Visual-Vestibular Sensory Integration During Congruent and Incongruent Self-Motion Percepts

by

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Abstract

This thesis examined the contribution of vestibular cues to self-motion perception and their integration with visual self-motion cues. The thesis is divided into five sections. In Section 1, a review of the illusory self-motion perception (i.e., 'vection') literature situates studies undertaken in this thesis. Topics reviewed include vection research, vestibular anatomy and physiology, visual-vestibular sensory integration, visual-vestibular neurophysiology and measurement methods to index vection. In Section 2, two experiments were reported. In E1, a virtual drum was displayed on a virtual reality headset. In E2, a novel measurement method consisting of a circular knob that participants rotated when experiencing vection was used to provide a direct measure of vection speed, direction, and duration. Results showed that vection strength and speed increased as visual stimuli moved faster. In Section 3, two experiments were reported in which circular vection was induced using vestibular air caloric stimulation. Participants had their eyes closed in E3 while receiving caloric vestibular stimulation. In E4 participants received caloric vestibular stimulation while viewing a stationary image in a VR headset. Participants perceived vection in the clockwise direction when cold air was applied to the left ear, and perceived counter-clockwise vection when caloric stimulation was in the right ear. Vection speed and duration measures were significantly smaller when participants viewed a stationary display (E4) than when their eyes were closed (E3). In Section 4, the goal was to determine if the visual or vestibular system prevailed in determining direction of self-motion perception during cue conflict. Participants observed an optic flow pattern that induced circular vection while receiving caloric vestibular stimulation also inducing vection. Visual and vestibular stimuli induced vection of approximately equal speeds in two conditions. In the 'congruent

motion' condition, visual and vestibular stimuli signaled vection in the same direction. In the 'incongruent motion' condition, visual and vestibular stimuli signaled vection in opposite directions. Results showed that in the incongruent condition, participants experienced vection in the direction signaled by the visual stimulus and vestibular stimulus equal amounts of times. In Section 5, a general discussion on these findings as they relate to optimal cue integration hypothesis is provided.

Keywords: self-motion perception; visual-vestibular sensory integration; vection; vestibular physiology.

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List of Acronyms

aPIC – Anterior posterior insular cortex

BOLD - Blood oxygenation level-dependent

CCW – Counter-clockwise

CSv - Cingulate sulcus visual area

CT – Computed tomography

CV - Circular vection

CW- Clockwise

EC - Egomotion-compatible

EEG - Electroencephalography

EI - Egomotion-incompatible

EV - Explanatory variable

fMRI - Functional magnetic resonance imaging

fNIRS – Functional near-infrared spectroscopy

FOV - Field of view

GVS - Galvanic vestibular stimulation

IOD – Inter-ocular distance

LCD – Liquid crystal display

LED – Light emitting diode

ME - Magnitude estimation

MEG - Magnetoencephalography

MST+ - Medial superior temporal complex

MT+ - Medial temporal complex

OKN – Optokinetic nystagmus

Pc - Precuneus (referred to as precuneus visual area)

PcM – Precuneus motion area

PET - Positron emission tomography

PIC – Posterior insular cortex

PIVC - Parieto-insular vestibular cortex

pPIC – Posterior posterior insular cortex

POs - Parieto-occipital sulcus

SCC - Semi-circular canal

TMS - Transcranial magnetic stimulation

VIP - Ventral intraparietal region

VOR – Vestibular ocular reflex

VR – Virtual reality

THESIS OVERVIEW

Sensory information from the visual, auditory, vestibular, proprioceptive, somatosensory, and kinesthetic systems must be continuously integrated in order to perform skilled motor actions. Sensory information provided by these systems for walking, running, and obstacle avoidance complement each other and is sometimes redundant. However, there are situations where sensory information from different systems conflicts with each other. An example of sensory conflict is when a person on a stationary train feels like they are moving when watching an adjacent train departing (Mach, 1875). In this example, the visual system receives optic flow information signaling self-motion, but the other sensory systems do not receive corresponding self-motion information. This visual illusion of perceived self-motion in a stationary observer is called 'vection'. The visual and vestibular systems are known to be the two sensory systems primarily involved in self-motion perception, though other sensory systems are involved to a lesser extent (Howard, 1982).

The visual system is sensitive to constant velocity motion, including self-motion and object motion (Previc, Kenyon, Boer, & Johnson, 1993). On the other hand, the vestibular system is sensitive to passive and active acceleration of the head (Howard, 1982). Importantly, the vestibular system is unable to differentiate moving at constant velocity from being stationary. This is because of the inertial properties of the vestibular system's mechanoreceptors (Lishman & Lee, 1973). The visual and vestibular systems' sensory capabilities are complimentary in that the visual system detects constant velocities and the vestibular system detects accelerations. However, to date, little is known regarding the vestibular system's contribution and integration with visual cues during self-motion perception. In contrast, there is a much better understanding

of the role of the visual system during self-motion perception. This lack of understanding in vestibular perception is problematic for understanding sensory integration and producing multisensory cueing systems such as flight simulation. For instance, there continues to be debate regarding the use of motion platforms for flight simulation that aim to provide complimentary vestibular information to produce more realistic flight experiences. The impact of motion systems on flight training is unclear (Hancock, Vincenzi, Wise, & Mouloua, 2008), in part, due to a lack of an understanding of how stimulation of the vestibular system affects the perception of self-motion.

The objective of the present thesis was to examine the vestibular system's contribution to self-motion perception and its integration with visual self-motion cues. In the present research, a series of experiments were completed in which visual and vestibular¹ circularvection were induced separately and then simultaneously. Perceived speed, direction, and duration of circularvection were measured. Visualvection was induced by a virtual optokinetic drum presented in a virtual reality (VR) headset. The virtual drum was a rendition of a physical optokinetic drum with alternating black and white vertical stripes. The stripes moved across the display in the clockwise or counter-clockwise directions thereby inducingvection. Vestibularvection was induced and measured separately by using air caloric vestibular stimulation of the horizontal semi-circular canals. To investigate sensory integration during congruent and conflicting visual-

¹ There is debate about the use of the term 'vection' when referring to illusions of self-motion in systems other than the visual system. 'Vection' will be used in this thesis to refer to self-motion induced in the vestibular system in a stationary individual (see Palmisano, Allison, Schira, & Barry, 2015 for a review on definitions of 'vection').

vestibular interactions, visual and vestibular self-motion stimuli were presented to participants together. In most experiments, vection speed, direction and duration were measured using an apparatus developed for this thesis called the rotating knob.

This thesis is divided into several sections. In Section One, the vection literature is reviewed in order to situate the present research. Early vection research that used optokinetic drums as a means to produce vection in laboratory environments is examined followed by a review of modern apparatus that has been used to measure new facets of vection. The anatomy/physiology of the vestibular system is then described followed by a review of studies on visual-vestibular sensory integration, visual-vestibular neurophysiology, and measurement methods that have been used to index vection.

In Section Two of the thesis, a virtual version of the optokinetic drum was implemented on a virtual reality (VR) headset. A novel methodology for indexing perceived vection speed was also developed and validated against standard magnitude estimation measures. This methodology involved having participants continuously rotate a knob to reflect the direction, speed and duration of perceived self-motion that was induced by the virtual drum in the VR display.

In Section Three, the role of the vestibular system in perceived self-motion was examined. This was done by using air caloric irrigation of the horizontal semi-circular canal of the vestibular system. The direction, speed and duration of perceived self-motion was measured using the rotating knob apparatus described in Section Two.

In Section Four, the visual and vestibular systems were simultaneously stimulated to examine how visual and vestibular cues to self-motion are integrated. In a congruent condition, visual and vestibular cues were configured to signal self-motion in the same direction. In an incongruent condition, visual and vestibular cues were configured to signal self-motion in opposite directions.

In Section Five a general discussion of the results, the contributions of this thesis, applications, future work and a conclusion are offered.

SECTION ONE: GENERAL INTRODUCTION

Research on Vection

Vection has been recognized and described with real world examples for over 100 years (Mach, 1875; von Helmholtz, 1867). Ptolemy described the self-motion experienced when an individual on a stationary boat watches a quickly moving body of water (in Howard & Rogers, 2002). Despite the boat being stationary, the visual information from the quickly moving water current can create a compelling illusion of self-motion. Wood (1895) described a self-motion illusion arising from an amusement park ride called the haunted swing. The haunted swing seated several observers. It was attached by a rod to the ceiling in a room. The room had furniture that was attached to the ground. The observers assumed that the swing moved and that the room was stationary. In reality, the swing moved very slightly but the room could move 360° in the pitch axis around the observers. The motion of the room around the observers created a very convincing illusion of self-rotation. Wood provided an informal description of the sensation when on this amusement park ride, but researchers have developed similar apparatus in laboratory environments to study vection.

In early laboratory studies, vection was primarily induced with optokinetic drums. These drums were illuminated and had black and white vertical stripes on the inner surface. They were powered by a motor. The observer was seated on a chair in the middle of the drum. When the motor rotated the drum, the movement of the stripes gave rise to a very powerful spinning illusion in the direction opposite to the motion of the stripes. This illusion is referred to as 'circular vection'. Mach (1875) compared circular vection with linear vection (i.e., vection

experienced in the forward/backward direction) and found that circularvection was more compelling to participants than linearvection. Aitken (1880) anecdotally noted that the drum induced a strong spinning sensation in participants and commented on the resulting motion sickness that some subjects experienced. Warren (1895) investigated the visual angle, lighting, speed of the drum and participant head orientation necessary to inducevection when in the supine posture. Results from this study were the first to confirm that participants experienced a convincing self-translation experience with bright lighting, full field visual angle of the room and stripe motion between $2\text{--}5^\circ/\text{s}$. These early studies were important in showing thatvection can be reproduced in a laboratory environment and provided some detail about the optimal conditions to inducevection.

Gibson (1966) described optic flow as the relative motion pattern sensed by the retina that is produced by an observer moving through the environment. Gibson noted an important distinction between optic flow for linear and circularvection. During linearvection producing forward self-motion, the images of objects in the scene radiate from the focus of expansion which lies in the direction of travel. This is not the same during self-rotation. Gibson noted that self-rotation does not often occur in a natural environment, but linear self-motion does. When self-rotation is experienced in natural settings, it is due to the individual moving, not objects in the world moving. When experiencing circularvection in the yaw axis, such as in the optokinetic drum, the optic flow pattern appears to move around the individual's spinal axis to make them feel like they are spinning in the opposite direction to the visual motion.

Brandt, Wist, and Dichgans (1975) used the optokinetic drum to investigate if certain features of the visual scene were being used by the visual system to determine one's relative

direction of self-motion. They reasoned that the background of a scene may drive self-motion perception because the background of a scene is generally stable. On the other hand, in the real world, motion in the foreground is usually caused by object motion. Therefore, Brandt et al. hypothesized that background motion would influence self-motion perception but not foreground motion. In one condition, Brandt et al. modified the drum so that the motion of the black and white stripes appeared to be in the background. In a second condition, Brandt et al. occluded the stripes with a frame. Moving the frame made the stripes appear to be in the foreground. Brandt et al. observed strongervection when motion of the stripes was in the background than in the foreground as hypothesized. It was not clear from these results if the actual or perceived background drove these results.

Ohmi, Howard, and Landolt (1987) demonstrated that the *perceived* background, not the actual background (i.e., not the more distant feature of the scene) drovevection. They did so by presenting displays to participants monocularly such that it was impossible to distinguish between closer and further visual stimuli. They ensured visual angles subtended by both stimulus patterns were the same and did not provide monocular depth cues such as occlusion. The patterns of the background and foreground stimuli used by Ohmi et al. differed slightly. The two stimulus patterns could spontaneously reverse their depth roles because of the lack of depth cues. Participants were asked to report the pattern of dots they perceived as the background or foreground. Participants were also to reportvection, which stimulus they perceived as background, and anytime there were perceived background-foreground reversals. Ohmi et al. found that participants feltvection in relation to the stimulus they perceived as being in the background. Work by Palmisano and Gillam (1998) further clarified the role of background and

foreground relationships in vection by demonstrating that there is an interaction between stimulus eccentricity (location of stimulus relative to the focal point), and stimulus frequency (pattern of the stimulus) on the perceived background.

To study how realistic visual features of the environment impact vection, Howard and colleagues created a fully furnished room that could turn around an individual in the roll axis (Allison, Howard, & Zacher, 1999; Howard & Childerson, 1994; Howard & Hu, 2001). This “tumbling room” was built on a platform that rotated in the roll axis relative to the Earth vertical axis. The tumbling room had a floor, ceiling and window. The room was fully furnished with chairs, a table, appliances, and human-like mannequins. Howard and Childerson (1994) argued that three types of visual information can drive visual vection: visual polarity, the visual frame and object motion. An object is said to have high visual polarity when there is a clear and distinct ‘top’ and ‘bottom’ to it, such as a chair. The visual frame refers to the principal vertical and horizontal lines of the environment such as the horizon, walls, corners, and ceilings. Visual motion or optic flow was the third type of visual information that contributes to vection perception. Howard and Childerson hypothesized that the tumbling room’s high-polarity objects (e.g., furniture), visual frame elements (e.g., floor and ceiling), and motion of the room should result in stronger vection than in a room without objects that have strong visual polarity. They compared vection strength responses when participants were in the tumbling room with a room with dots and a sphere with dots. The room with dots had a floor and ceiling and therefore had a visual frame but it did not possess polarity cues. The sphere with dots did not have visual polarity cues or a visual frame because there were no walls or edges in the room. Motion of the dots still provided optic flow information in the sphere. As predicted, Howard and Childerson

found the strongest vection in the tumbling room and weakest vection in the dotted sphere.

Allison Howard, and Zacher (1999) used the tumbling room to examine room rotation speed and visual field size on vection. Allison et al. showed that with faster speeds, and larger visual field size, subjects were more likely to experience vection (referred to as tumbling in their paper).

In sum, the evolution of physical apparatus to induce vection from the optokinetic drum to the dotted sphere, dotted room, and tumbling room has allowed the exploration and understanding of visual self-rotation perception and influential features of the visual scene such as background-foreground relationships, visual frame, and polarity. However, because of the difficulty in producing linear optic flow in a physical apparatus, there have been far fewer early studies published on linear self-motion perception (see Carpenter-Smith, Futamura, & Parker, 1995; Carpenter-Smith & Parker, 1992 for examples of linear vection in a physical apparatus). It was much easier to induce circular vection with an apparatus that rotated the visual stimulus such as the optokinetic drum but as display monitors and computer capability improved, the study of linear vection became more common. For instance, using a display monitor to present stimuli, Andersen and Braunstein (1985) found that visual angle, speed, and depth of linear displays did not increase vection durations and strength when presented to central vision. However, visual angle, speed, and depth do increase vection during full-field optic flow display. Palmisano (1996) showed that depth cues significantly enhanced linear vection perception in their study using graphically generated linear optic flow stimuli.

Other researchers have examined the relationship of visual vection to sensory conflict. Sensory conflict occurs when there is a mismatch between what is sensed in one sensory system compared to another. An example of sensory conflict is vection because the visual system

detects motion while the vestibular system does not. Giannopulu and Lepecq (1998) examined vection with visual stimuli that made participants feel like they were moving forward and backward, up or down while participants stood upright. The otolith organs of the vestibular system detect motion in line with the acceleration of gravity in Earth's 1-g environment. Therefore, Giannopulu and Lepecq hypothesized that there should be a weak visual-vestibular conflict when observing visual stimuli signaling up and down translations when standing upright while the head is in line with the body axis because up and down motions would be in line with gravitational acceleration detected by the otoliths when stationary. There should be a stronger visual-vestibular conflict when observing a visual stimulus signaling forward and backward motion because forward-backward visual vection would not be sensed by the otoliths when stationary. Giannopulu and Lepecq hypothesized that participants would experience stronger vection during up-down vection conditions than forward-backward conditions. Their results supported this hypothesis.

Giannopulu and Lepecq's (1998) results demonstrated that vection was stronger with reduced conflict. However, a study by Palmisano, Gillam, and Blackburn (2000) showed that vection can actually become stronger during visual-vestibular conflict. Palmisano et al. used a computer monitor to display an optic flow pattern of a simulated 3-dimensional array of spherical objects that expanded radially. Palmisano et al.'s stimulus induced linear vection in the forward direction. In a crucial condition, the radially expanding display was accompanied by random perturbations along the x and y axes in the scene. Perturbations made the radially expanding spherical objects appear to abruptly move up and down during forward vection. This resembled watching camera footage while the person filming was walking. Palmisano et al.

found that perturbations in the linear vection display strongly enhanced vection strength. Perturbations in the scene should cause an anticipated corroborant vestibular signal during real motion but this was not present. The visual stimulus used by Palmisano et al. therefore should have generated a strong visual-vestibular conflict that attenuated vection. This was not the case as they found stronger vection during conflict. Other studies have replicated this enhanced vection effect caused by perturbations in the scene (Allison, Zacher, Kirolos, Guterman, & Palmisano, 2012; Palmisano, Allison, & Pekin, 2008).

Vection has also been investigated using stereoscopic viewing devices (Allison, Ash, & Palmisano, 2014; Lowther & Ware, 1996; Palmisano, Davies, & Brooks, 2018; Seya & Shinoda, 2018; Wolfe & Held, 1980). Palmisano et al. (2018) investigated the impact of different depth perspectives on vection. The inter-ocular difference of two LED screens was manipulated. This changed the depth perspectives of the optic flow stimuli. The average eye separation or inter-ocular distance in humans is approximately 6.5 cm. Palmisano and colleagues presented optic flow patterns with varying disparities by manipulating IOD in four conditions. These conditions were no IOD (0 cm eye separation), a reduced IOD (3.25 cm eye separation), normal IOD (6.5 cm eye separation), and exaggerated IOD (13 cm eye separation). They found that vection strength increased with larger IODs. This was an interesting finding given that up to this point, it was thought that most cues to self-motion perception were primarily monocular. Previous studies also found that the simulated normal IOD of 6.5 cm increased vection, but this was assumed to be the case because it was close to true eye separation causing more natural and compelling vection. However, Palmisano et al.'s (2018) findings show that increasing the IOD incrementally beyond 0 cm and up to 13 cm increased vection strength ratings. Therefore, the

use of stereoscopic viewing devices in studying vection has shown that depth perception caused by eye separation enhances vection.

Virtual reality (VR) headsets are another class of apparatus that have been used to examine vection. In a study by DeSouza (1995), the tumbling room from Howard and Childerson (1994) was reproduced in a VR headset to examine roll-axis vection in different postures. Participants experienced vection more frequently in the upright position than in the supine position when viewing the tumbling room rotate around them in the roll-axis. Importantly, DeSouza's experiment demonstrated that vection can be experienced in a VR headset. Skwersky (1996) examined how scene polarity affected vection in a VR headset. This was done by comparing vection responses in VR headset renditions of a dotted sphere, dotted room and tumbling room. Skwersky found that participants reported vection more frequently in the VR tumbling room than in the dotted sphere and dotted room. This finding replicated Howard and Childerson's and provided additional evidence that VR headsets can elicit predictable vection experiences similar to those experienced with physical stimuli.

Although promising, the use of VR displays to study vection has been limited, in part because early VR headsets were large, heavy, and expensive. They had long refresh rates and limited graphic and resolution capabilities that significantly reduced vection and caused motion sickness. In recent years, however, there has been rapid improvement in the development of low-cost and high capability VR displays. At present, VR headsets have negligible lag times, high refresh rates and high-resolution displays and continue to rapidly improve. Accordingly, researchers are increasingly using VR to examine visually-induced vection.

