congenitally blind observers can use a stationary sound source to better detect and to reduce body and head sway (e.g., Easton, Greene, DiZio, & Lackner, 1998). It has also been demonstrated that producing acoustic flow by moving an array of speakers emitting white noise around a blind observer can induce postural instability (Stoffregen, Ito, Hove, Yank, & Bardy, 2010). This indicates that acoustic flow may be used to support postural control. Much like optic flow, acoustic flow can also induce vection or the illusory
perception of self-motion (see Väljamäe, 2009). Nevertheless, acoustic flow is not as compelling an indication of self-motion as optic flow. Most individuals can experience visually-induced vection and when they do, it is often indistinguishable from physical movement. Auditory vection gives rise to only a weak sensation of self-movement when it occurs (Väljamäe, 2009). Thus, it is not clear that acoustic flow plays a strong, independent role in the perception of self-motion in the way that optic flow does. However, there is evidence to suggest that auditory cues can augment the visual perception of self-motion. For instance, vection intensity is perceived to increase in the presence of congruent visual and auditory cues to self-motion compared to when only visual cues are available (Keshavarz, Hettinger, Vena, & Campos, 2014; Riecke, Schulte-Pelkum, Caniard, & Bulthoff, 2005; Riecke et al., 2008). This effect is most pronounced when the auditory cues that are provided are associated with self-motion in the real world (Larsson, Västfjäll, & Kleiner, 2004; Väljamäe, 2009). For instance, a clear example of a task in which observers associate auditory cues with self-motion is driving. Driving elicits a number of distinct auditory cues, including engine noise, tire noise, and wind turbulence. Because these sounds systematically increase in amplitude as the rate of travel increases, their intensity serves as a useful indication of speed (Merat & Jamson, 2011). Consequently, when auditory cues are not available, drivers travel faster than intended and become more variable in the speed that they maintain (Denjean, Roussarie, Kronland-Martinet, Ystad, & Velay, 2012; Hellier, Naweed, Walker, Husband, & Edworthy, 2011; Horswill & Plooy, 2008; Wang & Wang, 2012).

Unlike the visual and vestibular systems, comparatively less is known about the neural substrates underlying auditory self-motion perception. There has been much work to demonstrate that there are specific regions within and adjacent to the auditory cortex that specialize in detecting the motion of specific sound sources around an observer (e.g. Baumgart, Gaschler-Markefski, Woldorff, Heinze, & Scheich, 1999; Griffiths & Warren, 2002; Warren, Zielinski, Green, Rauschecker, & Griffiths, 2002). Warren and colleagues (2002) used a generic HRTF and headphones to simulate the movement of a single external sound changing in azimuth relative to the observer during Positron Emissions Tomography (PET) brain imaging in one experiment and during fMRI in another experiment (Warren et al., 2002). They demonstrated that the planum temporale (PT) was selectively activated by the simulated motion of a sound source to a greater extent than a stationary control stimulus or a control stimulus whose waveform was the mean of
the HRTF waveforms for both ears. Thus, the PT is thought to specialize in detecting the spectral and temporal changes that incoming sounds undergo as they move about the observer (Griffiths & Warren, 2002; Warren et al., 2002). However, it is not clear whether these neurons are in fact detecting motion or if they are merely sensitive to spatial changes (see Carlile & Leung, 2016). Moreover, it is not clear where or how the brain might utilize an entire field of dynamically changing cues to object position to make inferences about the movement of the self.

In summary, although multiple sensory systems are capable of conveying information about self-motion, no single sensory system is reliable across all possible behavioural and environmental circumstances in isolation. Because self-motion is often conveyed to by more than one sensory system simultaneously, these estimates can be combined to overcome the limitations associated with the individual sensory systems and to maintain an understanding of self-motion. That said, the availability of multiple, redundant estimates of self-motion not only allows observers to overcome instances in which information from one system or the other is broadly ineffective, the presence of congruent inputs also enables a more precise self-motion percept than that which could be achieved using any single sensory system in isolation (e.g., Butler et al., 2010; Fetsch et al., 2009). Having considered how each sensory system conveys self-motion, I will now consider behavioural and neurophysiological evidence to suggest that the independent estimates of self-motion provided by the individual sensory systems are integrated to optimize the precision of one’s self-motion percept. I will begin by providing a brief introduction to the general concept of optimal sensory integration.

2.1.2 Optimal integration during self-motion perception

2.1.2.1 What is optimal integration?

As previously discussed, the transduction and encoding of sensory information is subject to variability. Consequently, if an observer were to estimate the same environmental parameter repeatedly over many trials (e.g., the size of an unfamiliar object) using either the visual system (i.e., viewing the object) or the haptic system (i.e., grasping the object) in isolation of one another, the result would be a distribution of responses with some degree of variability (see Ernst, 2005; Ernst & Bülthoff, 2004). Some of this noise is due to the physical properties of the
environment. For instance, photons arrive at the retina in a stochastic fashion and thus the number of photons that are absorbed by any given area of the retina will vary over time (see Bialek, 1987; Faisal et al., 2008). Some of this noise is inherent to the nervous system. For example, the photoreceptors of the retina are subject to “dark noise” or spontaneous activity, even when no photons are absorbed (Bialek, 1987; Rieke & Baylor, 1998, 2000). Because a stimulus must surpass this baseline noise to be detected, dark noise is thought to limit human sensitivity to light under dark conditions (Bialek, 1987; Holcman & Korenbrot, 2005; Rieke & Baylor, 1998, 2000). Cortical neurons are also subject to noise because variability in their internal biochemical and electrophysiological processes can alter their responses on a trial-by-trial basis (see Faisal et al., 2008 for a review of neural noise). Furthermore, the initial state of an individual’s nervous system will be different each time a stimulus is encoded and this may also contribute to variability in the way that incoming sensory information is represented (Faisal et al., 2008). Consequently, if one were to present an observer with a specific visual stimulus (e.g., upward motion conveyed by a random dot display) while recording the firing rate of an individual cortical neuron that is tuned to respond to that particular stimulus (e.g., a neuron within the medial temporal cortex that responds preferentially to upward motion), repeatedly presenting the same stimulus would yield firing rates that vary on a trial-by-trial basis to form a distribution of possible responses (Churchland et al., 2011; Nienborg, Cohen, & Cumming, 2012; Snyder, Morais, & Smith, 2013).

Behavior is ultimately informed by internal representations of the environment and one’s position within it. Therefore, a representation that is noisy and uncertain could contribute to costly behavioural errors (see Munoz & Blumstein, 2012 for a review). For example, if instead of judging the size of an unknown object an observer is judging when and how quickly to cross the street to avoid being struck, unmitigated variability in their estimates of the rate of oncoming traffic, the width of the roadway, and/or their own walking speed and direction could have lethal consequences. One particular mechanism that plays a significant role insofar as allowing observers to mitigate the variability associated with individual sensory inputs is the nervous system’s capacity to integrate the redundant estimates provided by each sensory system to reduce the variability of perceptual estimates in a statistically optimal fashion (Ernst & Bülthoff, 2004).
From a computational perspective, there is accumulating evidence that the nervous system combines sensory estimates in a manner that is consistent with a Maximum Likelihood Estimation (MLE) model (Ernst, 2005; Ernst & Banks, 2002; Ernst & Bült Hoff, 2004). In the following sections, I will review what MLE is conceptually and how it applies to human multisensory perception. I will then consider behavioural evidence of optimal integration in the context of self-motion perception. Finally, I will consider the potential neural substrates of optimal integration as it relates to the perception of heading specifically.

### 2.1.2.2 Maximum Likelihood Estimation (MLE)

Generally speaking, MLE is a well-established inferential technique that is used in many science, technology, engineering, and mathematics applications as a method for estimating the true value of an unknown parameter, given a set of observations, while minimizing the variance associated with this estimate (Hamada, Wilson, Reese, & Martz, 2008; Myung, 2003). In the context of multisensory integration, maximum likelihood estimation was first applied to the estimation of visual-haptic object size (see Ernst, 2005; Ernst & Banks, 2002). When an observer is confronted with an unfamiliar object that they wish to grasp, they will have two independent estimates pertaining to the size of the object: a visual estimate and a haptic estimate. Due to sources of noise described above, each observation will differ and will have some level of associated variance. Nevertheless, the object has a true physical size and if the observer is to succeed in grasping the object, they must derive an estimate of object size that converges on this true value with the lowest level of variance possible. MLE dictates that this is achieved by taking the weighted average of the individual estimates, where the weights are proportional to their respective reliabilities or the inverse of their variances (see Ernst, 2005; Ernst & Banks, 2002).

To explain this in more practical terms, if the variance associated with a given estimate is conceptualized as perceptual uncertainty, the reliability of that estimate should be inversely proportional to its uncertainty. By weighting each estimate according to their reliabilities, this means that the observer is effectively attributing proportionally more weight the more reliable estimate (Ernst, Rohde, & van Dam, 2015). MLE then dictates that the reliability of the combined estimate is the sum of the unisensory reliabilities and therefore, the variance of the combined estimate is less than that associated with the component estimates. This is intuitive given that having multiple estimates of the same parameter, each with some level of associated
reliability, should generally serve to reduce perceptual uncertainty. The result is a combined estimate that is considered to be statistically “optimal” in that it represents the lowest variance and least biased estimate possible (Ernst, 2005; Ernst & Banks, 2002; Ernst & Bülthoff, 2004).

2.1.2.3 Behavioural evidence of optimal integration

Behavioural evidence of optimal integration has been observed in a number of different contexts including, but not limited to, visual-haptic integration as it relates to size estimation (Ernst & Banks, 2002), visual-auditory integration as it relates to speech perception (Alais & Burr, 2004), and visual-proprioceptive integration as it relates to body position (van Beers, Wolpert, & Haggard, 2002). More recently, there has been some emphasis on understanding how visual and vestibular estimates of self-motion are integrated to form a robust self-motion percept. Moreover, animal models of heading perception have also helped to elucidate the potential neural basis for optimal integration. Below I will review behavioural evidence of optimal integration as it relates to postural control and heading perception, followed by neurophysiological evidence of optimal integration.

2.1.2.4 Optimal multisensory integration for posture control

In order to maintain a stable posture, it is necessary to understand where one’s own center of mass (CoM) is relative to one’s base of support. No single sensory system encodes CoM directly and therefore, estimates of CoM must be derived from a combination of visual, vestibular, and proprioceptive input (Allison & Jeka, 2004). It has been proposed that the input from each of these sensory systems can be dynamically reweighted in order to achieve a stable posture, even under conditions of unreliable unisensory information pertaining to the position and/or orientation of the body in space (Assländer & Peterka, 2014; Bair, Kiemel, Jeka, & Clark, 2007; Nashner & Berthoz, 1978). This capacity can be demonstrated using a swinging room paradigm (see Lee & Aronson, 1974). When the walls of the room are moved around a standing observer, low-amplitude visual movements are thought to be interpreted by the brain as self-motion, as they generally lead to large compensatory postural adjustments. Conversely, high-amplitude visual movements are thought to be interpreted by the brain as the result of movement in the external environment, as they only have a small effect on the observer’s posture. This pattern of performance suggests that when necessary, visual cues to self-motion can be down-weighted to prevent them from undermining postural stability (see Carver, Kiemel, & Jeka, 2006; Keshner &
Kenyon, 2009). Dokka and colleagues (2010) formalized this dynamic weighting process by demonstrating that a Bayesian model of multisensory integration (see Ernst & Bülthoff, 2004) can be used to describe how an observer resolves the ambiguity surrounding whether visual motion arose due to the movement of the self or due to motion in the external environment. The observer will take into account the visual estimate and the vestibular estimates of self-motion, weighting each cue as a function of their respective reliabilities, as they would in the case of maximum likelihood estimation. In addition to the prevailing sensory information, the observer will also take into account a prior, or the probability that a given combination of visual and vestibular cues are due to self-motion or to the external environment based on previous experience (Ernst & Bülthoff, 2004; Körding et al., 2007). In the context of postural control, the prior dictates that external movement can be very fast (e.g., that of a passing car) but self-movements are comparatively slow. Consequently, the gain on visual input is 1:1 at low velocities, meaning that the postural response is equal in magnitude to the visual motion and increases in magnitude logarithmically with visual motion velocity. However, once the velocity exceeds 2.8 cm/s, visual input has little effect on posture because the visual motion is no longer attributed to the displacement of the body alone, but rather to the movement of external objects (Dokka, Kenyon, Keshner, & Kording, 2010). With respect to postural control specifically, it is not clear where this optimal weighting process occurs within the brain. However, parallel research on heading perception, or the process by which humans and non-human primates resolve the direction of self-motion, has provided behavioural evidence of optimal visual-vestibular integration and has also provided insight into the potential neural substrates of optimal visual-vestibular integration.

2.1.2.5 Optimal multisensory integration for heading perception
It has long been established that human observers utilize optic flow to extract information about self-motion, including their heading (Gibson, 1950; Warren & Wertheim, 1990; Warren et al., 1989; Warren & Hannon, 1988). Given that the vestibular system could detect linear (forward or backward) passive translation via the otoliths, Telford and colleagues (1995) hypothesized that humans are likely to receive information about their heading from both the visual system and the otoliths simultaneously. To test this hypothesis, they created a visual-vestibular heading perception task. Participants were seated on a cable-drawn cart and were passively translated
down a corridor via. The observers’ head and body were rotated relative to the axis of motion to create self-motion along different heading angles. Participants were fitted with a head-mounted display (HMD) that was fed by cameras mounted to their helmet that displayed the actual corridor. Wooden dowels were hung from the ceiling to create a dense optic flow field. The participants then had to indicate their heading angle using a pointer mounted to the cart. The task was performed under visual only conditions (passive translation below the vestibular threshold with the HMD active), vestibular conditions (supra-threshold translation without the HMD active), or with both cues combined. The task revealed that participants were in fact more precise at estimating their heading when both visual and vestibular cues were combined (see Telford, Howard, & Ohmi, 1995).

More recent work has built on this foundation by applying MLE techniques to demonstrate that visual and vestibular cues are combined in a statistically optimal fashion. Gu et al. (2008) trained macaques to perform a two-alternative-forced-choice task in which they were to discern whether their heading angle (i.e., their direction of self-motion) was to the left or to the right of center. Heading angle varied in increments ranging from ±0° to ±16°. The macaques received vestibular heading cues via forward translation on a motion platform (while seated), visual heading cues in the form of a visual optic flow stimulus presented on a display, or both cues presented simultaneously. Psychometric functions were fitted to the heading response data and the angle at which heading was correctly identified on 84% of trials was used as an index of the heading discrimination threshold (Gu et al., 2008; Wichmann & Hill, 2001). The results revealed that the macaques displayed increases in perceptual sensitivity, or decreases in the threshold at which they could reliably discern their heading correctly, when visual and vestibular inputs were combined. Critically, this gain in performance was consistent with maximum likelihood estimation. In other words, the heading detection threshold under bimodal conditions was lower than it was in either of the unimodal conditions and approximated the bimodal threshold predicted on the basis of the unimodal visual and vestibular inputs being weighted as a function of their respective reliabilities (Gu et al., 2008). Butler et al. (2010) used a similar heading discrimination paradigm to demonstrate that humans also exhibit optimal visual-vestibular integration. This variant utilized a two-interval, forced-choice paradigm in which the observer was asked to determine which of two consecutive movements was “more rightward” than the
other. Unimodal heading discrimination thresholds were used to establish a prediction of the reliability and theoretical weights for each cue. A bimodal condition consisting of congruent visual and vestibular cues was then used to determine whether there was an optimal reduction in perceptual variance associated with the presence of both cues. Finally, a bimodal condition consisting of conflicting cues (disparate visual and vestibular heading angles) was used to determine which cue took more weight in the final percept, and whether the unimodal inputs were being weighted according to their respective reliabilities. The results revealed that for humans, bimodal heading discrimination thresholds were significantly lower than unimodal heading discrimination thresholds. Moreover, the heading percept during the cue conflict condition was consistent with the visual and vestibular cues being weighted as a function of their respective reliabilities (Butler et al., 2010).

2.1.2.6 Neural substrates of optimal heading perception
In addition to providing strong behavioural evidence of optimal visual-vestibular integration, the macaque heading perception paradigm has also been implemented while obtaining single cell recordings of neurons within the dorsal medial superior temporal cortex (MSTd) to elucidate the neural substrates of optimal integration. The MSTd has long been implicated in mediating the perception of self-motion, given that it contains neurons that respond to visual motion cues (i.e., optic flow; Duffy & Wurtz, 1991a, 1991b) and to vestibular motion cues (i.e., physical motion in darkened environments; Bremmer et al., 1999). It has also been established that MSTd neurons encode heading specifically, as their response to optic flow stimuli is mediated by the location of the focus of expansion (Bradley, Maxwell, Andersen, Banks, & Shenoy, 1996; Duffy & Wurtz, 1995; Page & Duffy, 2003) and their response to physical translation is mediated by the vector of acceleration (Bremmer et al., 1999; Gu, DeAngelis, & Angelaki, 2007; Gu et al., 2006; Page & Duffy, 2003). More importantly, recent work has demonstrated that MSTd neurons integrate visual and vestibular heading cues in an optimal fashion. There are two primary variants of MSTd neurons: (i) incongruent cells that respond preferentially to nearly opposite visual and vestibular cues to heading and (ii) congruent cells that respond most vigorously to nearly matching visual and vestibular cues (Duffy, 1998; Gu et al., 2006). A given congruent cell may be tuned to respond most vigorously to a specific visual heading angle (e.g., ~21 degrees) and to a given vestibular heading angle (e.g., ~25 degrees). However, the MSTd neuron’s response will
dynamically shift toward the more reliable of the two inputs. For instance, when the optic flow cues are highly reliable (100% coherent), the response of the multimodal neuron is dominated by its visual heading preference. However, as the reliability of the visual input is degraded (i.e., the coherence or the total portion of the visual scene conveying the same heading is reduced to 50% or to 25%), the multimodal neuron’s response shift to align with its vestibular heading preference (see Morgan et al., 2008). This shift reflects the optimal integration of visual and vestibular inputs as 90% of the variance in the response of the MSTd neuron can be predicted by the linear summation of the unimodal responses weighted as a function of unisensory reliability (Angelaki, Gu, & DeAngelis, 2009). In other words, the MSTd neurons apply more weight to the more reliable of the two cues, maximizing the reliability of the final percept.

A prominent theory as to how the nervous system encodes the reliability associated with each sensory estimate is that it utilizes Probabilistic Population Coding (PPC, see Knill & Pouget, 2004; Ma, Beck, Latham, & Pouget, 2006). Under the PPC hypothesis, there are populations of unimodal visual and vestibular neurons and each neuron has a specific set of stimulus preferences that can be described by a Gaussian tuning curve. Each neuron is maximally sensitive (i.e., fires most vigorously) to optic flow conveying a specific heading angle and their sensitivity tapers off as the heading angle becomes increasingly disparate from its specific heading preference. Together, the entire population of unimodal neurons and their respective tuning curves represent all possible heading angles. In theory, if an experimenter was to present an observer with optic flow conveying a specific heading angle (e.g., via an HMD), and if they were to record and plot the firing rates of the entire population of neurons ranked in order of their heading preferences, they would observe a peak that centers on the neurons tuned to the heading angle of the visual stimulus and rapidly diminishing responses from adjacent neurons with increasingly disparate heading preferences. The overall result would be a Poisson-like distribution in which the mean of the distribution centers on the heading angle of the visual stimulus and where the variance is inversely proportionate to the amplitude of the peak response (see Knill & Pouget, 2004; Ma et al., 2006 for review). Therefore, the nervous system does not merely encode sensory estimates, it encodes distributions of responses that can be used to infer the most likely value of a given stimulus (i.e., the mean) and the associated reliability (i.e., the inverse of the variance) (Ma et al., 2006; Pouget, Beck, Ma, & Latham, 2013). One hypothesis as
to how the nervous system may perform optimal integration is that it may combine multiple population probability codes. Neural network modelling has been used to demonstrate that if the visual and vestibular population probability codes are combined by taking the sum of each code on a neuron by neuron basis, the result is a multisensory population probability code whose mean and variance are equivalent to those that would predicted by maximum likelihood estimation (Ma et al., 2006). Several different coding schemes have been described and therefore, further research is necessary to elucidate precisely which coding formats the nervous system utilizes (see Pouget et al., 2013 for review). However, the precise substrates of neural probability encoding notwithstanding, there is some evidence to suggest that there is a link between optimal integration at the neural level and optimal visual-vestibular integration as it is observed at the behavioural level.

There has long been evidence of a causal link between the responses of MSTd neurons and self-motion perception. For example, direct micro-stimulation of individual MSTd neurons systematically biases perceptual estimates of heading angle derived from an optic flow stimulus (e.g., Britten & van Wezel, 1998). Moreover, the ablation of the vestibular organs (i.e., labyrinthectomy) has been shown to abolish area MSTd’s response to physical translation, increasing heading perception thresholds (Gu et al., 2007). Similarly, the chemical inhibition of the MSTd increases the threshold at which differences in heading can be discerned (Gu et al., 2012). However, there is also evidence of a specific link between optimal integration at the level of the individual neuron and optimal visual-vestibular heading perception at the behavioural level. To determine how MSTd responses could account for optimal integration at the behavioural level, Fetsch and colleagues (2013) fitted psychometric functions to the neurophysiological data (i.e., firing rates) using the neuronal heading detection threshold and the point of subjective equality as the standard deviation and mean of the distributions, respectively. Using this simulation model, they observed a very similar dynamic reweighting process to that which has been observed in the behavioural heading discrimination data (Fetsch, DeAngelis, & Angelaki, 2013). Thus, research on heading perception has helped to reveal a plausible neural substrate for optimal integration observed at the behavioural level in the context of self-motion perception.
The role that multisensory integration plays in supporting reliable self-motion perception is becoming better understood, however, current knowledge is largely derived from research on younger adults and animal models of self-motion perception. In the following sections, I turn my attention to older adults and to the effect that aging has on the capacity to perform tasks involving self-motion.

2.2 Aging and self-motion perception

2.2.1 Overview

The mechanisms by which younger adults and non-human primates derive a reliable self-motion percept are becoming better understood. However, far less is currently known about how multisensory self-motion perception changes in adulthood and whether older adults integrate multisensory cues to self-motion in the same way that younger adults do. A rich and vast collection of empirical studies have demonstrated that older adults (65+ years of age), on average, exhibit broad declines in their performance on tasks involving self-motion. For example, older adults are prone to instability while standing and walking (e.g., Hausdorff et al., 2001; Horak, Shupert, & Mirka, 1989; Prince, Corriveau, Hébert, & Winter, 1997; Tinetti, Speechley, & Ginter, 1988). Among adults over the age of 70, up to 35% display some degree of gait abnormality, ranging in severity from unsteadiness or variable gait patterns to a tendency to lose balance outright (Verghese et al., 2006). It is estimated that 28% to 35% of adults over the age of 64 sustain a fall each year (Yoshida, 2007). In the context of driving, adults over age 60 are more likely to be involved in multi-vehicle collisions than all other groups of drivers, save for teenage, novice drivers (Hakamies-Blomqvist, 1993; Langford & Koppel, 2006) and have higher collision rates per kilometer travelled than all but teenage, novice drivers (Eberhard, 2008). Ultimately, both the risk of sustaining a fall and the risk of having a car accident represent major public health concerns. For those over the age 65 years, falls are the leading cause of accidental injury (Kannus, Sievänen, Palvanen, Järvinen, & Parkkari, 2005). Because of their physical frailty, older adults over age 65 are more likely than younger adults to sustain serious injuries from vehicle collisions (see Braver & Trempel, 2004; Li, Braver, & Chen, 2003). Once a fall or a collision has occurred, physical injury and/or the fear of being involved in future incidents can lead to activity restrictions that result in social isolation, a loss of independence,
and the deterioration of both physical and mental health (see Webber, Porter, & Menec, 2010 for review). Therefore, there is a clear need to understand the antecedents of age-related changes in performance on mobility-related tasks. While there are comprehensive bodies of literature that have considered the musculoskeletal, cardiopulmonary, and cognitive factors that influence older adults’ ability to perform mobility-related tasks, relatively little work has been done to explicitly characterize age-related changes in the perception of self-motion specifically.

It is well established that aging is typically associated with declines in the functioning of the individual sensory systems (e.g., declines in visual acuity or vestibular sensitivity), which may affect older adults’ capacity to detect specific self-motion parameters. These individual, modality-specific declines are where most of the research attention has focused when considering age-related changes in self-motion perception. Therefore, in the following sections, I will briefly present representative examples of work examining unisensory declines and the resultant age-related differences in the capacity to detect self-motion using each sensory system in isolation. I will then consider the need to examine age-related differences in terms of multisensory integration during self-motion perception.

### 2.2.2 Aging and visual self-motion perception

Aging is accompanied by broad changes in visual function that have important implications for performance on tasks involving self-motion. Within the eye, the iris becomes weaker with age, which can lead to the constriction of the pupil. Miosis is problematic under scotopic conditions where it can impair contrast sensitivity by broadly reducing retinal luminance (see Owsley, 2011 for a review). There are also important changes in the primary visual cortex that lead to reduced contrast sensitivity. For example, neurons within the primary visual cortex of senescent monkeys are less sensitive to contrast than those in younger monkeys (e.g., Zhang et al., 2008). Reduced contrast sensitivity has been linked to an increased risk of falls as it may impair the ability to detect changes in the position and orientation of one’s own body relative to the physical environment, and/or to detect and avoid obstacles such as potential tripping hazards (e.g., Lord, Clark, & Webster, 1991; Owen, 1985). Reduced contrast sensitivity may also be problematic during tasks such as nighttime driving because speed estimation is contrast dependent (e.g., Thompson, 1982). For instance, reducing the contrast of a visual scene during driving by
introducing fog in a driving simulator or by applying diffusing filters to the windows of a real vehicle can reduce perceived speed, which can lead drivers to travel faster than they would under high visibility conditions (e.g., Owens, Wood, & Carberry, 2010; Snowden, Stimpson, & Ruddle, 1998). Reduced contrast sensitivity may also impair older adults’ ability to detect and to avoid low contrast obstacles such as potholes, speed bumps, road debris, and pedestrians (e.g., Wood, Garth, Grounds, McKay, & Mulvahil, 2003). Additionally, the optic media, including the cornea and the lens, lose clarity with advancing age and this can contribute to the scattering of light within the eye (Elliott, Bullimore, Patla, & Whitaker, 1996). This stray light can broadly reduce retinal image contrast, creating a glare effect. This phenomenon is also problematic during tasks like night driving where the light emitted by the headlamps of oncoming vehicles, particularly high-intensity headlamps, can lead to blinding glare (Elliott et al., 1996; Mainster & Timberlake, 2003). The retina undergoes important changes as well. The overall density of photoreceptors and retinal ganglia decreases, as does the density of the retinal pigment epithelium (RPE). RPE cell loss, in particular, may compound older adults’ increased glare sensitivity by impairing the normal cycle of photopigment bleaching and regeneration, thereby increasing the amount of time required to recover normal contrast sensitivity following exposure to glare (Jackson, Owsley, & McGwin, 1999; Schieber, 1994).

There are also important age-related changes in the way that visual information is processed. Older adults tend to require more time than younger adults to detect and to identify visual targets, particularly in the presence of distractors or when they are required to spread their attention over different areas of the visual field (Owsley, 2011). Deficits in visual processing speed and divided attention are both associated with an elevated risk of collisions while driving (Owsley et al., 1998). Critically, older adults can also exhibit deficits that are specific to the visual perception of self-motion. For example, older adults are less precise than younger adults by 1 degree when using optic flow to judge whether their heading is to the left of to the right of a stationary target (Warren et al., 1989) and they are also less precise than younger adults when estimating absolute heading angle (Lich & Bremmer, 2014). Furthermore, there is evidence to suggest that older adults are impaired in their capacity to perceive optic flow. Specifically, they require a higher level of visual motion coherence to discern the direction of simulated self-motion on the basis of optic flow and they are thereby impaired in their capacity to discern
heading when non-coherent motion is added to the flow field (Atchley & Andersen, 1998; Kavcic, Fernandez, Logan, & Duffy, 2006; Kavcic, Vaughn, & Duffy, 2011; Snowden & Kavanagh, 2006; Tetewsky & Duffy, 1999). This may be consequential to the way that older adults perform real-world tasks that involve extensive object motion, such as walking through a densely-crowded environment, as this type of environment would effectively reduce the overall coherence of the available optic flow information.

One hypothesis as to why optic flow perception and the ability to estimate self-motion parameters such as heading diminishes in older age is that the perception of global patterns of visual information may be impaired by more general age-related visual impairments (e.g., impaired contrast sensitivity). Allen and colleagues (2010) presented older and younger adults with an optic flow stimulus comprised of a field of radially expanding dots. They manipulated both the coherence of the optic flow (the total portion of dots conveying flowing radially outward vs. those moving in random directions) and the contrast of the dots within the visual display. Participants were then asked to discriminate between inward and outward expansion. They found that at low levels of contrast, older adults required a higher level of coherence to discriminate the direction of motion compared to younger adults (Allen, Hutchinson, Ledgeway, & Gayle, 2010). They attribute older adults’ need for higher contrast levels to the decreased signal to noise ratio in the primary visual cortex described above. Due to deficits in terms of cortical inhibition (e.g., changes in acetylcholine regulation and diminished GABA levels; Leventhal, Wang, Pu, Zhou, & Ma, 2003), neurons in the primary visual cortex are less selective in their responses and show more spontaneous activity and thus higher levels of contrast may be necessary to overcome increased baseline noise (Allen et al., 2010; Falkenberg & Bex, 2007; Liang et al., 2010; Yang et al., 2009). However, other studies have indicated that deficits in optic flow perception are the result of selective declines in the neural mechanisms mediating self-motion perception. For example, experimentally degrading the visual acuity of younger observers does not affect heading discrimination, suggesting that optical factors do not play a significant role (Ball & Sekuler, 1986). Moreover, manipulating the coherence associated with large-field visual motion affects older adults’ ability to discern heading direction using optic flow (i.e., a field of dots expanding or contracting in a radial fashion), but does not affect their ability to discern the direction of horizontal motion (i.e., a field of dots travelling from the left...
side to the right side of the display; e.g., Kavcic et al., 2011). Others have shown that different forms of motion perception such as biological motion perception (i.e., the identification of point-light walker embedded in a field of dots) can be relatively spared whereas the perception of large-field visual motion (e.g., horizontal motion) declines (Billino, Bremmer, & Gegenfurtner, 2008). Together these observations suggest that aging leads to specific impairments to the perception of large-field visual motion that cannot be explained by general visual declines alone.

Deficits in terms of optic flow perception may be linked directly to the decline of the MST. It has been demonstrated that the neurons within the MST region that are tuned to respond to specific heading angles are less selective with respect to visual heading angle in elderly rhesus monkeys than they are in young monkeys (Liang et al., 2010). In humans, electrophysiological studies have shown that optic flow elicits distinct event-related potentials in the extra-striate visual cortices, but that these responses are different in older adults (Fernandez, Monacelli, & Duffy, 2013; Kavcic et al., 2006). Moreover, Lich & Bremmer (2014) used a neural network model to demonstrate that increased visual heading perception thresholds could also be tied directly to normal age-related cell loss in MST (Lich & Bremmer, 2014).