Riecke and Jordan (2015) compared vection using different display systems. They compared a stereoscopic projector, 3D LED TV, and two types of VR headsets. They measured vection onsets and strength responses. Field of view (FOV), resolutions, and refresh rates were different for these systems, but even when the VR headset systems' larger FOV was reduced to mimic that of the computer monitor and projector systems, no difference in vection intensity ratings across the apparatus were observed. The Riecke and Jordan results should not be interpreted to mean that all devices induce similar vection responses, but these findings suggest that provided sufficient FOV, resolution, and refresh rates are met, vection can be reliably produced in different display systems. These results further the case for the use of VR displays for inducing vection.

Kim, Chung, Nakamura, Palmisano, and Khuu (2015a) examined visual-vestibular sensory integration in a novel way by having participants move their head while viewing a display that induced forward vection in a VR headset. In this active viewing condition, participants were exposed to three different vection stimuli while they wagged their heads left and right. In a passive viewing condition, participants watched the same stimuli but kept their heads still. Kim et al. hypothesized that strongest vection ratings would be observed during the active head motion condition. This was hypothesized based on the assumption that corroborating visual (the spherical object motion) and vestibular (head motion) inputs would reduce sensory conflict and thereby increase vection. However, Kim et al. did not find a difference in the passive vs. the active viewing conditions. Surprisingly, passive viewing conditions in which the head did not move yielded slightly stronger vection. Kim et al.'s study highlights the capability of VR headsets to study visual-vestibular sensory integration in new ways as visual displays

synced to head movements are easily set up in a VR headset fixed to the head compared to a display monitor fixed to the real world.

To summarize, advancements in apparatus have allowed the study of new aspects of visual self-motion perception and visual-vestibular sensory integration. A growing body of research has shown that VR displays can be used to induce vection (DeSouza, 1995; Kim et al. 2015a; Riecke & Jordan, 2015; Skwersky, 1996). In the current thesis, circular vection was induced by presenting a virtual optokinetic drum on a VR display to explore vection speed perception, the relationship of vection speed to vection strength, and visual-vestibular sensory integration during combined vestibular self-motion stimulation. To understand how to produce vection in the vestibular system, the basic anatomical and physiological principles that underlie vestibular function are reviewed below.

The Vestibular System and Vestibular Perception

Anatomy and Physiology of the Vestibular System and its Fluid Dynamic Properties

The peripheral vestibular apparatus is located within the inner ear's bony labyrinth. It detects angular and linear, passive and active velocity changes of the head (Breuer, 1874; Camis, 1930; Howard, 1982; Mach, 1875). The peripheral vestibular apparatus is comprised of two primary sensing organs – the otoliths and the semi-circular canals (SCCs). Vestibular signals are initially processed at the cerebellum subcortically (Fay & Popper, 2004). The otolith organ is located in between the SCCs and the cochlea and is made up of two discrete sensors - the utricle and the saccule. These two sensors detect linear and translational accelerations of the head, including Earth's gravitational acceleration. The utricle specializes in detecting horizontal head

tilts while the saccule detects vertical head tilts (Ormsby, 1974). Within each of these two sensors is the otoconia. The otoconia (also called stratoconia) are salt crystals embedded in a viscous substance that causes hair cells' mechanoreceptors (stereocilia) to bend signaling head acceleration. When there is a translational head motion, the viscous fluid causes the hair cells' stereocilia to lag. It should be noted that the otoconia only moves with transient velocity changes (accelerations and decelerations) but cannot distinguish between being stationary and moving at constant velocity (Lishman & Lee, 1973; Mach, 1875). This is a result of the inertial fluid dynamic properties of the viscous substance surrounding the otoconia.

The SCCs comprise the second main organ that makes up the vestibular apparatus. Unlike the otoliths, which specialize in detecting linear head accelerations, the SCCs sense angular head accelerations. There are three canals in each ear that sense rotational changes in velocity in the yaw, pitch, and roll planes independently. These are the horizontal, the superior, and the posterior canals, respectively. Like the otolith organs, the SCCs detect acceleration due to the fluid dynamic properties of a viscous substance called the endolymph fluid. The three orthogonal canals, the saccule and utricle in each ear create a 3-dimensional configuration that permits detection of head acceleration with six degrees of freedom (Fay & Popper, 2004). The SCCs are blocked by the cupular membrane in which hair cells are embedded within the endolymph fluid. When the head rotates, the endolymph fluid lags causing the bending of hair cells and the stereocilia on the hair cells to bend. Bending of the stereocilia causes graded chemical ion (K^+ , Ca^{++} , and Cl^-) channel currents. When the ion channel currents generate a strong enough response, the 8th cranial nerve's (i.e., the vestibulocochlear nerve) vestibular contingent is stimulated, which signals head rotation. The otoliths, like the SCCs, also relay

motion signals to the vestibulocochlear nerve when there is a strong enough graded ion channel current. The configuration of the canals and otoliths permits stereocilia to bend in distinct directions based on the direction of head motion, signaling to the brain a unique pattern of activation for each type/direction of head motion. This is made possible because of the reciprocal configuration of the canals in each ear which produces an excitatory signal in the cupular membrane in one ear's canal and an inhibitory response in the other ear canal's cupular membrane.

The otolith organs detect linear/translational accelerations and the SCCs detect rotary accelerations. Therefore, head motion or physically displacing an individual is the simplest way to stimulate the vestibular system. To artificially stimulate the vestibular system, caloric vestibular stimulation and galvanic vestibular stimulation can be employed. Caloric and galvanic vestibular stimulation act directly on the vestibular apparatus to transduce a motion signal to the brain without the head or body physically moving, but hair cells and endolymph fluids in the otolith and semi-circular canals physically move with caloric vestibular stimulation. This allows the study and assessment of the vestibular system while the observer is stationary.

Physical Stimulation of the Vestibular System

The vestibular system is naturally stimulated by physical displacement of the head. An example of this is rotating an individual in a chair. The use of motion platforms is another method to displace individuals to activate the vestibular system. Motion platforms are often used for land vehicle and flight simulation, training and research to provide a realistic sensation of motion that accompanies visual cues to self-motion (Dahlstrom, Dekker, Van Winsen, & Nyce, 2009; Mohajer, Abdi, Nelson, & Nahavandi, 2015). A popular and widely used type of motion

platform is the Stewart platform. Stewart platforms consist of a raised plate held up by hydraulic, pneumatic or electrically powered actuators in a hexapod configuration that can move in six degrees of freedom. Motion platforms have limited motion ranges and therefore cannot simulate a large amount of motion experienced during real flight or driving (Kemeny, 2009). In the flight training literature, there is limited and at best mixed evidence suggesting that using motion platforms for flight simulation results in enhanced training outcomes (Hancock, Vincenzi, Wise & Mouloua, 2008). Motion platforms have often been used to understand visual-vestibular integration and study the role of the vestibular system in self-motion perception. However, motion platforms stimulate many sensory systems, thereby making it difficult to examine the unique contribution of the vestibular system to self-motion perception. To isolate the contribution of the vestibular system to self-motion perception, it can be stimulated artificially, or in other words, without real physical motion of the head. To this end, caloric and galvanic vestibular stimulation are methods to artificially stimulate the vestibular system.

Caloric Vestibular Stimulation

Caloric vestibular stimulation is a method by which cool or warm air or water enters the ear via the external auditory canal, stimulating the horizontal semi-circular canal. The air/water is cooler or warmer than body temperature. This creates a thermal gradient that changes the density of endolymph fluid in the horizontal semi-circular canal (Barany, 1906). Once there is a large enough temperature difference in the endolymph fluid from body temperature, there is a convection current that produces a pressure change across the cupula. This pressure change causes the semi-circular canal's mechanoreceptors to move, producing afferent neuron firing to the 8th cranial nerve. Therefore, changing the temperature of the endolymph fluid by using

caloric vestibular stimulation can perceptually result in an illusory rotary sensation in the yaw axis relative to the spine (von Brevern, Faldon, Brookes, & Gresty, 1997).

Calorics have been predominantly used in clinical settings to test balance. This can be done by examining eye movements that result from stimulating the vestibular system. When the vestibular system is stimulated there is typically a reflexive eye movement that is produced in individuals with healthy vestibular function. These reflexive eye movements are a result of the direct subcortical relationship between the optic nerve and the vestibular system and are called vestibular ocular reflexes (VOR). The VOR is a compensatory eye movement that functions to stabilize gaze, keeping the image steady on the retina when the head moves. VOR is characterized as a beating of the eyes when the set of SCCs (horizontal, superior, or posterior canals) inline to the axis of motion are stimulated when the eyes are closed. Therefore, when the horizontal canals are stimulated with air caloric irrigation the eyes beat laterally. When the eyes are open the VOR is accompanied by another type of involuntary eye movement called optokinetic nystagmus (Howard & Rogers, 2002). Optokinetic nystagmus occurs when the eye pursues an object in the visual field while in motion. The eyes move back to their original position to fixate on another moving object. Patients with peripheral vestibular damage or brainstem damage exhibit a limited VOR or do not exhibit an OKN when undergoing caloric testing (Goldberg, Highstein, Moschovakis, & Fernandez, 1987).

Caloric vestibular stimulation is frequently used to assess vestibular function but has also been used in biomedical engineering research to investigate fluid dynamic properties of the endolymph and semi-circular canal structural characteristics (Kassemi, Deserranno, & Oas, 2004; Kassemi, Deserranno, & Oas, 2005; Meiry & Young, 1967; Steer, 1967) and in the

investigation of psychiatric disorders such as schizophrenia, psychosis, and psychopathy (Jones & Pivik 1985; Levy, Holzman, & Proctor 1983). Caloric vestibular stimulation has been found to temporarily reduce spatial hemi-neglect in patients with brain injury (Ferré & Harris, 2017; Moon, Lee, & Na, 2006). In a study that investigated spatial updating, Karnath (1994) used caloric vestibular stimulation to compare perceived self-motion in participants with healthy vestibular function to participants with vestibular damage. Participants were instructed to point in the direction compensating for perceived motion generated by calorics in complete darkness. Results showed that participants with vestibular malfunction had significantly larger pointing deviations compared with healthy controls. This study demonstrated patients with vestibular damage's inability to update their position in space.

Galvanic Vestibular Stimulation

Galvanic vestibular stimulation is another method to artificially stimulate the vestibular system. Galvanic vestibular stimulation bilaterally stimulates the mastoid processes behind each ear with an electric current that acts directly on the primary vestibular afferents, not the mechanoreceptors of the otoliths and semi-circular canals as with caloric vestibular stimulation.

A study by Fitzpatrick, Marsden, Lord, and Day (2002) examined the use of galvanic vestibular stimulation to induce a self-rotation sensation in the roll axis relative to the participant's body axis while in the supine posture. Participants were blindfolded and secured to a platform that spun in the roll axis in two conditions. In one condition, participants received galvanic vestibular stimulation that made them feel like they were moving in the same direction of actual spinning. In another condition, galvanic vestibular stimulation made participants feel like they were moving in the opposite direction of the spinning. They hypothesized that if

galvanic vestibular stimulation could produce a robust and continuous spinning sensation, it would cancel out self-motion perception caused by the physical platform spinning in the opposite motion condition. In the same spinning condition, researchers hypothesized that galvanic vestibular stimulation would enhance self-rotation. To measure this, participants characterized any perceived self-motion on a 5-point scale to index the magnitude of their displacement. Participants were also required to verbally characterize the motion as a translation or a rotation. Participants reported stronger spinning when galvanic vestibular stimulation signaled motion in the same direction as the physical rotation than when in the opposite direction of the physical rotation but this was not significant. Participants reported that galvanic vestibular stimulation induced a rotary sensation when presented with a visual cue signaling motion in the same direction. However, participants in this study could not clearly distinguish their direction of perceived self-rotation.

The Fitzpatrick et al. (2002) study is one of the few that has shown that galvanic vestibular stimulation can induce modest spinning sensation (Maeda et al., 2005a; Maeda, Ando, & Sugimoto, 2005b). Findings of galvanic vestibular stimulation capable of inducing vection are at odds with the widely replicated finding that galvanic vestibular stimulation is mainly used to produce a sense of tilt rather than a compelling and clear sense of translation or rotation (Aoyama, Iizuka, Ando, & Maeda, 2015; Bense, Stephan, Yousry, Brandt, & Dieterich, 2001; Dilda, 2011; Dilda, Morris, Yungheer, MacDougall, & Moore, 2014). Galvanic vestibular stimulation stimulates the entire peripheral vestibular system simultaneously, creating a noisy vestibular signal (Fasold, et al., 2002). In sum, research suggests that galvanic vestibular stimulation can be appropriate for simulating a brief tilting sensation, and while its capability to

induce continuous self-motion is under investigation, presently it is limited. The following portion of this section will review how visual and vestibular signals are integrated during self-motion perception.

Sensory Integration

The visual and vestibular systems' role in self-motion perception were described above. A review of how the visual and vestibular systems integrate sensory input will inform the possible outcomes of experiments conducted in this thesis. A number of hypotheses have attempted to describe and predict sensory integration during conflict. One group of hypotheses is the traditional visual-vestibular sensory conflict hypotheses. Duringvection, the time between the start of an optic flow pattern and the experience ofvection is referred to asvection onset or latency. According to traditional sensory conflict hypotheses,vection onsets occur because the vestibular system does not receive self-motion cues but the visual system does. This conflict between visual input signaling self-motion and vestibular input signaling no self-motion information temporarily hindersvection. After a few moments, the display is moving at constant speed and the vestibular system is no longer in conflict with the visual system as the vestibular system cannot distinguish being stationary from moving at constant speed. This makes it possible forvection to be experienced under traditional sensory conflict accounts and results in observedvection onset times (Brandt, Dichgans, & Koenig, 1973; Telford & Frost, 1993; Weech & Troje, 2017; Wong & Frost, 1981).

Traditional sensory conflict hypotheses fail to explain Palmisano, Gillam, and Blackburn's (2000) findings. Palmisano and colleagues used a visual display with a simulated

camera shake effect and found that participants experienced shorter vection onsets during accelerating visual displays than with constant velocity display. This finding was surprising because according to traditional sensory conflict hypotheses, accelerating displays should create a conflict between the visual and vestibular systems and delay or attenuate vection. Instead, vection was stronger during accelerations/perturbations in the scene.

The visual dominance hypothesis is another hypothesis that attempts to explain visual-vestibular conflict. This hypothesis predicts that visual self-motion signals override vestibular inputs during visual-vestibular conflict (Berthoz, Pavard, & Young, 1975; Lee & Lishman, 1975; Lishman & Lee, 1973; Warren, 1895). Dominance is generally interpreted to mean that the other sensory system is completely inhibited from contributing to self-motion direction during conflict. Studies supporting visual dominance hypothesis have shown that wide field optic stimulation strongly influence perceived stance and that mechanical motion cues are generally ignored. Though this research finding comes from studies on visual-vestibular conflict during stance and postural control, it has led some researchers to conclude that the visual system dominates self-motion/self-orientation perception during conflict (Lishman & Lee, 1973). However, if visual dominance truly resolves visual-vestibular conflict, it would be expected that vection would be experienced immediately when an optic flow display is presented to an observer. There are no findings supporting this prediction as many researchers have shown a vection onset/latency time of several seconds. Visual dominance hypotheses are unable to account for commonly observed vection onset times.

In contrast to the visual dominance hypothesis, some research suggests that the vestibular system dominates during visual-vestibular sensory integration (Butler, Smith, Campos, &

Bülthoff, 2010; Harris, Jenkin, & Zikovitz, 2000). Studies that have found evidence suggesting visual dominance used mechanical cues generated by physical motion platforms to stimulate the vestibular system while viewing a conflicting visual display. Butler et al. investigated heading perception and found that heading direction was more consistent with vestibular direction of motion than visual direction of motion. Harris et al. looked at traversed distances as an indicator of experiencedvection. Harris and colleagues found that reported traversed distances were more consistent with vestibular cues to motion than visual cues to motion in the incongruent condition.

Researchers have proposed an optimal cue integration hypothesis to examine and explain cue conflict during linear (Fetsch, Turner, DeAngelis, & Angelaki, 2009; Gu, Angelaki, & DeAngelis, 2008) and rotational (De Winkel, Weesie, Werkhoven, & Groen, 2010 ; De Winkel, Soyka, Barnett-Cowan, Bülthoff, Groen, & Werkhoven, 2013; Jurgens, Kliegl, Kassubek, & Becker, 2015; Jürgens & Becker, 2011; Raymond, Droulez, & Kemeny, 2002; Telban & Cardullo, 2001) heading perception. In the optimal cue integration hypothesis, a weighted average is thought to be taken and optimally applied based on visual and vestibular sensory input. The modality that senses the most reliable input on average is likely to decide heading direction perception. The term ‘reliability’ in optimal cue integration hypothesis is defined as the inverse of the variance of a cue over trials. Therefore, cue reliability is tied to its strength or the level to which the cue is compelling.

De Winkel, Soyka, Barnett-Cowan, Bülthoff, Groen, and Werkhoven (2013) assessed human heading perception during cue conflict using accelerating visual stimuli in a two-interval forced-choice task. Researchers displayed vertical black and white stripes that moved clockwise or counter-clockwise on a LCD monitor. Participants sat in a chair that rotated. There was a

visual condition in which the stripes moved but the chair was stationary and a vestibular condition where the chair rotated but the stripes did not move. In a third visual-vestibular condition, both the chair and stripes moved. De Winkel and colleagues found that heading direction perception was most influenced in the visual-only cue condition for five of the eight participants. The three remaining participants made heading judgements based on the cue combination condition. None of the participants made heading predications based on vestibular cues presented alone. De Winkel et al.'s findings showed that observers were more likely to use visual cues even when visual-vestibular cues were provided. This result demonstrated that the optimal cue integration hypothesis does not always predict the observer's perceived heading or vection direction. If this was the case, participants would instead use visual-vestibular information equally. Other work from these researchers supports the notion that there can be deviations from optimal cue integration hypothesis (e.g., De Winkel et al., 2010; 2015).

Fetsch, Turner, DeAngelis, and Angelaki (2009) extended previous work on optimal cue integration hypothesis by investigating cue reliability. Cue reliability was defined as the inverse of the variance of the stimulus across trials. The goal of this study was to examine the extent to which varying visual and vestibular cue reliability across trials affects heading perception. Reliability was varied by manipulating the coherence of the visual display during conflict conditions in their experiment (i.e., the percentage of dots in the visual display that moved together to signal motion in a direction). They had human and primate subjects sit in a chair that moved linearly while watching a display indicating self-motion. It was found that participants chose the most reliable cue even when reliability varied from modalities across trials. This

suggests that optimal cue integration hypothesis is dynamic as it can change from one trial to the next for the same participants.

It is important to note that studies on optimal cue integration hypothesis did not examine vection but instead investigated heading. Heading is different than vection in that it does not require self-motion perception. Heading only requires that the observer is able to distinguish the direction of implied self-motion signaled by the optic flow pattern (Kirolos, Allison, & Palmisano, 2017; Lepecq et al., 2006). Heading perception occurs in much shorter periods than vection. Heading research is well-suited for study on physical motion platforms because heading display durations match the brief motions generated by mechanical motion platforms. In sum, the behavioural studies presented above support optimal cue integration hypothesis because they demonstrated that visual and vestibular cues are integrated in deciding heading direction instead of one system overriding cues from the other system. Therefore, there appear to be four hypotheses that have been used to explain self-motion perception during visual-vestibular conflict: traditional sensory conflict hypothesis, visual dominance hypothesis, vestibular dominance hypothesis, and optimal cue integration hypothesis.

A growing body of brain imaging research shows that visual and vestibular cortical areas become active during visual-vestibular conflict. The neurophysiological research on heading and self-motion processing and visual-vestibular integration are examined below.

Neural Correlates of Heading and Self-Motion Perception

Visual cortical regions like dorsomedial area V6, MSTd, precuneus motion area (PcM) and cingulate sulcus visual area (CSv) have been shown to be active during optic flow motion

where participants report vection, egomotion, or heading in neuroimaging studies (Furlan, Wann, Smith, & Smith, 2014; Pitzalis et al., 2010; Zeki, Watson, Lueck, Friston, Kennard, & Frackowiak, 1991). Other cortical areas have been shown to be involved in vestibular or visual-vestibular self-motion processing as well (Cardin & Smith, 2010b; Greenlee et al., 2016; Kirollos, Allison, & Palmisano, 2017). Vestibular processing areas include the parieto-insular vestibular cortex (PIVC) and the nearby posterior insular cortex (PIC). Findings of active vestibular processing regions during visual vection are interesting as these provide evidence in support of optimal cue integration hypothesis. This would converge with previously described findings from the behavioural literature presented above supporting optimal cue integration hypothesis. Neurophysiological findings on vestibular cortical activity converge with behavioural findings of optimal cue integration findings because during conflict, the visual and vestibular systems appear to be actively involved in self-motion perception.

Neuroimaging methods include functional magnetic resonance imaging (fMRI), positron emission tomography (PET), magnetoencephalography (MEG), electroencephalography (EEG), functional near-infrared spectroscopy (fNIRS) and computed tomography (CT). In fMRI and PET, clusters of high hemoglobin activity in parts of the brain are detected. The underlying assumption in fMRI and PET brain imaging is that metabolic activity in a localized brain region is correlated with some carefully controlled experimental event. The location of hemoglobin activity is analyzed by segmenting the brain into voxels (three-dimensional pixels) and statistically modeling voxel activity in experimental and baseline conditions. Conditions are then contrasted. It is assumed that if brain activity (e.g., % signal change) from the contrast in the statistical model exceeds the set threshold, brain activity is considered significant. In fMRI,

this activity is measured by the blood oxygenation level dependent (BOLD) signal. In PET, this is measured by administering and tracking a small dose of a radioactive tracer. It is important to note that whether activity is metabolic, such as in fMRI, PET or fNIRS, electrical such as in EEG, or magnetic such as in MEG, these brain imaging methods are all strictly correlational. Therefore, the stimulus associated with the brain activity in a certain area does not *cause* neurophysiological activity. To date, the only brain imaging technology from which causal activity can be inferred is transcranial magnetic stimulation (TMS).

Visual cortical regions associated with self-motion perception

Medial Temporal Complex (MT+)

The medial temporal complex or area MT+ is involved in processing coherent visual motion - an important characteristic ofvection. It is located at the anterior portion of the temporal lobe, bordering the visual and temporal lobes bilaterally. Many studies have reported increased activity in MT+ during coherent motion visual displays compared with incoherent motion or static stimulus displays (Rodman & Albright, 1989; Watson et al., 1993; Zeki et al., 1991). Studies on visual motion processing in monkeys' area MT (Rodman & Albright, 1989) were extended to humans by Zeki et al. (1991) and Watson et al. (1993). They observed a visual motion sensitive region homologous to monkeys V5/MT using PET and MRI in humans respectively. Zeki and colleagues found that V5/MT activity correlates with motion better than with stationary stimuli. Tootell et al. (1995) replicated these findings in fMRI and confirmed the same spatial coordinates for MT in humans as Zeki et al.

Morrone, Tosetti, Montanaro, Fiorentini, Cioni, and Burr (2000) reported that V5/MT is activated by changes in optic flow and to continuous translation in a fMRI study. Huk and

Heeger (2001) concluded that MT in humans has pattern motion cells that preferred perceived coherent motion compared to incoherent motion. Huk and Heeger did not specify the spatial coordinates of MT in their fMRI study. Pitzalis et al. (2013) reported greater activity in MT+ for translational and looming egomotion displays than for spiraling egomotion displays, replicating the Morrone et al. findings.

MST+ has neurons with larger receptive fields than the rest of the MT+ complex (Pitzalis et al., 2013). To functionally localize MST+ Pitzalis et al. used a stimulus that restricts optic flow to an aperture in the left or right hemifield. They hypothesized that there would be increased BOLD activity in the contralateral hemifield only for area MT+, but for both the contralateral and ipsilateral hemifield for area MST+. This is because the neurons in MST+ have larger receptive fields than MT+. As hypothesized, they found higher activation in MST+ for ipsilateral displays than in MT+. MT+ only responded to motion in the contralateral hemifield. Thus, MST+ responds to visual motion in both contralateral and ipsilateral hemifields but MT+ is only sensitive to motion in the contralateral hemifield. This finding is important as it suggests that MST+ is functionally and anatomically defined independently within the wider MT+ complex but that both regions respond to coherent visual motion.

Precuneus Motion Area (PcM)

The precuneus is located in the posterior medial region of the parietal lobe. Wolbers, Wiener, Mallot, and Büchel (2007) conducted an fMRI study in which they reported heightened BOLD signal in PcM during path-integration - a cognitive task believed to require self-orientation updating. Wolbers, Hegarty, Büchel, and Loomis (2008) found that PcM is involved in spatial updating. Studies have also shown increased BOLD activity in PcM during

egomotion-compatible (EC; displays that have the potential to induce heading or vection) visual displays and decreased BOLD activity with egomotion-incompatible displays (EI; displays that are not intended to induce heading or vection; Billington, Wilkie, & Wann, 2013; Cardin & Smith, 2010a). PcM therefore appears to be involved in processing cognitive aspects of vection processing.

V6

Pitzalis and colleagues confirmed that the human homologue to monkey V6 is located posterior to the dorsal end of the parieto-occipital sulcus (POs; Pitzalis, Sereno, et al., 2013). The precise function of V6 is still undetermined. Some studies have shown that V6 is sensitive to translational egomotion. Pitzalis et al. 2010 showed that V6 is involved in visually-guided motor control and distinguishing visually-induced self-motion from object motion (Pitzalis et al., 2010). Cardin, Hemsworth, and Smith (2012) reported that V6 is involved in obstacle avoidance. Others have reported its importance for estimating egomotion (Pitzalis, Sdoia, et al., 2013). Pitzalis and colleagues (2013) compared BOLD response to five types of optic flow: translational, circular, radial, spiral, as well as random motion and static dots. They found that % BOLD signal change in V6 was largest for translational optic flow displays compared to circular, radial, spiral, random motion, or static dots.

Although V6's function is not yet clearly defined, the dominant view is that it is involved in processing wide-field visual stimulation, disambiguating different types of optic flow and in visually-guiding motor control. Moreover, there is a functional distinction made between V6, and neighbouring V6a in the anterior bank of the parieto-occipital lobe (Pitzalis et al., 2013). Activity in V6a is driven by pointing and reaching in Pitzalis' study. V6 may not be directly

involved in processing self-motion and most research agrees that it does not integrate visual-vestibular signals nor vestibular signals in both humans and primates. Its proximity to the motor cortex makes it a candidate for processing visual information to be integrated with motor information (Smith, Greenlee, DeAngelis, & Angelaki, 2017).

Ventral Intraparietal Region (VIP)

The ventral intraparietal region (VIP) in macaques is regarded as a polysensory region because it responds to visual (Schaafsma & Duysens, 1996), vestibular, and somatosensory stimuli (Duhamel, Colby, & Goldberg, 1998). In a fMRI study by Bremmer et al. (2001), human VIP was functionally localized visually using optic flow in the frontal plane. Later studies also confirmed visual sensitivity of VIP (Cardin & Smith, 2010b; Smith, Wall, & Thilo, 2012) but reported slightly different coordinates for this region. Vestibular stimulation during fMRI in humans suggests that VIP is not a vestibular processing region (Fasold et al., 2002). However, VIP appears to be a visual processing area in monkeys (Colby, Duhamel, & Goldberg, 1993). Fasold's group functionally localized vestibular regions in humans by stimulating the inner ear with cold nitrogen caloric irrigation in fMRI. Their results point to strong involvement of the parieto-insular vestibular cortex (PIVC) in vestibular processing of caloric stimulation but not VIP. Similarly, Eickhoff, Weiss, Amunts, Fink, and Zilles, (2006) used galvanic vestibular stimulation, using a custom-made apparatus that is compatible with use with a MRI scanner. They found a significant change in BOLD activity compared to baseline in the parieto-insular cortex (an area approximating PIVC) but not in VIP.

In sum, VIP in humans does not seem to be activated during vestibular stimulation (Eickhoff et al., 2006; Fasold et al., 2002; Pitzalis et al., 2013). Therefore, rather than a general

polysensory integration area for self-motion signals, VIP could be principally involved in visually-guided obstacle avoidance in humans.

Cingulate Sulcus Visual Area (CSv)

CSv is the cortical region reported to anatomically separate the boundaries of the parietal and occipital lobes. CSv appears to be functionally involved in heading estimation. Wall and Smith (2008) reported that BOLD activity in CSv was greater with a full-field stimulus signaling self-motion than during a stimulus containing 9 smaller patches of the same display that did not signal self-motion. According to Furlan, Wann, and Smith (2014), activity in CSv seems to be correlated with activity in VIP. Smith's group argued that CSv is involved in motor planning, as opposed to motion perception, based on its anatomical and functional connectivity.

Furlan et al. (2014) noted that CSv responds well to changes of heading compared with other visual motion processing regions such as MST+ and V6. In contrast, MST+ responds better to continuous heading than to changes of heading. Fischer, Bühlhoff, Logothetis, and Bartels (2012) demonstrated the importance of CSv for processing visual self-motion during eye movements, compared with other known visual motion sensitive cortical regions. Fischer et al. argued that CSv integrates eye movements with retinal motion during self-motion displays. Wada, Sakano, and Ando (2016) showed that during oscillating horizontal motion of the visual scene, stronger BOLD activity was observed in area CSv. However, like other studies, their display did not last long enough to induce vection nor was vection measured.

In a recent study by Kirolos, Allison, and Palmisano (2017), behavioural measures of vection were obtained and BOLD activity was compared during oscillating vection, smooth vection and non-vection displays in fMRI. They found that CSv is strongly activated during

vertical oscillation vection displays compared to smooth vection displays. Kirollos et al. concluded that CSv appears to be a main candidate for visual self-motion processing in the brain.

Vestibular and polysensory cortical regions associated with self-motion perception

Parieto-insular vestibular cortex (PIVC)

PIVC is widely regarded as a polysensory region in both non-human primates (Guldin & Grüsser, 1998) and humans (Fasold et al., 2002). PIVC is known to be primarily involved in vestibular signal processing. It is reported to have strong right hemispheric dominance (Fasold et al., 2002). In PET studies, caloric irrigation has been used to localize PIVC (Bottini et al., 1994). PIVC was functionally localized using GVS in fMRI (Bense et al., 2001; Eickhoff et al., 2006). There have been reports of functionally localizing PIVC both with vestibular stimulation and visual stimulation separately.

Cardin and Smith (2010) reported increased PIVC activity during a visual stimulus signaling egomotion. In their experiment, they contrasted fMRI brain scans during ‘egomotion-compatible’ display presentations with ‘egomotion-incompatible’ display presentations. Egomotion-compatible stimuli were wide-field optic flow displays that lasted 3 s and were therefore too short to induce vection. The authors did not measure vection. Cardin and Smith found a significant change in activity for egomotion-compatible compared to egomotion-incompatible stimuli in PIVC. In line with this finding, Antal, Baudewig, Paulus, and Dechent (2008) reported that coherent optic flow displays activated similar insular areas to PIVC in a human fMRI study. Antal et al. did not record participant vection experience, however, there are fMRI studies that measured vection and reported increased PIVC activity during vection (Beer, Blakemore, Previc, & Liotti, 2002; Indovina, Maffei, Pauwels, Macaluso, Orban, & Lacquaniti,

2013; Kirollos et al., 2017; Kovács, Raabe, & Greenlee, 2008). As such, PIVC may not be spatially well-defined but there is convincing evidence of insular cortex activity during visual stimulation of this region. Kirollos et al. (2017) showed that PIVC/PIC is active during visual presentation of oscillating displays but not smooth displays. This finding suggests that PIVC may respond visually only to high-conflict vection displays such as oscillating vection, but not to low conflict displays such as smooth vection.

Posterior Insular Cortex (PIC)

Work by Frank, Wirth, and Greenlee (2016) clarifies reports of PIVC activity during visual and vestibular stimulation as they investigated cortical activity when viewing a vection inducing display and when receiving caloric irrigation separately in a fMRI study. Frank et al. found that area PIVC became active during caloric stimulation but not during visual self-motion display presentations. Frank and colleagues showed that an insular region directly adjacent to PIVC they called the posterior insular cortex (PIC) became active during visual and vestibular stimulation. Kirollos and colleagues (2017) found strong BOLD activity in PIVC during visual oscillating vection displays that induced high conflict between the visual and vestibular systems. Kirollos et al. reported that their stimulus may have localized nearby PIC. However, it is still possible that PIVC is responsive to high-conflict visual stimuli such as oscillation because Greenlee et al. did not examine this type of stimulus.

Schindler and Bartels (2018) demonstrated that region PIC showed significant activity during head motion (activating the vestibular system) compared to when the head was stationary (not activating the vestibular system) in a fMRI study. They did not measure vection in their study. Schindler and Bartels also found that PIC responded to coherent optic flow signaling self-

motion, replicating findings by Frank, Wirth, and Greenlee (2016). Schindler and Bartels attributed the activation of PIC with visual self-motion stimuli and vestibular motion caused by the head movements to activity in a different part of PIC. These PIC areas were anterior PIC (aPIC) which prefers coherent motion and appears to integrate visual and vestibular signals and posterior PIC (pPIC) which processes both visual and vestibular information separately and does not integrate these multi-modal signals. Evidence for connectivity differences defining PIVC, aPIC and pPIC will become clearer with further studies investigating cerebral connectivity (Smith, Greenlee, DeAngelis, & Angelaki, 2017; Wirth, Greenlee, & Beer, 2018).

In sum, there are several brain regions associated with self-motion processing. Some are purely visual regions (CSv, MT+, V6), some integrate both visual and vestibular signals (PIVC/PIC). Therefore, recent neuroimaging studies and behavioural heading research suggest that self-motion processing may be a distributed task between visual and vestibular systems and associated cortical areas supporting optimal cue integration hypotheses. However, it should be noted that some neuroimaging findings support visual dominance during conflict (Brandt, Bartenstein, Janek, & Dieteric, 1998). The remaining portion of this review describes some methods previously used to measure vection in behavioural studies, setting the stage for the vection measure developed and used in the current thesis.

Psychophysical measurement of vection

Stevens (1959) developed the magnitude estimation method to rate the subjective strength of perceived sensory experiences. In vection research the magnitude estimation rating technique involves exposing participants to a baseline optic flow stimulus display that induces

vection (referred to as the *modulus*). Participants monitor their subjective perception of vection strength on the modulus display and rate it on a scale (e.g., 1-10). Participants then rate subsequent vection trials, relative to the vection experienced during the modulus display. Magnitude estimation has been frequently used to measure vection, but this technique has limitations. First, magnitude estimation ratings rely on memory of the modulus display because it requires comparing vection experience in a recent trial to the vection experienced during the modulus viewed at the start of an experiment (Brindley, 1960; Poulton, 1968; Teghtsoonian, 1971). A second limitation of magnitude estimation ratings is that vection strength is a hypothetical construct. Therefore, it is interpreted and translated by the participant onto an arbitrary magnitude estimation rating scale. This can make magnitude estimation data difficult to interpret and compare across participants (Carpenter-Smith, Futamura, & Parker, 1995).

A nulling technique is another way to measure vection. Zacharias and Young (1981) had participants observe optic flow patterns that induced vection in a flight trainer. The trainer provided physical motion cues in a direction that conflicted with self-motion indicated by the optic flow trajectory. This physical motion was a rotation of the chair in which participants sat. Participants were required to rotate a knob in either a clockwise or counter-clockwise direction. Rotating the knob stopped the visual or vestibular stimulus depending on which direction the knob was rotated. Zacharias and Young hypothesized that participants would rotate the knob such that it would stop the stimulus participants felt provided the strongest cue to perceived self-motion. Zacharias and Young found that participants perceived self-motion to be driven by the visual display when stimulus input was a low temporal frequency pattern and by the vestibular system at with higher temporal frequency temporal patterns.

Palmisano and Gillam (1998) used a task similar to Zacharias and Young (1981). In an optokinetic drum, Palmisano and Gillam had participants null the visual or vestibular stimulus that made them feel like they were moving most, but nulling speed was also recorded. Palmisano and Gillam had participants rate perceived vection speed on a magnitude estimation scale. The nulling task was used to slow down the chair in relation to quickly moving circular vection visual stimuli.

The common thread among the nulling knobs (Huang & Young, 1981; Palmisano & Gillam, 1998; Zacharias & Young, 1981) used in experiments is that participants used a device to actively control (null) the source of stimulation during stimulus presentation. The advantage of nulling tasks compared to magnitude estimation ratings is that nulling tasks do not rely on memory. A drawback of nulling tasks is that they do not give a numerical value for vection strength, speed or experience. Though Palmisano and Gillam (1998) indexed speed of nulling, this should not be interpreted as speed of vection.

In this thesis, a new objective measure of vection perception was developed, validated and employed. This objective measure consisted of a circular knob apparatus. Participants rotated the knob in the direction and the speed at which they experienced circular vection. Knob rotation direction, speed, start time and duration were logged. The knob indexed the speed at which participants felt they were rotating but did not null the stimulus. Therefore, data from experiments in this thesis represent speeds at which participants felt vection. In Section 2 of this thesis, the circular knob methodology is introduced, validated and employed for data collection and analysis.

Summary of Section One

To summarize, vection research dates back to the late 1800's. The devices used to visually induce vection have evolved from physical optokinetic drums to tumbling rooms, dotted rooms, and spheres. Computer generated displays presented on monitors and more recently on VR headsets has allowed researchers to examine new facets of visually induced vection as in the experiments in this thesis. Artificial methods to stimulate the vestibular system such as caloric vestibular stimulation show promise in studying vestibular perception but have been under-utilized in perceptual research. As such, caloric vestibular stimulation is used in this thesis to examine vestibular self-motion perception. There are three competing hypotheses regarding how vestibular and visual cues are used to determine vection. The visual dominance hypothesis asserts that during visual-vestibular conflict, the visual system will decide self-motion. The vestibular dominance hypothesis states that during conflict, signals consistent with the vestibular direction of self-motion will be used. The optimal cue integration hypothesis predicts that during conflict the most reliable information from the visual or the vestibular system will be used to decide self-motion perception. Experiments in this thesis tested these hypotheses and determined the method by which visual-vestibular sensory integration is resolved. Neurophysiological studies on self-motion processing indicated that cortical regions associated with both the visual and vestibular systems are involved in self-motion processing rather than brain areas associated with one sensory system dominating the other sensory system and associated cortical processing regions. Understanding how the brain resolves conflict was expected to inform and converge with behavioural results on conflict in this thesis. Finally,

research on different behavioural measures to index vection was presented to justify the need for a methodology that measures vection speed.