### 2.2.3 Aging and vestibular self-motion perception

During normal healthy aging, the density of the hair cells within the vestibular organs declines. It is estimated that the saccule and utricle incur a 25% loss of hair cells and that the semicircular canals incur a 40% loss of hair cells by 75 years of age (see Matheson, Darlington, & Smith, 1999). While the mechanisms underlying hair cell loss remain unclear, hair cell loss is believed to cultivate broad declines in sensitivity to gravitational and linear acceleration (see Anson & Jeka, 2016). One of the major effects associated with the loss of vestibular sensitivity is an impaired in vestibulo-ocular reflex (VOR). The VOR refers to the reflexive counter-rotation of the eyes that occurs in response to the rotation of the head (see Fetter, 2007 for review). The VOR enables observers to maintain a stable retinal image during head movements, including those induced by tasks involving self-motion, like walking (Grossman, Leigh, Bruce, Huebner, & Lanska, 1989). Compared to younger adults, older adults tend to have VORs that are smaller in amplitude (e.g., Peterka, Black, & Schoenhoff, 1989) and that are comparatively delayed relative to the onset of head movements (Hirvonen, Aalto, Pyykkö, Juhola, & Jäntti, 1997).
Consequently, older adults have difficulty maintaining a stable gaze during movement. This can in turn manifest as decreased dynamic visual acuity (i.e., visual acuity tested under conditions where the head is moving; Demer, Honrubia, & Baloh, 1994; Honaker & Shepard, 2011). Diminished visual acuity during walking is thought to contribute to postural instability and an increased risk of falls (see Anson & Jeka, 2016; Zalewski, 2015 for reviews). Most pertinent to the current research, a loss of vestibular sensitivity is also thought to impair the capacity to detect passive self-motion. Adults over 50 years of age require a higher rate of acceleration to perceive the direction of passive self-motion (i.e., anterior-posterior translation and medial-lateral translation) performed in total darkness (Roditi & Crane, 2012). Recent work has also demonstrated that older adults have higher thresholds for the detection of passive 1-Hz rotations than younger adults, but not for simulated 1-Hz rotation induced via electrostimulation, where older adults are more sensitive than younger adults (Peters, Blouin, Dalton, & Inglis, 2016). This pattern of performance may indicate that declines in vestibular function stem from peripheral vestibular loss, while central vestibular processing may in fact be enhanced in older adults to compensate for peripheral loss (Peters, Blouin, Dalton, & Inglis, 2016). However, there is also evidence to suggest that central vestibular processing may decline as well. Older adults exhibit decreased functional connectivity in vestibular cortical regions (Cyran, Boegle, Stephan, Dieterich, & Glasauer, 2016) and atrophy in the hippocampus and temporo-parietal junction (TPJ), which are both thought to play an important role is transforming vestibular cues into spatial representations. The TPJ in particular has been implicated in the spatial disorientation experienced by older adults with dementia (see Arshad & Seemungal, 2016; Kaski et al., 2016).

### 2.2.4 Aging and proprioceptive self-motion perception

There is evidence to suggest that proprioceptive sensitivity also diminishes in late adulthood. For example, older adults tend to have a diminished sense of joint position as they exhibit nearly double the error of younger adults in estimating the angle of their ankles (Xu, Hong, & Chan, 2004) and are less precise when attempting to reproduce passive positioning of the knee (Ribeiro & Oliveira, 2007). Declines in muscle spindle sensitivity also reduce the capacity to detect changes in muscle length (Ribeiro & Oliveira, 2007). The capacity to detect the position and orientation of the lower limbs is paramount to the control of balance and to maintaining a stable posture. Thus, diminished proprioceptive function has been implicated as an antecedent to falls
in older adults (see Suetterlin & Sayer, 2013). The muscles of the neck are thought to play a particularly important role in self-motion perception (see Pettorossi & Schieppati, 2014). Due to their high spindle density, neck muscles are highly sensitive to changes in the orientation of the head, including those that arise during self-motion. The contribution that neck proprioception makes to self-motion perception is illustrated by research showing that stimulating the spindles via neck muscle vibration can alter the perceived magnitude of passive whole-body rotation (Panichi et al., 2011). There is some evidence to suggest that neck proprioception may be comparatively robust to age-related decline and may thereby help older adults to compensate for declines in vestibular self-motion perception (Schweigart, Chien, & Mergner, 2002). There has also been some work to suggest that compared to younger adults, older adults may be more reliant on proprioceptive cues than on visual and vestibular cues to control their posture. For example, Weismeier and colleagues (2015) compared older and younger adults in terms of their postural response while standing on a support surface that would tilt up to 0.5° or 1° anterior-posterior in a pseudorandom fashion. This procedure was repeated with eyes open and with eyes closed and the relationship between the angle of the support surface and the amplitude of body movement at the shoulders was used as an index of the gain on proprioceptive input. Both age groups increased the gain on proprioceptive input in the absence of visual cues to body orientation, but older adults displayed higher gains on proprioceptive input than younger adults in both eyes open and eyes closed conditions. This suggests that older adults may utilize proprioceptive input to alter their postural response to their support surface to a greater extent than younger adults (Wiesmeier, Dalin, & Maurer, 2015).

2.2.5 Aging and auditory self-motion perception

As discussed above, the auditory system provides several cues to the position of sound sources within the environment, including ITDs and ILDs associated with the HRTF. During self-motion, dynamic changes in each of these signals are thought to create a pattern of auditory information called acoustic flow that can, in turn, be used to make inferences about one’s own movement, analogous to the way that optic flow is used to make inferences about the parameters of self-motion. However, there is evidence to indicate that age-related hearing loss (ARHL) limits older adults’ sensitivity to ITDs and ILDs. In this section, I will consider the factors that
lead to ARHL, how ARHL affects auditory localization, and how ARHL may impact self-motion perception.

In the healthy ear, incoming sounds cause the basilar membrane to vibrate passively, creating a shearing motion against the overlying, stationary tectorial membrane. This movement deflects the outer hair cells (OHCs) of the basilar membrane, causing mechanically-gated ion channels to open and to allow an influx of positively charged ions from the endolymph-filled extracellular space within the cochlea (see Oghalai, 2004 for review). Because the endolymph maintains a relatively high resting potential of 80 mV (known as the Endocochlear potential or EP), and because the OHCs maintain a relatively large negative intracellular potential of -40 mV, this influx of positively charged ions causes the OHCs to depolarize (Oghalai, 2004). The OHCs are electromotile, which means that they behave as a form of piezoelectric device (Spector, Brownell, & Popel, 2003). When they depolarize, they change length rapidly and in doing so, they amplify the natural vibration of the basilar membrane. This mechanism is known as the cochlear amplifier and it is thought to greatly increase the sensitivity and frequency selectivity of human hearing (Oghalai, 2004). However, with advancing age, there are changes in the vasculature of stria vascularis, the capillary-rich lateral wall of the cochlea (see Shi, 2011). The blood supply to the stria vascularis diminishes and the stria vascularis begins to atrophy (Shi, 2011; Suzuki et al., 2006). Because the stria vascularis plays an important role in maintaining the EP, the atrophy of the stria vascularis causes the EP to diminish (Nin et al., 2016; Quraishi & Raphael, 2008). This loss of voltage is thought to diminish the cochlear amplifier, resulting in what is known as metabolic hearing loss or strial hearing loss (see Gates & Mills, 2005 for a review). Metabolic hearing loss can lead to diminished hearing across all frequencies but generally begins with a loss of hearing at high frequencies that eventually progress to lower frequencies (Gates & Mills, 2005; Schmiedt, 2010). It is this pattern of hearing loss that carries important implications for sound localization, and ultimately for self-motion perception. ILDs to sound location are most prominent among higher frequency sounds, whose short wavelengths cause them to be more heavily diffracted by the head and pinna. Thus, for older adults with high-frequency audiometric threshold loss due to metabolic ARHL, and/or OHC damage, a diminished sensitivity to high frequencies means that they will lose access to ILDs as a cue to the location of sounds within the environment (Akeroyd, 2014; Brimijoin & Akeroyd, 2016). With
reduced access to spatial auditory cues, older adults with high-frequency hearing loss may, in turn, become limited in their capacity to detect dynamic changes in their own position within the environment. For instance, spatial auditory cues play an important role in augmenting postural control (e.g., Vitkovic et al., 2016) and recent work has shown that ARHL may contribute to postural instability (e.g., Vitovik et al., 2016) and to an increased the risk of falling (Lin & Ferrucci, 2012; Viljanen et al., 2009; Vitkovic et al., 2016).

Elevated high-frequency audiometric thresholds alone are not necessarily a strong predictor of sound localization performance. That is because independent of peripheral sources of ARHL, such as metabolic ARHL, older adults can also suffer from central deficits in terms of auditory temporal processing that in turn limit their capacity to detect ITDs (see Freigang, Richter, Rübsamen, & Ludwig, 2015 for review). For instance, it has been demonstrated that compared to younger adults, older adults have higher thresholds for detecting ITDs (Strouse, Ashmead, Ohde, & Grantham, 1998), requiring up to twice the time delay that younger adults do in order to successfully localize the source of a sound (e.g., Herman, Warren, & Wagener, 1977). Moreover, when older adults are asked to localize narrow-band, lower frequency sounds that are relevant to ITDs (1,250 Hz to 1,575 Hz) in horizontal space, they are less precise than younger adults (Dobreva, O’Neill, & Paige, 2011). Age-related changes in auditory temporal processing and the sensitivity to ITDs could be related to changes in the overall rate at which auditory information is transmitted. This could be tied to an age-related decline in the number of spiral ganglia and/or nerve demyelination, both of which could affect transmission speed and integrity (see Freigang et al., 2015; Rance, 2005 for reviews). There may also be age-related changes in neural synchrony at different levels of the auditory system (see Pichora-Fuller, Alain, & Schneider, 2017 for review). For example, in the auditory nerve and in the brain stem, neurons engage in phase locking wherein neurons fire in phase (i.e., time-locked) with the features of incoming sounds. Andersen and colleagues (2012) submitted both older and younger adults to an electroencephalogram to record the auditory brainstem response elicited by the speech syllable /da/, given that this particular syllable is known to elicit a robust brainstem response. The syllable /da/ was presented at 80 dB repeatedly at a rate of 31.4 Hz. Results demonstrated that older adults had delayed and less consistent brain stem responses compared to younger adults. Moreover, phase locking power (i.e., response amplitude) was smaller in older adults than it was
in younger adults (Anderson, Parbery-Clark, White-Schwoch, & Kraus, 2012). Thus, the neural response to incoming auditory signals is less precise in older adults than it is in younger adults. There may be an increase in temporal jitter (Pichora-Fuller, Schneider, MacDonald, Pass, & Brown, 2007; Pichora-Fuller & Schneider, 1991, 1992) or variability in terms of the precision with which the brain encodes the temporal structure of incoming sounds (see Wang et al., 2012). Diminished neural synchrony could, in turn, undermine the reliability with which ITDs represent the spatial location of sound sources. This may be particularly problematic in noisy environments where ITDs are normally used to help parse different sound sources (Strouse et al., 1998).

It is important to note that an additional effect of ARHL may be that the resulting degradation of the quality of the incoming auditory signals leads to more effortful listening (see Pichora-Fuller, 2003; Pichora-Fuller & Singh, 2006 for reviews). Older adults may be forced to reallocate limited cognitive resources toward trying to disambiguate degraded auditory input, which then detracts from the resources that are available to perform other tasks (see Tun, McCoy, & Wingfield, 2009 for review). In the context of driving, ARHL can lead to diminished driving performance (e.g., diminished hazard perception and road sign recognition) when the driver is engaged in either a secondary auditory task (e.g., verbalizing the sum of pairs of digits presented auditorily) or a secondary visual task (e.g., verbalizing the sum of pairs of numbers presented over an in-vehicle display) (Hickson, Wood, Chaparro, Lacherez, & Marszalek, 2010). This may be because of the overhead cognitive resources necessary to perform the auditory task detract from the spare cognitive resources that would otherwise be free to perform the primary task of driving (Hickson et al., 2010).

In summary, there is ample evidence to indicate that the manner in which each sensory system conveys self-motion changes in old age. There is also evidence to indicate that sensory declines are associated with declines in cognition. For instance, older adults with Alzheimer’s disease often display impaired visual cognition (e.g., poor face discrimination, picture naming, etc.) but these deficits can be ameliorated by increasing image contrast. Increasing image contrast can promote near-normal visual cognition even among those who do not display clinically significant impairments in terms of visual acuity, cataracts, glaucoma, macular degeneration, etc. (see Albers et al., 2015 for a review). However, as discussed, most natural
forms of self-motion typically innervate multiple sensory systems simultaneously and-younger adults (and non-human primates) are known to achieve a robust self-motion percept by combining estimates of self-motion from across their sensory systems (e.g., Butler et al., 2010; Fetsch et al., 2009). Therefore, examining declines in the ability of individual sensory systems to convey self-motion in isolation of one another is not necessarily an ecologically valid representation of self-motion as it occurs during every day mobility-related tasks (see Campos & Bülthoff, 2012). In the context of simple stimulus detection and discrimination tasks, there is evidence to suggest that multisensory integration is heightened in older adults. For instance, when comparing reaction times to unimodal stimuli alone (e.g., visual only or auditory only), observers are slower than when both stimuli are presented together; however, older adults demonstrate a proportionally greater reaction time benefit under combined cue conditions (Laurienti et al., 2006; Mahoney, Li, Oh-Park, Verghese, & Holtzer, 2011; Peiffer et al., 2007). While these results demonstrate that there are performance benefits associated with heightened integration, heightened integration can also lead to performance decrements. Specifically, when multiple cues are presented simultaneously but one cue or the other contains information that is in conflict with or irrelevant to the task at hand, heightened integration can lead to negative performance outcomes (see Mozolic et al., 2012). There is also evidence to indicate that older adults may differ from younger adults in terms of how they weight sensory inputs relative to one another. Specifically, it has been demonstrated that older adults are more susceptible to performance declines when one modality or the other contains unreliable cues (e.g., Deshpande & Patla, 2007; Jeka, Allison, & Kiemel, 2010). Given that research on younger adults and animals has shown that robust and precise self-motion perception is contingent upon the capacity to combine redundant cues and to weight them as a function of their respective reliabilities, age-related changes in these mechanisms could have a significant effect on the way that older adults perceive their own movement. In the following sections, I will summarize evidence of age-related differences in the effect of multisensory cue combinations and in relative cue weighting and their potential neural substrates. I will then consider the consequences that these changes may have for self-motion perception. Finally, I will summarize gaps in current knowledge and the rationale for the series of experiments presented in this thesis.
2.3 Age-related differences in multisensory integration

Evidence of age-related differences in multisensory integration is largely derived from research examining age-related differences in performance on simple stimulus detection and stimulus discrimination tasks. Early behavioural research on multisensory integration is built within a framework that reflects the dynamics of multimodal neurons within the superior colliculus that integrate visual and auditory inputs to maximize their saliency. Therefore, it is necessary to briefly review this framework to provide the foundation necessary to conceptualize evidence of age-related differences in multisensory integration. I will begin by reviewing multisensory integration as it occurs within the superior colliculus and the behavioural manifestation of visual-auditory integration. I will then consider behavioural evidence of age-related changes in multisensory integration and leading theories as to the potential antecedents. First, I will consider how the decline of the individual sensory systems may cultivate compensatory multisensory responses. I will then consider the potential cognitive antecedents, including how age-related changes associated with the regulation of the default mode network may impact the way that sensory information is processed (Grady, Springer, Hongwanishkul, McIntosh, & Winocur, 2006), and how more generalized compensatory mechanisms such as the posterior-anterior shift with aging (PASA) may also lead to compensatory multisensory responses.

The superior colliculus mediates the capacity to detect and orient gaze toward salient external events. To this end, many of the neurons within the superior colliculus are sensitive to both visual and auditory inputs. The seminal work of Meredith and Stein (Meredith, Nemitz, & Stein, 1987; Meredith & Stein, 1986) used these neurons as a model by which to explore how individual neurons may serve to integrate cross-modal inputs in order to form a cogent, unitary percept. Using single-cell recordings, they established a series of guiding principles with respect to the function of multimodal neurons. Firstly, they observed that these neurons are tuned such that they are maximally sensitive to visual and auditory signals that are closely aligned in both time (Temporal Rule of integration) and in physical space (Spatial Rule of integration). These criteria are only likely to be met if the signals were caused by the same underlying event. Moreover, when the available visual and auditory signals are spatially and temporally congruent, the response of the multimodal neuron is highly vigorous (i.e., more spikes per second). This response can be super-additive, which is to say that they can be greater than the response that
would be predicted by the linear combination of the unisensory response rates. Thus, it is inferred that multimodal neurons only combine cross-modal signals that are causally related and that they will bolster the saliency of these events when they do occur (Krueger, Royal, Fister, & Wallace, 2009; Meredith et al., 1987; Meredith & Stein, 1986; Wallace, Meredith, & Stein, 1998). Another important tenet that has been established is the Principle of Inverse Effectiveness (PIE). Meredith and Stein (1986) observed that the most pronounced cross-modal signal enhancements occurred when the available visual and auditory signals were weak or were of limited efficacy (i.e., evoked only a low firing rate) in isolation (Meredith et al., 1987). Meredith and colleagues inferred that multimodal neurons maximize the salience of multisensory events when those events are only faintly detectable. Together these functions are thought to have conferred immense survival benefits during the era of evolutionary adaptation. Many events and objects that are important to human survival are conveyed by both visual and auditory signals (e.g., prospective mates, dangerous opponents, or potential predators). However, the reliability of these signals may vary widely depending on the prevailing environmental and behavioural circumstances. The cost of failing to detect such biologically significant events is perhaps far greater than the cost associated with false alarms. Thus selection pressures may have given rise to multimodal neurons within the superior colliculus that maximize the salience of biologically significant events, particularly when the constituent signals are weak, in order to minimize the costly possibility of failing to detect them (Munoz & Blumstein, 2012; Stein, Stanford, & Rowland, 2014).

At the behavioural level, stimulus detection tasks reveal a pattern of multisensory performance enhancement that is a close analog to the signal enhancements observed at the level of the individual neuron (Stanford & Stein, 2007). Healthy younger adults can identify events comprised of both visual and auditory cues faster and more precisely than they can detect either cue in isolation (e.g., Molholm et al., 2002; Molholm, Ritter, Javitt, & Foxe, 2004). Moreover, consistent with PIE, performance enhancements are even greater when the efficacy of the sensory inputs that are provided is diminished (i.e., when they are presented at an intensity that is close to their absolute detection threshold; Diederich & Colonius, 2004; Stanford & Stein, 2007). However, there is evidence to suggest that these same principles may lead to different performance outcomes in older adults. To illustrate, Laurienti et al. (2006) employed a forced choice discrimination task in which it was revealed that when congruent visual and auditory
stimuli were available (e.g., a red disk paired with the verbalized word “red”), both younger and older adults responded more quickly and more accurately than they could to either cue in isolation. Critically, they observed that the performance gains were greater among older adults than they were among younger adults. The observed age-related differences in performance could not be attributed to age-related differences in unisensory perceptual ability alone, as older adults were not different from younger in terms of the speed and accuracy with which they detected the visual or auditory cues in isolation of one another. Age-related differences in performance only emerged when both visual and auditory cues were available at the same time (Laurienti et al., 2006). Thus, Laurienti and colleagues inferred that age-related differences in performance may be driven by PIE. Given that aging is accompanied by declining unisensory abilities, including both vision (see Blanks & Dorrey, 2009; Owsley, 2011 for reviews) and hearing (see Pichora-Fuller et al., 2017 for review), the unimodal signals that older adults receive may be inherently weaker or less effective than those received by younger adults. As dictated by PIE, weaker unisensory signals should trigger a heightened multimodal response, which may then manifest as larger multisensory gains in stimulus detection speed and precision for older adults than for younger adults (Laurienti et al., 2006). Peiffer et al. (2007) corroborated this hypothesis by using a simple stimulus detection task to reveal that multisensory performance gains were so large among older adults that they were able to outperform younger adults under multisensory conditions (Peiffer et al., 2007). Thus, age-related differences in multisensory integration were conceptualized as older adults exploiting the principle of inverse effectiveness to bolster perceptual performance and to offset age-related declines in perceptual ability (Laurienti et al., 2006).

More recent work has revealed that heightened multisensory integration is not limited to congruent cues but rather extends to incongruent cues as well. Specifically, older adults have been shown, in some cases, to be more susceptible to audio-visual illusions. For example, Setti and colleagues (2013) demonstrated that older adults are more susceptible to the McGurk effect (Setti, Burke, Kenny, & Newell, 2013), a phenomenon wherein an auditory phoneme (e.g., /b/ in the syllable “ba”) and a simultaneous visual presentation of a different phoneme (e.g., /d/ in the syllable “da”) results in a unique illusory percept (e.g., /g/ in the syllable “ga”; see McGurk & Macdonald, 1976). This illustrates that older adults are more likely than younger adults to generate an erroneous percept when faced with spatially and temporally congruent cues that
provide conflicting information. Similarly, Deloss and colleagues (2013) employed a sound-induced flash illusion paradigm in which participants were presented with 0-3 auditory beeps in rapid succession along with 1-3 visual flashes that were congruent with the onset of the beeps. The participant’s goal was to report the number of visual stimuli that they perceived. In the presence of congruent beeps, older adults’ capacity to detect the number of stimuli onset events was enhanced. However, when there were fewer visual flashes than there were auditory beeps, older adults were more likely than younger adults to experience fission, the illusory appearance of additional visual flashes (DeLoss, Pierce, & Andersen, 2013). Once again, the observed age-related differences in multisensory performance could not be attributed to age-related differences in unisensory perceptual ability alone. Sekiyama and colleagues (2014) employed a McGurk paradigm in which they calibrated the auditory signal-to-noise ratio (SNR) to control for age-related hearing loss in older adults and to ensure that younger and older participants were equally precise in identifying auditory syllables in isolation of visual cues. They found that despite using perceptually equivalent auditory SNRs for younger and older adults, older adults were still more heavily influenced by the presence of incongruent visual syllables (i.e., they were more susceptible to the McGurk effect than younger adults) (Sekiyama, Soshi, & Sakamoto, 2014).

The pattern of observations described above has led to the overarching hypothesis that older adults may be exhibiting increased baseline processing of multisensory inputs compared to younger adults (Mozolic et al., 2012). To elaborate, multisensory integration is modulated by attention such that when a younger adult is instructed to explicitly attend to one modality over the other, the performance enhancements associated with the presence of multiple congruent sensory inputs are suppressed and the performance decrements associated with incongruent or distracting sensory inputs is also suppressed (Mozolic, Hugenschmidt, Peiffer, & Laurienti, 2008; Talsma, Doty, & Woldorff, 2007). At the neural level, modality-specific selective attention also results in a suppression of activity in the primary sensory cortex of the unattended modality (Mozolic, Joyner, et al., 2008). To assess whether older adults can engage cross-modal suppression, Hugenschmidt and colleagues (2009) submitted both older adults and younger adults to fMRI and had them perform a simple stimulus detection task in which they had to report whether a stimulus was red or blue. The stimulus consisted of either a visual presentation of a coloured circle, the auditory presentation of the word “red” or the word “blue”, or both cues combined. On a trial by trial basis, participants were prompted to attend to either the visual cue,
the auditory cue, or to divide their attention across both cues. The results revealed that for both age groups, modality selective attention reduced the multisensory performance benefits (i.e., enhanced reaction times) associated with the presence of multiple congruent cues. However, the multisensory performance benefits were higher among older adults in all attentional conditions. The results also revealed that older adults displayed greater activity in the auditory cortex in response to scanner noise during their resting state than younger adults (Hugenschmidt, Mozolic, Tan, Kraft, & Laurienti, 2009). Thus, Hugenschmidt and colleagues inferred that older adults can invoke modality selective attention and therefore age-related changes in terms of attentional control cannot account for age-related changes in multisensory integration. Instead, older adults may be processing more background sensory inputs than younger adults at baseline and modality selective attention may not be able to compensate for the overall increase in the processing of background auditory input observed during their resting state (Hugenschmidt et al., 2009).

2.3.1 Cognitive antecedents of age-related differences in multisensory integration

Mozolic and colleagues (2012) hypothesized that increased processing of task-irrelevant sensory information may be seated in the age-related dysregulation of the default mode network (DMN). The DMN is involved in mentation, but may also play a role in monitoring the external environment for important sensory signals (see Buckner, Andrews-Hanna, & Schacter, 2008 for review). Critically, the DMN must be suppressed in order for external or task-oriented attention to be engaged but age-related declines in functional connectivity within the DMN may preclude the successful deactivation of the DMN (Buckner et al., 2008; Stevens, Hasher, Chiew, & Grady, 2008), and this may promote greater processing of task-irrelevant environmental cues. At the behavioural level, this tendency to process more cross-modal sensory input, in general, is thought to then manifest as performance benefits when the available sensory inputs happen to be congruent, but lead to performance decrements when they happen to be incongruent or when one or more sensory inputs are task-irrelevant (Mozolic et al., 2012).

There is also some evidence to indicate that age-related changes in multisensory integration could be related to the posterior-anterior shift with aging (PASA; Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008). Under the PASA hypothesis, older adults recruit prefrontal cortical regions to
compensate for sensory processing deficits (Davis et al., 2008; Grady, 2012; Grady, 2008). Diaconescu and colleagues (2013) used magnetoencephalography to consider age differences in the neural response to auditory, visual, or multisensory stimulus presentations. They demonstrated that compared to unisensory visual cues (e.g., image of a lion) and auditory cues (e.g., sound of a lion roaring), both cues presented in combination yielded faster stimulus detection and the magnitude of the performance gains were greater among older adults, which replicated the age differences in multisensory integration described above (e.g., Laurienti et al., 2006; Peiffer et al., 2007). More importantly, older adults displayed larger responses in the posterior parietal and medial prefrontal cortices during multisensory stimulus presentations and larger responses predicted faster performance. Furthermore, larger posterior parietal and medial prefrontal responses were associated with reduced grey matter in cortical and sub-cortical brain regions, and reduced grey matter also predicted greater multisensory performance facilitation (Diaconescu, Hasher, & McIntosh, 2013). This suggests that heightened integration may be related to a compensatory recruitment of prefrontal cortical regions.

Additional evidence of the differential effects that incongruent or unreliable cues have on older and younger adults has also been observed within the domain of gait and posture control. It is important to note that research on age-related changes in gait and posture control has been carried out in isolation of research on age-related changes in multisensory integration, placing emphasis on the behavioural and environmental conditions that put older adults at risk for instability and falls more so than the underlying perceptual antecedents per se. Here I summarize key research from the domain of gait and posture control to illustrate that it provides analogous evidence of age-related differences in the capacity to contend with incongruent sensory inputs. I also consider the important insight that research on gait and posture control has provided into why age-related differences in the response to incongruent or unreliable sensory inputs may emerge. Specifically, I will consider the hypothesis that older adults may differ from younger adults in their capacity to weight sensory inputs according to their reliabilities.

Just as research on visual-auditory integration has demonstrated that older adults are prone to performance decrements in the presence of incongruent cues, research on postural control shows that older adults are more susceptible to performance decrements in response to incongruent or unreliable visual or vestibular cues. To illustrate, Deshpande & Palta (2007) had younger and
older adults walk toward a visual target straight ahead of them while vestibular cues to self-motion were manipulated via galvanic vestibular stimulation (GVS). For older adults, GVS resulted in greater path deviation and trunk tilt than it did for younger adults (Deshpande & Patla, 2007). Similarly, Jeka et al. (2010) provided older and younger adults with oscillatory visual cues while they attempted to maintain a stable posture. Relative to younger adults, healthy older adults and fall-prone older adults were more susceptible to postural instability while standing when presented with high amplitude, oscillatory visual information (Jeka et al., 2010).

Several explanations have been put forth as to why older adults are more susceptible to postural instability when faced with incongruent sensory inputs. A prevalent hypothesis is that older adults may be displaying systematic sensory biases. For example, it has been proposed that older adults are susceptible to visual perturbations because they are more reliant on visual cues for postural control (e.g., Simoneau et al., 1999; Sundermier, Woollacott, Jensen, & Moore, 1996; Wade, Lindquist, Taylor, & Treat-Jacobson, 1995). Conversely, other investigations have suggested that older adults are biased toward vestibular input and/or proprioceptive input (e.g., Wiesmeier et al., 2015). Ultimately, a systematic bias toward input from one modality or the other does not explain why older adults are more heavily influenced both visual and vestibular perturbations than are younger adults. A more inclusive explanation is that older adults are displaying altered sensory re-weighting (e.g., Berard, Fung, & Lamontagne, 2012; Berard, Fung, McFadyen, & Lamontagne, 2009; Berard, 2011). In other words, where younger adults can dynamically adjust the extent to which each sensory input contributes to their posture, older adults are perhaps more rigid in their relative weighting of sensory inputs.

To demonstrate this point, Berard and colleagues (2012) placed healthy older and younger adults in a room and asked them to walk in straight line in reference to the physical room. During the walking task, participants wore a head-mounted display that presented a virtual representation of the room. As the participant walked forward, the optic flow of the virtual room either matched their physical movement, or the focus of expansion was rotated to a conflicting angle of 40 degrees to the left or right of center. A motion capture system was used to record joint angles and center of mass trajectory during the walking task and these measurements were used to derive the observers’ heading orientation and center of mass. Results revealed that when the visual
scene depicted a conflicting heading angle, younger adults were able to maintain their intended straight forward heading orientation whereas older adults displayed greater heading deviations and greater deviations in terms of their center of mass (Berard et al., 2012). From this, the authors inferred that there may be age-related differences in the capacity to dynamically re-weight visual cues to self-motion. Where younger adults may have been able to assign less weight to the altered visual cues, age-related declines in the capacity to dynamically re-weight visual and vestibular inputs may have led older adults to incorporate the conflicting optic flow cues into their self-motion percept (Berard et al., 2012).

In summary, research examining visual-auditory stimulus detection and stimulus discrimination has revealed that older and younger adults are differentially affected by congruent and incongruent multisensory inputs. This signals that there may be age-related differences in multisensory integration. Older adults make invoke heightened integration to compensate for the decline of their individual sensory systems but older adults may also have greater difficulty inhibiting crossmodal inputs than younger adults. Research examining age-related differences in the effect of visual or vestibular perturbations during standing and walking has also revealed that older adults and younger adults are differentially affected by incongruent sensory inputs. Age-related differences in the capacity to contend with incongruent visual and vestibular input have been attributed specifically to changes in the ability for older adults to dynamically re-weight visual and vestibular inputs relative to one another. In the following sections, I will consider how age-related differences in multisensory integration could affect self-motion perception, the gaps in current knowledge pertaining to the generalizability of age-related differences in multisensory integration, and the rationale for the current thesis.

2.4 Potential consequences for self-motion perception

2.4.1 Age-related differences in cue integration

Research on how younger adults perceive their own movement has revealed that robust self-motion perception is enabled, in part, by the capacity to use combinations of sensory input from across different sensory systems to gather information about self-motion. Therefore, it stands to reason that age-related changes in the way that cues are combined could affect self-motion
perception. For example, two (or three) redundant cues to self-motion may allow both younger and older adults to perceive and to control self-motion with greater precision than they could with only a single cue to self-motion but, in light of evidence to suggest that multisensory integration is heightened in late adulthood (Laurienti et al., 2006; Peiffer et al., 2007), it is conceivable that the magnitude of this effect may be greater among older adults. However, very little is currently known about how self-motion perception is affected by age-related differences in multisensory integration. That is because age-related differences in multisensory integration have predominantly been characterized in the context of visual-auditory stimulus detection tasks. These tasks are not a strong representation of multisensory integration as it occurs during self-motion perception. Stimulus detection tasks often involve an observer seated at a desktop computer responding to the onset of highly discrete cues such as a stationary flash of light, a stationary tone, or both cues presented simultaneously. It is common to present either redundant cues that can be combined to facilitate performance or to present categorically unrelated cues that yield performance decrements, perhaps because they are combined to cultivate an inaccurate percept but also because they could distract the observer from the task at hand. Furthermore, stimulus detection tasks are often deliberately designed to invoke inverse effectiveness by utilizing weak or ineffective stimuli that are presented near the observer’s perceptual threshold (Holmes, 2009; Stanford & Stein, 2007). These highly specified task and sensory conditions may thereby overestimate age-related differences in multisensory integration. By contrast, multisensory integration as it occurs during self-motion perception involves far more complex sensory inputs. For example, when driving a car, the observer is immersed in sensory inputs that they must integrate dynamically over time and through physical space, not merely at discrete intervals, nor at a fixed location in space (Campos & Bülthoff, 2012). At present, few previous studies have examined whether the age-related differences in visual-auditory cue integration observed in the context of simple stimulus detection tasks generalize to more complex visual-auditory inputs, like the dynamic visual and auditory inputs experienced during self-motion perception.