SECTION TWO

A NEW SPIN ON THE OPTOKINETIC DRUM (EXPERIMENTS 1 & 2)

While stopped at a red light, a driver may feel that they are moving backward if an adjacent vehicle begins moving forward. The driver of the stationary car may frantically increase pressure on the brake pedal, only to realize that they did not move. This situation describes a visual illusion calledvection. Vection is thought to occur because the optic flow created by the forward motion of the adjacent vehicle signals to the driver that they are moving backward. In most situations, our senses relay congruent signals to the brain regarding our self-motion. However, duringvection there is a sensory conflict because the visual system receives information signalling self-motion, but the other sensory systems do not receive self-motion information.

Studies have investigated howvection strength (the perceived ‘convincingness’ of the illusion) is affected by visual angle of the stimulus (Allison et al., 1999; Warren, 1895), optic flow trajectories (Gibson, 1966; Mach, 1875; Palmisano et al., 2000), background-foreground scene relationships and stimulus eccentricities (i.e., stimulus distance relative to the fovea; Brandt, Wist, & Dichgans, 1975; Ohmi, Howard, & Landolt, 1987; Palmisano & Gillam, 1998). Typically, researchers have focused on measuringvection strength using magnitude estimations, how longvection lasts (durations) and the amount of time needed to experiencevection (onsets/latencies). However, there is little research that has directly obtained the speed of perceivedvection. Vection speed is important to consider for two reasons. First, quantifying the speed at which observers sense motion is a new dimension ofvection research that will give more detailed information on self-motion perception. Second, measuringvection speed is

important for multi-modal sensory stimulation in situations where information to the various sensory modalities should match. For instance, vection speed in the visual system should match vestibular, auditory, and proprioceptive cues to vection in situations of multi-modal self-motion perception such as in flight or vehicle simulation. This will ensure reliable and accurate simulation experiences. Moreover, multi-modal consistencies in simulation can be important for immersion and effective positive transfer of training. Sensory mismatches in simulation can cause safety concerns such as motion sickness and disorientation (Kennedy, Fowlkes, Berbaum, & Lilienthal, 1992), poor simulation fidelity, and negative transfer of training. Therefore, perceptual information such as perceived speed should match across modalities to ensure that simulation is an effective training tool. To ensure perceived speed matches across modalities, vection speed must first be measured across modalities. Vection speed is therefore measured across the visual and vestibular system in this thesis for the first time. A new methodology was developed in this thesis in which participants were required to rotate a knob in a manner that reflected their perceived vection speed, direction, and duration. Participants performed this task while they viewed a graphic display of an optokinetic drum.

In early vection experiments, an observer was seated in a large physical drum that had black and white vertical stripes on its inner surface (Aitken's 1880 study; Mach, 1875; Thalman, 1921). A motor rotated the drum around the participant in a clockwise or counter-clockwise direction at constant velocity. Participants typically experienced a compelling illusion of self-rotation, or circular vection in the direction opposite to the optic flow motion produced by the drum's stripes. Researchers have investigated depth perception and stimulus eccentricity by occluding parts of the rotating drum. For example, Brandt, Wist and Dichgans (1975) found that

vection is stronger when the background of the scene moves and the foreground is stationary than if the foreground of the scene moves and the background is stationary. Ohmi, Howard, and Landolt (1987) found that the perceived background, not the actual background, drives circular vection. Based on Ohmi et al.'s findings, it was not clear whether vection was driven by the display eccentricity or the spatial frequency of the stripes. Palmisano and Gillam (1998) showed an interaction between stimulus eccentricity, and spatial and temporal frequencies, whereby high frequency stripes drove stronger circular-vection in the far visual periphery (defined as 75° from center of fovea in Palmisano and Gillam's work). Low-frequency stripes enhanced vection strength when presented to foveal vision. The temporal frequency used in Palmisano and Gillam was 2.6 Hz and the spatial frequency was 0.2 cycles/deg⁻¹. Research by Held, Dichgans, and Bauer (1975) found that larger field of views generally enhanced vection strength.

The optokinetic drum has been useful for examining vection. However, the optokinetic drum has limitations. For instance, they are noisy, challenging to build, modify and accommodate in laboratory space. Wann and Rushton (1994) developed a 'virtual' rotating drum in which alternating black and white vertical stripes were presented on a VR display. Early-generation VR headsets had low resolution, limited field of view and long temporal lag during head movements which could result in motion sickness. These factors have become negligible because of improvement in VR display technology (Kim, Chung, Nakamura, Palmisano, & Khuu, 2015; Palmisano, Mursic & Kim, 2017). Several studies have shown that vection can be induced using VR displays (Riecke & Jordan, 2015; Kim, Chung, Nakamura, Palmisano, & Khuu, 2015; Wann & Rushton, 1994). Wann and Rushton (1994) used VR headsets to compare vection strength during realistic scenes with complex elements (i.e., such as

a virtual rendition of a busy city center) to simple scenes such as a virtual drum with vertical stripes. They found that vection was stronger when viewing a realistic scene than when viewing the drum pattern. VR headsets have also allowed researchers to compare vection while in different postures (Skwersky, 1995). The development of VR headsets gives researchers the potential to examine vection in new scenarios such as while walking, moving the head, and in different body positions.

The objective of the present section was to validate the use of a virtual optokinetic drum in a VR headset and to develop and validate a method that indexes circular vection speed in the visual system. In E1, the use of the virtual drum was validated by measuring vection strength using traditional magnitude estimation ratings (Stevens, 1959). Vection strength was hypothesized to increase as a function of drum speed. This would replicate the known linear relationship between perceived display speed and experienced vection strength (Palmisano & Gillam, 1998; Riecke, 2010; Uesaki & Ashida, 2015; Wada et al., 2016). In E2, the same stimuli as in E1 were used. However, instead of providing magnitude ratings, participants responded to stimuli with a knob that they rotated to reflect their perceived vection: vection direction, speed and duration were recorded. Vection speed was hypothesized to increase as drum speed increased.

Experiment 1: Magnitude Estimation Ratings of Vection in a VR Headset

The objective of the E1 was to validate the use of a virtual optokinetic drum for examining vection. A virtual rendition of the rotating drum was presented on a VR display. The virtual drum consisted of alternating vertical black and white stripes that appeared to move

clockwise or counter-clockwise on the display. Vection strength was measured using a magnitude estimation rating scale that has been widely used in vection research (Allison, Zacher, Kirolos, Guterman, & Palmisano, 2012; Apthorp, Palmisano, & Osorio, 2014; Kirolos, Allison, & Palmisano, 2017). It was predicted that faster virtual drum speeds would produce higher ratings of vection strength and longer vection durations.

Method

Participants

A total of 18 undergraduate students recruited from Carleton University's online study sign-up system participated in the experiment for course credit ($M_{AGE}=22.7$, $SD_{AGE}=5.7$). Two participants did not complete the experiment because they experienced slight nausea, leaving 16 participants (6 female, 10 male) in the final analysis. Three participants did not have normal or corrected-to-normal vision but reported seeing the display clearly. All participants responded that they did not have any previous history of vestibular disorders (Appendix 2).

Design

The experiment was a 3 (Drum Speed: 37.5 °/s vs. 56.25 °/s vs. 75 °/s) by 2 (Direction: clockwise vs. counter-clockwise) repeated measures design. The six conditions were presented six times each, totaling 36 trials that were presented in random order to each participant. The 36 experimental trials were split across four blocks (9 randomized trials per block). Each block lasted approximately 5 minutes and was followed by a 5-minute break.

Apparatus

VR headset. A virtual representation of the rotating drum with alternating black and white vertical stripes was presented on an Oculus Rift DK2 VR headset. The DK2 provided an 110° diagonal visual angle, a native resolution of 960 x 1080 pixels per eye, and a 75 Hz refresh rate. The left and right eye displays presented the same image at different perspectives permitting 3D perception of the stimuli. The inter-ocular distance (IOD) on the DK2 was set at 64 mm for all participants. IOD was held constant because it was assumed that small inter-subject differences in IOD would not impact stimulus perception. To ensure that the pattern was perceived as intended (i.e., the interior of a cylinder), participants were asked if the stimulus appeared convex, concave, or flat at the start of the experiment. All participants reported that it appeared concave. The graphics display simulated a drum with a 200-cm diameter. When wearing the VR headset, the observer's viewpoint was at the center of the virtual drum. Each stripe in the display corresponded to a width of 33 cm in the virtual graphics environment, and subtended a horizontal visual angle of 10.85° at a virtual viewing distance of 100 cm.

XBOX 360 Gamepad. A USB-integrated gamepad was used to record vection duration by having participants press and hold the top-right shoulder button when they experienced vection. Participants could select a value on the scale that represented the strength of experienced vection. This was done using the 'Y' button to navigate up on the scale and the 'A' button to navigate down on the scale. Participants could increase or decrease their rating on the scale by 5-point increments. The 'B' button was used by the participant to finalize the selection of their rating.

Figure 1. Controller used for Experiment 1.

Computer. A computer with an Intel Core I-7 processor, an NVIDIA GeForce GTX980 graphics card and 16 GB RAM was used to run the experiment. The graphics environment was built using Unreal Engine 4.8 software.

Stimuli and Procedure

The vertical stripe pattern that was presented on the VR display moved in the clockwise or counter-clockwise directions at three speeds: $37.5^\circ/\text{s}$ (slow), $56.25^\circ/\text{s}$ (medium) and $75^\circ/\text{s}$ (fast). This resulted in six conditions. Each trial lasted 30 s during which the display moved at one of the pre-selected speeds.

Figure 2. Sequence of a vection trial in E1. Participants rate vection strength with magnitude estimation scale controlled by a XBOX 360 controller.

Participants were seated on a chair in a dark room with their feet touching the ground and their heads supported by a pillow against a wall to keep it steady while wearing the VR headset. Once participants were comfortably seated, the display was adjusted in the headset to appear in front of the participant. Participants were given the instructions and completed 3-5 practice trials to ensure they understood their task.

Following the practice trials and at the start of the experimental session, participants were presented with a modulus display. This was a 40 s display of the stripes moving in the clockwise direction for 20 s and in the counter-clockwise direction for 20 s at the medium speed. Participants were instructed to monitor their experience of vection with the modulus display and assign it a value of '50' on a visually presented 0-100 scale. The value and associated vection strength experienced during the modulus display was used as a reference by the participant to rate all subsequent trials. Participants rated vection strength at the end of the trial when the 0-

100 rating scale appeared in the headset. They compared vection strength of the most recent vection display they had seen to the modulus display to rate the stimulus. Vection duration was measured by having participants hold the right trigger of the gamepad from the moment circular vection started until vection was no longer experienced.

In practice trials and experimental trials, a central fixation cross appeared on a grey background for three seconds at the beginning of each trial. Then the moving pattern of the drum appeared at one of the pre-selected speeds for 30 s. A grey screen appeared for 7 s after each trial and a ‘block complete’ message was presented at the end of each block. The headset display was mirrored on a monitor for the experimenter.

Results

Magnitude ratings of vection strength and vection duration were analyzed in separate 3 (Drum Speed: 37.5 °/s vs. 56.25 °/s vs. 75 °/s) by 2 (Direction: clockwise vs. counter-clockwise) repeated measures ANOVAs. Post-hoc comparisons were made using 95% confidence intervals (Jarmasz & Hollands, 2009). ANOVA tables containing full analyses for all ANOVA in this thesis are shown in Appendix 1.

Vection Strength

The vection magnitude ratings are shown in Figure 3. As predicted, there was a significant main effect of Drum Speed, $F(2, 30) = 25.04, p < .001, R^2 = .63$, where faster drum speeds resulted in greater ratings of vection strength. The 95% confidence intervals indicated a significant difference in perceived vection strength between all speeds in both the clockwise and counter-clockwise directions. As shown in Figure 3, vection strength did not differ between

clockwise and counter-clockwise presentation conditions ($F < 1$) and there was no interaction between Drum Speed and Direction ($F < 1$).

Figure 3. Magnitude estimation (ME) ratings of vection strength for three drum speeds in the clockwise (CW) and counter-clockwise (CCW) directions. Error bars indicate 95% confidence intervals for the analysis.

Vection Duration

As shown in Figure 4, participants indicated that vection lasted 10.9 s on average. Vection durations did not differ as a function of Drum Speed or Direction and there was no interaction between these factors (all F 's < 1). Some studies have shown that larger vection

magnitude estimation ratings correlate with longer vection durations, especially in linear vection studies, but this is not always the case and was not apparent in the present results.

Figure 4. Vection duration (in s) for three drum speeds in the clockwise (CW) and counter-clockwise (CCW) directions. Error bars indicate 95% confidence intervals for the analysis.

In summary, E1 validated the use of a virtual rotating drum for examining vection. Vection strength was measured using magnitude estimation rating which is a commonly used method to measure vection strength. Results showed that increasing the rotation speed of the virtual drum resulted in participants reporting stronger vection strength. This finding is consistent with previous vection research using a physical optokinetic drum (Palmisano & Gillam, 1998; Riecke, 2010; Uesaki & Ashida, 2015; Wada et al., 2016). It is concluded that

presenting a virtual drum on a VR display is a valid technique to induce and study circular vection.

Experiment 2: Measuring Speed of Circular Vection Using a Rotating Knob Task

Stevens (1959) developed the magnitude estimation method to rate the subjective strength of perceived sensory experiences. Magnitude estimation has been frequently used to study vection but is limited because it relies on memory. Moreover, vection strength is a hypothetical construct translated onto an arbitrary scale. These limitations can make magnitude estimation data difficult to interpret and compare across participants (Brindley, 1970; Carpenter-Smith et al., 1995; Poulton, 1968; Teghtsoonian, 1971).

In the present experiment, a rotating knob apparatus was developed to provide a direct measure of vection speed. Participants rotated the knob at the speed at which they experienced circular vection while watching a rotating virtual drum in a VR headset. Vection speed was hypothesized to depend on drum rotation speeds. That is, faster drum speeds would induce faster perceived vection which would be reflected in faster knob rotations.

When participants felt vection, they rotated the knob in the opposite direction and at the speed of their perceived self-motion. The knob apparatus recorded perceived vection speed, direction and duration. The drum moved at three distinct speeds (slow, medium, or fast) in the clockwise and counter-clockwise directions, identical to the conditions in E1. Faster drum speeds were hypothesized to result in faster knob rotation speeds by the participants.

Method

Participants

A total of 16 participants (4 female, 12 male) were tested ($M_{AGE}=19.0$, $SD_{AGE}=1.8$) were recruited. Fourteen were undergraduate students that received course credit in return for their participation. Two participants were experimenters involved with the experiment. Two participants did not experience vection and were excluded from the analysis. Therefore, 14 participants were included in the final analysis. All participants had normal or corrected-to-normal vision and no history of vestibular problems. Two participants were left-handed.

Stimuli & Design

Stimuli and design in this experiment were identical to E1.

Apparatus

Control Knob. A Spintrak rotary knob was used to index speed of circular vection. The knob was circular, had a 4.4 cm diameter and could be turned clockwise or counter-clockwise indefinitely. The knob had a tachometer and a high-resolution pulse rate of 1200 units over its 360° range for precise knob position tracking and recording. The knob was USB-integrated with custom-made software that logged measured turn rates in °/s at 75 Hz. The knob was housed in a wooden box and rested on the participant's lap during testing.

Figure 5. Knob controller used to measure vection speed. Knob can be rotated clockwise or counter-clockwise.

Computer. A computer with an Intel Core I 7920 processor with an ATI Radeon HD 5870 graphics card and 6 GB RAM was used for this experiment.

VR Headset. The VR headset was the same as in E1.

Procedure

Participants viewed the same stimuli from E1 and were seated upright in the dark. They underwent four blocks separated by 5-min breaks. Each block contained 9 randomized trials. Participants were instructed to turn the knob when they felt circular vection. They could rotate the knob continuously in the opposite direction to their perceived self-motion and were instructed to rotate the knob at the same speed they felt vection. They rotated the knob in the opposite direction of their perceived self-motion direction as this was thought to more directly engage the participant in an active task requiring constant monitoring of their perceived self-

rotation compared to simply mimicking the direction of their vection. The circular knob was used instead of other input methods such as a joystick because the motion of the knob (i.e., yaw axis rotation) closely represents the axis of perceived self-motion direction participants were thought to experience (i.e., yaw axis self-motion) compared to the linear motions of a joystick. Thus, it was thought that the knob would more readily capture perceived motion of the participant. Participants put their dominant finger on the top surface of the knob near its edge and held the knob on their lap with the other hand. If participants did not experience vection, they did not turn the knob.

Results

Vection speed and duration were analyzed in separate 3 (Drum Speed: 37.5 °/s vs. 56.25 °/s vs. 75 °/s) by 2 (Direction: clockwise vs. counter-clockwise) repeated measures ANOVAs. Post-hoc comparisons were made using 95% confidence intervals (Jarmasz & Hollands, 2009).

Vection Speed

Perceived vection speed was defined as the rate at which participants rotated the knob. There was a significant main effect of Drum Speed on knob rotation, $F(2, 28) = 34.21, p < .001, R^2 = .71$. As shown in Figure 6, participants turned the knob faster as the virtual drum speed was increased across the slow, medium and fast conditions. The 95% confidence intervals indicated differences between slow-fast and medium-fast speeds for both directions (e.g., clockwise and counter-clockwise). There was no main effect of Direction and no interaction between Drum Speed and Direction (F 's < 1) on knob rotation.

Figure 6. Knob Rotation Speed (°/s) for three drum speeds in the clockwise (CW) and counter-clockwise (CCW) directions. Error bars indicate 95% confidence interval for the analysis.

Vection Duration

Vection duration was measured as the amount of time (in s) that participants rotated the knob during a trial. There was a significant main effect of Drum Speed on vection duration, $F(2, 28) = 14.73, p < .001, R^2 = .51$. Based on the 95% confidence intervals (Figure 7) there were significant difference between slow-fast, and slow-medium conditions in both the clockwise and the counter-clockwise conditions. There were no observed interaction effects between Drum Speed and Direction ($F < 1$).

Figure 7. Vection duration (in s) for three drum speeds in the clockwise (CW) and counter-clockwise (CCW) directions. Error bars indicate 95% confidence interval for the analysis.

In summary, the goal of E2 was to develop and use a measure to index vection speed. This was done by having participants rotate a circular knob at the speed that reflected their experience of vection. As in E1, a virtual rotating drum was presented on a VR display in E2. The virtual drum was presented at three different speeds. Participants turned the knob device faster and for a longer duration as the speed of the rotating virtual drum was increased. In all, the rotating knob device can be used to obtain a measure of vection speed and is the first to provide vection speed data. This can be used to more specifically quantify vection perception for applications such as simulation.

Summary of Section Two

Experiments 1 and 2 showed that (a) vection can be produced by using a virtual drum presented on a VR display and (b) the knob rotation task can provide a direct measure of vection, including vection speed. In early studies, vection was induced by having participants sit in a large physical drum that had black and white vertical stripes on its inner surface. The optic flow produced by the moving stripes generated illusory rotary self-motion, or what is called circular vection felt in the direction opposite to the motion of the stripes. In the present experiments, vection was induced using a virtual optokinetic drum in which alternating black and white vertical stripes were presented on a virtual reality (VR) display.