Another important consideration is that previous work examining age-related changes in multisensory integration has primarily focused on visual-auditory integration whereas self-motion perception is largely seated in the integration of visual, vestibular, and proprioceptive
inputs, albeit with a peripheral contribution from auditory input. There is some evidence to suggest that age-related differences in multisensory integration extend to the integration of visual cues with other body-based cues. Specifically, Mahoney and colleagues had older and younger observers respond to the onset of visual cues (the appearance of an asterisk on a computer screen), somatosensory cues (electrical stimulation applied to the left and right index fingers), or both cues presented simultaneously as quickly as possible via a foot pedal under their right foot. They observed that 75% of older adults displayed multisensory performance enhancements (faster visual-somatosensory reaction times) whereas 25% did not. The 25% of individuals who did not experience multisensory performance enhancements had faster somatosensory reaction times that were comparable to those displayed by younger adults. Therefore, these individuals were likely performing at ceiling with somatosensory cues alone and were not able to gain from the addition of visual cues. Those who did display multisensory performance enhancements had slower somatosensory reaction times and thus these individuals may have exploited the additional visual cues to facilitate stimulus detection, perhaps as a compensatory mechanism (Mahoney, Holtzer, & Verghese, 2014). It is important to note that in the context of self-motion perception specifically, there may be important differences in terms of the manner in which visual and vestibular inputs are integrated. Specifically, self-motion perception is thought to necessitate a mandatory fusion of visual and vestibular sensory inputs (Kaliuzhna, Prsa, Gale, Lee, & Blanke, 2015; Prsa, Gale, & Blanke, 2012; de Winkel, Katliar, & Bülthoff, 2015). That is because during self-motion perception, visual and vestibular inputs both provide information that pertains to one’s own displacements and are thereby always share a common cause and are inherently redundant (Prsa et al., 2012). It follows from this principle that the age-related increase in multisensory integration observed in the context of visual-auditory cue integration may be more pronounced in the context of visual-vestibular cue integration. Ultimately, few previous studies have provided visual cues to self-motion and manipulated the presence or absence of congruent vestibular cues to determine how age-related differences in the integration of visual and vestibular inputs impacts older and younger adults’ capacity to perceive and to govern self-motion.

In a similar vein, most research that has examined how multiple sensory inputs convey self-motion has focused on how auditory cues augment the visual perception of self-motion, or how
vestibular inputs augment the visual perception of self-motion perception and vice versa. The reality is that many everyday tasks involve all three sets of sensory inputs together. It is conceivable that if there are performance gains associated with congruent cues across two sensory modalities, there could be even greater performance gains associated with three congruent sensory inputs. Although there has been some very limited work examining trimodal sensory integration in general, this work is subject to the same limitations associated with visual-auditory cue integration research in that it has focused on simple and highly discrete cues as opposed to the continuous and dynamic inputs experienced during self-motion.

2.4.2 Age-related differences in reliability-based cue weighting

A persistent challenge that observers face during self-motion is that the reliability with which their sensory systems estimate the parameters of their movement can vary (Knill & Pouget, 2004; Ma et al., 2006). Younger adults and non-human primates can maximize the precision of their self-motion percept by weighting visual and vestibular inputs as a function of their respective reliabilities. If older adults are unable to weight the available cues to self-motion as a function of their respective reliabilities, they may not be able to achieve the same optimal reduction in perceptual variance that younger adults achieve by integrating redundant cues to self-motion. Moreover, as Berard and colleagues (2012) alluded to, older adults may be relatively more susceptible than younger adults to performance declines during instances in which one sensory system provides unreliable cues to self-motion (Berard et al., 2012). That said, Berard et al. (2012) used changes in the orientation of body segments and in walking trajectory to infer that that older adults attributed more weight to visual inputs than to vestibular inputs while walking. There are two limitations associated with this interpretation. First, by only adding or removing incongruent cues to self-motion and measuring the resulting performance outcomes, this approach can only speak to age-related differences in the effect of presenting difference cue combinations. To tap into age-related differences in terms of optimal integration and relative cue weighting, it is necessary to characterize the reliability associated with the unimodal estimates of self-motion independently and to then determine how these estimates are reflected in the multisensory estimate of self-motion. In the case of optimal integration, the multisensory estimate is predicted by the sum of the unimodal estimates, each weighted as a function of their respective reliabilities, and the variance is lower than that of either unimodal
estimate. To date, no previous studies have implemented the rigorous, quantitative methods necessary to determine whether there are age-related differences in optimal integration during self-motion perception.

2.5 Rationale for the current thesis

Everyday mobility-related tasks require robust and precise self-motion perception. There is evidence to suggest that older adults exhibit broad changes in their performance on tasks involving self-motion but the perceptual factors underlying these changes are not fully understood. Previous studies have considered age-related changes in the capacity for the individual sensory systems to perceive self-motion, but have not systematically quantified how the sensory systems interact. Emergent evidence suggests that aging may lead to broad changes in terms of both the effect that different cue combinations have on performance and in the way that redundant cues are weighted. Given that younger adults rely on multisensory integration to derive robust and precise self-motion percepts, age-related differences in multisensory integration could have a significant effect on the way that older adults perceive and ultimately control their own movement. However, the extent to which older adults demonstrate optimal cue integration and/or reliability-based weighting of sensory inputs during self-motion is largely unknown. The purpose of this thesis was to examine age-related differences in multisensory integration within the context of self-motion perception. Specifically, my objectives were to determine (i) whether age-related differences in the effect of different sensory cue combinations can be observed during self-motion perception and (ii) whether age-related differences are observed with respect to optimal integration within the context of self-motion perception.

Thus, I utilized two distinct experimental methods. The first method employed a simple driving task that required participants to control their speed and their lane position. I selected this approach because driving is a multisensory, self-motion perception task that involves complex and dynamic sensory signals. Simulated driving was also an excellent model because it allowed me to systematically manipulate the presence or absence of auditory and vestibular inputs that were meaningful to the primary task while retaining a high degree of control over task complexity and other factors beyond the sensory manipulation that could influence performance. The primary research question was whether the age-related differences in multisensory
integration that are observed in the context of simple stimulus detection tasks extend to self-motion perception. I approached this question systematically with three experiments:

2.5.1 Chapter 3: Age-related differences in visual-auditory self-motion perception

In my first experiment, my goal was to determine whether the age-related differences in cue combination observed in the context of simple stimulus detection and stimulus discrimination tasks extend to the more complex and dynamic visual and auditory cues experienced during self-motion. I achieved this by presenting visual input (namely optic flow) and adding or removing congruent auditory inputs (i.e., engine, tire contact, and wind sounds) and measuring resulting age-related differences in driving performance. Previous investigations have demonstrated that when paired with visual inputs, auditory inputs augment speed perception (e.g., Denjean et al., 2012). Given that previous observations suggest that multisensory integration is heightened in older age and that older adults exhibit greater performance enhancements when redundant sensory inputs are available, I hypothesized that compared to visual input alone, the addition of congruent auditory input would have a greater impact on the driving performance of older adults compared to younger adults.

2.5.2 Chapter 4: Age-related differences in visual-vestibular self-motion perception

In my second experiment, I used the same multisensory driving paradigm to determine whether age-related differences in the effect of cue combination observed in the context of visual-auditory cue interactions extend to visual-vestibular interactions. I achieved this by presenting visual cues (optic flow) and adding or removing vestibular inputs (i.e., tilt and translation) designed to mimic some of the inertial forces encountered when driving a real vehicle (e.g., acceleration, deceleration, cornering). Previous studies on younger adults have shown that introducing vestibular cues during a driving task helps them to improve their capacity to maintain their lane position (Kemeny & Panerai, 2003) and their speed while turning (Reymond, Kemeny, Droulez, & Berthoz, 2001), but no previous work has examined age-related differences
in these outcomes. I hypothesized that adding or removing congruent vestibular inputs to visual cues would have a greater impact on the driving performance of older adults compared to younger adults.

2.5.3 Chapter 5: Age-related differences in trimodal self-motion perception

In my third experiment, I used the driving paradigm once more to determine whether three congruent cues to self-motion would yield additive or sub-additive effects and whether this would differ between older and younger adults. I achieved this by presenting the previously described visual, auditory, and vestibular cues simultaneously and comparing performance against the bimodal (visual-auditory and visual-vestibular) conditions. I hypothesized that if there are additive performance benefits associated with two congruent cues to self-motion (bimodal), there may be extended performance benefits associated with three congruent cues to self-motion (trimodal).

Overall, the driving task demonstrated that manipulating the combination of available cues to self-motion had a larger effect on the driving performance of older adults than that of younger adults. This observation raised some important questions that the driving task was not well-suited to address. For instance, it was not possible to perform the current driving task using auditory cues alone or vestibular cues alone and this precluded garnering the estimates of unimodal reliability necessary to assess how the available cues were integrated. Second, driving is a highly practiced task and therefore the effect of aging could be confounded by the effect of cumulative driving experience. Finally, the driving task involved active control (operating the steering wheel and pedals) and thus I could not exclude the role of proprioceptive cues and/or motor efference copies as additional cues to self-motion. Thus, I extended my driving research by implementing a task that would afford the higher level of experimental control and precision necessary to elucidate age-related differences in multisensory integration within the context of self-motion perception.
2.5.4 Chapter 6: Age-related differences in optimal integration during self-motion perception

In my second experimental method, I employed an adaptation of a well-established heading perception task (see Gu et al., 2007; Fetsch et al., 2009; Butler et al., 2009). This paradigm was selected because it has previously been used to establish behavioural evidence of statistically optimal visual-vestibular integration and it has also been used to elucidate the potential neural substrates of optimal integration (Fetsch et al., 2012; Gu et al., 2012; Morgan et al., 2008). Therefore, there was already a robust framework in place for interpreting heading perception outcomes to make inferences about multisensory integration. My goal was to use this rigorous psychophysical approach to test younger adults and, for the first time, older adults to determine whether older adults integrate visual and vestibular inputs optimally in that (i) their combined estimate is less variable than the constituent unimodal estimates and (ii) the combined estimate reflects the linear sum of each unimodal estimate weighted as a function of their respective reliabilities.

The heading perception paradigm consisted of a two alternative forced-choice task in which participants received two consecutive movements (while seated) and were asked to judge which of the two headings were more rightward than the other. The heading cues consisted of visual cues alone (optic flow via a head mounted display), vestibular cues alone (passive physical translational via a motion platform), congruent visual and vestibular cues combined, or incongruent visual and vestibular cues combined. My objective was to compare the heading discrimination performance of older and younger adults to determine whether older adults integrated optimally under congruent and incongruent cue conditions. Based on the findings of the studies described in Chapters 3 and 4, and based on previous work in the domain of gait and posture research (e.g., Berard et al., 2012), I hypothesized that while older adults may be able to integrate congruent cues to enjoy a reduction in perceptual variance, they may differ from younger adults in that they may not be able to integrate incongruent cues optimally.
Chapter 3

Age-related differences in visual-auditory self-motion perception

The study that appears in this chapter is published as:


3 Introduction

The events that occur around us typically stimulate more than one sensory system simultaneously. It is well established that these congruent signals can promote better perceptual performance (i.e., faster and more reliable) than the constituent sensory signals presented in isolation (see Rowland & Stein, 2014; Stein, Stanford, & Rowland, 2014 for reviews). A growing body of evidence indicates, however, that this process may change with age (Laurienti et al., 2006; Mozolic et al., 2012; Peiffer et al., 2007). This is evidenced by the observation that the magnitude of the performance gains associated with congruent visual and auditory inputs is greater among older adults than it is among younger adults (e.g., Laurienti et al., 2006; Peiffer et al., 2007). Moreover, the magnitude of the performance decrements associated with conflicting visual and auditory inputs is greater among older adults than it is among younger adults (DeLoss et al., 2013; Guerreiro, Murphy, & Van Gerven, 2013; Setti et al., 2013). That said, much of the current evidence to suggest that there are age-related differences in the integration of visual and auditory inputs is derived from stimulus detection and stimulus discrimination tasks (Ernst & Bülthoff, 2004). While precise and controlled, these tasks employ simple and highly discrete visual and auditory cues (e.g., flash of light, auditory beep; Shams, Kamitani, & Shimojo, 2002) and thus, it is not clear whether this pattern of performance generalizes to other multisensory tasks. More recent research has revealed that the purported age-related differences in the interaction between visual and auditory cues is contingent upon the nature of the task (McGovern, Roudaia, Stapleton, McGinnity, & Newell, 2014). For example, differences in multisensory enhancement have not been observed in tasks involving speech perception (Tye-
The potentially stimulus and/or task dependent nature of the observation that there are age-differences in visual-auditory interactions is particularly important when considering their functional implications. Ultimately, previous studies have utilized sensory cues that are very different from the visual and auditory inputs that we typically encounter in our daily lives. For example, many of the tasks that we perform routinely involve moving through our environment and thereby elicit dynamic sensory inputs that must be combined continuously over time and space, not merely at discrete intervals (Campos & Bülthoff, 2012). In order to determine whether the purported age-related differences in the interaction between visual and auditory cues extend beyond the simple stimulus detection type tasks in which they have typically been observed, it is necessary to evaluate these sensory interactions during more dynamic, realistic tasks.

There is a great deal of evidence to demonstrate that there are age-related differences in visual, proprioceptive, and vestibular interactions during self-motion. Several previous studies have attempted to quantify the relative influence of individual sensory cues during locomotion in older and younger adults by manipulating the reliability of, or the nature of simultaneously presented visual and vestibular/proprioceptive cues. For example, Deshpande and Patla (2007) introduced perturbations of the vestibular system during goal-directed walking using galvanic vestibular stimulation. Younger adults appeared to be better able to down-weight the perturbed vestibular inputs than older adults, demonstrated by their superior ability to maintain a linear path towards their visual target. Further, Berard et al. (2012) reported that, when visual heading angles were dynamically changed while walking through a virtual environment, older adults were more greatly affected by this visual manipulation than were younger adults (both in terms of their final heading angle and dynamic walking parameters such as head/trunk/pelvis yaw angles). These findings suggest that there may be age-related changes in the way that dynamic sensory inputs interact during mobility-related tasks. However, very little previous work has investigated potential age-related differences specifically in the interaction between dynamic visual and auditory cues during self-motion. This is an important distinction because the mechanisms underlying visual-vestibular/proprioceptive cue interactions likely differ from those underlying visual-auditory cue interactions. Specifically, visual and vestibular cues generated during self-motion are idiothetic, as the observer’s own movements are the source of both the visual and the
vestibular/proprioceptive cues that they receive. It has been posited that due to this inherent causal link between visual and vestibular/proprioceptive cues, they are integrated in a mandatory fashion (Prsa et al., 2012). Conversely, auditory cues are allothetic or generated by external sources and may thereby be integrated differently.

It is well established that visual cues can provide a robust indication of self-motion with respect to, for instance, distance and heading perception (Butler et al., 2010; Campos & Bülthoff, 2012; Fetsch et al., 2009; Frenz & Lappe, 2005; Gibson, 1950; Sun, Campos, & Chan, 2004; Warren & Hannon, 1988; Wilkie & Wann, 2002). Optic flow alone can also be strong enough to elicit a strong illusory perception of actual self-motion in the absence of physical displacement (i.e., vection; Brandt, Brandt et al., 1973). Growing evidence indicates that auditory cues can augment the visual perception of self-motion (Keshavarz et al., 2014; Riecke et al., 2005; Riecke et al., 2008). For example, auditory cues can help an observer differentiate visual displacements caused by egomotion from those caused by the movement of external objects (Calabro, Soto-Faraco, & Vaina, 2011; Väljamäe, Larsson, Västfjäll, & Kleiner, 2008). Moreover, auditory cues can strengthen the experience of vection (Keshavarz et al., 2014; Riecke et al., 2008). A representative example of a real-world task in which auditory cues demonstrably augment the visual perception of self-motion is driving a vehicle. When driving, we experience tire and wind turbulence noises that increase in amplitude relative to the rate at which we are traveling and therefore, these cues serve as a useful indication of relative speed (Merat & Jamson, 2011). The capacity for these cues to augment the visual perception of self-motion is illustrated by the fact that when no external feedback devices are available (i.e., speedometer) and auditory cues are removed, the perception of speed diminishes, causing drivers to underestimate their speed and/or to travel faster than intended (Horswill & Plooy, 2008). A number of investigations have also demonstrated that speed variability increases when driving without auditory cues (Horswill & Plooy, 2008; Matthews & Cousins, 1980; Merat & Jamson, 2011). Taken together, this evidence indicates that auditory cues bolster the perception of self-motion when presented in concert with visual motion cues. These observations also demonstrate that a visual-auditory driving task has the potential to help elucidate whether there are age-related differences in the interactions between visual and auditory cues that extend beyond simple stimulus detection tasks to more complex, continuous and dynamic sensory inputs under more realistic task conditions.
Therefore, in the current study, I used a driving simulator to provide older adults with visual cues to self-motion (i.e., optic flow) while manipulating the presence or absence of congruent auditory inputs (i.e., engine, tire, and wind noise). The driving simulator allowed me to move toward more complex sensory inputs without relinquishing the experimental control afforded by more traditional visual-auditory stimulus detection tasks, as the simulator affords highly repeatable conditions and, unlike real-world driving, a simulation allows for tight constraints on task complexity, distraction, and other factors that may confound age-related differences in performance. Driving performance metrics (speed maintenance and lane keeping) then served as an assay of age-related differences in the interactions between visual and auditory cues. Based on previous driving research, I hypothesized that compared to driving with visual cues alone, speed accuracy would be improved and speed variability would be reduced with the addition of congruent auditory input (e.g., Denjean, Roussarie, Kronland-Martinet, Ystad, & Velay, 2012). More importantly, based on previous evidence demonstrating age-related differences in the interaction between visual and auditory sensory inputs, I predicted that older adults would exhibit proportionally greater performance benefits than younger adults when congruent auditory and visual inputs were available compared to when only visual inputs were provided (e.g., Laurienti et al., 2006; Peiffer et al. 2007). While the auditory cues provided information about relative speed, they did not contain any information that was directly relevant to lane-keeping performance (e.g., no lane departure warning, rumble strips, etc.). Therefore, I predicted that lane-keeping performance would remain unchanged, unless auditory input was to promote more global changes in task performance by affecting, for instance, the participants’ general sustained attention, overall state of arousal, presence within the simulation or the perceived realism of the driving task (e.g., Cowan, Rojas, Kapralos, Moussa, & Dubrowski, 2015; Rojas, Cowan, Kapralos, Colllins, & Dubrowski, 2015).
3.1 Methods

3.1.1 Participants

Thirty-two older adults (65+ years) and twenty-three healthy younger adults (18-35 years) were recruited from the community. This study protocol was approved by the University Health Network research ethics board (REB 12-015-DE). All participants were pre-screened to ensure that they held a valid driver’s license and had no serious medical conditions (e.g., history of seizures, stroke, heart condition), no physical conditions that may affect their driving ability (e.g., arm or leg injuries), did not use medications that may impair driving performance and had no self-reported, uncorrected visual or hearing impairments. All participants passed the Montreal Cognitive Assessment screening for mild cognitive impairment (>26/30; Nasreddine et al., 2005). Participants were randomly assigned to one of two experimental groups: 1) visual cues alone or, 2) visual and auditory cues combined. Fourteen older adults (7 in the visual only condition, 7 in the visual + auditory condition) and 3 younger adults in the visual only condition withdrew prior to completing the experiment due to symptoms of simulator sickness (for detailed discussion, see Keshavarz, Ramkhalawansingh, Haycock, Shahab, & Campos, 2015). The simulator sickness rates found here (50% older adults, 13% younger adults) are comparable to those that have been reported in previous driving simulator studies (e.g., (Cassavaugh, Domeyer, & Backs, 2011; Reed-Jones, Vallis, Reed-Jones, & Trick, 2008; Stoner, Fisher, & Mollenhauer, 2011). Due to simulator malfunction, data was not recorded for 1 younger adult and for 2 older adults in the visual + auditory condition. All 17 cases of incomplete data due to simulator sickness and technical issues were excluded from data analyses. Table 3.1 summarizes the characteristics of the participants who had complete data and who were included in my analyses. Note that the high attrition rate led to a difference in the mean age between the older adults that comprised the visual only sensory condition and the older adults that comprised the visual auditory condition, but it is not expected to be confounded with the effects of sensory condition as will be discussed below.
Table 3.1

Participant demographics by age and sensory condition.

<table>
<thead>
<tr>
<th></th>
<th>Visual Only</th>
<th></th>
<th>Visual + Auditory</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Younger</td>
<td>Older</td>
<td>Younger</td>
<td>Older</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>M age (SD)</td>
<td>N</td>
<td>M age (SD)</td>
</tr>
<tr>
<td>Male</td>
<td>4</td>
<td>27.25 (1.70)</td>
<td>6</td>
<td>76 (6.92)</td>
</tr>
<tr>
<td>Female</td>
<td>6</td>
<td>25.67 (5.27)</td>
<td>2</td>
<td>70 (4.24)</td>
</tr>
<tr>
<td>Overall</td>
<td>10</td>
<td>26.30 (4.13)</td>
<td>8</td>
<td>74.50 (6.67)</td>
</tr>
</tbody>
</table>
3.1.2 Design

There were two between-subjects variables: age group (younger vs. older) and sensory condition (visual only vs. visual + auditory). Additionally, there were two within-subjects variables: drive number (acclimatization, 2, 3, 4, 5) and road geometry (straight vs. curved road segments). The result was a 2 (age) x 2 (sensory condition) x 5 (drive number) x 2 (road geometry) mixed factorial design.

3.1.3 Apparatus

The driving task took place within StreetLab, an immersive Virtual Reality laboratory housed within the Challenging Environment Assessment Laboratory at the Toronto Rehabilitation Institute’s iDAPT Centre for Rehabilitation Research (see Figure 3.1A). StreetLab was outfitted with a basic driving interface, consisting of a half-cab structure the approximate dimensions of a Smart car, which contained a car seat, a Logitech steering wheel and gas/brake pedals, and a digital speedometer (see Figure 3.1B). The dome-shaped lab contained an immersive, curved projection screen (see Figure 3.1C). The visual driving scene was rendered using the irrLicht engine and presented using six synchronized projectors (Eyevis ESP-LED; Figure 3.1D) each with a resolution of 1920x1200 for a total field-of-view of 240° horizontally and 105° vertically at 6.5 arcmins/OLP. The imagery was updated at 60Hz, with a total time delay of approximately 50 ms between the driver inputs and the visual display of the outside world. The visual driving scene consisted of clear daytime driving conditions on a two-lane rural road with guardrails and a series of left and right curves as shown in Figure 3.2. There was an equal number of left and right-hand curves, with one of three radii: 400 meters, 800 meters, or 1200 meters. The roadway was surrounded by an open grassy area with agricultural scenery (i.e., farms with barns and silos on the far horizon) that mainly provided optic flow information. This scenery was selected over other potential environments (e.g., a city scape) because complex scenery can exacerbate simulator sickness (e.g., Reed-Jones, Trick, Toxopeus, Reed-Jones, & Vallis, 2009). No other moving objects (e.g., vehicles, pedestrians, animals, etc.) or obstacles were in the scene. My goal was to capture a substantial duration of driving performance (≥25 minutes) to ensure that drivers had sufficient time to acclimatize to the simulator. This was an important consideration because older adults take a longer amount of time to acclimatize to driving simulators than younger
Figure 3.1. Solidworks™ rendered cutaway view of StreetLab, a fiberglass dome that can be configured into different virtual reality environments (A). The driving task configuration consisted of a mock cab comprised of a steel frame, plastic body panels, a real car seat, a Logitech steering wheel and pedals, and a digital speedometer (B). StreetLab contains a curved projection screen (C) and six Eyevision ESP-LED projectors (D) that generate a 240 degree horizontal x 105 degree vertical field of view image. Vehicle and road contact sounds were conveyed over a 7.1 channel sound system. The center channel speaker is depicted (E).
Figure 3.2. Screenshot of the driving scene consisting of a two-lane roadway with guardrails on either side and agricultural scenery on the horizon.
adults do (e.g., Kawano et al., 2012). To mitigate the risk of inattention, fatigue, and simulator sickness associated with driving for extended periods of time without interruption (e.g., Philip et al., 2003; Stoner et al., 2011; Yanko & Spalek, 2013), I created five separate courses that each took 5-7 minutes to complete. Each course was comprised of the same straight and curved road segments and thus each drive was identical in terms of their complexity and difficulty but the segments were arranged in different sequences so that drivers could not learn the courses. In addition to thwarting adverse effects, this approach allowed me to observe how participants' performance changed as they progressed through each subsequent drive and to discern whether the rate at which participants adapted to the driving simulator was affected by age and/or the available sensory inputs.

The vehicle dynamics were developed in the MathWorks’ Simulink environment and were then compiled and run in real-time using Quanser’s QUARC operating system. The auditory stimuli (presented only to the visual + auditory group) were created by the IrrKlang sound engine (Gebhardt, 2009) and consisted of looped, digital recordings of (i) the engine from a 2007 Volkswagen Passat diesel, (ii) tire-road contact sounds, and (iii) brown noise to represent air rushing over the vehicle (Freesound.org, 2010). The frequency of the engine sounds scaled according to the speed of the vehicle in a linear fashion. The amplitude of the road contact and wind sounds scaled according to speed in an exponential manner. Sounds were presented to the driver using a 7.1 channel sound system. The system consisted of seven, 4” inch satellite loudspeakers (Meyer Sound MM-4XP) located behind the sound-permeable surface of the projection screen and a 10” subwoofer (Meyer Sound MM-10XP) located on the floor of the lab. The center channel speaker was positioned near head height at 0° azimuth (see Figure 3.1E) and the subwoofer was positioned below it. The other six loudspeakers were distributed in an array along the same horizontal plane as the center channel speaker at ±28° azimuth (right front, left front), ±90° azimuth (right side and left side), and ±127.5° degree azimuth (right rear and left rear). Each speaker was positioned at a distance of 2.14 meters from the participant. At 80km/h, sound pressure level was 90 decibels (A-weighting). For each of the five drives, performance was measured by capturing speed (km/h), standard deviation in speed, and root mean squared error (RMSE) of lateral position (m) at a rate of 200Hz. Mean speed and speed variability were used as indices of accuracy and precision with respect to speed maintenance, respectively.
RMSE lateral position is a common index of steering performance. Performance measures were also separated by road geometry (i.e., straight vs. curved road segments), given that traversing curved road segments represented a higher level of task complexity.

3.1.4 Self-report measures

Participants were asked to rate the realism of the major components of the simulation including the steering, gas, brakes, accelerator, and the overall driving feel using a series of 7-point Likert scales. I also asked participants to report on the strength of their experience of vection (i.e., the sensation of self-motion in the absence of physical movement; see Hettinger, Schmidt, Jones, & Keshavarz, 2014) on a scale from 0 (none) to 10 (very strong). Additional control measures, including the Motion Sickness Susceptibility Questionnaire (MSSQ; Golding, 2006) were employed to measure proneness to motion sickness. The Fast Motion Sickness scale (FMS, (Keshavarz & Hecht, 2011) was used to track the severity of simulator sickness on a scale from 0 (no nausea) to 20 (severe nausea) during the simulation. After the driving task, the well-established Simulator Sickness Questionnaire (Kennedy, Lane, Berbaum, & Lilienthal, 1993) was administered to capture different symptoms of simulator sickness after completing the driving task. These measures were used to account for changes in sickness that may have coincided with age and/or with the available sensory input (see Keshavarz et al., 2015 for a full summary of the simulator sickness results).

3.2 Procedure

Once informed consent was obtained, the medical and driving history questionnaires were administered, along with the MSSQ and the MoCA. Participants were then randomly assigned to either the visual only or the visual + auditory condition of the driving task. A between-subjects design was used to avoid carryover effects between sensory conditions. Participants were seated inside the driving simulator where they were instructed to maintain a target speed of 80 km/h, to adhere to the center of their lane, and to drive the simulator as they would their own vehicle. The participant then embarked on each of the five road courses. The order in which the courses were presented was counterbalanced. The first course that participants received always served as an acclimatization period that allowed them to become familiar with the feel of the simulator’s
controls. During this acclimatization period, a digital speedometer was present to assist participants in achieving and maintaining their target speed of 80 km/h. Data from the acclimatization period were excluded from the statistical analyses. The four subsequent drives served as experimental drives in which the speedometer was occluded and participants were to rely only upon the available sensory inputs in order to estimate and maintain their 80 km/h target speed.

At the start of each drive, the vehicle was stationary and the participant was instructed to bring the vehicle up to 80 km/h and to maintain this speed to the best of their ability. They were instructed to then decelerate slowly and to bring the vehicle to halt at the end of the drive, which was demarcated by the discontinuation of the paved roadway and guardrails. These acceleration and deceleration periods were excluded from the data analyses. To limit the possibility of participants forgetting the 80 km/h target speed due to memory decay and to constrain the experience of speed adaptation, a phenomenon whereby the visual perception of speed diminishes with prolonged exposure (Evans, 1991), I included a refresher drive between each experimental drive. During the refresher drives, the speedometer was made visible again and the driver was instructed to accelerate to 80 km/h and to maintain 80 km/h for a period of 60 seconds. Once this period was complete, they were instructed to return to a complete stop and the subsequent experimental drive was initiated. Data from these refresher periods were also excluded from the analyses.

For the duration of the simulation, the researcher sat inside the lab and asked the participant to report their level of sickness on the FMS scale once every 60 seconds over the duration of the five experimental drives (each 5-7 mins in length) and the interleaving refresher sessions. At the end of each experimental drive, participants were offered a break from the simulation, which nearly all participants declined. Once all experimental drives were complete, participants were asked to rate the realism of the components of the simulation along with the strength of the vection that they experienced.
3.3 Results

My primary objective was to examine driving performance across the experimental drives during which the speedometer was occluded and participants were required to rely only on the available sensory information (drives 2-5). Thus, I employed a series of mixed factorial ANOVAs with the between-subjects factors age (younger vs. older) and sensory condition (visual only vs. visual + auditory) and the within-subjects factors road geometry (straights vs. curves) and drive number (2, 3, 4, 5). A priori alpha level was set to $\alpha=.05$. The Bonferroni correction for multiple comparisons was applied to all post-hoc tests.

3.3.1 Mean speed

Mauchly’s test of sphericity indicated that the assumption of sphericity had been violated for the factor drive number, $\chi^2(5)=11.38, p=.026$, therefore degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon=.78$). There was a main effect of age group, $F(1,32)=4.35, p = .045, \eta^2_p = .12$, in which older adults drove more slowly ($M=81.81, SE=2.19$) than younger adults ($M=87.94, SE=1.96$). I observed a main effect of road geometry, $F(1,32)=17.39, p < .001, \eta^2_p = .35$, in which drivers drove more slowly on curved road segments ($M=84.19, SE=1.44$) than on straight road segments ($M=85.56, SE=1.51$). I also observed a main effect of drive number, $F(2.37,76.09)=6.99, p < .001, \eta^2_p = .18$. A post-hoc Bonferroni test revealed that participants drove at higher speeds in the third, fourth, and fifth drives than in the second drive (see Figure 3). There was a significant three-way Age Group x Geometry x Sensory Condition interaction, $F(1,32)= 9.38, p = 0.004, \eta^2_p = 0.23$. Older adults drove significantly slower when traversing curved road segments compared to straight road segments in the visual only sensory condition, but not in the visual + auditory condition (see Figure 3.3). There was also a significant Age Group x Geometry interaction $F(1,32)=15.529, p<.001, \eta^2_p = 0.33$ in which older adults traversed curved road segments at a lower rate ($M=80.47, SE=2.16$) than they traversed straight road segments ($M=83.15, SE=2.25$), and at a lower rate than younger adults traversed curved road segments ($M=87.91, SE=1.93$). No other effects or interactions were significant ($F_{\leq3.73}, p_{\geq.062}$).
To more closely examine the impact of the available sensory inputs on speed accuracy, one-sample t-tests were used to compare mean speed in each sensory condition against the target value of 80 km/h for each age group and road geometry, aggregating performance across the experimental drives. For younger adults, speed was significantly greater than the target in all comparisons ($t \geq 3.49$, $p \leq 0.007$). For older adults, speed was only significantly greater than the
Figure 3.3. Mean speed separated by age group, sensory condition, road geometry, and drive number. Error bars are ±1SE. There were significant main effects of age group and of road geometry. Participants drove faster in drives 3, 4, and 5 than in drive 2 but drove slower on curved segments than on straight segments overall. There was an age x sensory condition x road geometry interaction in which older adults in the visual only condition traversed curved road segments at a lower rate than straight road segments.
80 km/h target when traversing the straight road segments in the visual-only condition \( t(7)=2.72, p=.030 \). Otherwise, older adults’ speed did not differ significantly from the 80km/h target.