In E1, vection strength was measured using magnitude estimation ratings. Increasing the speed of the optokinetic virtual drum resulted in higher magnitude estimation ratings, indicating stronger vection with faster drum speeds. This finding is in line with previous studies that have found increased vection strength with faster optic flow displays (Palmisano & Gillam, 1998; Riecke, 2010; Uesaki & Ashida, 2015; Wada et al., 2016). The virtual optokinetic drum was also used in E2. Rather than using magnitude estimation ratings, participants' perception of self-motion was measured with a newly developed apparatus in which participants turned a knob to coincide with their experience of vection speed. Participants spun the knob more quickly and for longer durations when the virtual drum rotated at higher speeds as hypothesized. The knob apparatus therefore provides a new index of perceived self-motion and its speed.

SECTION THREE

VESTIBULAR VECTION INDUCED BY AIR CALORIC VESTIBULAR STIMULATION (EXPERIMENTS 3 & 4)

The vestibular system has been informally referred to as the ‘sixth sense’ because of its roles in providing spatial orientation information, maintaining a stable image of the visual world during head motions and its involvement in cognitive tasks (Ferré & Harris, 2017). The vestibular system is even involved in basic physiological mechanisms such as blood pressure regulation (Howard, 1982; Spiegel & Démétriades, 1925). The otolith organs of the vestibular system sense gravitational acceleration. In space’s 0-g, gravitational accelerations are not present. Astronauts still sense vestibular cues to motion with active and passive head motions but without the gravitational acceleration acting on the otoliths, astronauts often become disoriented and can experience space motion sickness (Young et al., 1993). The visual environment can become blurry as a result of astronauts moving their head too quickly in the absence of gravitational acceleration acting as a reference to the vestibular system. Examples from reports in space highlight the important but often unrecognized role of vestibular function in our daily lives.

Researchers often use visual stimuli producing vection to make inferences about the vestibular system. However, comparatively little research exists examining sensation and perception in the vestibular system. In this section of the present thesis, the vestibular system was stimulated to generate vection. This was done by stimulating participants’ horizontal semi-circular canal with air caloric irrigation. Participants indicated the direction, speed, and duration of vestibular vection by spinning the knob apparatus used in Section 2.

Because the measurement and indexing of vestibular vection using air caloric irrigation has not previously been reported, the first objective was to examine whether caloric vestibular stimulation produces measurable vestibular circular vection. In E3, participants kept their eyes closed while undergoing caloric vestibular stimulation. If participants sensed vection, they indicated its direction, speed and duration with a knob during a designated response period after stimulation ended.

In E4, the objective was to investigate vestibular vection when viewing a stationary visual display. There was a presumed sensory conflict between the vestibular system and the visual system. This is because the vestibular system received self-motion information with air caloric vestibular stimulation, but the visual display did not indicate self-motion. Although optic flow information indicating vection is absent in both E3 and E4, it cannot be assumed that vection perception would be the same in these two experiments. In E3 (eyes closed) the visual system did not receive movement information. In E4 (eyes open) the visual system received information that there was no movement in that the displayed image was stationary. The two different visual conditions in E3 versus E4 may differentially affect vestibular vection. This was investigated in this section.

Information sensed and perceived by the vestibular system has important implications for human performance. This is exemplified in work on pilots conducted by Melvill Jones, Barry, and Kowalsky (1964) which compared post-rotational time constants for the horizontal, posterior and superior semi-circular canals of pilots' vestibular systems. Post-rotational time constants are perceived self-motion after-effects that occur in the opposite direction of an angular motion direction. Post-rotational time constants occur because during head rotation, the endolymph

fluid presses on the cupular membrane, deforming it temporarily. It can take several minutes for the cupula and endolymph to revert to resting state. Post-rotational time constants are a function of the cupular membrane's elastic properties and can last several minutes. Melvill Jones et al. observed that when pilots make a turn in the yaw axis, they had significantly longer turn overcompensations than when making a turn in the pitch or roll axes. Melvill Jones et al. suggested that the long post-rotational time constants in the horizontal semi-circular canal caused pilots to commit judgement errors of turn directions and speeds in the yaw axis.

Melvill Jones et al.'s (1964) findings underscore the importance of investigating the role of vestibular perception. Many flight simulators combine visual cues with vestibular cues to provide concomitant self-motion signals in attempt to achieve high fidelity flight simulation. Though many motion-based simulators are accredited and even required for certain aircraft simulators by the Federal Aviation Administration and other regulatory bodies, there are mixed findings in the literature on the benefit of motion-based simulators for training. There is no agreement on the training effectiveness of flight simulators because they are used in different domains to measure and study different phenomena. For example, Gundry's (1977) findings suggested that pilot cognitive workload mediates the threshold at which motion sensing is useful to pilots. Other researchers have suggested that the usefulness of motion cues during flight training depend on the pilot's level of experience (Brown, Kuehnel, Nicholson, & Futterweit, 1960; Mccauley, 2006). Research has also indicated that motion cues are only beneficial on certain types of tasks during flight training (Brown & Collins, 1958; Salas, Bowers &, Rhodenizer, 1998).

The impact of motion simulation for training may be poorly understood because there is

little research on vestibular perception and its contribution to self-motion. To this end, the current section investigates vestibular perception of self-motion. The use of motion platforms to study the vestibular system is not appropriate because motion platforms activate many sensory systems instead of isolating the unique contribution of the vestibular system.

A method that isolates the vestibular system is galvanic vestibular stimulation. Galvanic vestibular stimulation bilaterally stimulates the mastoid processes behind each ear with an electric current (Byrne & Marshall, 2016; Taro Maeda et al., 2005). The electric current acts directly on the primary vestibular afferents, not the mechanoreceptors of the otoliths and semi-circular canals. Galvanic vestibular stimulation is compact and portable, making it easy to integrate with visual self-motion displays to study multi-modal perception. A limitation of galvanic vestibular stimulation is that it stimulates the semi-circular canals and otolith organs simultaneously. This often results in an unclear sense of motion in no particular direction, instead of a compelling illusion of translating through space. Galvanic vestibular stimulation has also been reported to feel like standing on an unstable surface (Dilda et al., 2014). An alternate method to stimulate the vestibular system is caloric vestibular stimulation. Caloric vestibular stimulation was used to induce vestibularvection in E3.

Experiment 3: Vection Induced by Caloric Vestibular Stimulation

Caloric vestibular stimulation is a method by which cool or warm air or water enters the horizontal semi-circular canal via the external auditory canal. The air/water can be set to a temperature that is cooler or warmer than body temperature. The change in endolymph fluid temperature from regular body temperature ($\sim 37^{\circ}\text{C}$) creates a thermal gradient that changes the

fluid's density (Bárány, 1906). Changes in endolymph fluid density cause a convection current that produces a pressure change across the cupula. This pressure change causes the semi-circular canal's mechanoreceptors to move, in turn stimulating the 8th cranial nerve. Motion of the SCC's mechanoreceptors also occurs when the head rotates. This is why caloric vestibular stimulation can result in an illusory sensation of head rotation.

Caloric vestibular stimulation is commonly used by clinicians to assess vestibular health. Caloric vestibular stimulation has also been used in biomedical engineering research to investigate the fluid dynamic properties of the endolymph fluid and semi-circular canal structural characteristics (Kassemi, Deserranno, & Oas, 2004; Kassemi, Deserranno, & Oas, 2005; Meiry & Young, 1967; Steer, 1967).

Caloric vestibular stimulation has been used in neuroimaging studies to identify cortical regions associated with vestibular function (Fasold et al., 2002; Frank & Greenlee, 2014; Zu Eulenburg, Caspers, Roski, & Eickhoff, 2012). However, there are no known behavioural studies that use caloric vestibular stimulation to examine vestibular self-motion perception in individuals with normal vestibular function. In a study by Karnath (1994), self-motion perception was explored using calorics but the aim was to investigate vestibular malfunction as perceptions were compared to participants with vestibular damage.

In a fMRI study, Frank and Greenlee (2014) described a behavioural task where participants pressed a button to indicate perceived self-motion direction during caloric irrigation. However, behavioural data were not reported in their paper, presumably because the emphasis of the study was on fMRI findings. In the current research, cool air caloric vestibular stimulation was used to

inducevection. The rotating knob developed in Section 2 of this thesis was used to indexvection speed, direction and duration.

Method

Participants

Twenty-five Carleton University students participated in the experiment in exchange for course credit. Seventeen participants were female and two participants were left-handed ($M_{AGE}=22.7$, $SD_{AGE}=5.6$). No participants reported a history of vestibular malfunction. One participant dropped out of the study, leaving 24 participants in the final analysis.

Stimuli & Design

The experiment was setup as a one-way repeated measures design with ‘ear irrigated’ as the only factor. Irrigations were all performed at 18°C and delivered air at a rate of 10 l/min. Participants underwent two left-ear and two right-ear irrigations, totaling four trials per participant. Each irrigation lasted between 90-180 s depending on when the participant reported feeling a robust spinning sensation in either the clockwise or counter-clockwise direction.

Apparatus

ICS NCA 200 Air Caloric Irrigator. An irrigator generated air flow at 18°C at 10 l/min. As shown in pictured in Figure 8, a hose attachment delivered air via a glass speculum fitted with a disposable rubber tip to the participant’s ear.

Figure 8. ICS Air caloric irrigator used in Experiment 3. Temperature and pressure were set and displayed on main unit. Air travelled through the hose to speculum.

Control Knob. The Spintrak rotary knob was used to index circular vection from Section 2.

Computer. The computer had an Intel Core I 7 processor, an NVIDIA GeForce GTX980 graphics card and 16 GB RAM.

Procedure

Participants were tested individually in a quiet room with eyes closed and wore a blindfold. They laid down in the supine posture on a table with their heads rested on a 30° angle wedge pillow to optimally stimulate the horizontal canal. Participants rested the knob on their stomach and had their dominant index finger positioned on the knob. They held the knob with their other hand. Before the experiment began, participants demonstrated clockwise and counter-clockwise rotation of the knob with their dominant index finger to avoid confusion about direction during response periods. Once irrigation of the ear began, participants could verbally

communicate any self-motion they were experiencing throughout the trial. They described vection direction and strength to the experimenter without rotating the knob. When participants verbally reported a robust spinning sensation (within the 90-180 s trial), the experimenter removed the irrigator hose from the participants' ear. Participants could then rotate the knob in the direction of vection if they felt it while keeping their eyes closed. Participants rotated the knob as long as the sensed clear vection in one direction. If participants reported swaying, rotation but with no precise direction, or no self-rotation, they were instructed not to rotate the knob. The experimenter ended the trial once participants reported that the spinning sensation had stopped.

Breaks were taken after each trial to allow endolymph fluid to revert as close to normal body temperature as possible and to ensure that the participant no longer felt any motion or motion after-effects. Break durations were 25-min between same ear irrigations and 8-min between different ear irrigations. Longer breaks were needed between the same ear irrigations to ensure endolymph fluid was as close to normal body temperature as possible before the next irrigation began. Shorter breaks between different ears were needed as the temperature change of one ear's endolymph fluid was independent of the other. Therefore, break times just short enough for any motion after-effects to dissipate were required. During breaks, participants kept their eyes closed for the first two minutes to avoid any possible nausea and disorientation. The experiment lasted approximately 1.5 hours.

Results

Vection direction data was analyzed with a McNemar test. Vection speed and duration data were analyzed with within-subjects t-tests.

Vection Direction

Vection was experienced on 71 of 96 trials (74%). Of the 48 left-ear irrigation trials, participants reported experiencing vection in the clockwise direction on 23 trials and reported vection in the counter-clockwise direction on 13 trials. Participants did not report vection resulting from the 12-remaining left-ear caloric irrigation trials. Of the 48 right-ear irrigation trials, participants reported experiencing vection in the clockwise direction on 15 trials and reported vection in the counter-clockwise rotation on 20 trials. Participants did not report vection resulting from the 13-remaining right-ear irrigation trials. These data are summarized in the frequency plot in Figure 9. A McNemar test compared the proportions of vection direction based on ear irrigated and showed a significant difference for perceived direction based on ear irrigated, $p = .008$.

Figure 9. Frequencies of reported clockwise (CW) and counter-clockwise (CCW) vection based on the ear that was irrigated.

Vection Speed

Mean speed ($^{\circ}/s$) from each trial in the left ear ($112.2^{\circ}/s$) vs. right ear ($105.5^{\circ}/s$) were compared using a t-test collapsing across clockwise and counter-clockwise vection directions. The effect of ear irrigated (left or right) on speed of rotation was not significant, ($t < 1$, $df = 20$).

Vection Duration

Vection duration was calculated as the cumulative amount of time (s) within a trial that a participant rotated the knob during the response period following the stimulation period. Clockwise and counter-clockwise vection directions were collapsed. A within subjects t-test revealed that the effect of ear irrigated on speed of rotation was not significant, ($t < 1$, $df = 20$) for the left (54.7 s) and right (55.3 s) ears.

In summary, caloric vestibular stimulation produced vection on 74% of trials. This is important because it shows that vection can be produced with air calorics. Vection lasted roughly 55 s. This is much longer than the transient vection produced during galvanic vestibular stimulation or with the use of physical motion platforms. Longer vection produced by calorics will allow researchers to thoroughly investigate vestibular perception. The third main finding is that vestibular vection speeds were greater than $100^{\circ}/\text{s}$. This fast vection speed suggests that caloric vestibular stimulation is an effective method for producing convincing vection experiences.

There was a significant difference for vection direction on ear irrigated: cold left ear irrigation resulted in clockwise circular vection and cold right ear irrigation resulted in counter-clockwise circular vection in most trials. Observed vection directions based on ear irrigated from this experiment is consistent with known reports that cold air or water irrigation generally results in reflexive beating of the eye in the direction opposite to the irrigated ear (Jacobson & Newman, 1993). This means that cold irrigations in the left ear should result in left-to-right eye movements and that right-ear irrigation should result in right-to-left eye movements. Left-to-right eye movements are consistent with eye movements that would compensate for clockwise spinning. Right-to-left eye movements are consistent with eye movements that would compensate for counter-clockwise spinning. Therefore, vection direction data from E3 provide behavioural support that is consistent with clinically observed nystagmus direction patterns reported by Jacobson and Newman.

In some trials in E3, participants reported counter-clockwise vection when the left ear was irrigated and clockwise vection when the right ear was irrigated, which is opposite to the

general pattern of results. A possible reason for these results may be the use of monaural air calorics in this experiment. Monaural air caloric stimulation may have caused variability in vection direction because one ear receives thermal stimulation, changing endolymph fluid properties in the irrigated ear, but the other ear is not accordingly stimulated to signal consistent motion. During real spinning, the mechanoreceptors in each ear signal reciprocal motion, providing a more consistent self-motion direction. Though both ears were not stimulated simultaneously in this experiment, monaural calorics appeared to be sufficient in generating predictable vection in the clockwise or counter-clockwise directions that is consistent with reported nystagmus directions (Jacobson & Newman, 1993). Another possible reason for the variability in reported vection direction is that there are individual differences between each person's ear canal shape, distance to the shoulder and other physical factors that may make stimulating one individual's ear more or less challenging than stimulating another individual's ear. Because it is critical that the air caloric stimulation be transduced to the horizontal semi-circular canal at the correct temperature to obtain predictable results, it is argued that the physical variability in ear structure may make some ears more difficult to irrigate than others, potentially contributing to the observed variability in vection experience.

There was no significant difference of ear irrigated on vection speed and vection duration. This was expected as temperature and airflow pressure, two variables that would be predicted to mediate vection speed and duration, were held constant in E3. Finally, the long vection durations produced by calorics in E3 facilitated investigation of vestibular contributions to visual-vestibular self-motion integration in other experiments in this thesis.

Experiment 4: Vection Induced by Caloric Vestibular Stimulation While Viewing a Stationary Display

In E3, participants kept their eyes closed throughout the experimental response period when they spun the knob to indicate their vection experience. Vestibular caloric stimulation generated measurable vestibular circular vection. In E4, vection was induced using vestibular caloric stimulation as in E3. However, when participants responded using the knob to indicate vection, they opened their eyes and observed a stationary vertical black and white stripe pattern presented in a VR headset. The presence of a stationary visual display that did not signal self-motion coupled with a vestibular cue signaling self-motion was expected to create a sensory integration conflict.

Several visual-vestibular sensory integration hypotheses are presented to generate informed predictions for the results in E4. The visual dominance hypotheses suggests that the visual system is the modality relied upon during visual-vestibular conflict (Lee & Lishman, 1975; Lishman & Lee, 1973). Under assumptions made by the visual dominance hypothesis, participants in E4 should not experience vection because the ‘dominant’ visual system does not signal self-motion with a stationary display. On the other hand, the vestibular dominance hypothesis asserts that vestibular cues to self-motion dictate self-motion during cue conflict (Butler, Smith, Campos, & Bühlhoff, 2010; Harris, Jenkin, & Zikovitz, 2000). Under this hypothesis, the vestibular system will dominate the visual system: vestibular-induced vection will be experienced equally regardless of whether the visual system received no stimulation (E3) or when a stationary image (E4) was viewed. Researchers have also proposed an optimal cue integration hypothesis in which self-motion percepts are assumed to be influenced by the more

reliable of the visual and vestibular inputs (Angelaki, Klier, & Snyder, 2009; Fetsch, Turner, DeAngelis, & Angelaki, 2009; Gu, Angelaki, & DeAngelis, 2008; Reymond, Droulez, & Kemeny, 2002; Telban & Cardullo, 2001). Under optimal cue integration hypotheses, one sensory system does not dominate the other during cue conflict. Instead, vection will be determined by the most reliable cue (visual or vestibular) rather than one system shutting down and the other overriding it as is the case with visual and vestibular dominance hypotheses.

It was possible that eye movements caused by the vestibular ocular reflex could be a factor that alters vection perception in E4 (Reinhardt-Rutland, 1988). Because the horizontal canals were stimulated in E4, the eyes moved horizontally. When the eyes are open, the vestibular-ocular reflex is accompanied by another type of involuntary eye movement called optokinetic nystagmus (Howard, 2002). Cullen (2012) reported that optokinetic nystagmus is compensatory when participants are instructed to stabilize their gaze and suppressed when participants are instructed to redirect their gaze. This may make vection stronger when fixating on an element of the visual scene and weaker when the eyes follow the optic flow trajectory (Riecke, 2010). In E4, participants were expected to naturally fixate on some element of the visual stimulus, suppressing nystagmus more quickly than when the eyes are closed. If this is the case, vection should be shorter and slower in E4 than in E3.

Method

Participants

A total of 25 undergraduate students from Carleton University participated in this experiment in exchange for course credit. Two participants did not complete the experiment,

leaving 23 participants in the final analysis ($M_{AGE}=22.6$, $SD_{AGE} = 8.0$). Six participants were male and three participants were left-handed. None of the participants reported any vestibular disorders.

Stimuli & Design

The experiment was setup as a repeated measures design where ear irrigation was the only factor manipulated. The graphic visual stimuli presented on the VR headset consisted of a black and white vertical stripe pattern simulating the interior of a drum. The visual pattern subtended the observers' entire visual field. The virtual drum had a 200-cm diameter. When wearing the headset, the observer's viewpoint was at the center of the virtual drum. Each stripe in the display corresponded to a width of 33 cm in the virtual graphics environment, and subtended a horizontal visual angle of 10.85° at the virtual viewing distance of 100 cm.

Apparatus

VR Display. The Oculus Rift DK2 VR headset from Section Two was used with the same settings.