### 3.3.2 Standard deviation in speed

Mauchly’s test of sphericity indicated that the assumption of sphericity had been violated for the factor drive number, \( \chi^2(5)=38.85, p<.001 \), therefore degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity (\( \varepsilon=0.56 \)). All main effects were significant. There was a main effect of age group, \( F(1,32)=19.00, p<.001, \eta_p^2=0.37 \), in which older adults exhibited a higher standard deviation in speed (\( M=9.33, SE=0.70 \)) than younger adults (\( M=5.20, SE=0.63 \)). There was a main effect of sensory condition in which standard deviation in speed was lower in the visual + auditory condition (\( M=5.12, SE=0.67 \)) than in the visual-only condition (\( M=9.41, SE=0.670 \)). There was a main effect of road geometry, \( F(1,32)=6.24, p=0.018, \eta_p^2=0.16 \), in which standard deviation in speed was greater on curved road segments (\( M=7.72, SE=0.602 \)) than on straight road segments (\( M=6.81, SE=0.39 \)). There was a main effect of drive number, \( F(3,96)=6.60, p<0.001, \eta_p^2=0.17 \). A post-hoc Bonferroni test (\( \alpha=0.05 \)) revealed that the standard deviation in speed was lower in the fourth (\( M=6.13, SE=0.501 \)) and fifth (\( M=6.14, SE=.528 \)) drives than in the second drive (\( M=8.67, SE=.76 \)), see Figure 3.4. I also observed a significant Age Group x Sensory Condition interaction, \( F(1,32)=4.49, p=0.042, \eta_p^2=0.123 \). For older adults, the addition of auditory inputs yielded a lower standard deviation in speed than visual input alone. For younger adults, there was no difference in performance between sensory conditions (see Figure 3.4). No other interactions were significant (\( F<4.08, p \geq 0.052 \)). Older adults in the visual-only condition maintained a significantly greater mean speed than those in the visual + auditory condition. This greater speed could have inflated speed variability, thereby confounding the effect of sensory condition on speed variability. Thus, I transformed SD speed into z-scores to normalize SD speed across groups and submitted them to the 4-way ANOVA to confirm my observations. The Age Group x Sensory Condition interaction remained significant, \( F(1,32)=5.19, p=0.029, \eta^2=0.140 \), and post-hoc Bonferroni tests confirmed that older adults in the visual only condition (\( M=1.08, SD=1.9 \)) were significantly more variable in the speed that they maintained than those in the visual +auditory condition (\( M=-1.9, SE=.19 \)).
Figure 3.4. Standard deviation in speed separated by age group, sensory condition, road geometry and drive number. Error bars are ±1SE. There was an age x sensory condition interaction in which older adults exhibited less variability in speed when both visual and auditory inputs were available compared to when only visual inputs were available. Note also main effects of age group and of sensory condition.
3.3.3 Lateral control

RMSE lateral position was examined for the experimental drives, comparing between age groups, sensory conditions, and road geometry. No effects were significant for this parameter. There were no significant main effects of age group, \( F(1,32)= 3.00, p = 0.09, \eta^2_p = 0.09 \); sensory condition, \( F(1,32)= 2.87, p = 0.09, \eta^2_p = 0.08 \); road geometry, \( F(1,32)= 2.76, p = 0.11, \eta^2_p = 0.08 \); or drive number, \( F(1,32)= 1.85, p = 0.14, \eta^2_p = 0.05 \). No interactions were significant.

3.3.4 Baseline performance across groups

Older adults in the visual-only condition were significantly older \((M=74.5, SE=2.36)\) than older adults in the visual + auditory condition \((M=66.75, SE=1.41)\), \(t(14)=2.82, p=.014\). The mean age of the visual only older adult group was inflated by three older adults who were above the age of 75. To ensure that differences in performance were due to the available sensory inputs and not due to baseline differences in performance related to the disparities in the demographic composition of each group within my design, I first examined driving performance across groups within the acclimatization drive. In this drive, all participants were able to view the speedometer and thus any differences in the capacity to maintain the target speed would ostensibly stem from participants’ inherent performance variability. Ultimately, there were no differences across all groups in mean speed, standard deviation in speed, or RMS lateral position within the acclimatization period \((t \leq -1.15, \min p \geq .268)\). Further, I also used bivariate correlations to examine the relationship between age and each of the driving performance measures aggregated across the four experimental drives. There were again no significant correlations observed for any of the driving parameter measures across all of the groups, apart from one significant positive correlation between age and speed variability for the older adult visual only group \((r=.83, p=.010)\), which I address in the Discussion.

3.3.5 Perceived realism

To examine how the experience of realism changed across the available sensory conditions, I analyzed each of the self-report measures pertaining to realism using a series of two-way, Age x Sensory Condition ANOVAs. Non-parametric analyses were also performed to confirm the
veracity of my ANOVA results. For “overall driving feeling” there was no effect of age group, $F(1,30)=2.33, p=.14, \eta_p^2=0.07$, but there was a main effect of sensory condition, $F(1,30)=10.51, p=.003, \eta_p^2=0.26$, in which the visual + auditory condition was rated as being significantly more realistic ($M=5.2, SE=.36$) than the visual only condition ($M=3.5, SE=.38$). This observation was confirmed with a Mann-Whitney U test, ($U=60.50, p=.003$ two-tailed). For the realism of the steering, braking, gas pedal, and the strength of vection, no effects were significant.

3.3.6 Simulator sickness

To assess the relationship between simulator sickness and driving performance, I took the total SSQ score and the peak FMS score of the participants who completed the experiment and correlated those scores with each driving performance measure, aggregated across the experimental drives and across road geometry. There were only two significant bivariate correlations: for younger adults in the visual only condition, peak FMS score was negatively correlated with standard deviation in speed ($r=-.83, p=.003$) and for older adults in the visual auditory condition, total SSQ score was negatively correlated with mean speed ($r=-.77, p=.035$). Note that there was no effect of sensory condition on dropout rates (see Keshavarz et al., 2015). Ultimately, the current evidence does not suggest that increased simulator sickness led to diminished driving performance or that poor driving performance exacerbated simulator sickness.

3.4 Discussion

There is growing evidence to suggest that the manner in which visual and auditory sensory inputs are integrated may change in late adulthood, but most of this evidence is derived from simple stimulus detection or stimulus discrimination tasks (e.g., Laurienti et al., 2006). These tasks are powerful and highly controlled, but much remains to be understood about how these effects generalize to other types of tasks and/or whether there are functional consequences associated with age-related changes in multisensory integration. Thus, I developed a multisensory driving task in which I systematically manipulated the presence or absence of congruent auditory input and used subsequent driving performance to index age-related differences in the interaction between visual and auditory cues. I predicted that auditory input
would affect driving performance measures associated with speed (but not with lane keeping) and that these effects would be proportionally greater among older adults. When I examined standard deviation in speed during the experimental drives, I observed that speed variability was lower in the visual + auditory condition relative to the visual-only condition for both younger and older adults. This pattern of observations aligns well with previous driving research indicating that compared to driving with visual input alone, speed variability is reduced in the presence of congruent auditory input (e.g., Denjean et al., 2012). More importantly, the magnitude of these benefits was greater among older adults compared to younger adults. This observation is generally consistent with the findings reported by basic psychophysical studies exploring age-related changes in multisensory integration. Specifically, they mirror the principle of inverse effectiveness and the observation that congruent visual and auditory cues confer greater gains in performance for older adults than for younger adults, compared to the constituent unisensory inputs presented in isolation of one another (e.g., Laurienti et al., 2006; Peiffer et al., 2007).

When I examined mean speed, I observed that older adults drove at significantly slower speeds than younger adults, ultimately traveling under the target speed of 80km/h at the outset of the driving task. Older drivers have a tendency to self-regulate their behaviour in order to minimize crash risk (see Charlton, Oxley, Fildes, Oxley, & Newstead, 2003). This can include reducing speed when faced with challenging scenarios (e.g., Trick, Toxopeus, & Wilson, 2010). In the current investigation, older adults may have traveled at a lower rate of speed compared to younger adults to maintain broad safety margins as they acclimatized to the driving task, a process that can take longer for older adults to complete (e.g., Kawano et al., 2012). Conversely, younger adults are known to drive faster than older adults in both real vehicles and in driving simulators (see Mullen, Charlton, Devlin, & Bedard, 2011 for review) and do so regardless of the prevailing task demands (e.g., Trick et al., 2010). Therefore, the overall differences in speed between older and younger adults were generally consistent with previous driving research examining age-related differences in performance. More importantly, I also observed evidence to suggest that older adults were more greatly affected by the presence of combined visual and auditory inputs when estimating and maintaining their speed. In the visual-only condition, older adults significantly reduced their speed to traverse the curved road segments but in the visual +
auditory condition, older adults maintained nearly identical speeds on the straight and curved road segments. The presence of auditory cues allowed older adults to maintain speeds that were lower on average and ultimately closer to their 80 km/h target speed. This speed may have been more suitable for negotiating both straight and curved road segments and thus no changes in speed were required. In the visual only condition, the absence of auditory cues may have left older adults with a diminished capacity to estimate their speed, leading them to drive faster than intended (e.g., Evans, 1970; Horswill & Plooy, 2008) and thereby requiring them to reduce their speed in order to retain control over their vehicle when negotiating curved road segments. That is not to say that auditory cues provided an absolute measure of speed, but rather that the combination of visual and auditory input augmented older adults’ perception of relative speed.

The interaction between age and sensory condition that I observed, particularly in the dimension of speed variability, suggests that age related changes in the interaction between visual and auditory cues as observed in the context of simple stimulus detection and discrimination tasks may extend to the continuous and dynamic visual and auditory cues that we encounter in our daily lives. This also suggests that age-related changes in the interaction between visual and auditory cues may have important implications for the way that older adults perform everyday multisensory tasks including, but not limited to, driving a motor vehicle.

That said, there are several additional factors that may have contributed to the pattern of observed performance that must be addressed. For instance, the presence of auditory cues may have had a broad influence on task performance by modulating more global factors, such as enhanced sustained attention, an increased state of arousal, a greater sense of presence in the simulation, or a greater sense of perceived realism. However, I did not observe evidence of global changes across all aspects of driving task performance, rather, only the driving parameters that I predicted would be affected by auditory feedback (i.e., speed perception) were influenced by the availability of auditory cues. Lane keeping, a driving parameter that I predicted would not be affected by auditory feedback was not influenced by the availability of auditory cues. The specificity of these performance outcomes indicates that auditory cues influenced driving performance by augmenting speed perception rather than by exerting a global influence on task performance. However, an important factor that may have contributed to age-related differences in performance was cumulative driving experience. While the age-related differences in
performance that I observed may stem from age-related differences in multisensory self-motion perception, they may also reflect age-related differences in years/km lifetime driving experience. As driving experience accumulates, a number of important cognitive and perceptual changes occur as a function of this experience. For instance, drivers who have traveled between 10,000 and 50,000 km begin to develop the ability to rely on the ambient or peripheral visual channel to govern lateral position (Horrey, Wickens, & Consalus, 2006; Summala, Nieminen, & Punto, 1996). It is also possible that in parallel, drivers learn with increasing experience how the frequency and amplitude of engine and road/tire noises scale according to speed and learn to use this information help govern speed (e.g., Merat & Jamson, 2011). This learned reliance on auditory information for speed perception may lead older adults to be more susceptible to changes in performance due to the presence or absence of auditory cues. Thus, future research in this domain should seek to employ multisensory tasks in which the relative effects of age and previous experience can be parsed.

3.5 Limitations

The high attrition rate coupled with my between-subjects design made it difficult to maintain groups that were well matched in terms of age and gender. For example, there was a difference in the mean age of the older adults in the visual-only condition and the older adults in the visual + auditory condition. This is an important consideration because performance becomes increasingly variable with advanced age across several domains (e.g., Hultsch, MacDonald, & Dixon, 2002). Indeed, I observed a positive correlation between age and speed variability within the visual only older adult group. However, age-related differences alone cannot account for the effect of sensory condition, given that the two groups were no different in their driving performance at baseline. Gender differences in driving performance are also an important factor to consider but the modest number of men and women and relative imbalance within each cell of my design does not permit me to make meaningful comparisons between men and women. Future investigations should consider gender differences in unisensory and multisensory driving performance.

An additional limitation associated with my sample was that I utilized self-report measures to screen for sensory impairment, which can be unreliable. While I assume that the older adults in
my sample were within the normal hearing range, it is possible that a clinical audiometric examination would reveal some degree of age-related hearing loss (see Pichora-Fuller & MacDonald, 2009; Pichora-Fuller et al., 2017). Hearing loss is an important factor to account for in the context of driving performance, given associations have been shown between the risk of having a collision and hearing loss (e.g., Hickson, Wood, Chaparro, Lacherez, & Marszalek, 2010; Picard, 2008). Future studies should incorporate central and peripheral audiometric testing to better understand the association between hearing status and driving performance during multisensory driving tasks.

Finally, the driving task was not able to precisely quantify the relative contributions of visual and auditory inputs to this task or to determine whether they were optimally integrated. In order to achieve this, one would have to obtain performance measures during both unimodal (vision alone and auditory alone) and bimodal conditions. Because it is impossible to control a motor vehicle with auditory cues alone, I was only able to examine how combining visual cues with congruent auditory cues affected driving performance and age-related differences therein.

3.6 Conclusions and future directions

The goal of the present study was to determine whether evidence of age-related differences in visual-auditory cue integration would be observed in the context of real-world multisensory tasks that involve continuous and dynamic sensory inputs. I found that both younger adults and older adults exhibited a reduction in speed variability in the presence of congruent visual and auditory cues compared to visual cues alone, but this effect was greater among older adults. This finding provides preliminary evidence to suggest that age-related differences in multisensory integration may generalize to more complex sensory inputs and that heightened multisensory integration may carry functional implications for older adults in the context of self-motion and mobility-related tasks. These observations could also have important implications for the design of real vehicles. For example, automakers are moving toward quieter interiors by utilizing advanced sound deadening materials (Hellier et al., 2011) and even by employing active noise cancellation technologies (Hansen, 2002; Hansen & Snyder, 1996; Wang & Wang, 2012). The initiative to dampen or to eliminate vehicle and road noises could be inadvertently removing information that otherwise helps drivers to retain control over the speed of their vehicle (Hellier et al., 2011). The
current findings suggest that this may be particularly true for older adults, who appear to rely more heavily than younger adults upon the presence of congruent auditory input in order to govern their speed effectively and consistently. More recent initiatives have highlighted the need to be selective in terms of the frequencies that are attenuated, such that useful auditory information (e.g., engine rpm) is still transmitted to the driver, while repetitive and overrepresented sounds (e.g., road and tire noise at high speed) are reduced (e.g., Duan, 2011). This selective approach to active noise cancellation could be important for the safety of older drivers who may rely more heavily on auditory cues for accurate and reliable speed control. In the current investigation I only considered the impact of congruent sensory cues and thus future research should endeavor to explore the outcomes associated with incongruent sensory cues. In our daily lives, we are immersed in sensory signals and good performance is contingent not only upon our capacity to combine related sensory cues but also upon our capacity to segregate unrelated cues (Meredith et al., 1987). In light of the observation that the performance facilitation associated with congruent cues (e.g., Laurienti et al., 2006; Peiffer et al., 2007) appears to generalize to more complex multisensory tasks, it stands to reason that the performance decrements associated with incongruent cues (e.g., Guerreiro et al., 2013; Setti et al., 2013) may also generalize to real-world, multisensory tasks. Future investigations will aim to characterize both the performance enhancements and the performance decrements associated with age-related differences in multisensory integration in order to fully appreciate the functional consequences that they may carry.
Chapter 4
Age-related differences in visual-vestibular self-motion perception

The study that appears in this chapter is published as:


In Chapter 3, I observed that presenting visual cues to self-motion and adding or removing congruent auditory cues to self-motion had a differential effect on the driving performance of older and younger adults. From this, I inferred that the age-related differences in multisensory integration observed in the context of simple visual-auditory stimulus detection and stimulus discrimination extend to the continuous and dynamic cues that we experience during self-motion. This provides some preliminary evidence to suggest that there could indeed be age-related differences in terms of multisensory self-motion perception that are observable at the behavioural level. However, auditory cues tend to play more of an auxiliary role in self-motion perception (Stoffregen et al., 2009; Väljamäe, 2009). Auditory cues can facilitate self-motion perception in contexts like driving where the observer can learn the relationship between auditory cues and self-motion (e.g., Merat & Jamson, 2011) but auditory cues may not provide meaningful cues to self-motion in every behavioural context. Instead, in most natural behavioural contexts, observers tend to rely upon the visual and vestibular systems for reliable self-motion perception. The visual and vestibular systems typically present tightly congruent cues to self-motion and a synergistic relationship exists between the two systems in that the strengths associated with the vestibular system can be used to overcome the limitations associated with the visual system and vice versa (see DeAngelis & Angelaki, 2012). Thus, having established that age-related differences in the effect of cue combination may extend to the more continuous and dynamic cues experienced during self-motion (Chapter 3), my goal moving forward was to determine whether they also extend to the cue combinations that are more central to self-motion perception as it occurs in our daily lives. In Chapter 4, I will review current knowledge pertaining to visual-
vestibular integration in the context of self-motion perception and I will then discuss my simulated driving paradigm designed to characterize any age-related differences in the effect of combining visual and vestibular cues to self-motion.

4 Introduction

In order to navigate effectively, we must maintain a precise and accurate representation of our own movement. Our brain achieves this by integrating information about our speed, heading, and traveled distance from across our sensory systems (see Campos & Bülthoff, 2012). The important role that multisensory integration plays in self-motion perception has been well-illustrated by, for example, past research studying the interactions between the visual and vestibular systems. Both systems can detect self-motion but, due to their respective limitations, neither sensory system is perfectly reliable across all possible behavioral and environmental conditions (Butler, Campos, & Bülthoff, 2015; Butler et al., 2011, 2011, 2010; Cullen, 2012; Ernst & Bülthoff, 2004). For example, visual cues to self-motion are diminished under low contrast conditions, such as darkness (e.g., Warren, Kay, Zosh, Duchon, & Sahuc, 2001) or fog (e.g., Snowden, Stimpson, & Ruddle, 1998) and vestibular input is diminished when travelling at a constant velocity (see Berthoz, Pavard, & Young, 1975; Goldberg, 2012; Siegle, Campos, Mohler, Loomis, & Bülthoff, 2009). By integrating visual and vestibular input, it is possible to achieve a self-motion percept that is more precise than that afforded by either sensory system in isolation (Butler et al., 2010; Cullen, 2012; Fetsch et al., 2012, 2009; Gu et al., 2008; Morgan et al., 2008), and one that is more robust to conditions in which one or both systems can no longer provide reliable information (DeAngelis & Angelaki, 2012a; Dichgans & Brandt, 1978; Siegle et al., 2009). While this process has recently been characterized for younger adults (Butler, Campos, & Bülthoff, 2014; Butler et al., 2010; Campos, Butler, & Bülthoff, 2012; Fetsch et al., 2009) and non-human primates (Fetsch et al., 2009; Gu et al., 2008), less is understood about how visual-vestibular integration changes with age and how these changes might affect the way that older adults perceive and govern their own movement. Because aging can lead to declines in both vision and vestibular functioning (Iwasaki & Yamasoba, 2015; Owsley, 2011), it is likely that in addition to transient, context and environmentally dependent changes in the reliability of visual and vestibular input, older adults also contend with gradual, but persistent age-related declines in sensory and perceptual reliability. This is evidenced, for instance, by the fact that...
when using optic flow (see Gibson, 1950) alone to make relative heading judgments (i.e.,
determining whether a linear egocentric movement was to the left or to the right of a visual
target), older adults exhibit greater perceptual thresholds than younger adults (Warren &
Hannon, 1988). Older adults are also less precise than younger adults when making absolute
heading judgments such that, when asked to indicate the angle of a linear motion on a scale, their
mean heading estimation errors are greater than those displayed by younger adults (Lich &
Bremmer, 2014). Furthermore, when physically translating in total darkness and thereby relying
predominantly upon the vestibular system to perceive the direction of their movement (i.e., left-
right, forward-backward, up-down, or yaw left-right), older adults require a higher rate of
acceleration in order to reliably discern the direction of their movement (Roditi & Crane, 2012).
Ultimately, the potentially diminished reliability of the visual and/or vestibular information that
older adults receive could lead them to utilize redundant visual and vestibular inputs to a
proportionally greater extent than younger adults to achieve a reliable self-motion percept and to
thereby govern self-motion.

Empirical evidence to support the hypothesis that older adults demonstrate heightened
multisensory integration originally stems from research in the domain of visual-auditory
integration. Specifically, when visual cues (i.e., flashes of light) are combined with congruent
auditory cues (i.e., beeps), this yields faster stimulus detection times compared to when either
cue is presented in isolation (e.g., Hughes, Reuter-Lorenz, Nozawa, & Fendrich, 1994); the
magnitude of the multisensory performance gains being greater among older compared to
younger adults (e.g., Laurienti et al., 2006; Peiffer et al., 2007). More recent work has
demonstrated that these performance outcomes may be task dependent, such that other studies
have shown no age-related differences in multisensory relative to unisensory performance in the
context of, for example, speech perception (Tye-Murray et al., 2010). My own research has
suggested that age-related changes in visual-auditory integration may extend to some tasks
involving self-motion perception (i.e., Chapter 3). Specifically, I observed that when driving in a
simulator, younger and older adults were more precise and more accurate in the speed that they
maintained when they were provided with both visual motion cues (i.e., optic flow) and auditory
motion cues (i.e., engine, tire, and wind noise), compared to when only visual cues were
available. Importantly, the performance gains were greater among older compared to younger
adults (See Chapter 3). Thus, there is evidence to suggest that older adults may utilize redundant visual and auditory cues to a proportionally greater extent than younger adults to inform their self-motion percept.

However, it is not clear whether this same pattern of performance generalizes when combining visual and vestibular cues to self-motion, given that there may be fundamental differences in the way that visual and vestibular cues are integrated compared to visual and auditory cues. Because self-motion creates an inherent causal link between dynamic visual and vestibular input, they may be more tightly integrated compared to externally generated visual and auditory cues (Campos et al., 2012; Frissen, Campos, Souman, & Ernst, 2011; Prsa et al., 2012). Thus, a closer examination of how older and younger adults utilize congruent visual and vestibular inputs during self-motion perception is warranted to ascertain whether age-related differences are again observed, as they have been in the context of visual-auditory integration.

There is evidence from research examining age-related changes in mobility indicating that there may be changes in the way that older adults utilize and combine visual and non-visual, body-based cues (i.e., proprioceptive and vestibular cues). For instance, older adults often exhibit broad declines in their capacity to maintain a stable posture (see Maki & McIlroy, 1996) and to maintain a steady gait (see Winter, 1991) and it has been posited that these declines may relate, at least in part, to age-related differences in the way that the constituent visual, vestibular, and proprioceptive cues are combined (see Horak et al., 1989; Jeka et al., 2006; Setti, Burke, Kenny, & Newell, 2011; Teasdale, Stelmach, & Breunig, 1991; Woollacott, 2000). For instance, varying the congruency of visual, vestibular, and proprioceptive inputs relative to one another can have differential effects on older and younger adults, wherein older adults exhibit larger changes in their postural responses or navigational strategies when faced with incongruent sensory feedback compared to younger adults (Berard et al., 2009; Deshpande & Patla, 2007; Jeka et al., 2006; Stapleton, Setti, Doheny, Kenny, & Newell, 2014). Further, when having to use self-motion cues to update their position in space (i.e., path integration; Mittelstaedt & Mittelstaedt, 1980), older adults demonstrate greater performance decrements relative to younger adults when they are restricted to using either vestibular/proproprioceptive input alone (e.g., Adamo et al., 2012) or visual input alone (e.g., Harris & Wolbers, 2012) compared to when both cues are available. Taken together, these observations provide some evidence to suggest that older adults may use and
combine coincident visual and vestibular cues differently than younger adults. Previous experiments have focused on very basic mobility tasks (e.g., postural stability while standing or path integration over short trajectories). Therein, they have typically utilized highly controlled, albeit relatively simple and transient visual and vestibular cues. Self-motion perception as it occurs in our daily lives typically involves actively generated, comparatively more complex, and sustained motion cues. Thus, my objective was to determine whether evidence of age-related differences in the way that visual and vestibular cues contribute to self-motion perception could be observed under more realistic task constraints.

As mentioned above, I previously utilized a simulated driving task to assess how older and younger adults’ self-motion perception changes when driving with visual and auditory cues combined, compared to a control condition in which only visual motion cues were available (Chapter 3; Ramkhalawansingh et al., 2016). In the current experiment, I built upon this research by examining how older and younger adults’ self-motion perception differed when a combination of visual and vestibular cues was available, using the same visual only control group as a point of comparison. During the simulated driving task, participants were required to maintain a prescribed target speed and govern their lateral position. Driving performance was then used to make inferences about age-related differences in the use of visual and vestibular cues to perceive and control self-motion. Previous driving research on younger and middle-aged adults (ranging in age from 20-47 years) have demonstrated that optic flow conveys information that is relevant to both speed maintenance and lateral control (Kountouriotis et al., 2013; Mourant, Ahmad, Jaeger, & Lin, 2007), but that the addition of congruent vestibular cues can bolster lateral control over visual cues alone and can improve speed governance when traversing curves, during which lateral acceleration and the resulting innervation of the semicircular canals is most pronounced (Reymond et al., 2001; Winsum & Godthelp, 1996). Thus, I predicted that both younger and older adults would exhibit changes in lateral control and in speed maintenance as a function of whether vestibular cues were available and that the magnitude of the performance differences across sensory conditions would be greater among older adults.
4.1 Methods

4.1.1 Participants

Thirty-two older adults and twenty-six younger adults were recruited from the community. The study protocol was approved by the University Health Network Research Ethics Board (REB 12-015-DE). All participants were prescreened by telephone interview to ensure that they held a driver’s license and that they had no serious medical conditions (e.g., seizures, stroke), and no self-reported uncorrected visual or hearing impairments. Participants were compensated at a rate of $15 per hour. On site, informed consent was obtained and the Montreal Cognitive Assessment was administered to screen for mild cognitive impairment (inclusion criteria was >26/30; (Nasreddine et al., 2005). There were two experimental groups (between-subjects): 1) visual cues alone or, 2) visual + vestibular cues combined. The visual only control group was the same group that appeared in Chapter 3 whereas the visual + vestibular condition group is the novel extension of this previous work and these data have not previously been reported. Sixteen older adults (7 visual only, 9 visual + vestibular) and five younger adults (3 visual only, 2 visual + vestibular) withdrew prior to completing the experiment due to simulator sickness (for complete simulator sickness findings, see Keshavarz et al., 2015). These sickness rates (50% older adults, 15% younger adults) are comparable to those reported in previous investigations (e.g., (Cassavaugh et al., 2011; Reed-Jones et al., 2008). Due to a technical issue, data was not recorded for one younger adult in the visual + vestibular condition. Cases of incomplete data due to simulator sickness or technical issues were excluded from the analyses. Ultimately, there were 8 older adults (6 male, 2 female; $M=74.50$, $SD=6.67$) and 10 younger adults (4 male, 6 female; $M=26.30$, $SD=4.13$) in the visual only condition and 8 older adults, (6 male, 2 female; $M=65.62$, $SD=1.59$) and 10 younger adults (6 male, 4 female $M=23.9$, $SD=3.18$) in the visual + vestibular condition. Note that the high attrition rate led to a difference in the mean age between the older adults in the visual only condition and the older adults in the visual + vestibular condition. This does not appear to be confounded with the effects of sensory condition, as will be discussed below.

4.1.2 Design

There were two between-subjects variables: age group (younger vs. older) and sensory condition (visual only vs. visual + vestibular). Additionally, there were two within-subject variables: drive
number (1, 2, 3, 4) and road geometry (straight vs. curved road segments). The result was a 2 (age) x 2 (sensory condition) x 4 (drive number) x 2 (road geometry) mixed factorial design. A mixed factorial design was used to avoid carryover effects between the sensory conditions.

### 4.1.3 Apparatus & Stimuli

Note that the same apparatus, driving task, visual stimulus and dependent measures that were utilized in Chapter 3 are also utilized here. The experiments are nearly identical with the exception that instead of adding or removing congruent auditory cues as I did in Chapter 3, in the current study I add or remove vestibular cues (described in greater detail below).

To implement the driving task and present the constituent sensory information, I utilized StreetLab, a dome-shaped virtual reality laboratory at the Toronto Rehabilitation Institute’s iDAPT Centre for Rehabilitation Research (see Figure 4.1A). StreetLab was outfitted with a half-cab structure that contained a car seat, a Logitech steering wheel, gas/brake pedals, and a digital speedometer (see Figure 4.1B). The visual driving scene was rendered using the irrLicht engine and displayed on StreetLab’s curved projection screen (see Figure 4.1C) using six synchronized projectors (Eyevis ESP-LED; Figure 4.1D), each with a resolution of 1920x1200. This created an immersive virtual driving environment with a total field-of-view of 240° horizontally and 105° vertically at 6.5 arcmin/OLP. The imagery was updated at 60Hz and there was a time delay of approximately 50 ms between the driver inputs and the visual display of the outside world. The driving scenario consisted of clear daytime conditions on a two-lane rural road with guardrails, surrounded by an open grassy area with agricultural scenery (i.e., farms with barns and silos on the far horizon) that mainly provided optic flow information (see Figure 4.1C). There were no other moving objects (e.g., vehicles, pedestrians, animals, etc.) or obstacles in the scene. This scenery was selected over other potential environments (e.g., a cityscape) because complex scenery can exacerbate simulator sickness (e.g., Reed-Jones, Trick, Toxopeus, Reed-Jones, & Vallis, 2009).
Figure 4.1. Solidworks™ rendered cutaway view of StreetLab, a fiberglass dome that can be configured into different virtual reality environments (A). The driving task configuration consisted of a mock cab comprised of a steel frame, plastic body panels, a real car seat, a Logitech steering wheel and pedals, and a digital speedometer (B). StreetLab contains six Eyevis ESP-LED projectors (C) that generate a 240 degree horizontal x 105 degree vertical field of view image on a curved projection screen (D). StreetLab is shown here mounted on a 6 degree-of-freedom hydraulic motion platform that was used to provide physical motion cues (E).
My goal was to capture a reasonably large body of driving performance data for each subject (≥25 minutes), but to mitigate the risk of inattention, fatigue, and simulator sickness associated with driving for extended periods of time without interruption (e.g., Philip et al., 2003; Yanko & Spalek, 2013). Thus, I created five separate drives that each took 5-7 minutes to complete. To ensure that each drive was nearly identical in terms of their complexity and difficulty, I created a series of straight road segments and curved road segments 400 meters, 800 meters, or 1200 meters. Each course was comprised of the same straight and curved road segments but arranged in different sequences to prevent drivers from becoming too familiar with any given sequence. In addition to thwarting adverse effects, this approach allowed me to observe whether participants’ performance changed as they adapted to the simulated driving task, and to determine whether this adaptation process was affected by age and/or the available sensory inputs. The first course that participants received always served as an acclimatization period that allowed them to become familiar with the feel of the simulator’s controls. During this acclimatization period, a digital speedometer was present to assist participants in achieving and maintaining their target speed of 80 km/h. The four subsequent drives served as experimental drives in which the speedometer was occluded and participants were to rely only upon the available sensory inputs in order to estimate and maintain their 80 km/h target speed. Data from the acclimatization period were excluded from the statistical analyses.

In order to provide vestibular cues to self-motion, the laboratory was mounted on a Bosch-Rexroth HyMotion 11000 6-degrees-of-freedom hexapod motion platform (Figure 4.1E). This enabled me to introduce a combination of pitch and longitudinal translation to convey the forces associated with acceleration and braking and to introduce a combination of roll, yaw, and lateral translation to convey the centrifugal forces associated with cornering. A classic motion drive algorithm was employed (see Reid & Nahon, 1985), with a moderate gain of 0.4 and second-order high-pass filters in all axes. The filter break frequencies were set at 2 rad/s for the translational degrees of freedom, while roll and pitch were set at 0.05 rad/s and 0.7 rad/s in yaw. The low-pass tilt-coordination filters for surge and sway were third order, combining a 2 rad/s second order and 50 rad/s first order filter, with rate limits of 6°/s. The vehicle dynamics model that dictated the handling characteristics of the vehicle was developed in the MathWorks’
Simulink environment and were then compiled and run in real-time using Quanser’s QUARC operating system.

Note that while I characterize the driving task as consisting predominantly of visual and/or vestibular stimulation, I recognize that the task involves some concomitant somatosensory and proprioceptive sensory inputs, particularly from the muscles and tendons of the neck.

4.1.4 Driving performance measures

Driving performance was measured by capturing speed (km/h), standard deviation in speed, and root mean squared error (RMSE) in lateral position (m) at a rate of 200Hz. Mean speed and speed variability were used as indices of accuracy and precision in terms of speed maintenance, respectively. RMSE lateral position is a common index of steering performance. Performance measures were separated by road geometry (i.e., straight vs. curved road segments), given that traversing curved road segments represented a higher level of task complexity and a different pattern of vestibular stimulation.

4.1.5 Self-report measures

Following the completion of the driving task, participants were asked to rate the realism of the major components of the simulation including the steering, gas, brakes, accelerator, and the overall driving feel using a series of 7-point Likert scales. They were also asked to report on the strength of their experience ofvection (i.e., the illusory sensation of self-motion; Brandt, Dichgans, & Koenig, 1973) on a scale from 0 (none) to 10 (very strong). Finally, the well-established Simulator Sickness Questionnaire (Kennedy et al., 1993) was administered to capture any persisting symptoms of simulator sickness. Sickness was also captured over the duration of each drive using the Fast Motion Sickness scale (Keshavarz & Hecht, 2011). See Keshavarz et al., 2015 for a full summary of the simulator sickness results.

4.1.6 Postural stability

Balance testing was performed pre and post driving simulation to ensure that participants did not have serious balance impairments that could, in turn, affect driving performance (e.g., Gaspar et
al., 2013), or lead to biases in each of the sensory conditions or age groups. Participants stood on a force plate (AMTI BP12001200) with their feet aligned in parallel (spread 17 cm at the heel) for two, 30 s intervals, first with eyes open then with eyes closed. These data were subjected to a second-order dual-pass Butterworth filter with a 6-Hz cutoff frequency in Matlab to filter out high-frequency noise. Matlab was then used to derive mean position (cm), standard deviation position (cm), and root mean squared position (cm) both in the X and Y axes and for both intervals (eyes open/closed). Matlab was also used to derive center of pressure (COP) path length (cm) for each interval (eyes open/closed; see Winter, 1995).

4.1.7 Procedure

Once informed consent was obtained, the medical and driving history questionnaires were administered, along with the MSSQ and the MoCA. Participants were then randomly assigned to either the visual only or the visual + vestibular condition of the experimental driving task. Sensory condition was a between-subjects factor to avoid carryover effects. Participants were seated inside the driving simulator where they were instructed to maintain a target speed of 80 km/h, to adhere to the center of their lane, and to drive the simulator as they would their own vehicle. The participant then embarked on each of the five drives. The order in which the drives were presented was counterbalanced across participants. The first drive always served as an acclimatization period that allowed participants to become familiar with the feel of the simulator’s controls. During this period, a digital speedometer was present to assist participants in achieving the 80 km/h target speed. The four subsequent drives served as experimental drives in which the speedometer was occluded and participants were to rely only upon the available sensory inputs to estimate and maintain the target speed.

At the start of each drive, the vehicle was stationary and the participant was instructed to bring the vehicle up to 80 km/h and to maintain this speed to the best of their ability. They were instructed to then decelerate slowly and to bring the vehicle to halt at the end of the drive, which was demarcated by the discontinuation of the paved roadway and guardrails. These acceleration and deceleration periods were excluded from the data analyses. To limit the possibility of participants forgetting the 80 km/h target speed due to memory decay and to constrain the experience of speed adaptation (Evans, 1991), I included a refresher drive between each
experimental drive. During the refresher drives, the speedometer was made visible again and the driver was instructed to accelerate to and maintain 80 km/h for 60 seconds before returning to a complete stop before the subsequent experimental drive was initiated. Data from these refresher periods were also excluded from the analyses.

For the duration of the simulation, the researcher sat inside the simulator and asked the participant to report their level of sickness on the FMS scale once every 60 seconds over the duration of the five drives and the interleaving refresher sessions. At the end of each experimental drive, participants were offered a break from the simulation, which nearly all participants declined. Once all experimental drives were complete, participants were asked to rate the realism of the simulation along with the strength of the vection that they experienced.

4.2 Results

I examined driving performance over the course of the four experimental drives. A mixed-factorial ANOVA including the between-subjects factors age group (younger vs. older) and sensory condition (visual alone vs. visual + vestibular) and the within-subjects factors road geometry (straight vs. curved) and drive number (drives 2, 3, 4, 5) was performed. For all statistical analyses, a priori significance level was set to $\alpha = .05$. Post-hoc tests were corrected using the Bonferroni adjustment for multiple comparisons.

4.2.1 Mean speed

There was a main effect of road geometry, $F(1,32) = 8.947, p = .005, \eta_p^2 = .22$, in which drivers traversed curved road segments more slowly than straight road segments. As was previously reported (Ramkhalawansingh et al., 2016), there was a three-way Age Group x Sensory Condition x Road Geometry interaction, $F(1,32) = 6.89, p = .013, \eta_p^2 = 0.18$. Older adults drove slower ($p < .001$) on the curved road segments than on the straight road segments in the visual only sensory condition, but here I also observed that no such change in speed related to road geometry was observed in the visual + vestibular sensory condition (see Figure 4.2). Younger adults displayed no differences in speed across sensory conditions or road geometry. No other effects were significant.
4.2.2 Standard deviation in speed

Due to violations of sphericity, degrees of freedom were corrected (Greenhouse-Geisser, $\varepsilon = .72$) for analyses involving the factor drive number. There was a main effect of age group, $F(1,32) = 13.83, p < .001, \eta_p^2 = 0.30$, in which older adults exhibited greater speed variability ($M = 10.29$, $SE = .77$) than younger adults ($M = 6.47$, $SE = .69$). There was a main effect of drive number, $F(2.15,68.79) = 5.36, p < .001, \eta_p^2 = .14$, with post-hoc comparisons demonstrating that speed variability decreased over the course of the four experimental drives, ultimately becoming significantly lower ($p = .009$) in the final drive ($M = 7.02$, $SE = .53$) compared to the first experimental drive ($M = 10.37$, $SE = .87$) for both older and younger adults. As previously reported in Chapter 3, I observed a significant Age x Sensory Condition interaction, $F(1,32) = 5.08, p = .031, \eta_p^2 = 0.14$, revealing that in the visual only sensory condition, older adults were significantly more variable in their speed than were younger adults (see Figure 4.3). I also observed a significant three-way Age x Sensory Condition x Road Geometry interaction, $F(1,32) = 6.25, p = .018, \eta_p^2 = 0.16$, in which older adults in the visual only condition were significantly more variable in their speed on the curved road segments than they were on the straight road segments (see Figure 4.3). No other effects were significant.
Figure 4.2. Mean speed (km/h) across age group, sensory condition and road geometry. Error bars are ±1SE. There was a three-way interaction in which older adults in the visual only sensory condition travelled more slowly on curved road segments than on straight road segments.
Figure 4.3. Standard deviation in speed (km/h) across age group, sensory condition and road geometry. Error bars are ±1SE. ** p<.001, *p=0.05. In the visual only sensory condition, older adults were more variable in the speed that they maintained than were younger adults. Additionally, for older adults in the visual only condition, speed was more variable on curved road segments than it was on straight road segments.
4.2.3 Root mean squared error lateral position

There were three cases in which RMSE lateral position was exceptionally high (i.e., > 2.5 SD beyond the mean). Two older adults from the visual-only condition experienced a loss of control, which I operationally defined as instances in which the vehicle’s heading diverged from the heading of the roadway by > 90 degrees. Additionally, one older adult in the visual + vestibular condition drove in the left and right lanes interchangeably. All three cases were omitted from the analyses. Degrees of freedom were corrected for the factor drive number (Greenhouse-Geisser, $\varepsilon = .38$). There was a main effect of age group, $F(1,29) = 4.93, p = .034, \eta_p^2 = .15$, in which older adults were more variable in their lateral position than younger adults (see Figure 4.4). There was a significant Age x Sensory Condition interaction, $F(1,29) = 4.30, p = .047, \eta_p^2 = 0.13$ such that, in the visual + vestibular condition, older adults were significantly more variable in their lateral position than younger adults. No other effects were significant.

4.2.4 Postural stability

A two-way age x sensory condition between-subjects ANOVA was used to examine the pre-simulation COP path length with eyes open and with eyes closed in order to compare the baseline postural stability between participants in the two sensory conditions and between the different age groups. Force plate data were corrupt for three younger adults in the visual-only condition and for one older adult in the visual-only condition and were excluded from the analysis. The ANOVA revealed that there was a main effect of age, $F(1,28) = 4.94, p = .034, \eta_p^2 = 0.15$, in which older adults exhibited greater baseline postural instability than younger adults overall. There was also a main effect of eyes open versus closed, $F(1,28) = 6.05, p = .020, \eta_p^2 = 0.18$, in which postural stability decreased with eye closed. No other effects were significant. I also examined changes in postural responses pre-simulation versus post-simulation to determine whether there were adaptation effects, but no comparisons were significant.
Figure 4.4. RMSE lateral position (m) by age group, sensory condition and road geometry. Error bars are ±1SE. Older adults in the visual + vestibular condition were more variable in their lateral position than were older adults in the visual only condition.
4.2.5 Baseline driving performance across groups

Older adults in the visual-only condition were significantly older ($M = 74.5, SE = 2.36$) than older adults in the visual + vestibular condition ($M = 65.37, SE = .46$), $t(14) = 3.79, p = .002$. To ensure that the pattern of performance that I observed was due to the sensory manipulation and not due to the unintended age difference between the older adult groups, I examined driving performance within the acclimatization drive. In this initial drive, all participants were permitted to view the speedometer and therefore, any differences in speed maintenance would reveal inherent group differences in performance variability. T-tests revealed that there were no differences in mean speed, standard deviation in speed, or RMSE lateral position between the older adults who comprised the visual only condition and those who comprised the visual + vestibular condition ($t \leq -1.88, \min p \geq .101$).

4.2.6 Self-report measures

To examine how the experience of realism compared across sensory conditions, I analyzed the self-report measures pertaining to realism using a series of two-way, age x sensory condition between-subjects ANOVAs. Note that non-parametric tests were also performed and verified the ANOVA’s main effects. However, I report the results of the ANOVA here as my primary goal was to detect interactions between the age and sensory condition factors. For “steering feel”, there was a significant Age x Sensory Condition interaction, $F(1,31) = 5.97, p = .020, \eta_p^2 = 162$, in which younger adults rated steering feel in the visual + vestibular condition as being significantly more realistic ($M = 5.10, SE = .47$) than older adults ($M = 2.88, SE = .52$). For “braking realism”, there was a significant main effect of age group, $F(1,31) = 8.85, p = .006, \eta_p^2 = 0.22$, in which younger adults rated the braking as more realistic ($M = 5.45, SE = .35$) than older adults ($M = 3.82, SE = .41$). For “overall driving feeling”, there was main effect of sensory condition, $F(1,31) = 8.77, p = .043, \eta_p^2 = .139$ such that the visual + vestibular condition was rated as more realistic ($M = 4.53, SE = .33$) than the visual only sensory condition ($M = 3.50, SE = .354$). No other effects were significant.

To determine how simulator sickness influenced driving performance, I took the highest level of sickness that participants reported on the FMS scale (i.e., peak FMS score) and the total SSQ
score and correlated them with each driving performance measure aggregated across the experimental drives and across road geometry. No correlations were significant for FMS score ($r \leq -0.204, p \geq 0.233$) or for total SSQ score ($r \leq -0.24, p \geq 0.160$).

4.3 Discussion

Effective self-motion perception is typically achieved through the integration of visual and vestibular input (DeAngelis & Angelaki, 2012), but age-related changes in their respective reliabilities (e.g., Lich & Bremmer, 2014; Roditi & Crane, 2012) and/or the mechanisms underlying multisensory integration could result in age-related differences in multisensory self-motion perception. To assess this, I employed a basic simulated driving task that required participants to maintain a target speed and maintain lateral position. I then compared a novel condition under which visual information was combined with vestibular information to my previously observed data for which only visual inputs were available. Driving performance measures (speed, standard deviation in speed, and RMSE lateral position) were used as indices of self-motion perception. It was hypothesized that adding vestibular inputs would have a proportionally greater impact on the performance of older adults than that of younger adults.

4.3.1 Mean speed and standard deviation in speed

When I examined performance across the four experimental drives I observed that performance varied as a function of both age group and sensory condition. When sensory information was limited to only visual input, older adults displayed a distinct pattern in which they traversed straight road segments at a higher rate of speed and significantly reduced their speed in order to traverse curved road segments (see Chapter 3). The novel finding in the current study was that no such difference in speed on straight versus curved road segments was observed in the visual + vestibular sensory condition and no such effect was observed for younger adults. Previous research has indicated that vestibular cues serve as a useful indication of speed when negotiating turns as they convey information about lateral forces and thus help to inform safety margins (e.g., Kemeny & Panerai, 2003; Reymond et al., 2001). Thus, my findings may indicate that when both visual and vestibular inputs were available, vestibular cues augmented the perception of speed and this allowed older adults to select a speed that was conducive to safely traversing
both straight and curved road segments. Conversely, when vestibular cues were absent, older adults drove faster on straight road segments and this may have in turn necessitated a significant reduction in speed on curved road segments to negotiate them safely and effectively.

When examining speed variability across the four experimental drives when only visual inputs were available, older adults exhibited greater variability when traversing curved road segments compared to straight road segments (a finding previously reported in Chapter 3). The novel observation in the current study was that, when both visual and vestibular inputs were available, older adults demonstrated no such difference in speed. This may indicate that the lateral forces that older adults experienced when traversing curved road segments improved their capacity to detect changes in speed. As previously mentioned, drivers adjust their speed while cornering by taking into account lateral force (Reymond et al., 2001) and thus, in the current investigation, older adults may have exploited the presence of vestibular input to exercise tighter control over their speed on curved road segments. This would have allowed them to avoid experiencing the high levels of lateral force associated with cornering at excessive speeds and to thereby constrain the perceived risk of losing control over the vehicle (Reymond et al., 2001). This pattern of behavior aligns well with previous research indicating that older drivers are often aware of some of their own limitations (e.g., reaction time) and tend to modify their driving behavior accordingly in order to minimize crash risk (Nishida, 1999). Importantly, younger adults did not demonstrate any differences in speed variability as a function of either sensory condition or road geometry. It is possible that younger adults were performing close to ceiling with visual cues alone, given the relative simplicity of the current driving task, and therefore vestibular cues may not have afforded many performance benefits above and beyond visual input alone.

4.3.2 Lateral control

Older adults exhibited greater variability in lateral position in the visual + vestibular condition compared to the visual-only condition. This observation ran contrary to my original hypothesis that the addition of vestibular input would improve lateral control over visual inputs alone (e.g., Curry, Artz, Cathey, Grant, & Greenberg, 2002) and that the magnitude of these performance benefits would be greater among older adults (e.g., Laurienti et al., 2006). There are two possible explanations for these performance outcomes, which I introduce here and elaborate upon below.
The first relates more directly to the hypothesis that there are inherent age-related differences in multisensory self-motion perception. While I endeavored to provide matching visual and vestibular cues as much as possible, it should be acknowledged that there may have been occasional unintended, but ultimately unavoidable discrepancies between the visual and vestibular cues that participants received (as is the case for most driving simulation studies employing motion). That is because no motion base is capable of perfectly replicating the physical motion experienced in a real vehicle under all conditions. Age-related differences in the way that visual and vestibular cues are combined may have thereby resulted in greater detriments to lateral control in older adults under possibly discrepant sensory conditions. The second explanation relates to differences between the sensory inputs that occur during simulated driving compared to the sensory inputs experienced during one’s history of real-world driving. Specifically, age-related differences in cumulative driving experience could have led to differences in the strength of the learned associations between the visual and motion inputs experienced when driving a real car. For older adults, a higher level of cumulative real-world driving experience could have promoted stronger learned associations and an inability to accommodate the novel visual-vestibular associations presented during the simulated driving task. In the following sections, I address each hypothesis and reflect on a global explanation for the observed age effects with respect to both lateral control and speed-related metrics.

4.3.3 Age-related differences in multisensory self-motion perception

A driving simulation paradigm was chosen for the current experiment because a) driving is a realistic multisensory task, b) it enabled me to systematically manipulate the available sensory inputs, and c) it is a commonly employed technique used within applied areas for which there are important real-world implications. Such implications apply to any research study or application that utilizes motion-based simulation technologies and/or that includes different populations. While even a basic simulator can typically present compelling visual cues simulating self-motion, no motion platform is capable of perfectly replicating the physical forces experienced in a real vehicle under all conditions. For example, motion platforms are generally accurate at conveying onset accelerations (see Pinto, Cavallo, & Ohlmann, 2008), but they cannot replicate the sustained lateral forces associated with protracted turning maneuvers (see Greenberg &
Blommer, 2011). Therefore, some level of discrepancy between visual and vestibular cues is to be expected. In practice, these discrepancies can potentially be partially mitigated by having the driver perform a predefined set of maneuvers (e.g., following a lead vehicle; Stoner et al., 2011), for which visual-vestibular congruency can be more easily maintained. In the current experiment, I utilized an open-ended task in which participants were largely free to dictate the movements of their vehicle. This approach was selected because it is less contrived and because rigid task constraints could have limited the range of observable performance outcomes, or oversimplified the driving task to the extent that participants would perform at ceiling. However, an open-ended driving task likely created opportunities for subtle discrepancies to emerge between the visual and vestibular cues. These discrepancies may have affected older adults’ performance in terms of lateral control more so than younger adults. This may relate directly to the hypothesis that there are age-related differences in the way that visual and vestibular cues are combined during self-motion perception.

As discussed, in the context of stimulus detection/discrimination tasks, there is some evidence to suggest that multisensory integration is heightened in older adults compared to younger adults (Mozolic et al., 2012) and this heightened integration may also leave older adults more susceptible to performance declines than younger adults under conditions of conflicting sensory inputs (e.g., during visual-auditory integration; (DeLoss et al., 2013; Guerreiro et al., 2013; Stapleton et al., 2014). This pattern may also extend to visual-vestibular integration (e.g., Berard et al., 2012; Deshpande & Patla, 2007) and may be, in part, related to older adults’ poorer abilities to ignore or to inhibit irrelevant or conflicting cross-modal sensory information (see Freiherr, Lundström, Habel, & Reetz, 2013; Weeks & Hasher, 2014). Because older adults may allow cross-modal inputs to interact more freely when the available sensory inputs are congruent, older adults may exhibit performance gains but when sensory inputs are incongruent, older adults may exhibit performance losses (see Mozolic et al., 2012 for review). Therefore, the findings of the current investigation may be evidence that this same general pattern extends to visual-vestibular cues relating to self-motion. Younger adults may have been able to combine visual and vestibular cues strategically to retain lateral control whereas older adults may have been unable to ignore or to inhibit vestibular input when it varied relative to visual input, causing them to experience declines in lateral control with motion. This observation aligns with Deshpande.
and Patla's (2007) observation that when older and younger adults were instructed to walk toward a visual target but were presented with discrepant vestibular cues (i.e., vestibular innervation via galvanic stimulation), older adults deviated from their path to a greater extent than younger adults did.

4.3.4 Age-related differences in real-world driving experience

An alternative (but not exclusive) explanation for the observed age-related differences in the way that vestibular input affected lateral control relates to cumulative driving experience. The current driving task may have been a departure from the visual-vestibular interactions historically experienced by each participant during their lifetime of real-world experience. In addition to the physical motion parameters, an additional discrepancy between the simulator and real driving relates to the high gain on the steering input caused by the small physical diameter of the steering wheel (11”) and the lower number of wheel rotations from lock-to-lock (2.5). Because the older adults had more lifetime driving experience than the younger adults, they may have had stronger, implicit expectations pertaining to the sensory inputs that they should receive while driving compared to younger adults. These expectations may have limited their capacity to accommodate for discrepancies between the simulation and real-driving, leading to declines in lateral control. This hypothesis is consistent with research in the domain of simulator sickness. A prevailing theory pertaining to the cause of simulator sickness is that the central nervous system generates an internal representation of the inputs normally associated with self-motion perception tasks like driving and flying (Oman, 1990; Reason, 1978). However, the inherent discrepancies between the sensory inputs provided by the simulator and the user’s internal model of the real task create a mismatch that can result in a pattern of discomfort, disorientation, and nausea called simulator sickness (e.g., Keshavarz & Hecht, 2011; Reason & Brand, 1975). It has also been demonstrated that pilots with more cumulative real-world experience (e.g., flight instructors) are more susceptible to simulator sickness compared to less experienced pilots and this is attributed to their greater experience resulting in a stronger internal representation of real flight motion cues (Johnson, 2005). It is possible that the older adults’ in the current investigation, given their greater lifetime experience with real-world driving, had a stronger internal representation of real vehicle motion. For that reason, they may have had more difficulty reconciling any inaccurate or inconsistent non-visual cues that the simulator provided. Younger adults may have been better
able to adapt to the novel cues having had less cumulative driving experience and perhaps possessing a less rigid internal representation of vehicle motion cues. Ultimately, both age-related differences in multisensory integration and age-related differences in experience are likely to have played a role in how the available sensory inputs influenced performance on my simulated driving task. Future investigations should extend the approach used here by employing tasks for which the potential influence of previous experience is limited as much as possible.

The current findings have clear implications within the context of vehicle and simulator design when considering older users. For instance, driving simulators are now being regarded as a viable alternative to on-road driving when assessing or training older drivers for the purpose of driver recertification (see Ball & Ackerman, 2011). However, my findings suggest that the sensory cues that the simulator provides will have a differential impact on the driving performance of older and younger adults. While it has been established that physical motion cues improve younger adults’ speed maintenance when traversing curves (Reymond et al., 2001), my findings revealed that older adults benefited from motion cues with respect to speed maintenance but younger adults did not. Thus, fixed-based driving simulators that rely predominantly upon visual cues to convey motion may leave older adults at a disadvantage by eliminating the physical motion cues that older adults use to govern their speed. The effect that vestibular cues have on performance could also have important implications with respect to the design of real vehicles.

Manufacturers have been moving toward technologies such as adaptive suspension that minimize body roll while turning (Cao, Liu, Li, & Brown, 2008). This system is designed to improve driver safety and comfort, however, it may inadvertently reduce important vestibular cues to vehicle motion that older drivers utilize in order to control their speed effectively. That said, I also observed in this study that vestibular cues had a negative impact on lateral control for older adults but not younger adults. I attributed the negative performance outcome associated with vestibular cues to older adults’ greater sensitivity to discrepancies between the available visual and vestibular cues and/or discrepancies between the motion of the simulator and real vehicle motion. Therefore, the extent to which vestibular cues have a negative impact on older adults’ lateral control will largely depend upon the application(s) for which the driving simulation is
being utilized and the nature of the vestibular cues involved. For example, driving scenarios intended for driver training or assessment may involve more complex maneuvers than those utilized in the current investigation and these maneuvers could lead to more pronounced visual vs. vestibular and/or simulator vs. reality discrepancies, thereby exacerbating the negative effects that vestibular cues have on older adults’ lateral control. These effects should be taken into account when designing simulator-based driving research studies and training/assessment protocols with older users in mind.

4.4 Conclusions

In summary, my findings suggest that adding vestibular cues to visual self-motion stimuli has a different effect on the driving performance of older adults compared to younger adults. When vestibular inputs were added to visual inputs, older adults demonstrated more accurate and less variable speed, whereas younger adults did not demonstrate any differences in speed with the addition of vestibular cues. Older adults also demonstrated more variable lateral control overall compared to younger adults, but their performance was the most variable when vestibular inputs were introduced compared to when visual cues were presented alone. These effects may have stemmed from changes in the way that older adults integrate visual and vestibular inputs in support of self-motion perception and/or age-related differences in overall driving experience and changes in the ability to adapt to a novel driving task. These findings may have important implications within the context of vehicle and simulator design and use, particularly when considering older users.
Chapter 5
Age-related differences in trimodal self-motion perception

In Chapters 3 and 4, I observed that compared to visual motion cues alone, the addition of congruent auditory cues bolstered speed-keeping performance for both younger and older adults and that the performance gains were greater among older adults. I also observed that the addition of congruent vestibular self-motion cues bolstered speed-keeping performance but undermined lane-keeping performance and, once again, the effect of the available sensory inputs was greater for older adults than it was for younger adults. Taken together, these observations indicate that the age-related differences in multisensory integration that have previously been observed in the context of simple stimulus detection extend to the continuous and dynamic cues experienced during self-motion. Such age-related differences could have important practical implications for how older adults perform everyday mobility-related tasks. However, a noteworthy difference between self-motion as it occurs in the real world and self-motion as it was conveyed in the experiments presented in Chapters 3 and 4 is that self-motion typically innervates many sensory systems simultaneously, not just the visual and auditory systems, or the visual and vestibular systems. Self-motion through the environment leads to optic flow, acoustic flow, proprioceptive cues, inertial cues, and even olfactory cues that each help to convey how one’s own position in space is changing (see Wozny, Beierholm, & Shams, 2008). Thus, an important question is whether the observed age-related differences in multisensory self-motion perception extend to the more complete cue combinations typically encountered during self-motion. Furthermore, while there is an extensive literature exploring the neural substrates and behavioural manifestation of the integration of sensory inputs from two separate sensory modalities, there is a dearth of research concerning the integration of three or more sensory inputs. There is an implicit understanding that in most natural behavioural contexts, observers receive input from many sensory systems simultaneously and integrate them to form a unitary percept. However, there has been little effort to examine systematically whether there is a differential effect of presenting an observer with two compared to three sensory inputs. In Chapter 5, I briefly review current knowledge pertaining to trimodal cue combination in the context of stimulus detection and in the
context of self-motion perception. I will then discuss the experiment designed to investigate the effects of aging on trimodal self-motion perception compared to bimodal self-motion perception.

5 Introduction

It has been established that in the context of simple stimulus detection, two congruent cues can yield faster and more reliable performance than that afforded by either constituent sensory input in isolation (Stanford & Stein, 2007; Stein & Alex, 1993; Stein & Stanford, 2008; Stein et al., 2014 for reviews). There is also a growing body of evidence to suggest that older adults differ from younger adults in the way that they are affected by the presence of two congruent multisensory cues, and in the way that they are affected by two incongruent multisensory cues. Compared to younger adults, older adults generally garner greater performance in the presence of two congruent cues but they are also more adversely affected by the presence of two incongruent cues (see de Dieuleveult, Siemonsma, van Erp, & Brouwer, 2017; Mozolic et al., 2012 for reviews). However, while there is a wealth of knowledge pertaining to the effect that bimodal cue combinations have on the performance of older and younger adults, comparatively little work has considered the effect that trimodal cue combinations have on the performance of either age group. There has been some work to demonstrate that when younger observers are asked to press a button in response to the onset of a visual, an auditory, or a haptic signal either in isolation, in bimodal combinations, or in trimodal combination, trimodal detection is faster than both unimodal and bimodal detection (Diederich & Colonius, 2004; Hecht, Reiner, & Karni, 2008). There has been at least one study showing that trimodal cues (visual-auditory-tactile) yield faster response times than bimodal cues (Lee & Spence, 2008). That said, these trimodal benefits appear to be highly task and stimulus-dependent. For example, other investigations have shown that trimodal emergency braking warning systems are no better that bimodal warning systems (Politis, Brewster, & Pollick, 2015). It has also been demonstrated that an emergency braking warning system that employs four cues in tandem (a visual icon, an auditory tone, and two forms of haptic feedback [vibration and brake pedal pulsation]) can actually lead to slower reaction times compared to visual and auditory alerts presented in isolation (Lee, McGehee, Brown, & Marshall, 2006). It is important to note that, although these studies are concerned with driving performance, they are primarily concerned with how quickly drivers detect the onset of highly discrete multisensory signals that alert them to hazards. These studies are not concerned
with multisensory integration as it relates to the perception of self-motion per se. An important distinction between the multisensory inputs received in the context of hazard detection and the multisensory inputs received during self-motion is that warning systems present cues that are a proxy for or a presage to naturally occurring signals. Therefore, warning signals do not necessarily yield implicitly related and redundant estimates of a given movement parameter (e.g., speed or heading). Given that warning signals comprised of three coincident, albeit not implicitly related cues, can yield additive performance benefits, an important question is whether the presence of trimodal cues to self-motion that are essentially redundant lead to additive or sub-additive performance outcomes.

Research explicitly examining the effect of trimodal cues on self-motion perception is also limited. It has been demonstrated that, when attempting to induce vection or the illusory experience of self-motion, the combination of visual, vestibular, and vibrational cues to self-motion can lead to stronger self-reports of vection (i.e., more convincing and higher maximum intensity) compared to only visual and vibration cues combined (Schulte-Pelkum, 2007). Similarly, it has been demonstrated that auditorily induced circular vection (the illusory experience of rotation; see Riecke, Feuereissen, Rieser, & McNamara, 2015 for review) can be enhanced by vibrations and by the perceived potential for physical motion created by priming participants with passive physical rotations prior to presenting auditory and vibrotactile cues in tandem (Riecke et al., 2008). However, this body of work is limited in that it considers only subjective ratings of self-motion (e.g., vection strength). To determine whether the differences in the subjective experience of self-motion associated with the combination of available cues have any functional relevance, it is necessary to consider how they affect behaviour during self-motion.

My objective was to utilize the same driving paradigm employed in Chapters 3 and 4 to present visual, vestibular, and auditory cues to self-motion in unison and to compare performance under trimodal sensory conditions (visual + auditory + vestibular) to the performance observed under the two bimodal conditions (visual + auditory and visual + vestibular) presented in Chapters 3 and 4, respectively. Diederich & Colonius (2004) and Hecht and colleagues (2008) demonstrated that the performance gains conferred by trimodal cues over bimodal cues are modest compared
to those conferred by bimodal cues over unimodal cues. Therefore, I predicted that trimodal cues may yield modest gains in driving performance over bimodal cues. Specifically, I predicted that the trimodal condition may lead to further improvements in speed maintenance because, in Chapters 3 and 4, I demonstrated that auditory and vestibular cues were both beneficial to older adults in terms of speed maintenance. However, because vestibular cues were detrimental to older adults’ lane-keeping performance and because auditory cues were not expected to affect lane-keeping performance in either age group, I predicted that older adults’ lane-keeping performance would not benefit from trimodal cues.

5.1 Methods

5.1.1 Participants

In the trimodal condition, 14 older adults and 11 younger adults were recruited. Of these, 6 older adults and 1 younger adult were excluded due to simulator sickness. A total of 10 younger adults (7 male, 3 female; $M=25.1$ years) and 8 older adults (3 male, 5 female; $M=71.6$ years) completed the trimodal sensory condition.

5.1.2 Materials, Apparatus, and Procedure

The materials, apparatus, procedure, and dependent measures were the same as those used in Chapters 3 and 4 were used. The novel aspect of the current experiment was that the visual cues that were used in Chapters 3 and 4 were simultaneously presented with the auditory cues described in Chapter 3, and the vestibular cues described in Chapter 4 to create a trimodal sensory condition. Performance in the trimodal condition was compare against performance in the visual + auditory and visual + vestibular conditions that were already reported in Chapters 3 and 4, respectively.

5.2 Results

A series of mixed-factorial ANOVAs, including the between-subjects factors age group (younger vs. older) and sensory condition (visual + auditory vs. visual + vestibular vs. trimodal) and the within-subjects factors road geometry (straight vs. curved) and drive number (experimental drives 2, 3, 4, 5) were performed, one for each dependent variable (mean speed, standard
deviation in speed, and RMSE lateral position). For all statistical analyses, a priori significance level was set to $\alpha=.05$. Post-hoc tests were corrected using the Bonferroni adjustment for multiple comparisons.

### 5.2.1 Mean Speed

There was a main effect of age group, $F(1,48)=7.49, p=.009, \eta_p^2=.135$, in which older adults drove slower ($M=79.87, SE=1.72$) than younger adults ($M=86.18, SE=1.54$). There was a main effect of road geometry in which participants traveled slower on the curved road segments ($M=82.45, SE=1.17$) than on the straight road segments ($M=83.60, SE=1.16$). There was also a main effect of drive number, $F(3,144)=4.26, p=.007, \eta_p^2=.081$. Post-hoc comparisons revealed that participants traveled faster in experimental drives 3, 4, and 5, compared to drive 2. Note that drive order was counterbalanced. However, there was no main effect of sensory condition $F(2,48)=.195, p=.824, \eta_p^2=.008$, and no interactions were significant.