Procedure

In E4, participants received caloric irrigation while their eyes were closed. When ear irrigation ended participants were prompted to open their eyes and look at a stationary vertical black and white stripe pattern. Participants rotated the knob to expressvection if they perceived it. Participants rotated the knob at the speed and in the direction in which they experiencedvection. Participants closed their eyes when they no longer sensedvection and stopped rotating the knob, ending the trial. Participants underwent two left-ear and two right-ear irrigations.

They were given 8-min breaks between alternate ear irrigations, and 25-min breaks between same ear irrigations. The experiment lasted approximately one hour and a half.

Results

Vection Direction

Vection was experienced in 63 of 92 trials (68%). A McNemar test showed a significant difference for ear irrigated on direction of perceived circular vection, $p = 0.008$. Of the 46 left-ear irrigation trials, participants reported experiencing clockwise rotation on 23 trials and reported counter-clockwise rotation on 8 of the trials. Of the 46 right-ear irrigation trials, participants reported experiencing clockwise rotation on 15 trials and reported counter-clockwise rotation on 17 trials. Participants did not experience vection on 15 left ear and 14 right ear trials. These data are summarized in Figure 10.

Figure 10. Reported vection direction (clockwise; CW or counter-clockwise; CCW) based on the ear that was irrigated (left or right ear) while viewing a stationary drum pattern.

Vection Speed

Data for knob rotation speed were collapsed across vection direction (CW and CCW) for each ear. There was no difference in average speed reported in left (78.8 °/s) vs. right (86.3°/s) ear, $t(21) < 1$.

Vection Duration

Data for vection duration was collapsed across vection direction (CW and CCW) for each ear and analyzed in a within subjects t-test for the left (44.6 s) and right (45 s) ears showing that there was no significant difference for duration on irrigated ear ($t < 1$, $df = 21$).

Comparing Vection Speed and Duration across Experiments 3 and 4

To further examine how visual-vestibular conflict impacts vection, mixed-factor ANOVAs were used to analyze vection Speed and Duration across E3 (eyes closed: visual-vestibular conflict not present) versus E4 (eyes-open: visual-vestibular conflict present). The within-subjects factor was ear irrigated (left vs. right ear). The between-subjects factor was Experiment (E3: eyes closed vs. E4: eyes open).

There was a significant effect of Experiment on Speed, $F(1, 41) = 51.36, p < .001, R^2 = .56$ and on Duration, $F(1, 41) = 158, p < .001, R^2 = .79$. Vection was faster (Figure 11) and lasted longer (Figure) when participants had their eyes closed (E3) compared to when their eyes were open (E4) and viewing a stationary display. There were no significant differences of ear irrigated, nor any interactions (all $F_s < 1, df = 1, 41$).

Figure 11. Vection speed displayed in °/s for left (L) and right (R) ear irrigations for E3 (eyes closed) and E4 (eyes open). Error bars represent 95% confidence intervals for the analysis.

Figure 12. Vection duration displayed in s for left (L) and right (R) ear irrigations for E3(eyes closed) and E4 (eyes open). Error bars represent 95% confidence intervals for the analysis.

In E4, participants responded to vestibular vection while viewing a stationary display of the optokinetic drum. It was unknown if participants would experience vection during the conflict. Results indicated that vection was experienced in E4. Vection direction showed the same pattern as in E3: CW motion perceived for left ear irrigation and CCW motion perceived for right ear irrigation. Vection speed was approximately $84^{\circ}/s$ and duration was 45 s, which were slower and shorter compared to E3 where there was no conflict from the visual system. This suggests that while the vestibular system determined self-motion perception in E4, the stationary visual stimulus affected vection perception

Summary of Section Three

The first goal of this section was to determine if vection can be induced using caloric vestibular stimulation. To this end, E3 demonstrated that vection can be produced with cold air caloric vestibular stimulation. Left cold ear irrigation resulted in clockwise vection while right cold ear irrigation resulted in counter-clockwise vection. Vection speed was roughly $109^{\circ}/s$ and durations 55 s long in E3. The second goal was to determine whether a conflicting visual display signaling no self-motion would impact vestibular-induced vection. In E4, after the vestibular system was stimulated with air caloric irrigation, participants viewed a stationary visual display in a VR headset. Results showed that vection persisted despite the presumed visual-vestibular conflict. Vection direction showed the same pattern of results in E4 as in E3; left ear irrigation resulted in clockwise vection and right ear irrigation resulted in counter-clockwise vection. However, in E4 (eye open) vection speed ($84^{\circ}/s$) was $15^{\circ}/s$ slower and vection duration (45 s) was 10 s shorter than in E3 (eye closed). This comparison across experiments suggests that vestibular-induced vection was reduced when participants viewed a stationary visual display. This shows that the vestibular system played an important role in self-motion perception during conflict because participants continued to experience vection in E4 even when there is a visual signal indicating no self-motion. Visual dominance hypotheses do not explain results in E4. If they did, in E4 participants would have not experienced vection or would have experienced extremely short-lived vection when they opened their eyes. Vestibular dominance hypothesis also does not explain these results because vection was shorter and slower in E4 than in E3. If vestibular dominance hypothesis was correct, then vection speed and duration in both

experiments would have been identical. Results from E4 therefore suggest that the visual stimulus, despite being stationary, still provides conflicting sensory input that impacts vection experience. It therefore appears based on results in this section, that optimal cue integration hypotheses best explain these results. This is because during conflict, both the visual and vestibular systems both appear to contribute to vection perception. However, because the visual stimulus did not induce vection in E4, further experiments should test vection when visual and vestibular stimuli indicate a conflict when both signal vection in different directions. This was tested in Experiment 8.

In related research, Lepecq et al. (2006) have shown that perceived self-motion direction can be altered when a visual display is presented simultaneously with galvanic vestibular stimulation that induces the perception of tilting. Research by Weech and Troje (2017) has shown that visual vection latency can be reduced when GVS signals that do not induce self-motion in any particular direction are administered to participants. Cress et al. (1997) reported significantly higher motion fidelity ratings by participants when galvanic vestibular stimulation that induced roll axis tilt was combined with a visual display indicating tilt in the same direction. This is in comparison to viewing the visual display without a galvanic vestibular signal. Taken together, these studies indicate that vestibular cues for self-motion perception can alter visual vection perception when they are presented at the same time. Findings from E4 build on results from these studies by demonstrating that vestibular cues presented before visual cues also alter vection by reducing its durations and speed when a visual stimulus signaling no self-motion is presented.

To summarize, the purpose of this section was to determine if measurable vection can be induced with air caloric vestibular stimulation (E3) and determine if vection changed when there was a conflicting visual stimulus (E4). Circular vection was successfully induced and measured in both experiments. Results from E4 suggest that the vestibular system is heavily relied upon for self-motion perception even when observers receive conflicting visual self-motion information. However, vection was slower and shorter when the visual stimulus was present in E4. The finding that vection persisted in E4 but was slower and shorter than in E3 suggests that vestibular and visual signals contribute to self-motion perception during conflict instead of one system dominating the other. Notably, in E3 and E4 long vection durations were obtained with air caloric vestibular stimulation. Based on this finding, it appears that using caloric irrigation in combination with visual presentations in VR headsets is a promising method to investigate visual-vestibular sensory integration.

SECTION FOUR

VISUAL-VESTIBULAR SENSORY INTEGRATION DURING CONGRUENT AND INCONGRUENT VECTION PERCEPTS (EXPERIMENTS 5-8)

Introduction

In the present section, the goal was to examine how visual-vestibular conflict is resolved during perceived self-motion. This was determined in an experimental condition in E8 where visual and vestibular cues to self-motion created a conflict: visual and vestibular stimuli indicated vection in opposite directions at equal speeds. Three experiments were conducted leading up to E8. All participants in E8 had all completed E5 – E7. In E5, the goal was to ensure participants could experience circular vection with caloric vestibular stimulation. Participants received cold air caloric vestibular stimulation and used the knob to index vection experience with their eyes closed. This experiment replicated E3. To ensure these participants also experienced visual vection, the same participants from E5 also underwent E6. In E6, the procedure used in E2 was replicated wherein vection was induced visually by having participants observe a virtual optokinetic drum pattern presented on a VR headset and indexed vection experience with the knob. In sum, E5 and 6 identified participants that experienced vestibular and visual vection and provided baseline data on visual and vestibular vection perception for each participant. In E7, the goal was to match vestibular vection speeds generated by caloric vestibular stimulation with visual vection speeds generated by the virtual optokinetic drum presented on the VR headset. Therefore, visual and vestibular vection were matched to be of

approximately equal speeds. Each participant's visual vection speed obtained in E7 was then used in E8.

The main experiment was E8. This experiment examined how visually-induced and vestibular-induced signals for vection are integrated. To this end, visual and vestibular vection were experienced simultaneously in E8 at the predetermined matched speed from E7 for each participant. Two conditions were examined. In the congruent condition the visual and vestibular systems were stimulated to signal vection in the same direction. Therefore, visual and vestibular stimuli were 'congruent' and there was no presumed visual-vestibular conflict. In another condition, the visual and vestibular systems were stimulated to signal vection in opposite directions and thus there was a presumed visual-vestibular conflict. This was the incongruent condition.

It was predicted that E8 would test three hypotheses on visual-vestibular integration: visual dominance, vestibular dominance, or optimal cue integration hypothesis. In dominance hypotheses (visual or vestibular), one system dominates self-motion perception while the other becomes inhibited. Cues from the inhibited sensory system appear to play no part in deciding self-motion. Research in support of visual dominance hypothesis has even shown that cortical activity in vestibular processing regions becomes inhibited during conflict (Brandt et al., 1998). Both visual and vestibular dominance hypotheses support that one system is not involved in vection perception during conflict. Moreover, dominance hypotheses assert that one system does not contribute at all to self-motion while the other decides self-motion. On the other hand, optimal cue integration hypothesis predicts that both visual and vestibular cues are used during

conflict to decide self-motion and that one system does not become inhibited. Instead, self-motion perception is decided by a weighted average of cues across trials. Cue reliance can be defined by characteristics such as cue strength, speed and consistency. E8 tested visual dominance, vestibular dominance and optimal cue integration hypotheses.

Experiment 5: Vection Induced by Caloric Vestibular Stimulation

The objective of the present experiment was to identify a group of participants who experience vestibular vection. As in E3, caloric vestibular stimulation with cold air was used to induce vection. Participants who experienced vestibular vection in this experiment were selected to participate in subsequent experiments.

Method

The apparatus, stimuli and procedure were identical to Experiment 3.

Participants

A total of 16 participants were recruited from the Carleton University community. Of these, three participants were removed because they did not sense vestibular vection and an additional three participants were removed because they experienced discomfort and did not wish to continue. Accordingly, a total of 10 participants (4 female and 3 left-handed, $M_{AGE}=26.2$, $SD_{AGE}=3.1$) were included in the final analysis. All participants were paid.

Results

Vection direction data was analyzed with a McNemar test. Vection speed and duration data were analyzed with within-subjects t-tests.

Vection Direction

Vection direction data are summarized in a frequency plot in Figure . Participants experienced vection on 33 of 40 trials (82.5%). Of the 20 left-ear irrigation trials, participants reported experiencing clockwise rotation on 12 trials and reported counter-clockwise rotation on four trials. Of the 20 right-ear irrigation trials, participants reported experiencing clockwise rotation on 10 trials and reported counter-clockwise rotation on seven trials. A McNemar test revealed that there was no significant difference for ear irrigated on direction of perceived vection, $p=0.50$.

Figure 13. Number of times clockwise (CW) or counter-clockwise (CCW) circular vection was reported based on irrigated ear.

Vection Speed

Mean speed ($^{\circ}/s$) from each trial in the left vs. right ear were compared. The effect of ear irrigated on speed of knob rotation was not significantly different ($t < 1$, $df = 9$).

Vection Duration

A within subjects t-test that showed that the effect of ear irrigated on speed of rotation was not significantly different ($t < 1$, $df = 9$). In summary, E5 determined which individuals could perceive vestibular vection. Vection, speed and duration data largely resembled those of E3, as expected.

Experiment 6: Vection Induced with an Optokinetic Drum in a VR Headset

The objective of E6 was to ensure all participants could experience visual vection with the virtual optokinetic drum displayed on a VR headset. In E6, vection was induced in the visual system with the same 10 participants that experienced vestibular vection in E5. As in E2, a virtual optokinetic drum was presented in a virtual reality headset. The drum moved at three speeds in a clockwise or counter-clockwise direction, totaling 6 conditions. Vection direction, speeds, and durations were measured with the rotating knob. Participants were hypothesized to experience faster vection with faster drum speeds, replicating results from E2.

Method

The same 10 participants from E5 participated in this experiment. All apparatus, stimuli, and procedure were identical E2 including the VR headset display of the optokinetic drum

Results

Vection speed and duration were analyzed in separate 3 (Drum Speed: 37.5 °/s vs. 56.25 °/s vs. 75 °/s) by 2 (Direction: clockwise vs. counter-clockwise) repeated measures ANOVAs. Post-hoc comparisons were made using 95% confidence intervals (Jarmasz & Hollands, 2009).

Vection Speed

Vection speed data are shown in Figure . There was a significant main effect of Drum Speed, $F(2, 18) = 4.96, p < .05, R^2=0.36$, where faster drum speeds resulted in faster knob rotations. There was no significant main effect of Direction ($F < 1$) on knob rotation speed and no significant interaction between Drum Speed and Direction ($F < 1$) on knob rotation speed. As shown in Figure , the 95% confidence intervals indicated a significant difference between slow-fast and medium-fast conditions in the clockwise direction. In the counter-clockwise direction, there was a difference between all drum speed conditions.

Figure 14. Knob Rotation Speed (°/s) when viewing three Drum Speeds in the Clockwise ('CW') and Counter-clockwise ('CCW') directions. Error bars represent 95% confidence intervals for the analysis.

Vection Duration

Vection duration data are shown in Figure . There was a significant main effect for Drum Speed on vection duration, $F(2, 18) = 4.98, p < .05, R^2 = .36$. The 95% confidence intervals indicated that there was a significant difference between the slow-medium and slow-fast conditions in the clockwise direction. There was a significant difference for slow-fast and medium-fast conditions in the counter-clockwise direction. There were no observed interaction effects between Drum Speed and Direction ($F < 1$).

Figure 15. Vection Duration (s) when viewing the three Drum Speeds (slow, medium and fast) in the Clockwise ('CW') and counter-clockwise ('CCW') directions. Error bars represent 95% confidence intervals for the analysis.

In sum, E6 showed that participants from E5 experienced visually-induced vection when viewing a rotating virtual drum. As found previously in E2, faster drum speeds resulted in faster and longer vection. Results from E5 approximately replicate those of E3, and E6 replicated E2. These results helped ensure that participants would perceive self-motion in both the visual and vestibular modalities in E7 and E8.

Experiment 7: Matching Visual and Vestibular Vection Speeds

The objective of E7 was to determine an approximately equal vection speed across the visual and vestibular modalities for each participant. In the current experiment, participants from E5 and E6 underwent a vestibular caloric trial at the start of the experiment with their eyes closed. They were asked to monitor and remember the speed at which they felt they were moving during this vestibular caloric trial. After a short break, participants watched the virtual drum stimulus in a VR headset and adjusted the drum's speed using a gamepad. The participants' task was to repeatedly select the visual vection speed that best represented the vestibular vection speed experienced during caloric vestibular stimulation. The mean matched visual vection speed obtained in this experiment was used in E8.

Method

Apparatus & Stimuli

The Oculus VR headset and ICS 200 Air Caloric Irrigator were used with the same presets as in E5 and E6. The optokinetic drum moved in the clockwise or counter-clockwise directions equal amounts of times at speeds ranging from 20-350°/s. An XBOX 360 controller was used to select the visual drum speed that produced visual vection most similar to vection experienced during the caloric irrigation trial.

Procedure

Participants underwent one vestibular caloric trial and 36 visual trials. The irrigation trial lasted 90-180 s. During the irrigation trial, participants reported to the experimenter when they

felt vestibular vection and were instructed to monitor and remember the speed of vection while their eyes were closed. Participants were then given a 2-min break. Participants put on the VR headset and were given a XBOX 360 controller. They watched the optokinetic drum rotate at various speeds and were instructed to identify the visual display that induced vection at the speed most similar to vection experienced during the caloric trial by selecting it with the XBOX controller. The drum speed was randomly assigned each trial. Participants used the left and right shoulder buttons of the XBOX 360 controller to slow down (left shoulder button) or speed up (right shoulder button) the optokinetic drum on each trial until they matched it to the vestibular vection speed. The left and right shoulder buttons changed the speed of the display by increments of $5^\circ/\text{s}$. When participants identified the visual display that induced vection at the same speed experienced during the caloric trial, they pressed the 'A' button on the XBOX controller to log their response. Participants repeated the task of identifying the visual display speed that matched their vestibular vection experience 36 times. Participants could select a visual speed 10 s after the start of the first display to ensure they experienced vection and could select a display anytime thereafter. The 36 trials were evenly split over four blocks each containing 9 trials. Each block was separated by 5-min breaks to limit potential VR sickness. The experiment lasted approximately 45 minutes.

Results

Each participant's mean visual vection speed is displayed in Figure .

Figure 15. Means of visual display speed that best represented each participant's vestibular vection experience in °/s. Error bars represent standard deviations.

Results from E7 determined the approximate visual vection speeds that best matched vestibular vection speeds for each participant. There was little within-subject variability, as the error bars representing standard deviations in Figure show. This implies that participants are reasonably sure of the speed at which they felt they were moving during vestibular vection trials. However, Figure 16 highlights the substantial between-subject variability in perceived self-rotation perception by air caloric vestibular. This emphasizes the importance of performing the present experiment as visual-vestibular vection matching is experienced very differently between

individuals. The mean visual speeds for each participant obtained in this experiment were used in E8.

Experiment 8: Self-motion Perception During Congruent and Incongruent Directional Cues

The goal of E8 was to determine how self-motion is decided when visual and vestibular signals are in conflict. In the current experiment, the average visual vection speed each participant selected in E7 was set as the drum speed for that participant. Participants received air caloric stimulation for 90-180 s with their eyes closed to induce vestibular vection. Vestibular vection takes time to induce as the temperature change resulting in perceived vection is slow. Once participants felt vestibular vection, they viewed the optokinetic drum display in VR. Therefore, participants experienced visual and vestibular vection at approximately the same time in E8. Participants responded using the rotating knob apparatus in order to measure vection speed, duration, and direction.

There were two conditions in E8. In the congruent condition, vestibular and visual vection were signaled in the same direction. This was done by stimulating the participant's ear with calorics first, asking the direction in which they sensed motion, then setting the visual display such that it would induce visual vection in the same direction as the vestibular vection. Participants were expected to experience vection in line with visual and vestibular direction of vection in the congruent condition because there was no conflict. In the incongruent condition, vestibular and visual vection were signaled in opposite directions. This was done by stimulating the ear with calorics first, asking the direction in which the participant sensed motion, then

setting the visual display such that it would induce visual vection in the opposite direction as their experienced vestibular vection. Results from the incongruent condition were expected to shed light on how visual-vestibular conflict is resolved. If visual dominance resolves visual-vestibular conflict during the incongruent condition, then participants were expected to rotate the knob in accord with the visual cues to vection on all or most trials. On the other hand, if participants spun the knob in the direction corresponding to vestibular vection on all or most trials, this would suggest that vestibular dominance hypothesis explains visual-vestibular conflict resolution in the incongruent condition. If participants do not experience vection this would suggest that sensory stimuli cancel each other out to resolve conflict and that vection is not experienced.

Method

Apparatus & Stimuli

The apparatus used were the Oculus VR headset, the ICS 200 Air Caloric Irrigator, and the rotating knob from E5 and E6. The vestibular stimulus was 18°C air caloric irrigation. The visual stimulus was a VR headset display of a spinning virtual optokinetic drum. The experimenter set the speed of the visual display for each participant at the start of the experiment based on the participant's mean drum speed obtained in E7. Therefore, each participant saw the visual stimulus that they reported was of the matched vestibular speed from E7. Each participant underwent two congruent trials and two incongruent trials. Left and right-ear irrigations were alternated across trials and congruent and incongruent conditions were counter-balanced. Participants were naïve as to the conditions they were in and were not aware of an incongruent

condition. Counter-balancing condition orders for each participant avoided participants determining which condition they were in.

Procedure

Participants laid down in the supine posture with their heads pitched 30° forward with a wedge pillow. They held the knob against their stomach with their non-dominant hand. Participants received caloric irrigation with eyes closed while wearing the VR headset. The headset displayed a dark screen during caloric irrigation phases. After 90-180 s of caloric stimulation the irrigator was removed and the participant verbally reported the direction of vestibular vection. The experimenter set the motion of the virtual drum in either the direction congruent with participant's reported vection direction or opposite to the direction of their vection based on whether participants were in a congruent or incongruent condition. The direction of visual vection was controlled by the experimenter using left and right arrow keys on a keyboard. Participants opened their eyes and viewed the moving drum in the VR headset. Participants rotated the knob in the direction and at the speed at which they felt they were moving. Breaks were taken after each trial to allow endolymph fluid to revert to normal body temperature and to ensure that the participant no longer felt any motion or motion after-effects. Break durations were 25-min between same ear irrigations and 8-min between different ear irrigations. During breaks, participants kept their eyes closed for the first two minutes to avoid any possible nausea and disorientation. The experiment lasted approximately 1.5 hours.

Results

Vection Direction

Two of the ten participants did not experience vestibular vection and were excluded from the analysis. Each of the remaining participants completed four trials: two congruent and two incongruent trials. This totaled 32 trials in the experiment. Self-rotation was reported on 31 of the 32 trials. The vection direction data is summarized in **Error! Reference source not found.**

. For 15 of the 16 trials in the congruent condition, participants experienced vection in the direction that the visual and vestibular cues signaled as expected. In the remaining congruent trial, the participant did not experience vestibular vection.

In the incongruent condition, participants reported vection matching the direction indicated by vestibular stimulation on 8 trials and reported vection matching the visual direction in the remaining 8 trials². Of the eight participants, three reported vection consistent with the visual cues for vection on both incongruent trials and three reported vection consistent with the vestibular cues for vection on both incongruent trials. The two remaining participants experienced vection consistent with visual direction of vection in one trial and based on vestibular direction of motion in the other trial.

² No inferential analyses were performed on vection direction data as there were equal amounts of responses for the visual incongruent as for the vestibular incongruent responses.

Table 1. Vection direction reports during congruent and incongruent conditions. Incongruent trials are split into responses consistent with visual vection direction and responses consistent with vestibular vection direction.

<i>Congruent</i> <i>(Visual + Vestibular)</i>	<i>Incongruent</i> <i>(Direction consistent with visual vection)</i>	<i>Incongruent</i> <i>(Direction consistent with vestibular vection)</i>
15	8	8

Vection Speed

Data for knob rotation speed were analyzed in a one-way repeated measures ANOVA with three conditions. These conditions were labeled ‘congruent’, ‘incongruent (vis)’ referring to incongruent conditions in which participants reported visual vection and ‘incongruent ves’, referring to responses in the incongruent condition that were in accordance with vestibular cues to vection direction. There were no significant differences for speed whether participants were in the congruent condition, used visual cues to decide self-motion, or used vestibular cues to decide self-motion, $F(2,8)=1.61, p>0.05$. Data for vection speed are presented in Figure .

Figure 17. Vection speed when perceived as congruent, visual incongruent, or vestibular incongruent. The error bars represent 95% CI for the analysis.

Vection Duration

The same three conditions used to analyze vection speed data were used to analyze vection duration data. There was no effect of condition on duration in a one-way repeated measured ANOVA, $F(2,8)=0.82$, $p>0.5$. Data are displayed in Figure .

Figure 18. Vection duration when perceived as congruent, visual incongruent, or vestibular incongruent. The error bars represent 95% CI for the analysis.

To summarize, the objective of E8 was to determine how self-motion direction is determined when the visual and vestibular systems received cues that are in conflict. This was examined in the incongruent condition of E8. Results for the incongruent condition showed that three participants used visual cues to indicate self-motion, three participants used vestibular cues, and the remaining two participants used visual cues on one incongruent trial and vestibular cues on the other incongruent trial.

In this experiment, the visual and vestibular cues were matched to indicate vection at the same speeds but in opposite directions. Vection speed and duration data for congruent trials was somewhat faster than vection speed data for incongruent trials, but this was not significant. This was consistent with previous experiments wherein vection was faster and longer when there was no conflict. Slower speeds and shorter durations during conflict in previous findings of this thesis and between incongruent and congruent trials in E8 suggest that one system does not dominate the other. If the visual or vestibular systems dominated, then vection speed and duration would have been the same in congruent and incongruent trials for the system that dominates during conflict. This is because information from that system is not being processed and used to determine self-motion. However, the trend showing slower and shorter vection during conflict suggests that information from both sensory systems is being used to decide self-motion rather than one system becoming inhibited and not contributing to deciding self-motion. In summary, E8 demonstrates that dominance hypotheses are insufficient in explaining the current results and that findings from E8 fit best with optimal cue integration hypothesis which is explained in detail in Section Five.

Summary of Section Four

The goal of the present section was to examine how visual-vestibular conflict is resolved during perceived self-motion. In Experiment 5, vestibular vection was induced using caloric vestibular stimulation. Vestibular vection direction, speed and duration were measured with the rotating knob. As reported in E3, long vestibular vection durations were observed. Six individuals did not participate in further experimentation as three did not experience vection in

E5 and three experienced motion sickness. In E6, a virtual rendition of the optokinetic drum was used to induce and record visual vection in a VR headset. As in E2, virtual drum speeds significantly impacted visual vection speeds. In E7, the goal was to identify vection speeds for the visual and the vestibular systems that were approximately equal for each participant. Visual vection speeds from E7 for each participant were then presented in E8.

The objective of E8 was to investigate how self-motion direction is determined when visual and vestibular stimuli to self-motion direction are present. In the congruent condition, visual and vestibular cues signaled self-motion in the same direction. In the incongruent condition, visual and vestibular cues signaled self-motion in opposite directions. Results from E8 showed that visual cues were used for deciding self-motion on half of the trials and vestibular cues were used in the other half of the trials. Therefore, there was no evidence for either visual or vestibular dominance. The results are most consistent with optimal cue integration hypothesis in which it was predicted that participants would use the most reliable cue (visual or vestibular) in each trial to determine self-motion direction. In optimal cue integration hypothesis, cue reliability is defined as the inverse of the variance of a cue, or the strength of the cue. The extent to which knob responses would be consistent with the visual or vestibular direction under optimal cue integration hypothesis would therefore depend on the reliability of each cue set by the experimenter. Because vection speeds across the visual and vestibular systems were matched in E7 and these matched stimuli were used in E8, visual and vestibular cues were set to be of approximately equal speed. Moreover, because there were an equal number of responses

indicating visual and vestibular cue reliance, this suggests that the cue matching from E7 successfully attained equal speeds ofvection as intended.

SECTION FIVE

GENERAL DISCUSSION

In summary, the overall objective of the present thesis was to examine the vestibular system's contribution to self-motion perception and its integration with visual self-motion cues for self-motion perception. These objectives were attained over a series of experiments where vestibular and visual circular vection were induced separately and then simultaneously.

In E1, the objective was to determine if participants could sense vection using a VR rendition of a head-mounted optokinetic drum. The VR optokinetic drum displayed in the headset was inspired by early physical optokinetic drums used to study vection in laboratory environments. Vection strength was measured in E1 with a widely used methodology called magnitude estimation ratings. The speed of the drum was manipulated and participants rated vection strength after each trial. Results from E1 indicated that faster drum speeds produced greater vection ratings. This suggests that vection can be produced in a VR headset version of the rotating drum yielding predictable results.

In E2, the objective was to develop and implement a methodology capable of measuring vection speed for the first time. The VR optokinetic drum was used again to induce vection. A methodology used to record perceived vection speed was developed. This was a knob that participants rotated at the speed at which they experienced vection. Results indicated that faster drum speeds yielded faster vection recordings from the knob. The knob apparatus was validated

in this experiment to measure vection speed and was used to measure vestibular vection speed percepts in subsequent experiments.

In E3, the objective was to determine if vection can be induced and measured in the vestibular system when there is no visual-vestibular conflict. Air caloric irrigation was administered to participants while they kept their eyes closed. They spun the knob when they experienced vection to express the experienced speed and direction of vection. These results are the first to demonstrate that vestibular vection with long durations can be produced and measured with air calorics.

In E4, the objective was to investigate visual-vestibular conflict during vection. In E4, a visual-vestibular conflict was assumed because the visual cue did not signal self-motion but the vestibular cue did. Participants experienced vection despite the visual stimulus indicating no self-motion. However, results from this experiment showed that vection speed and responses were significantly slower during conflict compared to when there is no visual-vestibular conflict (e.g., E3). This suggests that although vestibular cues were relied upon to determine vection, visual information still played a role as evidenced by the slower and shorter vection responses. Accordingly, information provided by the vestibular system does not dominate the perception of vection when conflicting visual information is present.

Experiments 5 - 8 were conducted to further examine how self-motion direction is determined during visual-vestibular conflict. Experiments 5 and 6 were designed to screen participants and E7 was conducted to match the strength of perceived self-motion across visual

and vestibular conditions leading to E8. Experiment 5 replicated E3: participants received air caloric vestibular stimulation while their eyes were closed and indexed their vection experience using the rotating knob. A total of 16 participants were initially recruited. Of these, 3 participants were removed because they did not sense vestibular vection and an additional 3 participants were removed because they experienced discomfort and did not wish to continue. Accordingly, 10 participants continued to E6. Experiment 6 replicated E2: participants viewed an optokinetic drum in a VR headset and indexed their vection experience using the rotating knob. In E7, visual vection speed was matched to vestibular vection speed for each participant.

In E8, participants observed the optokinetic drum signaling visual vection while experiencing vestibular vection generated by air calorics at the same time. There were two conditions. In the congruent condition, the visual and vestibular stimuli signaled motion in the same direction at equal speeds. In the incongruent condition, visual and vestibular stimuli signaled motion in opposite directions at equal speeds. Findings in the incongruent condition showed that in half of responses, participants experienced vection in accordance with visual cues. In the other half of incongruent responses, participants experienced vection in accordance with vestibular cues. Vection speed was fastest in the congruent condition and slowest in visual incongruent condition, though this was not significant. These data follow a consistent trend with the results in Section 2 (E3 & E4): vection is faster when there is no visual-vestibular conflict and suggests that visual and vestibular dominance hypotheses cannot explain the results.

Experiments 4 and 8 both examined vection during cue conflict because participants attended to a visual stimulus while receiving incongruent vestibular self-motion cues in both

experiments. In E4, participants experienced vestibular vection while looking at a stationary display. Results from that experiment indicated that participants still experienced vection despite a conflicting visual cue indicating no self-motion. Vection speeds and durations were slower and shorter in E4 than when participants did not have a conflicting visual cue as in E3. E8 builds on findings from E4. The results from E8 suggest that optimal cue integration hypothesis explains visual-vestibular conflict when visual and vestibular vection speeds were equal in the incongruent condition and are inconsistent with visual and vestibular dominance hypotheses. Cue reliability is defined as the inverse of the variability of a cue. Therefore, factors such as strength, speed, and consistency can all contribute to a cue's reliability. In E8, cues were equally reliable because vection speeds were matched. This is evidenced by findings in E8 indicating that visual and vestibular cues were used equal amounts of times to determine self-motion direction.

In a study on heading perception by Fetsch, Turner, DeAngelis and Angelaki (2009) cue reliability was directly manipulated. Monkeys were positioned on a motion platform and watched a display showing an optic flow pattern signaling forward motion. This forward motion could be off center (slightly left or right to varying degrees from a central fixation point on the screen). Accordingly, the vestibular forward motion stimulus could move left and right off center as well at the same time as the visual optic flow stimulus creating a visual-vestibular conflict. Coherence was manipulated by changing the amount of elements in the visual optic flow stimuli that moved together. For instance, 25% coherence would mean that 25% of the dots moved in the same direction to indicate heading. A highly coherent visual optic flow stimulus

(e.g., 100%) made the visual stimulus more reliable (less variability in the elements in the display), whereas a low coherent visual display made the vestibular stimulus more reliable (more variability in the elements in the display). Fetsch et al. looked at the heading responses during conflict with varying levels of coherence or cue reliability where coherence changed on every trial. They found that heading responses were mediated by the level of coherence of the visual display. Therefore, the more coherent the visual display, the more heading reports were based on visual stimulus heading direction. The less coherent the visual display, the more the vestibular heading direction was relied upon across trials.

To summarize, cue reliability is a representation of the strength of a cue. In the Fetsch et al. (2009) experiment this was mediated by manipulating coherence of the elements in the optic flow display. In E8 of the present research, reliability was modulated by setting the speed to be perceptually equal across the visual and vestibular systems in all trials. Findings demonstrating an optimal cue integration decision making model by humans has also been demonstrated in many studies on human heading perception (De Winkel, Weesie, Werkhoven, & Groen, 2010 ; De Winkel, Soyka, Barnett-Cowan, Bühlhoff, Groen, & Werkhoven, 2013; Gu, Angelaki, & DeAngelis, 2008)

Results from this thesis extend findings by Fetsch, Turner, DeAngelis and Angelaki (2009) and others on optimal cue integration hypothesis as they indicate that when reliability or strength is characterized by the speed of the stimuli and those speeds are approximately equal, visual and vestibular cues are used to decide self-motion direction equal amounts of times. This suggests that visual and vestibular cues were perceived to be equally reliable. Interestingly,

debate regarding visual dominance, vestibular dominance, and optimal cue integration is analogously taking place in the current neuroimaging literature.

A PET study by Brandt, Bartenstein, Janek, and Dieterich (1998) found that during conflict generated from visualvection, metabolic activity in vestibular cortical processing regions such as the insula becomes inhibited. Brandt and colleagues reported that activity in visual cortical regions increased significantly during visualvection. Authors suggested that these results provide neurophysiological support for visual dominance hypotheses for resolving conflict duringvection. Nishiike et al. (2002) used magnetoencephalography (MEG) during visualvection displays and showed that both vestibular and visual regions became more active duringvection. Brandt et al. found that vestibular cortical regions became inhibited, but Nishiike et al. found that vestibular regions were active during visual-vestibular conflict. Therefore, findings from Brandt et al. and Nishiike et al. appear to contradict one another.

Kirollos, Allison, and Palmisano (2017) resolved the discrepancies between Brandt et al. (1998) and Nishiike et al. (2002) findings as they found that vestibular regions PIC/PIVC became active during high-conflict displays but not low-conflictvection displays. In their experiment, high-conflict displays simulated forwardvection with an up-down oscillation component. Low-conflict displays simulated smooth forwardvection.

Frank, Wirth and Greenlee (2016) showed that PIC activity correlated with both visual and vestibular stimulation, whereas PIVC activity correlated with vestibular self-motion stimuli only. Results from Kirollos et al. agree with those of Nishiike et al. and Frank et al. (2016) as

they all show that some vestibular processing areas (PIC and/or PIVC) become active during visual vection processing. These findings are consistent with behavioural findings from E8 that showed that during conflict visual and vestibular cues are used to determine self-motion direction (see Frank & Greenlee, 2018, for a recent review of visual-vestibular cortical interaction during conflict). This was evidenced by the distributed responses indicating that in half of trials participants used visual cues to decide self-motion and in the other half of trials participants used vestibular cues to decide self-motion.

In sum, the findings of the present thesis are consistent with neuroimaging results showing that both visual and vestibular systems and their neural correlates are involved in processing and deciding self-motion direction. In E4 of the present thesis it was unclear whether vestibular dominance or optimal cue integration explained results during conflict in which the visual display signaled no motion as the visual cue was less reliable. However, E8 showed that when the visual stimulus is matched for vection speed to the vestibular stimulus, both visual and vestibular systems are used to determine self-motion equally.

Contributions of this Thesis

The first contribution of this thesis was that it successfully reproduced the classic optokinetic drum as a virtual optokinetic drum in a VR headset. Rotation of the virtual drum induced circular vection. This finding supports the use of VR headset technologies for self-motion research.

The second contribution of this thesis was that it demonstrated the successful development and validation of the first vection speed measurement apparatus – the rotating knob. The knob can be used to measure circular vection across the visual and vestibular systems separately and simultaneously. This can help identify vection speed perception patterns through comparison across the visual and vestibular systems.

The third contribution of this thesis was that vestibular vection was successfully induced and measured using air caloric irrigation. Observed vestibular vection perception directions (e.g., left ear cold irrigation caused clockwise vection on most trials and right ear cold irrigation caused counter-clockwise vection on most trials) were consistent with eye movements reported in the literature on clinical assessment of vestibular function (i.e., right-to-left beating of the eyes during left ear cold irrigations and left-to-right beating of the eyes during right ear cold irrigations; Newman & Jacob, 1993).

A fourth contribution of this thesis is that it demonstrated that vection durations generated by caloric irrigation were ~ 45 s. These long vection durations will allow researchers to study vestibular vection and couple the vestibular stimulus with other experimental stimuli and tasks. Self-motion cues provided by methods such as galvanic vestibular stimulation and physical motion are transient, making vestibular motion perception difficult to study.

The fifth contribution of this thesis is that it uncovered the relationship between visual and vestibular cue conflict. In E4 (i.e., vestibular vection while watching stationary display), vection speeds and durations were slower than in E3 (i.e., vestibular vection with eyes closed).

This was explained by the stationary visual display hinderingvection and suggests that during conflict, cues to both sensory systems are being used to decide self-motion. In E8 – when participants experienced visual and vestibularvection in opposite directions, results showed that the visual and vestibular system were relied upon equal amounts of times for self-motion perception. These results, along with recent neuroimaging findings on visual-vestibular sensory integration, provide converging evidence suggesting that dominance hypotheses do not adequately explain sensory integration. Instead, optimal cue integration hypothesis best explains visual-vestibular sensory integration during conflict. Taken together, this thesis contributes to the growing body of research supporting visual-vestibular sensory integration during self-motion perception in the behavioural and neurophysiological literatures.

Applications of Findings from this Thesis

In the flight training and simulation industry, the value of motion platforms for generating self-motion cues have repeatedly been called into question because evidence is mixed regarding their training value and high costs. The effectiveness of motion platforms is mixed arguably because of the lack of understanding of the contribution of the vestibular system on self-motion perception. Findings from this dissertation have shown that vestibular cues play an important role in deciding self-motion direction when cues producevection of the same speed across modalities. During real flight, vestibular cues may therefore be used in situations where these are perceived to be more reliable in deciding self-motion. This can be dangerous when incorrect vestibular information is relied on. Therefore, vestibular perceptual research results such as those in this thesis should be used to make informed decisions about designing motion

cueing systems that will allow the study of vestibular contributions of self-motion, sensory integration and training to appropriately use spatial orientation cues.