### 5.2.2 Standard deviation in speed

Mauchly’s test of sphericity approached significance for drive number, $\chi^2(5)= 10.75, p=.057$, and thus the Greenhouse-Geisser corrected values are reported for the factor drive number. There was a main effect of age group, $F(1,48)=7.38, p=.009, \eta_p^2=.133$, in which older adults exhibited a higher standard deviation in speed ($M=7.04, SE=.41$) than younger adults ($M=5.54, SE=.366$). There was a main effect of sensory condition, $F(2,48)=5.54, p=.007, \eta_p^2=.188$, with post-hoc comparisons revealing that speed was less variable in the visual + auditory condition than in the visual + vestibular condition, but no other comparisons were significantly different. There was no effect of road geometry, $F(1,48)=3.51, p=.067, \eta_p^2=.068$. However, there was a main effect of drive number, $F(2.65,127.56)=3.86, p=.011, \eta_p^2= 0.074$, in which standard deviation in speed gradually declined over the course of the experimental drives. Post-hoc tests revealed that speed variability diminished over the course of the drives, resulting in significantly lower speed variability in the last drive ($M=5.47, SE=.35$) compared to the first drive ($M=7.07, SE=.38$). There was a significant three-way interaction of age by sensory condition by road geometry, $F(2,48)=6.06, p=.004, \eta_p^2 = 0.202$. In the visual + auditory condition, older adults were more variable in their speed on curved road segments than on straight road segments. In the visual + vestibular condition, younger adults were more variable in their speed on curved road segments.
that on straight road segments whereas older adults were more variable in their speed on straight road segments than on curved road segments. These results are consistent with the findings reported in previous chapters. Notably, in the new trimodal condition, there was no significant difference in speed variability between straight and curved road segments for either age group (see Figure 5.1).

5.2.3 Lateral position

There was no significant effect of age group, $F(1,48)=2.37, p=.130, \eta_p^2 = 0.047$, or sensory condition, $F(2,48)=1.73.15, p=.187, \eta_p^2 = 0.067$, and there was no significant interaction, $F(2,48)=3.15, p=.052, \eta_p^2 = 0.116$.

5.3 Discussion

My goal was to determine whether trimodal cues to self-motion would have a different effect on older and younger adults compared to bimodal cues. I observed that younger adults were relatively consistent in terms of their mean speed, speed variability, and variability in lane position across all sensory conditions. For older adults, speed variability and variability in lateral position were highest in the visual + vestibular condition and were significantly lower in the visual + auditory and visual + vestibular conditions. However, contrary to my hypothesis, trimodal performance was not significantly better than visual + auditory performance for any dependent measure.
Figure 5.1. Standard deviation in speed (km/h) across age group, sensory condition and road geometry. Error bars are ±1SE. *p=0.05.
5.3.1 Speed and speed variability

I predicted that that because auditory cues and vestibular cues both improved speed maintenance over visual cues alone that there may be additive benefits associated with the presence of both cues. However, no such improvement emerged. For younger adults, this is likely because they were already performing at ceiling with visual cues alone. On this simplified driving task, the available optic flow cues may have been sufficient for younger adults to estimate their relative speed and lateral position such that there was little appreciable benefit associated with the addition of auditory and/or vestibular cues. According to the principle of inverse effectiveness, multisensory performance enhancements are typically the greatest when the available cues are of limited efficacy in isolation (Meredith et al., 1987; Meredith & Stein, 1986). Thus, for younger adults, the presence of additional sensory inputs would have conferred very little benefit over using visual cues alone.

For older adults, it is possible that age-related declines in individual sensory systems decreased the reliability of the estimates of self-motion provided by each sensory system. Thus, older adults were able to benefit from multiple congruent cues to self-motion and this is why the addition of auditory or vestibular cues resulted in improved speed maintenance. However, the question remains as to why the combination of visual, auditory, and vestibular cues to self-motion did not yield performance benefits to the older adults above and beyond those associated with visual and auditory cues. One plausible explanation is that the combination of visual and auditory cues may have been sufficient for older adults to attain robust estimates of speed. There is a body of evidence to suggest that in the context of driving, auditory cues are highly informative with respect to speed and greatly improve speed perception and maintenance over visual cues alone (Davis & Green, 1995; Denjean, Roussarie, Kronland-Martinet, Ystad, & Velay, 2012; Hellier, 2011; Evans, 1970; Horswill & Plooy, 2008; Matthews & Cousins, 1980; Merat & Jamson, 2011; Wang & Wang, 2012). I corroborated this observation in Chapter 3 and I also demonstrated that these benefits may be proportionally greater for older adults. There is evidence to suggest that vestibular cues can convey information about speed but in the current task, participants would have only received vestibular cues when accelerating or decelerating and performing turns because these were the instances in which the lab was tilted to convey the
associated linear or lateral forces. Otherwise, when driving at a constant velocity, vestibular cues would have been very minimal. Thus, the combination of visual and auditory cues may have been sufficiently informative with respect to speed that there would have been little additional benefit to be gained from the presence of vestibular cues to self-motion.

Ultimately, there is a ceiling on the level of multisensory enhancement that can be achieved. Hecht and colleagues (2008) demonstrated that although trimodal cues yielded modest improvements in terms of stimulus detection time over bimodal cues, trimodal performance gains over bimodal performance were far smaller than the bimodal performance gains over unimodal performance (Hecht et al., 2008). Hecht and colleagues projected that no additional performance benefits would have emerged had they added a fourth cue. The diminishing returns associated with the addition of a third cue suggested that the onset of three congruent cues was sufficiently salient that participants were likely performing at ceiling and had thereby reached the limit for potential multisensory performance enhancements (Hecht et al., 2008). In the current experiment, speed may have become sufficiently salient to the older adults in the presence of visual and auditory cues and thus there was little to be gained from the addition of vestibular cues. It is also important to consider that the investigations that have provided evidence of multisensory performance enhancement, and evidence of age-related differences therein, have generally presented cues at or near perceptual thresholds (Holmes, 2009; Stanford & Stein, 2007). In accordance with the principle of inverse effectiveness, testing under sensory conditions where the available inputs are less salient should maximize the resulting multisensory performance enhancements and may be more sensitive to age-related differences. It is conceivable that if I had presented visual, auditory, and vestibular cues to self-motion near older adults’ perceptual thresholds, I may have been able to elicit performance enhancements in the trimodal condition, especially for the older adults. However, in the current task, I did not manipulate the level of reliability associated with the individual cues to self-motion because one of the primary goals associated with using a driving paradigm was to move away from the highly specified sensory conditions that have traditionally been used to explore age-related differences in multisensory perception and to provide more natural and dynamic cues, akin to those experienced during real-world self-motion tasks. This approach was intended to shed light on
whether age-related differences in multisensory integration are restricted to highly controlled stimulus detection type tasks or if they extend to real-world tasks.

5.3.2 Lateral control

In Chapter 4 I demonstrated that the addition of vestibular cues was detrimental to lane-keeping performance relative to visual cues alone, likely owing to conflicts between the visual and vestibular cues and/or between the vestibular cues presented in the simulation and those encountered during real driving. The present experiment revealed that although vestibular cues were present in the trimodal condition, lane-keeping performance did not decline. It is possible that the presence of auditory cues helped drivers to reduce speed variability and that improved speed maintenance made it easier to steer the vehicle. Therein, an important consideration is that because drivers controlled their speed and lane position themselves, each participant could have received different vestibular cues and thus the level of vestibular conflict that was experienced may have differed between individuals and most critically, the level of conflict may have also differed between the bimodal (visual + vestibular) and trimodal conditions. The use of a between-subjects design and unconstrained motion cues makes it difficult to ascertain whether the differences in lateral control between the visual + vestibular and trimodal conditions were due to the extent to which the combination of available sensory cues informed lane-keeping performance or differences in the way that the individuals in each condition controlled their vehicle and the resulting vestibular cues.

In the current series of experiments, the between-subjects design was advantageous for avoiding carryover effects between sensory conditions. Allowing participants to control their own speed and lane position was also imperative because the goal was to observe performance under more naturalistic task constraints. Nevertheless, to pinpoint the bases of the observed age-related differences in the integration of visual and vestibular cues to self-motion, future research should seek to ensure that all participants receive the same vestibular cues. This can be achieved by using predefined, passively generated motion instead of actively controlled and thereby unconstrained motion cues. Furthermore, a within-subjects approach would control for inter-individual differences in performance.
5.4 Conclusions

The goal of this study was to determine whether trimodal cues to self-motion lead to different performance outcomes for older and younger adults compared to bimodal cue combinations. Results demonstrated that younger adults were consistent in their performance across sensory conditions, likely owing to the fact that they were performing at ceiling with visual cues alone. Older adults’ speed maintenance was not superior in the trimodal condition compared to the visual + vestibular condition, likely because the combination of visual and auditory cues allowed older adults to perform near ceiling in terms of their speed perception. Older adults’ lane keeping performance was superior in the trimodal and visual + auditory conditions compared to the visual + vestibular condition. Where vestibular cues were detrimental to lateral control in the visual + vestibular condition, they were not detrimental in the trimodal condition. The precise motion cues that participants received may have differed between the visual + motion and trimodal conditions because of the use of a between-subjects design and the ability of participants to control the vehicles themselves. Thus, follow-up studies should use passive motion cues and a within-subjects design to ensure that motion cues are consistent across sensory conditions.
Chapter 6

Age-related differences in visual and vestibular perception and integration for heading estimation

The study that appears in this chapter has been submitted for publication as:


In Chapters 4 and 5, I observed some evidence to indicate that compared to younger adults, older adults may combine visual and vestibular cues to self-motion, despite instances where they may be incongruent. I considered the possibility that this may be due to underlying age-related differences in the way that visual and vestibular cues to self-motion are weighted relative to one another. However, despite the fact that the driving task was highly valuable in providing insights into the effects of cue combination during a more complex and dynamic everyday task, this paradigm was also limited in other key dimensions. For example, because participants actively controlled their vehicle, and because a between-subjects design was used, the precise motion cues that participants received may have differed between individuals or between sensory conditions. Driving is also a highly contextualized, well-practiced task and, as such, the effects of driving experience are confounded with the effects of age, thereby limiting the extent to which conclusions can be made specifically about age-related differences in multisensory integration.

Furthermore, to evaluate the two main tenets of optimal multisensory integration, (i) reduced variance in bimodal relative to unimodal conditions and (ii) combined perceptual estimates that reflect reliability-based cue weighting, it is necessary to establish the reliabilities of the individual sensory inputs separately in order to predict what the bimodal percept and associated reliability should be if the sensory inputs are integrated in an optimal fashion. In the current driving task, participants would not have been able to control both the vehicle’s speed and direction with the auditory cues alone or the vestibular cues alone and therefore it was not
feasible to establish the estimates of unimodal reliability necessary to formally test model predictions.

As discussed in Chapter 1, previous work has used a psychophysical heading perception task to precisely characterize how non-human primates and younger adults integrate visual and vestibular cues to self-motion. This task was ideally suited to elaborate upon the findings of my driving experiments because it allowed me to avoid age-related differences in prior task-specific practice/exposure, it involved passive self-motion and would thereby ensure that all participants received the same motion stimuli, and it also employed a within-subjects design that included both unisensory and bimodal cue conditions. In this final experimental chapter, I will review current knowledge pertaining to visual-vestibular integration during heading perception and I will describe my experiment designed to enable a closer examination of age-related differences in visual-vestibular integration.

6 Introduction

Many everyday tasks such as walking and driving involve self-motion through space. To perform these tasks effectively, it is necessary for the observer to maintain reliable estimates of their own movement parameters, including their speed, the relative distance that they have travelled, and their heading (Campos & Bülthoff, 2012; Cullen, 2014; DeAngelis & Angelaki, 2012; Frenz & Lappe, 2005; Greenlee et al., 2016; Larish & Flach, 1990; Page & Duffy, 2003; Sun, Campos, Young, Chan, & Ellard, 2004; Warren & Wertheim, 1990). Multiple different sensory systems can estimate self-motion parameters (e.g., visual, proprioceptive, vestibular). Due to noise within the nervous system and changing behavioural and environmental conditions, the reliability associated with each of these estimates can vary (Ernst & Bülthoff, 2004; Knill & Pouget, 2004; Ma, Beck, Latham, & Pouget, 2006). Research on younger adults and non-human primates has provided evidence to suggest that observers can constrain the variability of their perceptual estimates by integrating redundant sensory estimates in a statistically optimal fashion (Butler et al., 2011, 2010; Fetsch et al., 2009; Gu, Fetsch, Adeyemo, Deangelis, & Angelaki, 2010). This phenomenon has been particularly well-characterized at both the behavioural and neurophysiological levels in the context of heading perception (Butler et al., 2011, 2010; Fetsch et al., 2009; Gu et al., 2010).
When presented with visual cues (i.e., optic flow; Gibson, 1950) and vestibular cues (i.e., passive translation) pertaining to the direction of self-motion, macaque monkeys and young adult humans integrate them such that each estimate is weighted as a function of their relative reliabilities. This yields a bimodal estimate of heading that is said to be optimal in that the variance is lower than that associated with either unimodal estimate alone, and the final heading estimate is proportionally closer to the more reliable unimodal estimate (Butler et al., 2011, 2010; Ernst, 2005; Ernst & Banks, 2002; Ernst & Bülthoff, 2004; Fetsch et al., 2009; Gu et al., 2010). Optimal integration has been observed in numerous behavioural contexts and across different sensory cue combinations but optimal integration as it occurs during self-motion perception may be uniquely robust. Because self-motion simultaneously introduces highly correlated visual and vestibular motion cues, it has been suggested that these cues may be integrated in a more mandatory fashion than, for instance, exteroceptive visual and auditory cues (see Prsa, Gale, & Blanke, 2012; Frissen et al. 2011; Campos & Bülthoff, 2012). Optimal integration of visual and vestibular cues to self-motion also tends to be robust to modest spatial discrepancies between these cues (see Butler et al., 2011, 2010; Fetsch et al., 2009; Kaliuzhna et al., 2015; de Winkel et al., 2015) and to discrepant visual and physical velocity motion profiles (Butler et al., 2015).

In the context of self-motion perception, the reduction in perceptual variance associated with optimal integration has traditionally been demonstrated by providing congruent visual cues to self-motion (e.g., optic flow) and vestibular cues to self-motion (e.g., physical translation) and observing the resulting gains in precision (e.g., Butler et al., 2010, 2011; Fetsch et al., 2009). Optimal reliability-based cue weighting has been demonstrated by introducing subtle angular conflicts between visual and vestibular heading directions (Butler et al., 2010, 2011; Fetsch et al., 2009) and by artificially degrading the reliability of the visual cues (e.g., introducing non-coherent motion; Fetsch et al., 2009) during spatial conflicts. However, little is currently known about whether age-related changes in sensory reliabilities and/or age-related changes to central sensory integrative mechanisms affect whether older adults experience an optimal reduction in perceptual variance in the presence of congruent cues to self-motion. Furthermore, little is known about whether age-related changes to central sensory integrative mechanisms affect the
range of spatial and temporal discrepancies that older adults can tolerate before optimal integration will no longer occur. Age-related changes to optimal integration could be consequential to the way that older adults perceive self-motion and how they perform tasks such as standing, walking, and driving.

There is much evidence to suggest that older adults experience functional declines in performance on tasks that require reliable self-motion perception. Compared to younger adults, older adults are more prone to instability and falls while standing and walking (Hausdorff et al., 2001; Horak et al., 1989; Prince et al., 1997; Tinetti et al., 1988) and they have increased difficulties with spatial navigation (Adamo et al., 2012; Allen, Kirasic, Rashotte, & Haun, 2004; Harris & Wolbers, 2012). Older adults are also more likely to be involved in multi-vehicle collisions than all but young, novice drivers (Hakamies-Blomqvist, 1993; Langford & Koppel, 2006) and have higher collision rates per kilometer traveled than all but young, novice drivers (Eberhard, 2008). Although much emphasis has been placed on the unimodal, cardiopulmonary, musculoskeletal, neurophysiological, and cognitive factors associated with age-related declines in performance on mobility-related tasks, changes to perceptual, and multisensory integrative processes are also likely to contribute to these declines and yet these contributions are not well understood.

Older age is characterized by broad changes in sensory functioning and perceptual abilities relevant for self-motion perception. For instance, there are age-related differences in the processing of visual motion cues that cannot be explained by changes in peripheral visual functioning alone (Ball & Sekuler, 1986; Bennett, Sekuler, & Sekuler, 2007; Fernandez, Monacelli, & Duffy, 2013; Kavcic, Vaughn, & Duffy, 2011; Lich & Bremmer, 2014; Snowden & Kavanagh, 2006; Tetewsky & Duffy, 1999; Warren, Blackwell, & Morris, 1989). Consequently, older adults have higher perceptual thresholds for discerning their heading on the basis of optic flow cues to self-motion (Atchley & Andersen, 1998; Lich & Bremmer, 2014; Warren et al., 1989). In the vestibular system, a loss of hair cells within the semicircular canals and the otoliths (see Anson & Jeka, 2016; Zalewski, 2015 for reviews) can lead older adults to experience greater perceptual thresholds for passive self-motion in darkness or while blindfolded.
Therefore, older adults may generally be subject to declines in the reliability with which the individual sensory systems convey self-motion.

There is also evidence from basic stimulus detection and discrimination tasks indicating that there may be age-related changes in the way that multiple sensory inputs are integrated to form a coherent, unitary percept (e.g., Diederich, Colonius, & Schomburg, 2008; Laurienti, Burdette, Maldjian, & Wallace, 2006; Peiffer, Mozolic, Hugenschmidt, & Laurienti, 2007). Younger and older adults’ performance in terms of stimulus detection and stimulus discrimination is differentially affected by the combination of available sensory inputs. This has been observed for a number of different sensory cue combinations but has primarily been observed in the context of visual-auditory stimulus detection (see de Dieuleveult, Siemonsma, van Erp, & Brouwer, 2017 for a review). However, in chapters 3-5, I found evidence to suggest that the age-related differences in the effect of the available sensory inputs that have been observed in the context of visual-auditory stimulus detection tasks may extend to self-motion perception. Specifically, I used a basic simulated driving paradigm to provide visual motion cues alone (via projected image) or in combination with congruent vestibular cues (i.e. moved via a hydraulic motion platform), or auditory cues (i.e. wind, tire, engine sounds). I then used measures of speed and lane-keeping performance to make inferences about age-related differences in multisensory self-motion perception. The results demonstrated that the addition of congruent vestibular cues to self-motion had a more pronounced effect on older adults’ speed maintenance and lane-keeping performance than it did on younger adults’ (Chapter 4). Likewise, the addition of auditory cues had a more pronounced effect on older adults’ speed maintenance performance than it did on younger adults’ (Chapter 3). Parallel research examining age-related differences in gait and postural control has also demonstrated that older adults are more susceptible to performance declines when presented with incongruent visual or vestibular cues to self-motion (Berard et al., 2012; Deshpande & Patla, 2007). Taken together, these observations suggest that older adults may be reliant on multiple congruent cues (i.e., visual + vestibular) to perform self-motion tasks and that they are less tolerant to sensory conflicts. The extent to which these behavioural outcomes reflect age-related differences in underlying cue integration strategies has not been examined.
Age-related changes in performance on mobility-related tasks has often been attributed to sensory biases either toward visual cues (e.g., Simoneau et al., 1999; Sundermier, Woollacott, Jensen, & Moore, 1996; Wade, Lindquist, Taylor, & Treat-Jacobson, 1995) or vestibular cues to self-motion (Wiesmeier et al., 2015). However, a systematic bias toward input from one modality or the other does not explain why older adults are more heavily influenced by both visual perturbations (e.g., Berard et al., 2012) and vestibular perturbations (e.g., Deshpande & Patla, 2007) than are younger adults. An alternative explanation is that older adults differ from younger adults in terms of which cues they integrate and how. Specifically, it is possible that when visual cues become uninformative or unreliable (e.g., spatially incongruent or noisy), younger adults may be better able than older adults to strategically assign more weight to the more reliable or more relevant sensory input(s). However, most previous studies that have examined age-related differences in the use of different sensory cues to guide self-motion have done so by simply adding or removing congruent or incongruent cues to self-motion and measuring the resulting performance outcomes. To better quantify age-related differences in multisensory integration during self-motion perception, it is necessary to first characterize the unimodal estimates of some parameter of self-motion (e.g., speed, heading, distance) and to then determine how these estimates are combined when more than one is available and they are redundant. To date, no previous studies have used rigorous psychophysical techniques within the context of self-motion perception to evaluate whether older adults’ multimodal self-motion estimates are optimal.

To summarize, previous studies involving younger adults have shown that visual and vestibular inputs are combined to yield an optimal reduction in perceptual variance (e.g., Butler et al., 2010; Fetsch et al., 2009) but no previous studies have evaluated whether the same is true for older adults. Likewise, previous studies have demonstrated that younger adults weight visual and vestibular cues as a function of their relative reliabilities (e.g., Butler et al., 2010; Fetsch et al., 2009) but no previous studies have established whether the same is true for older adults. Finally, whereas a few previous studies have explored the types and magnitude of visual and vestibular spatial conflicts that younger adults will tolerate before they no longer integrate (de Winkel, Correia Gracio, Groen, & Werkhoven, 2010; de Winkel, Katliar, & Bülthoff, 2017; Kaliuzhna et al., 2015), the characteristics of the spatial window of integration are unknown for older adults.
In fact, age-related changes to the spatial (rather than temporal) window of integration have generally not been well explored; even when considering other types of cue combinations (e.g., visual-auditory) or tasks (e.g., detection time) (see de Dieuleveult et al., 2017).

The goal of the current investigation was to utilize the above-mentioned, well-established heading perception paradigm to investigate whether there are age-related differences in visual-vestibular integration. I employed a heading discrimination task in which visual cues to heading (optic flow) were provided via a head-mounted display and vestibular cues to heading (passive translation in the dark) were provided via a motion platform. A two-interval forced-choice (2IFC) task was used in which participants were presented with two movements and reported which movement was more rightward. There were three primary study objectives:

1. Measure performance under each unimodal condition (visual and vestibular alone) as a way of a) investigating age-related differences in the reliability of each sensory estimate and b) to quantify the reliability of unimodal estimates to make predictions about optimal integration during the bimodal conditions.

2. Present congruent visual and vestibular cues simultaneously to determine whether both age groups exhibited optimal integration defined as a reduction in variance relative to the unimodal estimates.

3. Introduce two levels of inter-sensory spatial conflict between the visual and vestibular cues, a) a subtle 5º conflict and b) a larger 20º conflict. This allowed me to determine whether reliability-based cue weighting occurred and whether there were age-related differences in the magnitude of spatial conflict that was tolerated.

6.1 Methods

6.1.1 Participants

A total of 35 adults over age 65 (M=70 years, SD=4.45) and 17 younger adults aged 18-35 (M=22.3, SD=4.2) were recruited from the community. A telephone prescreening interview was used to screen for self-reported visual, hearing, and/or balance impairments. On-site, older adults
were screened for cognitive impairment using the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005; >26/30 indicating possible cognitive impairment). Participants completed a comprehensive questionnaire pertaining to their overall physical health (e.g., activity level, history of health conditions) and to capture demographic information (e.g., sex, occupation, level of education). Participants were excluded if they reported serious medical issues (e.g., history of stroke, seizures/epilepsy, recent heart attack, etc.) that could affect performance or compromise safety during the experiment. Of those recruited, 24 older adults ($M=69.6$ years, $SD=4.1$) and 17 younger adults ($M=22.3$, $SD=4.2$) were eligible to participate. Participants gave their informed consent before taking part in the experiment and were compensated at a rate of $10 per hour. This research was approved by the University Health Network’s Research Ethics Board (REB 14-8264) and was performed in accordance with the ethical standards specified by the Canadian tri-council research ethics guidelines.

Of those who met the necessary inclusion criteria, 10 older participants (42%) were excluded from the analysis 2 younger participants (12%) were excluded from the analysis because their unimodal heading discrimination performance was near chance, which either made it impossible to fit a psychometric function, or resulted in extreme heading discrimination thresholds (greater than 2.5 standard deviations beyond the mean). The two younger adults who were eliminated had extreme visual heading discrimination thresholds. Of the ten older adults who were excluded, six were eliminated because their visual JNDs were extreme. Four older adults were excluded because they had extreme JNDs in all sensory conditions. In total, 14 older and 15 younger adults were included in the analyses (see Table 6.1 for a summary of participant characteristics). Older adults who were deemed eligible to participate and who were included and older adults who were deemed eligible but who were excluded because their data were unusable were compared in terms of their age, visual acuity, contrast sensitivity, stereo vision, and MoCA scores (see below for details regarding these assessments) using a series of independent samples $t$-tests. No comparisons revealed significant differences. The critical $p$ value for all analyses was $\alpha = 0.05$. 

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Table 6.1

*Summary of participant characteristics*

<table>
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<tr>
<th></th>
<th>N</th>
<th>Age (years)</th>
<th>Male: Female</th>
<th>MoCA</th>
<th>ETDRS (logMAR)</th>
<th>Randot graded circles (arcssec)</th>
<th>Pelli-Robson (logCS)</th>
<th>TUG (s)</th>
<th>COP path (cm) Eyes open : eyes closed</th>
<th>Stroop interference (s)</th>
<th>UFOV total (ms)</th>
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<td><strong>Older adults</strong></td>
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<td>14</td>
<td>14</td>
<td>69.8 (4.2)</td>
<td>9:5</td>
<td>28.1 (1.5)</td>
<td>0.05 (0.19)</td>
<td>161.4 (142)</td>
<td>1.63 (0.13)</td>
<td>8.66s (0.94)</td>
<td>24.67 : 32.57</td>
<td>66.28 (22.76)</td>
<td>210.5 (115.05)</td>
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<td><strong>Younger adults</strong></td>
<td></td>
<td>15</td>
<td>22.6 (4.5)</td>
<td>9:6</td>
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<td>-0.07 (0.17)</td>
<td>29.4 (15.9)</td>
<td>1.78 (0.13)</td>
<td>--</td>
<td>29.54 : 47.04</td>
<td>49.33 (25.38)</td>
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<td><strong>Older vs. Younger (t-tests)</strong></td>
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Mean and standard deviation (in parentheses). Columns include sample size, age, ratio of men to women, Montreal Cognitive Assessment (MoCA) scores, Early Treatment Diabetic Retinopathy Study (ETDRS) log minimum angle of resolution, Randot graded circles (arcssec). Pelli-Robson log contrast sensitivity, Timed Up and Go (TUG) scores in seconds, Center of Pressure Path Length for eyes open and eyes closed (cm), Stroop task interference score (seconds), and Useful Field of View task total score (ms).
Figure 6.1. A depiction of the iDAPT lab (A) used for this study located at the Toronto Rehabilitation Institute. This lab consists of an 8m x 8m x 8m fiberglass cabin with a steel floor mounted on a 6 degree-of-freedom hydraulic motion platform (B) used to provide vestibular cues to heading through passive translation. Participants were seated in a chair that was bolted to the floor (C), where they wore an Oculus Rift™ Head-Mounted Display and noise isolating headphones. The HMD provided optic flow via stereoscopic imagery of an expanding starfield (D).
6.1.2 Apparatus

The experiment was conducted at the Toronto Rehabilitation Institute’s iDAPT Centre for Rehabilitation Research. The experiment took place in a modular, 8 m x 8 m x 8 m laboratory space comprised of a fiberglass body and a steel floor (see Figure 6.1A) that is mated to a Bosch-Rexroth HyMotion 11000 6-degrees-of-freedom hydraulic hexapod motion platform (see Figure 6.1B). The lab was outfitted with a chair equipped with a height and position adjustable headrest to help reduce the movement of the head and neck (see Figure 6.1C). White noise was delivered over a pair of Koss QZ99 passive noise isolating headphones to mask the sounds of the hydraulic platform. The experimenter was able to speak to the participant through the headphones using a Buddy Microphones DesktopMini 7G USB microphone. The visual motion was presented to participants using an Oculus Rift™ Developer Kit 2 stereoscopic head-mounted display (HMD). The organic light emitting diode (OLED) display panel within the HMD has a 90° horizontal and a 100° vertical field of view with a resolution of 960 x 1080 pixels per eye, a refresh rate of 60Hz, and a persistence of 2ms.

6.1.3 Cognitive and perceptual performance assessment battery

Several baseline measures of vision, mobility/balance, and cognition were taken to better characterize the participant groups and to use as potential covariates for data analyses associated with the heading estimation responses across the different sensory conditions (See Table 6.1 for summary statistics).

6.1.3.1 Vision

The ETDRS eye chart (see Ferris, Kassoff, Bresnick, & Bailey, 1982) was administered to evaluate visual acuity, the Pelli-Robson eye chart (Pelli, Robson, & Wilkins, 1988) was used to evaluate contrast sensitivity, and the Randot Stereo test (Stereo Optical Company, 1995) was used to evaluate stereovision. The Early Treatment Diabetic Retinopathy Study (ETDRS) visual acuity test indicated that all participants had visual acuity within the near-normal range of vision or better (see Colenbrander, 2010; Colenbrander, 2002). Older adults and younger adults did not differ significantly in terms of their visual acuity. On the Pelli-Robson contrast sensitivity test, older adults’ mean logCS of 1.63 was lower than younger adults’ mean of 1.78, indicating poorer
contrast sensitivity. On the Randot stereo acuity test, older adults’ mean arcsec was 161.4 which was larger than younger adults’ mean of 29.4, indicating poorer stereoacuity. Note that the performance on the Pelli-Robson and Randot tests may have been affected by lower than optimal lighting conditions. On the Useful Field of View task (UFOV) older adults’ score was 210.5 ms, which was larger than younger adults’ score of 56.25 ms, indicating that older adults were slower to process peripheral visual targets (Ball & Owsley, 1993).

6.1.3.2 Mobility and balance
To reveal any mobility or balance impairments that could affect vestibular heading perception, participants completed the Timed Up and Go (TUG) test (Podsiadlo & Richardson, 1991). All participants completed the task in less than 12 seconds, which is the cut-off score beyond which falls risk increases (see Bischoff et al., 2003; Shumway-Cook et al., 2000). I also performed posturography wherein participants stood on a force plate with their feet together but separated by 17 cm at the heels for 30 seconds, first with their eyes open and again with their eyes closed. The force in Newtons along the x and y-axis over time were used to derive several measures of postural stability including length and area of Center of Pressure (CoP) path length. This test was administered as excessive sway, or an outright loss of balance, could indicate deficits with respect to the visual, proprioceptive, and/or vestibular perception of self-motion that could affect performance on the heading perception task. Note that older and younger adults did not differ significantly in terms of their CoP path length.

6.1.3.3 Cognition
A paper and pencil Stroop task (Stroop, 1935) was used to assess participants’ speed of information processing and capacity for response inhibition. Specifically, the Stroop Neuropsychological Screening Test (SNST) variant was utilized (Trenerry et al., 1989). The SNST consists of two parts, each of which are timed: (i) a colour task in which participants verbally identify the colour of 112 sets of coloured stimuli (asterisks) and (ii) a colour-word task in which they must identify the colour of the ink in which words naming incongruous colours are printed. The Stroop interference, or the increase in the amount of time required to perform the color-word task over the colour task, is used as an index of inhibitory control (Trenerry et al., 1989).
6.1.4 Stimuli

The vestibular stimulus consisted of physical translations via the motion platform that were 7.8 cm in magnitude and that followed a smooth, sinusoidal acceleration/deceleration profile (Equation 1),

\[ s(t) = 0.049 \left( \frac{2\pi t - \sin(2\pi t)}{4\pi^2} \right), \quad 0 \leq t \leq 1 \text{s}, \quad (1) \]

where the maximum rate of acceleration/deceleration was 0.49 m/s\(^2\) and the peak velocity was 0.15 m/s (Butler et al. 2010). I utilized a rate of acceleration that was well above human detection thresholds (see Benson, Spencer, & Stott, 1986) to ensure that older adults would be able to detect the vestibular heading cues. Note that these passive translations also innervate the proprioceptive system (e.g., the neck) but are assumed to be discriminated primarily using vestibular cues. This is supported by the fact that labyrinthectomized macaques undergoing passive translation in the dark display heading perception thresholds ten times higher than when their labyrinths are intact (Gu et al., 2007).

The visual stimuli were generated using Unity™ version 5.2.0 by Unity Technologies Inc. (Unity, 2015). Unity is a video game and VR development platform. A 1000 m x 1000 m x 1000 m virtual space was populated with 200 white Gaussian blobs that were spawned at random locations to create a starfield (See Figure 6.1D). Each blob was the same size, but their visual angle could vary depending on their depth within virtual space. At the maximum depth, a blob could be as small as a single pixel or 0.2° horizontal visual angle. At the minimum depth, a blob could occupy nearly the entire field of view. A virtual camera was placed at the face of the starfield and then traveled toward the stars. The camera followed the same acceleration/deceleration profile as the motion platform. This perspective was then displayed on the HMD in stereo, giving the observer the visual impression that they were translating through the starfield and creating optic flow.
Figure 6.2. Depiction of 2-interval forced choice task in which participants were asked to judge which of two headings was more to the right. Panel A depicts the congruent condition where the standard heading was always 0°. Panel B depicts the incongruent condition where the standard contained a 0° vestibular heading and a visual heading that was either 5° rightward or 20° rightward. The comparison heading angles were centered on 2.5° and 10°, respectively (or Δ/2).
6.2 Procedure

6.2.1 Baseline assessment session

The experiment was divided into two sessions, each lasting approximately 2 hours. In the first session, I obtained informed consent and performed on-site screening using the medical history questionnaire and the MoCA. I then administered the visual, mobility/balance, and cognitive assessment battery.

6.2.2 Experimental heading perception task

The second session consisted of the heading perception task. The heading perception task was comprised of a 2-interval forced choice (2IFC) task in which participants were asked to judge “in which of the two intervals did you move more to the right?” Each trial consisted of a standard heading interval (0°, 5°, or 20°) and a comparison heading interval (± 2°, 5°, 10°, 20°; see Figure 6.2). The order in which the standard and comparison intervals were presented was counterbalanced. All participants performed the task under three sensory conditions: visual, vestibular, and bimodal (visual and vestibular combined). Two levels of inter-sensory incongruencies were also introduced wherein the vestibular cues were straight ahead (0°), but the visual cues were offset to the right by either 5° (subtle conflict), or 20° (larger conflict). Hereinaforward, the unimodal conditions will be denoted using Θ followed by the standard heading angle (e.g., Θ= 0°) and the bimodal conditions will be will be denoted using Δ followed by the visual offset angle (e.g., Δ = 0°).

6.2.2.1 Unimodal and congruent conditions

To establish the unimodal reliability of visual estimates and vestibular estimates of heading, participants completed a block of visual only trials and a block of vestibular only trials. Participants also completed a block of congruent bimodal trials where the standard consisted of congruent visual and vestibular cues. For each of these conditions, the standard heading angle was Θ=0° and the comparison heading angles varied around the standard in increments of ±2°, 5°, 10°, 20°.
6.2.2.2 Incongruent conditions

To quantify the relative weights of the visual and vestibular estimates of heading, I introduced a block of bimodal trials in which the standard heading contained a subtle $5^\circ$ inter-sensory conflict. Specifically, the standard consisted of a vestibular heading angle of $0^\circ$ and a visual heading angle that was offset by $5^\circ$ to the right ($\Delta = 5^\circ$). The comparison heading angle centered around a heading angle of $\Delta/2 (2.5^\circ)$ and varied in increments of $\pm 2^\circ$, $5^\circ$, $10^\circ$, and $20^\circ$. This level of inter-sensory conflict is comparable to that which has previously been utilized to introduce slight spatial disparities as a strategy for quantifying sensory cue-weighting, but while keeping the spatial disparity subtle enough to be largely unnoticeable (see Fetsch et al., 2009; Butler et al., 2010). To determine whether the weighting was optimal, the observed bimodal estimates were compared against those predicted by the observed unimodal estimates. To establish an estimate of reliability for unimodal visual estimates when the standard was $5^\circ$, participants completed a visual only block with a $\Theta=5^\circ$ rightward standard. The comparison heading angle centered around $5^\circ$ rightward and varied in increments of $\pm 2^\circ$, $5^\circ$, $10^\circ$, $20^\circ$.

Participants also completed a block of bimodal trials for which a larger inter-sensory conflict of $20^\circ$ was introduced. Here the aim was to use a larger level of inter-sensory conflict than that used in previous studies in order to explicitly determine whether there are age-related differences in the level of spatial conflict for which optimal integration no longer occurs. This allowed me to gain novel insight into possible age-related differences with respect to the spatial window of integration. For these trials, the standard consisted of a vestibular heading angle of $0^\circ$ and a visual heading angle that was offset by $20^\circ$ to the right ($\Delta=20^\circ$). The comparison heading angle centered on a heading angle of $\Delta/2 (10^\circ)$ and varied in increments of $\pm 2^\circ$, $5^\circ$, $10^\circ$, $20^\circ$. Once again, to determine whether the weights were optimal, the observed bimodal estimates were compared against those predicted by the observed unimodal estimates. Participants also completed a visual only block where the standard was $\Theta=20^\circ$ rightward as a benchmark for comparison. The comparison heading angle centered on a heading angle of $\Delta/2 (10^\circ)$ and varied in increments of $\pm 2^\circ$, $5^\circ$, $10^\circ$, $20^\circ$ around the standard.
All participants completed seven experimental blocks in total: one vestibular block, three visual blocks (0°, 5°, 20° standards), and three bimodal blocks (0°, 5°, 20° visual offset). The blocks were grouped into three bins, one for each level of angular offset (0°, 5°, 20°). Each bin contained a visual block, a vestibular block, and a bimodal block. There were eight trials for each of the eight possible comparison angles (± 2°, 5°, 10°, 20°), resulting in a total of 64 trials per block, for a total of 460 trials across all 7 blocks. Because there was only one type of vestibular only trial (0°), those 64 trials were distributed as evenly as possible across the three bins. Within each bin, the constituent blocks were always presented in the same order: visual, bimodal, vestibular. However, the order in which the three bins were presented was counterbalanced. See Figure 6.3 for a depiction of the counterbalancing scheme.

The presentation of each trial was triggered by the experimenter using a tablet computer. Within each trial, the first movement interval was presented, followed by a one-second pause before the onset of the second movement interval. Once both intervals were complete, the participant verbalized their judgment as to which of the two headings was more to the right (“first” or “second”). The experimenter recorded their response via the tablet computer. Once the response was entered, there was a 750-ms pause before the next trial was initiated. In the vestibular alone and bimodal conditions, a longer delay after each trial was necessary because, after each trial, the motion platform required 5 seconds to return to its starting position, moving at a rate that was below the perceptual threshold.
Figure 6.3. Depiction of counterbalancing scheme. The order in which participants experienced each angular offset (0°, 5°, 20°) was counterbalanced. The order in which participants experienced each sensory condition was the same.
6.3 Data analyses

The portion of rightward responses that the participant made was plotted for each comparison heading angle within each block and the data were fitted with a cumulative Gaussian function using the psignifit toolbox (Wichmann & Hill, 2001a, 2001b). The cumulative Gaussian functions were used to derive the point of subjective equality (PSE), the point at which the heading was selected as more rightward 50% of the time, and the just noticeable difference (JND),

\[ JND = \sqrt{2} \sigma. \]  

(2)

The JND was defined as the difference in heading angle between the PSE and the point at which heading was selected as more rightward 84% of the time, or a threshold of one standard deviation above the mean (Ernst, 2005; Rohde, van Dam, & Ernst, 2016; Wichmann & Hill, 2001). The JND is inversely related to reliability (the larger the JND, the less reliable the estimate of heading).

MLE (see Ernst, 2005; Ernst & Banks, 2002; Ernst & Bülthoff, 2004) dictates that the bimodal likelihood, \( \hat{\mathbf{S}^\text{Bimodal}} \), can be predicted by the linear weighted sum of the visual heading estimate, \( \hat{\mathbf{S}^\text{Vis}} \), and the vestibular heading estimate, \( \hat{\mathbf{S}^\text{Vest}} \):

\[ \hat{\mathbf{S}^\text{Bimodal}} = w_{\text{Vis}} \hat{\mathbf{S}^\text{Vis}} + w_{\text{Vest}} \hat{\mathbf{S}^\text{Vest}}, \]  

(3)

where the weights \( w_{\text{vis}} \) and \( w_{\text{vast}} \) are derived from the reliability (inverse variance) of the unimodal cues,

\[ w_{\text{Vis}} = \frac{1/\text{IND}^2_{\text{Vis}}}{1/\text{IND}^2_{\text{Vis}} + 1/\text{IND}^2_{\text{Vest}}}, \]  

(4)

\[ w_{\text{Vest}} = 1 - w_{\text{Vis}}. \]  

(5)
and where $\text{JND}_{\text{vis}}$ and $\text{JND}_{\text{vest}}$ represent the JND of the unimodal visual cues and vestibular cues, respectively, and serve as estimates of unimodal variance. The observed weights are calculated by determining the proximity of the bimodal PSE relative to each unimodal PSE,

$$w_{\text{vis}} = \frac{\text{PSE}_{\text{bimodal}} - \text{PSE}_{\text{vest}}}{\text{PSE}_{\text{vis}} - \text{PSE}_{\text{vest}}},$$

(6)

and

$$w_{\text{vest}} = \frac{\text{PSE}_{\text{bimodal}} - \text{PSE}_{\text{vis}}}{\text{PSE}_{\text{vest}} - \text{PSE}_{\text{vis}}}.$$

(7)

The observed weights, Equation 6 & 7, can then be compared against the predicted weights, Equations 4 & 5. MLE then dictates that the bimodal reliability is the sum of the unimodal reliabilities,

$$\frac{1}{\text{JND}_{\text{bimodal}}^2} = \frac{1}{\text{JND}_{\text{vis}}^2} + \frac{1}{\text{JND}_{\text{vest}}^2},$$

or

$$\text{JND}_{\text{bimodal}}^2 = \frac{\text{JND}_{\text{vis}}^2 \cdot \text{JND}_{\text{vest}}^2}{\text{JND}_{\text{vis}}^2 + \text{JND}_{\text{vest}}^2}.$$

(8)

and thus, the bimodal JND should be less than or equal to the lowest unimodal JND,

$$\text{JND}_{\text{vis-vest}} \leq \min (\text{JND}_{\text{vis}}, \text{JND}_{\text{vest}}).$$

(9)

(Formulae adapted from Butler et al., 2010)

6.3.1 Statistical analyses

To compare precision between age groups, the visual unimodal JNDs and the vestibular unimodal JNDs were submitted to a 2 age (older vs. younger) x 4 unimodal condition (vestibular; visual 0°, 5°, 20°) mixed factorial ANOVA. To determine whether younger and older adults were matched with respect to the point of subjective equality of the unimodal heading estimates, the differences between the objective heading angle of the unimodal motion stimuli (i.e., offset angle) and participants’ estimates of heading angle (i.e., PSEs) were calculated and submitted to
a 2 (older vs. younger) x 4 (vestibular; visual 0°, 5°, 20°) mixed factorial ANOVA. To determine whether participants’ individual characteristics as determined by baseline sensory, cognitive and motor tasks influenced the precision with which they estimated their heading, bivariate correlations were used to examine the relationship between age, visual acuity, contrast sensitivity, stereo acuity, TUG, COP path length, and JND at each visual offset and for each unisensory condition and each standard heading angle.

To test for increases in precision observed in the bimodal condition relative to the unimodal conditions, I ran a series of 2 age (older vs. younger) x 3 sensory condition (visual, vestibular, bimodal) ANOVAs, one for each visual offset (0°, 5°, and 20°). To determine whether the gains in precision associated with bimodal cues were consistent with optimal integration, I then followed up with paired-samples t-tests comparing the observed JNDs to the predicted optimal JNDs for the 0°, 5°, and 20° offsets within each age group. Likewise, to test whether the available cues were weighted in a manner that was consistent with optimal integration, I used paired–samples t-tests to compare the predicted optimal PSEs to the observed PSEs for the 5° and 20° offsets within each age group. The 0° offset was omitted because the PSEs associated with the visual and vestibular cues should be the same and thus there can be no observable differences in terms of their relative weighting.

6.4 Results

6.4.1 Reliability (JNDs)

JNDs for the two age groups, the vestibular condition, and each of the three visual conditions (i.e., Θ= 0°, 5°, and 20°), were submitted to a 2 (older vs. younger) x 4 (unimodal conditions) mixed factorial ANOVA. There was a main effect of age group, $F(1,27)=7.16, p=.013, \eta_p^2=.210$, in which older adults had higher JNDs overall compared to the younger adults. There was also a main effect of sensory condition, $F(3,81)=15.52, p<.001, \eta_p^2=.365$. Post-hoc t-tests using the Bonferroni correction revealed that vestibular JNDs ($M=4.37, SE=.46$) were lower than the visual JNDs at Θ=0° ($M=7.34, SE=.65, p=.002$) and Θ=20° ($M=9.46, SE=.95, p<.001$), and that visual Θ=20° JNDs were higher than the visual Θ=0° ($p=.044$), and Θ=5° JNDs ($M=6.08, SE=.63, p=.002$). There was also a significant age by sensory condition interaction, $F(3,81)=3.06,$
Post-hoc Bonferroni tests comparing age groups within each sensory condition demonstrated that vestibular only JNDs did not differ significantly \( (p=.559) \) between older \( (M=4.65, \ SE=.661) \) and younger adults \( (M=4.11, \ SE=.639) \). Likewise, visual \( \Theta=5^\circ \) JNDs did not differ \( (p=.171) \) between older \( (M=6.96, \ SE=.89) \) and younger adults \( (M=5.20, \ SE=.86) \). However, visual \( \Theta=0^\circ \) JNDs differed \( (p<.001) \) between older \( (M=9.67, \ SE=.93) \) and younger adults \( (M=5.02, \ SE=.89) \), and visual \( \Theta=20^\circ \) JNDs differed \( (p=.049) \) between older \( (M=11.42, \ SE=1.36) \) and younger adults \( (M=7.51, \ SE=1.32) \). Post-hoc Bonferroni tests comparing sensory conditions within each age group revealed that older adults were driving the effect of sensory condition. Younger adults’ JNDs did not differ significantly across any of the unimodal conditions \( (p=.104) \). Conversely, older adults had lower JNDs in the vestibular condition \( (M=4.65, \ SE=.661) \) than in the visual \( \Theta=0^\circ \) \( (M=9.67, \ SE=.93, \ p<.001) \) and \( \Theta=20^\circ \) conditions \( (M=11.42, \ SE=1.36, \ p<.001) \), but not the visual \( \Theta=5^\circ \) \( (M=6.96, \ SE=.89, \ p=.173) \) condition. Also, they had lower JNDs in the visual \( \Theta=5^\circ \) condition than in the visual \( \Theta=0^\circ \) \( (p=.032) \) and \( \Theta=20^\circ \) \( (p=.005) \) conditions.

### 6.4.2 Weighting (PSEs)

To determine whether younger and older adults were matched with respect to the point of subjective equality of the unimodal heading estimates, the difference between the objective heading angle of the unimodal motion stimuli (i.e., offset angle) and participants’ estimates of heading angle (i.e., PSEs) was calculated. The mean differences were then submitted to a 2 (older vs. younger) x 4 (unimodal conditions) mixed factorial ANOVA. As expected, there was no significant effect of age group, \( F(1,27)=1.31, \ p=.262 \), or unimodal condition, \( F(3,81)=.462, \ p=.710 \), and no interaction, \( F(3,81)=1.59, \ p=.198 \).
6.4.3 Correlations between unimodal JNDs and participant characteristics

Bivariate correlations were used to examine the relationship between age, visual acuity, contrast sensitivity, stereo acuity, TUG, COP path length, and JND at each visual offset and for each unisensory condition and each standard heading angle to determine whether age-related sensory declines predicted unimodal heading perception. No correlations were significant ($r \leq .283, p \geq .077$) and thus there is no evidence that these particular participant characteristics were predictive of unimodal precision, but this was likely due to the modest sample size.

6.4.4 Unimodal vs. bimodal JNDs

6.4.4.1 Congruent conditions

Unimodal and bimodal JNDs for the $0^\circ$ standard were submitted to a 2 age x 3 sensory condition (visual, vestibular, bimodal) mixed factorial ANOVA. Mauchly’s test of sphericity indicated that the assumption of sphericity was violated for the factor sensory condition, $\chi^2(2)=13.51, p=.001$; therefore, degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon=.71$). There were significant main effects of age group, $F(1, 27)=9.25, p=.005, \eta^2_p=.255$, and sensory condition, $F(1.42, 38.43)=19.87, p<.001, \eta^2_p=.424$, and a significant age by sensory condition interaction, $F(1.42, 38.43)=7.02, p=.006, \eta^2_p=.206$. Post-hoc Bonferroni tests revealed that for older adults, bimodal cues ($M=4.38, SE=.411$) yielded a significantly lower ($p<.001$) JND than visual cues ($M=9.67, SE=.931$) as shown in Figure 6.4B. No other comparisons were significant.

6.4.4.2 Incongruent conditions

Unimodal and bimodal JNDs for the $5^\circ$ standard were submitted to a 2 age x 3 sensory condition (visual, vestibular, bimodal) mixed factorial ANOVA. Mauchly’s test of sphericity indicated that the assumption of sphericity had been violated for the factor sensory condition, $\chi^2(2)=6.99, p=.030$; therefore, degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon=.81$). There was a significant main effect of sensory condition,
Figure 6.4. Mean unimodal, bimodal, and predicted optimal just-noticeable differences (y-axis) for younger adults (A) and older adults (B), each plotted as a function of visual offset angle (x-axis). Just noticeable difference (JND) is an index of reliability; larger mean JND indicates lower reliability. Note that because the vestibular heading was always 0° during conflict trials, the vestibular JND only appears at 0°. The key observation was that younger adults’ mean bimodal JND was near predicted optimal JND at the 0° and 5° offsets whereas older adults’ mean bimodal JND was only near optimal at the 0° offset. Error bars are ±1SE.
F(1.62, 43.70) = 7.99, p < .001, η² = .228; however, there was no significant main effect of age group, F(1,17) = 3.48, p = .073, η² = .114, and no significant interaction, F(1.62, 43.70) = .597, p = .554, η² = .022. Post-hoc Bonferroni tests exploring the effect of sensory condition revealed that Bimodal JNDs (M = 3.88, SE = .261) were significantly lower (p = .002) than visual JNDs (M = 6.08, SE = .625) as shown in Figures 6.4A and B. No other comparisons were significant.

Unimodal and bimodal JNDs for the 20º standard were submitted to a 2 age x 3 sensory condition (visual, vestibular, bimodal) mixed factorial ANOVA. Mauchly’s test of sphericity indicated that the assumption of sphericity had been violated for the factor sensory condition, χ²(2) = 15.69, p < .001; therefore, degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity (ε = .68). There were significant main effects of sensory condition, F(1.38, 37.16) = 17.00, p < .001, η² = .386, and age group, F(1, 27) = 6.01, p = .021, η² = .182, but no significant interaction, F(1.38, 37.16) = 1.83, p = .182, η² = .064. Post-hoc Bonferroni tests exploring the effect of sensory condition revealed that Bimodal JNDs (M = 7.52, SE = .51) were significantly greater than (p < .001) vestibular JNDs (M = 4.38, SE = .46). Post-hoc tests exploring the effect of age group revealed that overall, older adults had greater JNDs (M = 8.21, SE = .640) (p < .001) than younger adults (M = 6.03, SE = .618) as shown in Figures 6.4A and 6.4B.

### 6.4.5 Observed vs. predicted optimal JNDs

Predicted optimal JNDs were calculated from the unimodal JNDs using Equation 8. The observed and predicted JNDs were submitted to paired-samples t-tests for each heading angle and for each age group. Younger adults’ observed and predicted bimodal JNDs did not differ significantly at Δ = 0º, t(14) = -1.58, p = 0.136, or at Δ = 5º, t(14) = 2.10, p = .055. However, their observed and predicted JNDs did differ at Δ = 20º, t(14) = -6.69, p < .001 (see Figure 6.4A). Older adults’ observed and predicted JNDs did not differ significantly at Δ = 0º, t(13) = -1.10, p = .291. However, their observed and predicted JNDs did differ significantly at Δ = 5º, t(13) = 2.41, p = 0.031, and at Δ = 20º, t(13) = 5.22, p < .001 (see Figure 6.4B).
6.4.6 Observed vs. predicted optimal PSEs

For the conflict conditions $\Delta=5^\circ$ and $\Delta=20^\circ$, equations 4 and 5 were first used to derive estimates of the relative weights associated with the constituent visual and vestibular heading estimates on the basis of their respective JNDs. No predictions were made for $\Delta=0^\circ$ because a spatial conflict is necessary in order to determine relative weights. The predicted optimal PSE was then calculated by taking the linear weighted sum of the visual and vestibular PSEs (Equation 3). I used two-tailed $t$-tests to compare the observed bimodal PSE against the optimal PSE. At $\Delta=5^\circ$, the observed bimodal PSEs for younger adults ($M=2.41$, $SE=.404$) were not significantly different from the predicted PSEs ($M=1.97$, $SE=0.55$), $t(14)=-.82$, $p=0.426$ (see Figure 6.5A). At $\Delta=5^\circ$, the observed bimodal PSEs for older adults ($M=.99$, $SE=.58$) were not significantly different from the predicted PSEs ($M=1.22$, $SE=0.37$), $t(13)=.301$, $p=.768$ (see Figure 6.5B). At $\Delta=20^\circ$, younger adults’ observed PSEs did not differ from their predicted optimal PSEs, $t(14)=.652$, $p=.525$ (see Figure 6.5A). At $\Delta=20^\circ$, older adults’ observed PSEs ($M=6.09$, $SE=1.11$) were significantly greater (i.e., closer to the observed visual PSE) than their predicted optimal PSEs ($M=3.20$, $SE=.70$), $t(13)=2.27$, $p=.041$ (see Figure 6.5B).

6.5 Discussion

The purpose of the current investigation was to determine whether healthy older adults differ from younger adults in terms of how they integrate multisensory information during self-motion perception. Specifically, my objectives were to consider whether older adults integrate visual-vestibular cues optimally such that (1) congruent cues yield a reduction in variance and (2) cues are weighted according to their respective reliabilities. Moreover, my objective was to consider whether (3) older adults demonstrate differences in visual-vestibular integration under varying levels of spatial conflict compared to younger adults. I observed evidence to indicate that older and younger adults did not differ in terms of their vestibular heading discrimination thresholds but did differ in terms of their visual heading discrimination thresholds. I also observed that while congruent cues allow both older and younger adults to reduce perceptual variance, incongruent cues reveal different cues integration strategies among older and younger adults. In the following sections I will consider why the observed pattern of age-related differences in
Figure 6.5. Mean unimodal, bimodal, and predicted optimal point of subjective equality (y-axis) for younger adults (A) and older adults (B), each plotted as a function of visual offset angle (x-axis). The PSE is an index of what the perceived heading angle is. Note that for this reason, the visual, vestibular, and bimodal PSEs are overlapping at the 0°. Note that no prediction for optimal PSE was generated for 0° because no spatial conflict was present. The key observation was that younger adults’ mean bimodal PSE was near optimal at both the 5° and 20° offset, whereas older adults’ mean bimodal PSE was only near optimal at the 5° offset. Error bars are ±1SE.
unimodal heading thresholds and in bimodal cue integration strategies may have emerged. I will then consider the potential functional implications that different cue integration strategies may have for older adults and important areas for future research.

6.5.1 Age-related differences in unimodal thresholds

6.5.1.1 Vestibular JNDs

In the current investigation, older and younger adults did not differ with respect to their heading discrimination thresholds when they were passively moved in the dark. There is a large body of work indicating that age-related declines in the vestibular system (e.g., hair cell loss, nerve cell loss) changes older adults’ capacity to detect inertial cues to self-motion (Anson & Jeka, 2016), but the nature of these perceptual declines likely depends on the characteristics of the inertial cues that are provided. Roditi and Crane (2012) presented older adults (50 years +) and younger adults (21-50 years) with passive anterior or posterior sinusoidal translations that ranged in magnitude from 0.12cm to 15cm at either 1Hz or a 0.5Hz and asked them to report the direction of self-motion. At 0.5 Hz, older adults had greater thresholds for detecting passive translations than younger adults, but at 1 Hz, older adults and younger adults did not differ significantly. Older adults’ mean perceptual threshold at 1Hz was 0.9 ± 0.3 cm/s and younger adults’ mean perceptual threshold at 1Hz was 0.7 ± 0.3 cm/s (Roditi & Crane, 2012). This suggests that in the current study, age-related differences in vestibular precision did not emerge because I knowingly utilized a rate of acceleration that well exceeded both younger and older adults’ perceptual thresholds. Ultimately, more systematic investigations using varied motion profiles are required to disentangle age-related differences in vestibular function as it relates to self-motion perception.

6.5.1.2 Visual JNDs

At Θ=0° older adults were significantly more variable than younger adults when using visual cues alone to discriminate heading. Older adults’ mean visual JND at Θ=0° was 9.67°, which was nearly twice as high as younger adults’ mean visual JND. Previous work on optic flow perception has shown that even when carefully controlling for visual impairments, older adults
display higher perceptual thresholds for optic flow wherein they require faster flow rates and a higher level of coherence in order to derive reliable estimates of their speed and heading (Atchley & Andersen, 1998; Bennett, Sekuler, & Sekuler, 2007; Snowden & Kavanagh, 2006; Tetewsky & Duffy, 1999; Warren et al., 1989). Animal models of heading perception have established that the medial superior temporal cortex contains neurons that respond to visual (and to vestibular cues) pertaining to heading (Duffy & Wurtz, 1995; Gu et al., 2007; Gu, Watkins, Angelaki, & DeAngelis, 2006) and studies on senescent monkeys in particular have shown that the neurons within MST become less selective with respect to visual heading with age (Liang et al., 2010). More recently, neural network modeling has been used to demonstrate that typical rates of global cortical cell loss within area MST can be used to predict the increased heading perception thresholds observed in older adults (Lich & Bremmer, 2014). There is also evidence that in MST there is a neural overrepresentation for angular headings, which biases heading perceptions away from 0° (i.e., straight forward) (Cuturi & MacNeilage, 2013; Gu et al., 2010). Many behaviours involve maintaining straight forward movement and therefore, this systematic bias in heading perception may enable observers to more readily categorize headings as left or right of center, making them more sensitive to deviations from their intended path (Cuturi & MacNeilage, 2013). However, this heading bias may also lead to the overestimation of headings that are close to 0° (Cuturi & MacNeilage, 2013). For older adults, the confluence of heading overestimation and broad changes in neural mechanisms that mediate optic flow perception may lead to increased heading discrimination thresholds at 0°, although this has not been empirically tested.

The observation that older adults’ visual JNDs were lower at Θ=5° than at Θ=0° may reflect the different properties of visual motion present during each respective standard (e.g., the retinal eccentricity of the focus of expansion, the prevalence or salience of dynamic occlusion). It is also possible that because standard headings of Θ=5° conveyed directionality, these headings were more easily categorized as rightward and were less susceptible to perceptual biases than standard headings of Θ=0°. That said, for standard headings of Θ=20°, older adults had significantly greater visual JNDs than at Θ=5° (whereas younger adults did not). Previous studies have shown that heading discrimination thresholds increase with a more eccentric point of reference and are
thereby much higher at standard headings of 20° than they are at standard headings of 5° (Crowell & Banks, 1993; Gu et al., 2010). This may be because many MST neurons are tuned such that their peak heading discriminability is for headings near 0° (forward) and 180° (backward) (Gu et al., 2010). The higher eccentricity of the Θ=20° standard in concert with decreased heading selectivity may have increased older adults’ heading discrimination thresholds relative to the Θ=5° standard (Gu et al., 2010).

6.5.2 Predicted optimal vs. observed performance

6.5.2.1 Congruent sensory cues

To assess whether younger and older adults integrate visual and vestibular cues to heading optimally, I compared observed bimodal JNDs against the predicted optimal JNDs. Consistent with previous findings (Butler et al., 2010; Fetsch et al., 2009), younger adults integrated congruent visual and vestibular cues in a manner consistent with optimal integration and, for the first time, this pattern was also evidenced in older adults. That said, although the observed JNDs did not differ from the predicted optimal JNDs, younger adults also did not display a significant reduction in variance over visual or vestibular cues alone when comparing the average JND values across conditions. For older adults, bimodal cues yielded a significant reduction in variance over visual cues alone but not vestibular cues alone. Participants may have performed close to ceiling within one or both of the unimodal conditions and therefore, there was not enough room for a statistically significant improvement in averaged precision values. The basic principles of multisensory integration indicate that bimodal performance gains are the largest when the two unimodal reliabilities are equal and near threshold and thus, the most sensitive approach would be to map the threshold values for each unimodal cue and to try to equate unimodal estimates (within and between age groups) a priori. Future investigations could seek to implement this approach when investigating the integration of visual and vestibular cues in order to maximize sensitivity to age-related differences in optimal integration (although see also “Future Directions” below).
6.5.2.2 Incongruent sensory cues

For the subtle conflict ($\Delta=5^\circ$), younger adults exhibited optimal integration as indicated by no significant differences between the observed and optimal predicted estimates. This observation is consistent with previous work demonstrating that younger adults integrate optimally in the presence of spatial conflicts of 4°, 6°, and 10° (Fetsch et al., 2009; Butler et al., 2010). However, the bimodal JNDs were not significantly different from the vestibular JNDs, suggesting that vestibular inputs were used more heavily. On the other hand, at the 5° conflict older adults’ observed bimodal JNDs were significantly greater than their predicted optimal JNDs. This suggests that even at relatively small spatial conflicts, there may be a lower bimodal benefit in terms of increased reliability afforded by redundant sensory inputs, compared to that which can be observed in younger adults. Note that for the 5° trials specifically, there was no significant difference in the unimodal visual and unimodal vestibular JNDs between older and younger adults, or within older adults. Again, because the greatest gains in precision occur when unimodal reliabilities are matched, this condition was the most sensitive to evidence of age-related differences in optimal integration, and indeed age-related differences were observed. Notably, the PSE values demonstrated that neither age group displayed biases in their absolute thresholds during the 5° conflict condition and both groups showed evidence of reliability-based cue weighting at this subtle cue conflict level.

For the larger conflict ($\Delta=20^\circ$), both age groups had bimodal JNDs that were significantly greater than the predicted JNDs. Although younger adults did not demonstrate greater precision for bimodal relative to unimodal estimates, their PSEs did match the predicted PSEs, suggesting they utilized reliability-based cue weighting. Older adults, however, had bimodal PSEs that were not consistent with the predicted optimal PSEs based on reliability-based weighting. Because the vestibular estimates were far more reliable than the visual estimates, optimal integration would dictate that the bimodal PSE is weighted in favour of the vestibular estimate. However, older adults’ bimodal PSE was pulled toward the visual heading estimate, meaning that the highly unreliable visual inputs had a larger than predicted influence on their heading estimate. There are a number of plausible explanations as to why a more substantial spatial conflict had differential effects on the performance of older and younger adults in terms of relative cue-weighting. In the
following sections, several non-exclusive or exhaustive interpretations are offered. First, I will consider how aging may affect the interpretation of visual motion cues as being caused by self-motion or object motion. I will then consider how age-related differences in cumulative experience may affect expectations pertaining to the spatial congruency between cues arising from self-motion. Finally, I will consider the potential role of broader age-related changes in terms of central multisensory integrative mechanisms.

A persistent challenge faced by the perceptual system is to determine which sensory inputs are caused by the same movement or event and should be integrated, versus those that are caused by independent movements or events and should be segregated (i.e. causal inference; see Kayser & Shams, 2015; Körding et al., 2007; Parise, Spence, & Ernst, 2012; Shams & Beierholm, 2010; Spence & Squire, 2003). Generally, sensory inputs that occur close together in space and in time are more likely to have originated from the same event and are thereby more likely to be causally related and thus integrated (Wallace & Stevenson, 2014; Körding et al., 2007; Shams & Beierholm, 2010). As discussed above, the range of physical space and time over which integration is likely to occur is commonly referred to as the spatial and temporal windows of integration, respectively (Diederich & Colonius, 2004; Wallace et al., 2004). However, much of the previous research concerning the spatial and temporal binding windows has focussed on the integration of discrete visual and auditory inputs. The processes underlying visual-auditory integration and visual-vestibular integration, however, may be distinct. Visual and auditory stimuli are exteroceptive (i.e., generated externally) and therefore their spatial and temporal proximity can be used to make inferences about whether they are causally related and should be integrated (Blanke, Slater, & Serino, 2015). The integration of interoceptive cues (i.e., those generated internally) such as vestibular and proprioceptive inputs may be subject to additional constraints (see Blanke et al., 2015 for review). Visual and vestibular cues to self-motion may be unique in this respect because under most natural conditions involving self-motion, the visual and vestibular systems will provide highly congruent information (Kaliuzhna et al., 2015; Prsa et al., 2012). There is some evidence to suggest that because dynamic visual and vestibular cues associated with self-motion are essentially redundant, observers may discard the individual visual and vestibular estimates (i.e., sensory fusion; Prsa et al., 2012). Previous work has
demonstrated that visual-vestibular integration is robust to the introduction of different types of inter-sensory incongruencies including conflicting heading angles (e.g., Butler et al., 2011, 2010; Fetsch et al., 2009), conflicting movement axes (i.e., forward translation vs. roll; Kaliuzhna et al., 2015) and conflicting velocity profiles (Butler, Campos, & Bülthoff, 2014). Taken together, this evidence suggests that visual and vestibular cues to self-motion may be integrated in a more mandatory fashion than exteroceptive cues typically are.

Recent evidence indicates that while visual-vestibular integration may be robust to the introduction of various types and levels of multisensory incongruencies, integration is not observed under more significant visual-vestibular spatial conflicts (de Winkel et al., 2017). To demonstrate this, de Winkel and colleagues (2017) created an absolute heading estimation task in which participants were presented with stereoscopic optic flow clues conveying a broad range of headings of (± 180° in increments of 5°) along with physical motion conveying headings that were offset from the visual heading angles. The magnitude of the offset was selected randomly from a uniform distribution of headings ranging from -90° to +90°. Observers then used an instrumented wand to point in the direction of perceived self-motion. de Winkel and colleagues demonstrated that younger adults’ heading percepts were best predicted by a causal inference-model averaging model (CI-MA; Kayser & Shams, 2015; Körding et al., 2007; de Winkel et al., 2015; Wozny, Beierholm, & Shams, 2010). Visual motion cues will always have one of two causal interpretations: they could reflect self-motion or they could reflect the movement of external objects (see Brandt, Dichgans, & Koenig, 1973). Visual and vestibular motions cues that are highly spatially congruent are likely to have both been caused by self-motion and should thereby be integrated whereas highly spatially discrepant visual and vestibular cues are unlikely to have both been caused by self-motion (i.e., the visual cues may reflect object motion) and thus they should be segregated. The CI-MA model dictates that the observer will derive heading estimates for both causal structures, including a multisensory integration heading estimate that assumes that both the visual and vestibular cues were caused by self-motion and a sensory segregation heading estimate that assumes that the visual and vestibular heading estimates were caused by discrete events. The final heading percept then reflects the sum of the multisensory integration estimate weighted according to the probability that the visual and
vestibular cues were both caused by self-motion, and the sensory segregation estimate weighted according to the probability that the visual and vestibular cues were causally distinct. The probability associated with either causal structure is informed by a prior that dictates that as the magnitude of the spatial conflict increases, the probability of a common cause decreases. This prior is informed by the observers’ past experiences with visual and vestibular cues to self-motion (see Salinas, 2011 for review). Thus, at small spatial discrepancies of less than ±14°, the observer will infer a common cause and their heading percept will reflect the integration of the visual and vestibular heading estimates. At intermediate spatial discrepancies (±14° to ±45°), their heading percept will be intermediate to the multisensory integration and the sensory segregation estimates and at more substantial spatial conflicts (±45° to ±90°), their heading percept will reflect sensory segregation (Körding et al., 2007; de Winkel et al., 2015, 2017). This is consistent with the observation in the current study that younger adults continued to optimally integrate in the presence of a 5° spatial conflict, but not a 20° conflict. At a 5° conflict, the probability that both cues were causally related to self-motion may have been sufficiently high that younger adults integrated them. A 20° conflict may have led to ambiguity as to whether the cues were causally related to self-motion or to object motion. This could also explain why younger adults’ bimodal JNDs at Δ=20° were sub-optimal and were closer to their Θ=20° visual JNDs than their vestibular JNDs. On bimodal trials where visual motion was attributed to the movement of external objects, younger adults may have been judging which interval of object motion was more rightward and therefore, they were only as precise as their Θ=20° visual estimate. However, there have been no comparable studies that have introduced large visual-vestibular conflicts to older adults.

In the current study, unlike younger adults, older adults did not demonstrate evidence of optimal integration during large or even subtle visual-vestibular conflicts. One possible explanation is that older adults may be less flexible than younger adults in terms of the inferences that they make about the causality of temporally coincident motion cues. As discussed above, during most natural forms of self-motion, the visual and vestibular systems will typically provide highly temporally and spatially congruent cues. It is conceivable that as older adults accumulate a lifetime of exposure to self-motion experiences and the associated congruency between visual
and vestibular cues, they may develop more rigid expectations. This may result in a greater sensitivity to spatial discrepancies and thus a reduced tolerance to even modest spatial conflicts.

Previous work in other sensory domains has also shown that multisensory integration may be broadly heightened in older age and that when older adults are presented with incongruent or task-irrelevant cues, they may continue to combine them in an obligatory fashion, resulting in greater performance decrements compared to younger adults (DeLoss et al., 2013; Guerreiro et al., 2013; McGovern et al., 2014; Sekiyama et al., 2014). Thus, in the current task, older adults may have incorporated both the visual and vestibular cues into their heading percept, even during large spatial conflicts, despite the comparatively low reliability of the visual cues. Previous evidence of heightened multisensory integration has largely been derived from visual-auditory stimulus detection and stimulus discrimination tasks. Therefore, the results described here are some of the first evidence to support this interpretation for visual-vestibular integration, and in the context of tasks involving self-motion perception.

An important caveat is that older adults may be capable of appropriately reconciling or adapting to conflicting cues to self-motion, but that they are slower to do so than younger adults. Previous work has demonstrated that when older adults are presented with oscillatory visual cues while attempting to maintain a stable posture they are more susceptible to postural sway than younger adults. However, when exposed to the conflicting cues for an extended duration, they can eventually adapt (e.g., Jeka et al., 2006; Jeka, 2010). This is perhaps because as stimulus duration increases, the observer can accumulate more evidence pertaining to whether or not the available cues are in fact causally related (see Winkel et al., 2015, 2017). In the current investigation, each movement was 1 s long. It is conceivable that if older adults were presented with motion cues over a longer duration (e.g., ≥ 2 s), their response to the spatial conflict may have been different. It has also been demonstrated that stereoscopic cues are very important for optimal integration. Without stereoscopic cues to provide a sense of depth and to thereby add scale to the magnitude of visual motion cues, observers are more inclined to interpret visual motion as object motion (see Butler et al., 2011). For older adults, stereopsis takes longer to build up, such that older adults do not typically benefit from stereoscopic cues to self-motion unless the duration is longer.
than two seconds (Lich & Bremmer, 2014). Further, binocular cues can serve to enhance the detectability of visual stimuli embedded in noise (i.e., binocular unmasking; Schneider, Moraglia, & Jepson, 1989) but binocular unmasking is reduced in older adults because age-related differences in spatial frequency tuning may lead older adults to process more visual noise than younger adults (Speranza, Moraglia, & Schneider, 1995). Therefore, future studies should seek to examine the effect that longer duration motion cues have on older adults’ capacity to reconcile spatial conflicts.

6.6 Implications

The current findings suggest that older adults are less tolerant to spatial conflicts than younger adults and older adults do not demonstrate reliability-based estimation when faced with large spatial conflicts. This observation may help to better characterize previous observations pertaining to age-related differences in performance on tasks involving multisensory self-motion perception. In the context of gait and balance, it has been demonstrated that when older adults are presented with incongruent cues to self-motion, they experience greater performance variability than younger adults (e.g., Berard et al., 2012; Deshpande & Patla, 2007; Jeka, 2010). One hypothesis is that this may reflect age-related differences in the ability to down-weight unreliable visual cues specifically, perhaps due to a bias toward visual cues to self-motion (e.g., Berard et al., 2012; Simoneau et al., 1999; Sundermier et al., 1996). In the current study, I provide evidence to suggest that age-related differences in multisensory self-motion perception are nuanced. In general, older adults integrate congruent cues to self-motion optimally and are therefore able to account for cue reliabilities when forming their multisensory self-motion percept. However, in the presence of an inter-sensory spatial conflict, younger adults continue to account for relative cue reliabilities in forming their self-motion percept, whereas older adults do not. This pattern of performance is not likely to be problematic under most real-world situations where self-motion is typically experienced with congruent visual and vestibular cues. Compared to younger adults, older adults may be more susceptible to performance declines during instances for which the available cues to self-motion are unreliable, discrepant, or irrelevant. This includes experimental conditions that introduce spatial conflicts, but it can also include real-world
instances of global visual flow that is discrepant with self-motion (e.g., facing a moving train, virtual reality environments, dynamic signage, moving crowds).

6.7 Future directions

A key consideration when interpreting the results of the current investigation is the inequality of the reliability measures for unisensory visual and vestibular estimates of the older adults (apart from the 5° offset conditions). To provide the most sensitive and robust test of optimal integration, it is important to match, as best as possible, unimodal thresholds. This is because multimodal performance gains are most obvious when the unimodal precision is equal and because largely mismatched unimodal cues can result in the more reliable cue capturing the bimodal percept or leading to a winner takes all approach (Ernst, 2005; Ernst, Rohde, & van Dam, 2015). In the current investigation, the stimulus parameters were carefully selected to coincide with previous investigations that matched visual and vestibular cues in terms of their psychometric properties (e.g., Butler et al., 2010). I also conducted pilot testing with younger adults where I adjusted the gain on the rate of the visual motion relative to the physical motion until the visual and vestibular thresholds were well-matched for the younger adults. Ultimately, due to the heterogeneity of the older adult sample, on average, the reliability of the unisensory estimates were not well-matched to each other. By not intentionally and artificially equating unisensory performance in each group, I was able to examine age-related changes to sensory integration strategies under arguably more natural sensory conditions. In this regard, the current investigation provides interesting first evidence to suggest that age-related sensory/perceptual declines (even within non-clinical cut points) might affect the integration strategies that older adults utilize. However, future work should seek to better disentangle the effects of central and peripheral age-related changes to sensory functioning by intentionally matching unisensory reliabilities. One method of accomplishing this is to artificially degrade the more reliable of the two estimates by adding noise to the signal such as introducing non-coherent motion into the flow field (e.g., Fetsch et al., 2009) or adding noise to the vestibular cues via subtle lateral oscillations during translation.
Further, because the congruent bimodal cue trials were embedded within a larger set of trials that included both subtle and large spatial conflicts, these dynamic changes in the spatial congruency between cues over the course of the experiment may have also affected the weighting strategies that participants utilized (e.g., through rapid recalibration, which is known to change with older age; e.g., Noel, De Niear, Van der Burg, & Wallace, 2016). Previous research in multisensory traveled distance estimation has demonstrated, for instance, that the history of previously experienced cue relations can affect relative cue weightings. Specifically, when a sensory cue is more stable across trials it receives greater weight in the final estimate than when it is constantly changing relative to another redundant sensory cue (see Campos, Butler, & Bülthoff, 2014). In the case of the current study, during cue conflict trials, the vestibular heading was always 0º and the visual cues were offset by either 5º or 20º. Therefore, because the vestibular cues were stable across cue conflict trials whereas the visual cues were more transient, observers may have learned to assign more weight to the vestibular estimate. Using an experimental design in which both visual and vestibular cues are manipulated equally as often, and/or by examining trial-by-trial effects on how cue congruencies affect immediately subsequent trials, could provide more nuanced insight into the dynamics of any age-related differences in multisensory integration during self-motion.

6.8 Conclusions

The objective of the current investigation was to determine whether there are age-related differences in multisensory integration within the context of self-motion perception. When presented with spatially congruent cues, younger adults’ heading estimates were generally consistent with optimal integration. For the first time, it was demonstrated that older adults also integrate congruent cues to self-motion in a manner that is consistent with optimal integration. When presented with a subtle spatial conflict, only younger adults demonstrated optimal bimodal reductions in variance. In the presence of a large spatial conflict, a) younger and older adults did not demonstrate optimal reductions in variance for bimodal compared to unimodal conditions and b) older adults no longer weighted visual and vestibular cues according to their relative reliabilities but were instead biased towards the less reliable visual cues. This pattern of older adults’ performance is not likely to be problematic under most real-world situations where self-
motion is typically experienced with congruent visual and vestibular cues. But it could mean that they are more susceptible to performance declines during instances for which the available cues to self-motion are unreliable, discrepant, or irrelevant. This includes experimental conditions that artificially introduce spatial conflicts, but it can also include real-world instances of visual flow that is discrepant with self-motion (e.g., facing a moving train, virtual reality environments, dynamic signage, moving crowds). Age-related changes in the integration of multisensory cues to self-motion could have important implications for older adults as they could contribute to age-related changes in performance on critical everyday mobility-related tasks like standing, walking and driving.
Chapter 7
General Discussion

7 General Discussion

Previous research has established that younger adults and non-human primates integrate information about their movement from across their sensory systems to maximize the precision of their self-motion percept. Although there is growing evidence to suggest that multisensory integration may be heightened among older adults, this phenomenon has largely been observed in the context of simple, stimulus detection type tasks. Therefore, the broad objective of the present research was to ascertain whether age-related differences in multisensory integration as they have been observed in the context of stimulus detection could extend to self-motion perception, which could in turn influence the way that older adults perceive and ultimately control their own movement.

In Chapter 3, I demonstrated that for both younger and older adults, the presence of both visual and auditory cues while driving improved speed maintenance over visual cues alone, but that the magnitude of the performance gains appeared to be greater among older adults. Therefore, this study extended current knowledge in the domain of multisensory integration by demonstrating that the heightened integration that older adults exhibit in the context of visual-auditory stimulus detection and stimulus discrimination tasks extends to more complex tasks that involve continuous and dynamic visual and auditory cues. I inferred that if age-related changes in visual-auditory integration generalize to self-motion, this may have immediate practical implications as the presence of auditory cues to self-motion may be of comparatively greater importance to older adults. Accordingly, during tasks like driving, it may be necessary to consider that specific vehicle design choices with respect to the auditory cues to self-motion that are transmitted to the driver may differentially affect the performance of older and younger adults.

Having established that age-related changes in multisensory integration extend to more dynamic visual and auditory cues, the next important question was whether these age-related differences
would extend to different sensory cue combinations. In most natural behavioural contexts, humans rely upon the synergy between the visual and vestibular systems for reliable self-motion perception (see DeAngelis & Angelaki, 2012). Thus, the goal was to determine whether a similar pattern of performance would extend to the cue combinations that are more central to self-motion perception as it occurs in the real world. In Chapter 4, I demonstrated that while adding vestibular cues to visual cues benefitted older adults in terms of the reliability of their speed maintenance, it led to diminished lane-keeping performance. There were two potential interpretations for this outcome. It may have been that older adults, given their greater cumulative driving experience were more sensitive to any discrepancies between the vestibular cues experienced during the simulation and those experienced during real driving. However, because the combination of available cues had a differential effect on older adults, this pattern of performance may also signify that age-related differences in multisensory integration extend from visual-auditory cue integration to different cue combinations. I inferred that this may have important implications insofar as designing simulators for evaluating or remediating older adults’ driving performance, as well as for the design of real vehicles. In both contexts, careful consideration should be given to the differential effect that the available vestibular cues will have on older and younger adults. In Chapter 5, my goal was to consider whether all three cues would lead to greater performance benefits relative to the combination of two congruent cues, but I observed that there were no appreciable differences between bimodal and trimodal cue conditions (apart from some differences in the lane-keeping performance of older adults).

The interim conclusion based on my multisensory driving research was that older adults display a similar pattern of performance to that which has been observed in the context of simple stimulus detection type tasks in that they are differentially affected by the combination of available sensory inputs. Therefore, age-related differences in multisensory integration are not limited to the oversimplified task and stimulus conditions in which they have traditionally been observed but rather appear to be robust and generalize to more complex and dynamic cues presented under more realistic task constraints. However, because driving is a highly practiced task, and because the older adults may have had more cumulative experience than the younger adults, I could not distinguish age-related changes in multisensory integration from age-related
differences in previous experience. This limitation was particularly problematic insofar as interpreting the effect that vestibular cues had on older adults’ steering performance. Moreover, although the driving task revealed age-related differences in performance outcomes associated with presenting different cue combinations, this particular driving task could not be performed with auditory cues alone or with vestibular cue alone. Therefore, the driving task could not quantify underlying age-related differences in the way that the available sensory inputs were actually integrated.

In a follow-up experiment, I employed a more controlled psychophysical heading perception task which allowed me to apply MLE techniques to assess whether older adults employ an optimal integration strategy, as younger adults have been previously shown to do. The heading perception task demonstrated that both older and younger adults integrated congruent visual and vestibular cues in a statistically optimal fashion, thus resulting in greater bimodal precision than unimodal precision. In the presence of a modest spatial conflict, younger adults continued to integrate optimally whereas older adults did not. In the presence of a more substantial spatial conflict, older adults assigned a disproportionate weight to visual cues, despite their lower reliability relative to the vestibular cues. Thus, there are limits to the level of spatial conflict that both older and younger adults will tolerate before visual and vestibular inputs are no longer integrated to form a unitary self-motion percept. Overall, it seems that older adults may be less tolerant to spatial conflicts between sensory inputs than younger adults.

Taken together, the current research indicates that multisensory self-motion perception differs between older and younger adults. Both older and younger adults will experience performance gains under circumstances where the prevailing sensory inputs provide congruent estimates of self-motion. However, during instances where the available inputs happen to be incongruent, older adults may be more likely than younger adults to incorporate these inputs into their percept and to experience performance declines. For example, under conditions that result in global visual flow that is unrelated to self-motion (e.g., facing a moving train, virtual reality environments), or circumstances that render the available cues to self-motion unreliable (e.g., walking or driving in low visibility conditions caused by darkness, fog, or glare), younger adults
may be able to assign proportionally more weight to vestibular cues to self-motion whereas older adults may not. Thus, older adults may allow sensory inputs that are unrelated to self-motion to add variability to their perceptual estimates of self-motion. This could, in turn, lead to an increased risk of potentially costly behavioural errors.

7.1 Limitations

There were several important limitations associated with the driving paradigm. Specific limitations are discussed in Chapters 3-5, but here I consider some overarching limitations associated with using driving to quantify age-related differences in multisensory perception.

Participants actively controlled their speed and lane position throughout the driving task. Although the vehicle control dynamics were the same across age groups and sensory conditions, because participants controlled the vehicle themselves, not every participant would have received precisely the same pattern of sensory inputs. For instance, a driver who traveled at a higher rate and traversed the curved road segments at a higher rate would receive higher magnitude tilt/translation and associated vestibular innervation than a driver who traversed the curved road segments at a lower rate. Another important limitation associated with the driving task was that the effect of age was possibly confounded by age-related differences in cumulative driving experience. I recruited fully licensed younger and older adults to ensure that differences in performance on the driving task were due to the sensory conditions and not due to complete inexperience. However, many of the older adults were licensed for much longer and had greater exposure to driving, which may have cultivated strong expectations as to the pattern of sensory inputs that should be present while driving, but also strong expectations in terms their own ability to control their vehicle. In that vein, an important overarching limitation associated with the driving paradigm was that, while I made inferences about self-motion perception, I was not able to fully discount the possibility that context and task-specific experiential factors may have also affected performance and the associated age-related differences that were observed. For example, despite giving older adults clear instructions as to their objectives (i.e., maintain a specific target speed and lane position), it is possible that other factors including their awareness of their own limitations influenced their driving (e.g., choice of speed when negotiating turns).
Another issue associated with using a driving simulator to compare performance between older and younger adults is that younger adults are said to be ‘digital natives’ in that they were raised with computer technology whereas older adults are ‘digital immigrants’ in that they have adapted to computer technology (see Prensky, 2001 for a review). It may have been easier for younger adults to adapt to the simulator given their greater familiarity with computer technology than older adults. There is empirical evidence to show that older adults can take longer than younger adults to adapt to driving simulators. Older adults will often require more cumulative time in the simulator or repeated visits before their performance (e.g., steering, speed maintenance) will approximate that of younger adults (e.g., Dickerson, Mullet, Avanesova, & Keyes, 2017; Domeyer, Cassavaugh, & Backs, 2013; Kawano et al., 2012). Nevertheless, the benefits associated with the simulated driving task were that it was a reasonable representation of self-motion as it occurs in the real-world yet it still allowed me to apply a high level of experimental control in so far as eliminating extraneous cues. These attributes made this task an excellent starting point in terms of examining the tenability of age-related differences in multisensory integration extending to multisensory self-motion perception.

The heading perception task was motivated by the outcomes of the driving studies as a way to examine the effects of age on multisensory self-motion perception with a level of control that was not possible to achieve using the driving paradigm. For example, by providing participants with passive self-motion cues, I could ensure that all participants received identical visual and vestibular cues to self-motion. By moving away from a highly practiced, real-world task, I could also ensure that the effect of age was not confounded by previous exposure/experience. However, the heading perception task also carried some important limitations. For instance, there was a mismatch between the visual and vestibular cues in terms of their relative reliabilities. When investigating optimal integration, typically an effort is made to ensure that the unisensory reliabilities are roughly equal because the gains in precision associated with redundant estimates is largest when the estimates are equal in terms of their reliability and thereby receive equal weight (see Ernst, 2005; Rohde, van Dam, & Ernst, 2016 for reviews). Therefore, by ensuring roughly equal reliabilities, the experimenter can maximize the chance of observing the performance gains associated with the presence of multiple, congruent sensory inputs. More
importantly, if the objective is to consider age-related changes in central integrative mechanisms in isolation of other factors that may contribute to changes in multisensory interactions, such as the decline of the individual sensory systems, then it is ideal to ensure that there are no age-related differences in unimodal performance. In the current set of experiments, differences in terms of unimodal estimates were interesting in that they revealed age-related differences in the ability to use otherwise identical cues to estimate self-motion. However, the observed age-related differences in perceptual performance could be due to peripheral factors influencing multisensory integration (e.g., peripheral sensory declines) in addition to more central factors (e.g., heightened integration). Future research may be able to parse central and peripheral factors influencing multisensory integration by matching unisensory reliabilities. Another important limitation was that although I make inferences about age-related differences in terms of the tolerance to spatial conflict, the degree of spatial conflict was not manipulated with a high enough spatial resolution to precisely quantify the level of conflict that adults will tolerate. Specifically, because I used conflict intervals of 0° (no conflict), 5° and 20° degrees, it is not possible to systematically evaluate differences in the magnitude of the spatial binding window as a function of age.

Another overarching limitation was the prevalence of simulator sickness and the associated attrition rate. This was a major concern in the multisensory driving experiments where 29.75% of all participants across the three experiments dropped out (see Keshavarz et al., 2015 for a detailed summary of simulator sickness), with 25.6% dropping out due to high levels of sickness (FMS≥15). A leading hypothesis as to the cause of simulator sickness is that it is the physiological response to the presence of a conflict either between sensory inputs or between the pattern of prevailing sensory inputs and the observer’s implicit expectations (see Johnson, 2005; Oman, 1990; Reason, 1978 for reviews). As discussed above, different driving styles may have elicited different patterns of sensory input and therefore it is possible that individuals who were less tolerant to these unintended but unavoidable sensory conflicts were different in terms of their pattern of driving performance compared to those who completed the experiment. This would have biased my sample toward those who drove in a manner that constrained sensory conflicts. That being said, among those who completed the driving experiment, I considered
whether driving performance was correlated with measures of simulator sickness severity. Based on these analyses, there was no evidence to indicate that higher levels of simulator sickness were associated with diminished driving performance or vice versa. When considering both those who remained in the experiment and those who dropped out due to symptoms of simulator sickness (see Keshavarz et al., 2015), there was no evidence to suggest that the severity of simulator sickness differed between sensory conditions. Furthermore, although there was a relatively high attrition rate due to simulator sickness, the attrition rate did not differ between sensory conditions (see Keshavarz et al., 2015) and thus the participants remaining in each sensory condition was not biased by differences in the susceptibility to simulator sickness. Taken together, the simulator sickness data indicates that group differences in the prevalence and severity of simulator sickness was not driving the effect of sensory condition and thus, the observed driving performance outcomes were likely due to the effect of the available sensory inputs on self-motion perception as opposed to simulator sickness.

Finally, in both the driving experiments and the heading perception experiments, older adults were screened for sensory and cognitive impairments. In the heading perception experiment specifically, a large portion of the older adults who participated were ultimately excluded from the analyses because their visual heading perception, vestibular heading perception, or both were highly unreliable. Therefore, the sample of older adults in the current series of experiments is comprised of a group of older adults who are perhaps high performers and who are not necessarily representative of the broader older adult population. It will be important for future investigations to consider how older adults with age-related cognitive and/or sensory declines perform in these same domains.

7.2 Directions for future research

7.2.1 Mapping older adults’ spatial binding window

A fruitful area for future research will be to precisely characterize age-related differences in terms of the spatial binding window. Specifically, it may be of value to determine the magnitude of intersensory spatial conflict that older and younger adults can tolerate before optimal
integration no longer occurs. As discussed in Chapter 5, previous work has shown that older adults may have a broader temporal binding window for visual-auditory integration and that they will integrate cues that have a greater temporal disparity than younger adults (e.g., Colonius & Diederich, 2004; DeLoss et al., 2013; Diederich et al., 2008; Laurienti et al., 2006; McGovern et al., 2014; Peiffer et al., 2007; Setti et al., 2011). However, comparatively little work has been done to explore age-related differences in terms of the spatial binding window. Whether temporal and/or spatial binding changes with age is perhaps of even greater importance in the context of visual-vestibular cue integration than it is in the context of visual-auditory cue integration. During self-motion, visual-vestibular integration is essential if not mandatory and thus, changes in the spatial and temporal criteria that must be satisfied before visual and vestibular inputs are integrated are likely to have a considerable effect on how older adults perceive their own movement and how they, in turn, perform tasks involving self-motion.

In the current body of work, I inferred that older adults may be less tolerant to spatial conflicts between visual and vestibular cues to self-motion (Chapter 3 and Chapter 5). However, as discussed, I did not vary the magnitude of the spatial conflict at a high enough spatial resolution to hone in on the precise magnitude at which optimal integration breaks down. de Winkel and colleagues (2017) recently demonstrated that for younger adults, as the spatial conflict becomes progressively larger over a range from ± 0-90°, and the probability of the cues being causally related to self-motion decreases, the observer will begin to segregate them (de Winkel et al., 2017). If applied to older adults, this paradigm could help to elucidate the precise level of spatial conflict at which older adults reliably segregate visual and vestibular cues, thus revealing the limits of their spatial binding window.

Another important question is whether the spatial binding window is malleable. Previous work has demonstrated that the temporal binding window is malleable and that both younger adults and older adults can be trained to adopt narrower temporal binding windows (e.g., Mégevand, Molholm, Nayak, & Foxe, 2013; Powers, Hillock, & Wallace, 2009; Powers, Hillock-Dunn, & Wallace, 2016; Setti et al., 2014; Stevenson & Wallace, 2011; Stevenson, Wilson, Powers, & Wallace, 2013). The malleability of the temporal binding window has primarily been
demonstrated using temporal order judgment (TOJ) tasks (e.g., Setti et al., 2014; Stevenson et al., 2013). In the TOJ task, observers are presented with a flash of light and a tone in rapid succession and are asked to judge whether the flash or the tone was presented first. The portion of correct responses is observed relative to different time intervals between the visual and auditory cues. In the presence of a relatively brief inter-stimulus time interval (e.g., 15 ms), the observer is more likely to infer that the visual and auditory cues were caused by the same event and to integrate them (Stevenson et al., 2013). Consequently, brief inter-stimuli time intervals do not permit observers to reliably discern the order in which the visual and auditory were presented. As the inter-stimuli interval is increased (e.g., 300 ms), the observer is more likely to perceive them as discrete events and thus they can reliably discern the order in which the cues were presented (Stevenson et al., 2013). The inter-stimuli interval at which the observer can reliably identify the correct order (e.g., on 75% of trials) can then be used to infer the size of the observer’s temporal binding window (Powers et al., 2009; Stevenson & Wallace, 2011; Stevenson et al., 2013). Older adults tend to have larger temporal binding windows than younger adults, possibly to accommodate the longer amount of time it takes for older adults to process individual sensory inputs (Diederich et al., 2008; Mozolic et al., 2012). However, by having older adults perform the TOJ task and by providing feedback as to whether each order judgment is correct, it is possible to reduce the size of the temporal binding widow such that temporal order judgments can be made at smaller inter-stimuli intervals than they could prior to training (Powers et al., 2009; Setti et al., 2014; Stevenson et al., 2013). This is perhaps because training improves visual temporal acuity (Powers et al., 2016) Therefore, it may be possible to undertake an analogous form of training relating to the spatial binding window. For example, it may be possible to utilize an absolute heading estimation paradigm in which older adults are exposed to visual and vestibular cues to heading at different levels of spatial conflict, and at different levels of relative cue reliability, and are then asked to reproduce their perceived heading direction via pointing (e.g., de Winkel et al., 2017). In instances where older adults report a sub-optimal heading estimate, remediation may be provided by presenting an objective indication of the optimal heading estimate, perhaps via the presentation of congruent and highly reliable visual and vestibular cues in the direction of the optimal heading estimate. Analogous to TOJ feedback training, spatial feedback training could help older adults to improve their spatial acuity when
estimating heading angle and may help older adults to become more sensitive to spatial incongruency and/or differences in the relative reliability of visual and vestibular cues to self-motion. It would also be interesting to determine whether spatial feedback training could help older adults to become more robust to instances where incongruent or unreliable cues to self-motion are provided during tasks that are contingent on reliable self-motion perception, including standing and walking. The practical benefit of spatial feedback training is that it could help older adults to become more robust to real-world instances in which the available cues to self-motion become discrepant and/or unreliable.

7.2.2 Elucidating the neural substrates of age-related differences in optimal visual-vestibular integration

Another important pursuit may be to consider the potential neural substrates of age-related differences in visual-vestibular self-motion perception. Lich and Bremmer (2014) used neural network modeling to demonstrate that age-related atrophy within the medial temporal cortex could account for age-related declines in terms of the precision of visual heading perception (Lich & Bremmer, 2014). Specifically, Lich and Bremmer employed an established neural network simulation that uses a population of motion detectors, each with specific heading preferences, to approximate the way that neurons within the primate MSTd encode the heading angle of an optic flow stimulus (see Lappe & Rauschecker, 1994). They used this model to test the effect of randomly deactivating of 1-10% of detectors, thus simulating the effect of cell loss within MSTd. They compared the model output against older and younger adults’ performance on an absolute heading estimation task where observers were presented with optic flow and had to then report their perceived heading angle using a visual scale. They observed that older adults had a higher error when estimating their absolute heading angle compared to younger adults and that older adults’ elevated heading error was consistent with the random deactivation of 6-8% of MST neurons. They inferred that if the rate of cortical cell loss is roughly 1-2% per decade of life beyond the age of 30 (e.g., Raz et al., 2005), a cell loss of 6-8% would be typical for the older adults in their sample, whose mean age was 67.8 years. Thus, they concluded age-related declines in heading estimation could be linked to the atrophy of MSTd. In animal models, it has been demonstrated that neurons within the MSTd mediate the integration of visual and vestibular
cues to heading (see Gu et al., 2008). It is conceivable that changes in the optimal integration of visual and vestibular cues could also be related to age-related changes in the integrity of the MSTd. Previous work has shown that the chemical inhibition of the MSTd can lead to broad declines in the precision with which non-human primates discern their heading (Gu et al., 2012). Age-related atrophy could have a similar effect and therefore it would be interesting to test senescent primates to see if they exhibit analogous deficits to younger primate undergoing temporary (or permanent) lesions to the MSTd. That said, it is also important to note that the function of the individual neurons within the medial temporal cortex may also change. Liang and colleagues (2010) used senescent primates to demonstrate that medial temporal neurons are less selective for visual headings, perhaps owing to a decreased signal-noise ratio (Liang et al., 2010). It is not clear whether these neurons are also less selective for vestibular cues and/or for bimodal cues pertaining to heading.
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