Future Work

In the current thesis, vestibular vection was induced using 18°C air calorics. Future experiments should investigate vestibular vection using caloric vestibular stimulation at different temperatures. This can be done measuring vection with the rotating knob. This will determine how temperature differences across the cupula affect perceived vestibular vection speed, duration and variability in experienced vection direction and increase knowledge of how temperature gradients can impact vestibular vection. It is hypothesized that larger temperature differences would result in faster vection experience.

In Experiment 8, optimal cue integration hypothesis best explained results from the incongruent condition. In this condition, visual and vestibular vection speeds were set to be equal but signaled vection in opposite direction. Visual and vestibular cues were used equal amounts of time to decide self-motion direction. However, it is unclear if some participants prefer using visual cues or vestibular cues during conflict. Therefore, this experiment should be replicated with more participants to understand why some participants used visual cues to self-motion, why others used vestibular cues, and some used both visual and vestibular cues to decide self-motion.

To further explore if optimal cue integration explains cue conflict during self-motion, researchers should manipulate cue reliability. Reliability would be predicted to be reflected

proportionally in vection direction responses. For instance, setting the vestibular stimulus to be faster than the visual stimulus on most trials should result in vection responses corresponding to the direction signaled by the vestibular cue on most trials. Results from such experiments can help researchers predict how manipulating stimuli can influence vection responses and inform how participants determine cue reliability.

In E8, participants received caloric stimulation before they viewed the visual display. Experiencing vestibular vection before visual vection may have affected the experience of vection when a visual stimulus was presented slightly afterward. Future experiments should focus on better synchronizing visual and vestibular self-motion cues to more carefully test conflict occurring at the same time.

Finally, caloric vestibular stimulation currently induces vection in the yaw axis of motion relative to the body axis as it stimulates the horizontal semi-circular canals most effectively. Future research should focus on testing and developing compact and effective stimulation technologies capable of stimulating the posterior and superior canals to investigate vection in the roll and pitch axes. This requires substantial research and development from engineers and scientists. However, this will result in the development of apparatus capable of inducing complex and realistic vection that could replace motion platforms for simulation and training. Moreover, such wearable vestibular apparatus can aid in the discovery of functions of the human vestibular system not yet known. Experiments in this thesis are a first step toward informing new experiments on vestibular perception and understanding visual-vestibular integration.

Conclusion

The aim of this dissertation was to investigate the role of the vestibular system in self-motion perception and visual-vestibular interactions during conflict. Vection was therefore induced in the vestibular system and visual system independently. Then, vestibular stimuli were paired with conflicting visual displays. The rotating knob developed and validated in this thesis indexed speeds, durations, and directions of visual and vestibular vection. During cue conflict, visual and vestibular systems were involved in deciding self-motion perception. This is contrary to the notion that one system dominates the other. There appears to be converging evidence that the visual and vestibular systems are involved in deciding self-motion in the neuroimaging literature. Research conducted in this thesis is an important step in investigating vestibular perception and demonstrates that caloric vestibular stimulation can induce robust vection percepts. Continued vestibular perceptual research will undoubtedly produce a better understanding of the vestibular perception, visual vestibular sensory integration, and technologies that can effectively simulate physical motion for applications such as flight simulation.

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Appendix 1: ANOVA Tables

Table 2. ANOVA for vection strength in experiment 1.

Predictor	Sum of Squares	<i>df</i>	Mean Square	F	<i>p</i>	R ²
Speed	9075.021	2	4537.510	25.035	0.000	.625
Direction	6.510	1	6.510	.232	0.637	.015
Interaction	19.396	2	9.698	.232	0.794	.015

Table 3. ANOVA for vection duration in experiment 1.

Predictor	Sum of Squares	<i>df</i>	Mean Square	F	<i>p</i>	R ²
Speed	129.486	2	64.743	2.142	.135	.125
Direction	59.525	1	59.525	1.894	.189	.112
Interaction	14.215	2	7.108	.638	.535	.041

Table 4. ANOVA table for vection speed in experiment 2.

Predictor	Sum of Squares	<i>df</i>	Mean Square	F	<i>p</i>	R ²
Speed	165089.982	2	82544.991	34.212	0.000	.710

Direction	9114.362	1	9114.362	4.566	0.051	.246
Interaction	867.308	2	433.654	1.079	1.079	.072

Table 5. ANOVA for vection duration in experiment 2.

Predictor	Sum of Squares	<i>df</i>	Mean Square	F	<i>p</i>	R ²
Speed	226.563	2	113.282	14.730	0.000	.513
Direction	9.237	1	9.237	1.181	.296	.078
Interaction	27.323	2	13.662	3.010	.065	.177

Table 7. Mixed factors ANOVA comparing E3 with E4 results for vection speed.

Predictor	Sum of Squares	<i>df</i>	Mean Square	F	<i>p</i>	R ²
Between Factors (Experiments)	806538.58 1	1	806538.58 1	51.358	0.000	.556
Within Factors (Ear Irrigated)	6.489	1	6.489	0.004	.948	0.00
Interaction	1125.896	1	1125.896	.742	.394	.018

Table 8. Mixed factors ANOVA comparing E3 with E4 results for vection duration.

Predictor	Sum of	<i>df</i>	Mean	F	<i>p</i>	R ²
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	Squares		Square			
Between Factors (Experiments)	214023.34	4	214023.34	158.003	.000	.794
Within Factors (Ear Irrigated)	5.268	1	5.268	0.011	.916	0.000
Interaction	.176	1	.176	0	.985	0.000

Table 6. ANOVA for vection speed in experiment 6.

Predictor	Sum of Squares	<i>df</i>	Mean Square	F	<i>p</i>	R ²
Speed	64659.85	2	32329.929	4.958	0.019	.355
Direction	1007.286	1	1007.286	1.103	.321	.109
Interaction	1883.669	2	941.835	.518	.604	.054

Table 7. ANOVA for vection duration in experiment 6.

Predictor	Sum of Squares	<i>df</i>	Mean Square	F	<i>p</i>	R ²
Speed	124.198	2	62.099	4.980	0.019	.356
Direction	.005	1	.005	0.001	.975	0.000
Interaction	18.134	2	10.749	.843	.447	.086

Table 8. ANOVA for vection speed in experiment 8.

Predictor	Sum of Squares	<i>df</i>	Mean Square	F	<i>p</i>	R ²
Condition	609.582	2	304.791	1.606	.384	-

Table 9. ANOVA for vection duration in experiment 8.

Predictor	Sum of Squares	<i>df</i>	Mean Square	F	<i>p</i>	R ²
Condition	3153.859	2	1576.930	.824	.548	-

Appendix 2: Informed Consent and Ethics for Optokinetic Drum Experiments and Caloric Vestibular Experiments

SONA POSTING

Study Name: Inducing Vection Using a Head-Mounted Display

Experimenters: Ramy Kirollos, Ph.D. Student, Institute of Cognitive Science

Dr. Matthew Brown, Research Scientist, Carleton University

Experimenter's Phone: 613-520-2600 ext. 2487

Experiment Location: VSIM Building, room 2201

Description: The Oculus Rift is an emerging technology that is making waves in the video game

industry, private/government sectors for training purposes, and in academic research as well.

Help us learn more about the potential of fully immersive head mounted displays by participating in our study. In this experiment, you will be shown a 3D virtual environment that consists of alternating black and white stripes that rotate clockwise or counter-clockwise. You will be asked to monitor for a sensation of self-motion and to indicate the direction and speed of your perceived self-motion by turning a control knob. The study will take approximately one hour to complete. This research was approved by the Carleton University Research Ethics Board – B (Project Approval 15-156) on September 18, 2015.

Eligibility Requirements: Normal or corrected-to-normal visual acuity. No history of any vestibular disorders.

Duration: One hour

Remuneration: 1.0 % course credit

Preparation: None

Exclusions: Please do not sign up for this study if you are prone to motion/car sickness.

Informed Consent Form

Project Title: Inducing Vection Using a Head-Mounted Display

Faculty Sponsor: Dr. Chris Herdman, Department of Psychology, Carleton University, tel. 520-2600 x. 8122

The purpose of this informed consent form is to ensure that you understand both the purpose of the study and the nature of your participation. The informed consent must provide you with enough information so that you have the opportunity to determine whether you wish to participate in the study. This research was approved by the Carleton University Research Ethics Board – B (Project Approval 15-156) on September 18, 2015. Please ask the researcher to clarify any concerns that you may have after reading this form.

Research Personnel: In addition to the Faculty Sponsor named above, the following people are involved in this research and may be contacted at any time should you require further information about this study:

<u>Name</u>	<u>Title</u>	<u>Department</u>	<u>Email</u>	<u>Phone</u>
Ramy Kirollos	Ph.D. Student	Cognitive Science	ramykirollos@cmail.carleton.ca	520-2600 x. 2487
Matthew Brown	Research Scientist	Psychology	matthew.brown@carleton.ca	520-2600 x. 2487

Other Contacts: If you have any ethical concerns regarding this study, then please contact:

<u>Name</u>	<u>Contact Info.</u>
Carleton University Research Office	ethics@carleton.ca
Dr. Shelly Brown, Chair, Carleton University Research Ethics Board - B	520-2600 x. 1505

Purpose: The purpose of this study is to determine whether the feeling of self-motion can be induced using a 3D virtual environment presented on a head-mounted display. This experiment will use a novel method of measuring the perception of self-motion to understand differences between how the body responds to motion cues in real and virtual environments.

Task: We are interested in measuring the illusion of perceived self-motion. This is calledvection. An example of experiencingvection occurs when you are sitting on a stationary bus/train when an adjacent bus/train begins to move and you feel as though you are moving. In this experiment, a 3D virtual environment consisting of alternating black/white stripes will be presented on an Oculus head-mounted display. These stripes will rotate clockwise or counter-clockwise. Your task is to indicate whether or not you are experiencing any self-motion. That is, do you feel like you are rotating within the virtual environment? If and when you sensevection, you are to turn a knob in the **opposite direction**, but at the **same speed**, of your perceived self-motion to null or “cancel-out” the motion you are experiencing. For instance, if you feel like you are rotating clockwise, then turn

the knob counter-clockwise. Note that turning the knob does not control what you see in the 3D environment. If the illusion of self-rotation disappears within a trial, then stop rotating the knob.

Duration, Locale & Compensation: Testing will take place in VSIM 2210 and will take approximately one hour. You will receive 1.0% course credit for your participation.

Potential Risks/Discomfort: Because this study investigates the illusion of self-rotation in virtual environments, you may become nauseous/motion sick. To reduce the chances of this occurring, you will be provided with three 10-minute breaks during the experiment as it has been shown that interrupting exposure to the visual stimuli can alleviate nausea/motion sickness. However, if you begin to feel nauseous/motion sick, please inform the researcher immediately, at which point the experiment will be paused or terminated depending on the severity of the motion sickness and you will be asked to remain seated for 10 minutes during which the nausea/motion sickness should abate. If the nausea/motion sickness persists beyond 10 minutes, you will be referred to Carleton University Health Counselling Services. You will be given full credit (1.0%) for your participation even if the experiment has not been completed.

Anonymity/Confidentiality: All data collected in this experiment will be kept strictly confidential through the assignment of a coded number and securely stored on a local computer for a maximum of ten years. Similarly, this Informed Consent form will be kept for a maximum of ten years before being destroyed. The information

provided will be used for research purposes only. You will not be identified by name in any reports produced from this study. Further, the information is made available only to the researchers associated with this experiment

Benefits: As virtual reality becomes an increasingly viable option for training, exploration, and learning, understanding the similarities and differences between how we perceive and interact with real and virtual environments (e.g., how our bodies respond to motion cues) will inform the design and implementation of virtual environments to improve realism and immersiveness.

Right to Withdraw/Omit: You have the right to withdraw from this experiment at any time without academic penalty. Your participation in this experiment is completely voluntary.

I have read the above description of the study on inducing vection using a head-mounted display. By signing below, this indicates that I agree to participate in the study, and this in no way constitutes a waiver of my rights.

Name: _____

Date: _____

Signature: _____

Witness: _____

Debriefing

Inducing Vection Using a Head-Mounted Display

Thank you for your participation! This study is designed to investigate illusions of self-motion (vection) that are induced using a virtual environment presented on an Oculus Rift head-mounted display. More specifically, this experiment will explore the similarities and differences between motion that is experienced in real and virtual environments. This research is fundamental to understanding virtual environment immersion, and the strengths and limitations of immersive virtual environment technology for video games and training.

If you experience any nausea/motion sickness following this experiment, then it is recommended that you find a comfortable place to sit down and close your eyes. Feelings of nausea or motion sickness typically dissipate after 10 minutes. If the nausea/motion sickness persists beyond these 10 minutes of rest, then it is recommended that you see Carleton University Health and Counseling Services:

<u>Name</u>	<u>Contact Info.</u>
Carleton University Health and Counselling Services	520-6674

If you are interested in learning more about this study or the topic, please see the following:

Palmisano, S., Allison, R. S., Kim, J., & Bonato, F. (2011). Simulated viewpoint jitter shakes sensory conflict accounts of vection. *Seeing and Perceiving*, 24(2), 173-200.

Wong, S. C. P. & Frost, B. J. (1978). Subjective motion and acceleration induced by the movement of the observer's entire visual field. *Perception & Psychophysics*, 24(2), 115-120.

This research was approved by the Carleton University Research Ethics Board – B (Project Approval 15-156) on September 18, 2015. Should you have any ethical concerns regarding this study then please contact:

<u>Name</u>	<u>Contact Info.</u>
Carleton University Research Office	ethics@carleton.ca
Dr. Shelly Brown, Chair, Carleton University Research Ethics Board - B	520-2600 x. 1505

Should you have any other concerns about this study then please contact any of the following individuals:

<u>Name</u>	<u>Title</u>	<u>Department</u>	<u>Study Role</u>	<u>Contact Info.</u>
Ramy Kirolos	Ph.D. Student	Cog. Science	Principal Researcher	ramykirollos@cmail.carleton. ca
Dr. Matthew Brown	Researcher	Psychology	Co-Investigator	matthew.brown@carleton.ca
Dr. Chris Herdman	Professor	Psychology	Faculty Advisor	chris_herdman@carleton.ca

SONA POSTING

Study Name: Inducing a Spinning Sensation by Stimulating the Ear with Warm Airflow

Experimenters: Ramy Kirollos, Ph.D. Student, Institute of Cognitive Science

Dr. Matthew Brown, Research Scientist, Carleton University

Faculty Supervisor: Dr. Chris M. Herdman, Professor of Psychology, Carleton University

Experimenter's Phone: 613-520-2600 ext. 2487

Experiment Location: VSIM Building, room 2201

Description: The contribution of the balance system to our ability to walk, run, orient ourselves, and navigate through space remains poorly understood. Help us learn more about the balance system's contribution to spatial orientation by participating in our study. In this experiment, you will be presented with warm airflow into your ear, which may induce a spinning sensation,

despite actually being stationary (lying down). You will be asked to monitor your sensation of self-rotation (if any) and express this experience by turning a knob relative to the direction of your perceived self-motion. Warm air stimulation of the inner ear will be achieved using an air caloric irrigator that relays warm air to the ear via a tube and earpiece designed to fit comfortably in your ear like an earbud. Stimulation will occur for one to two minutes. After this stimulation period, you will be asked to spin the knob relative to the direction of your perceived self-rotation for approximately two to eight minutes. This procedure of administering warm air to the ear and recording your knob-turn response will be repeated three times. Throughout the experiment, you will lie on your back with your head tilted slightly forward and eyes closed. You will wear a portable EEG system on your head throughout the experiment to record brain data related to eye-movements during stimulation. The study will take approximately one hour to complete. This research was cleared by the Carleton University Research Ethics Board – B (Protocol Clearance # 104652) on June 23, 2016.

Duration: One hour

Remuneration: 1.0 % course credit

Preparation: None

Exclusion Criteria: Please do not sign up for this study if you are prone to motion/car sickness, have a history of vestibular problems (e.g., clinically diagnosed vertigo), or require a hearing aid.

Physical Risks: Nausea, motion-sickness, dizziness, temporary ringing of ears after the experiment.

Informed Consent Form

Project Title: Inducing a Spinning Sensation by Stimulating the Ear with Warm Airflow

Faculty Sponsor: Dr. Chris Herdman, Department of Psychology, Carleton University, tel. 520-2600 x. 8122

The purpose of this informed consent form is to ensure that you understand both the purpose of the study and the nature of your participation. The informed consent must provide you with enough information so that you have the opportunity to determine whether you wish to participate in the study. This research was cleared by the Carleton University Research Ethics Board – B (Project Protocol Clearance # 104652) on June 23, 2016. Please ask the researcher to clarify any concerns that you may have after reading this form.

Research Personnel: In addition to the Faculty Sponsor named above, the following people are involved in this research and may be contacted at any time should you require further information about this study:

<u>Name</u>	<u>Title</u>	<u>Department</u>	<u>Email</u>	<u>Phone</u>
Ramy Kirolos	Ph.D. Student	Cognitive Science	ramykirollos@cmail.carleton.ca	520-2600 x. 2487
Matthew Brown	Research Scientist	Psychology	matthew.brown@carleton.ca	520-2600 x. 2487

Other Contacts: If you have any ethical concerns regarding this study, then please contact:

<u>Name</u>	<u>Contact Info.</u>
Carleton University Research Office	ethics@carleton.ca
Dr. Shelly Brown, Chair, Carleton University Research Ethics Board - B	Shelley.Brown@carleton.ca 613-520-2600 ext. 1505

Purpose: The purpose of this study is to understand how the perception of self-motion manifests itself in the vestibular (balance) system. To this end, this study will induce the sensation of self-rotation by stimulating the inner ear using warm air. The ability to induce the feeling of self-rotation has important implications for user immersion in virtual reality environments such as simulators.

Task: The experimenter will use an air caloric irrigator to administer a gentle current of warm air into your ear as you lay on your back with your eyes closed. An caloric irrigator relays air from the machine to the ear via a hose, tube, and earpiece designed to fit comfortably into your ear like an earbud. The administration of warm air to your ear will last one to two minutes. Although the airflow may be a bit loud, it will not be painful or harmful. After one to two minutes of constant airflow, you may begin to sense that you are moving, or rotating, despite being stationary. Your task is to monitor this sensation of movement or rotation. If and when you sense that you are moving/rotating, you will be asked to turn a knob in the direction opposite to your sensed direction of movement. For example, if you feel that you are moving to the right/clockwise, then turn the knob to the left (counter-clockwise). You will be asked to monitor for the feeling of movement/rotation for several minutes from when the air has stopped flowing. If you feel that you have stopped moving/rotating during this period, then stop rotating the knob. Only rotate the knob if you feel that you are moving/rotating. Once you have completed the first trial, you will be given an eight-minute break during which you will be asked to continue

lying down with your eyes closed. This is to allow your vestibular system to “reset” itself before repeating the procedure and will reduce the likelihood of becoming motion sick. You will be asked to remain lying down with your eyes closed during this break. There will be a total of three trials.

Duration, Locale & Compensation: Testing will take place in VSIM 2210 and will take approximately one hour to complete. You will receive 1.0% course credit for your participation.

Potential Risks/Discomfort: Because this study involves the perception of self-rotation, you may begin to feel disoriented, nauseous or motion sick. A slight and temporary ringing in the stimulated ear may occur after the experiment, similar to that experienced when listening to music with earbuds. This should subside within an hour. Careful consideration has been taken to minimize the chances of this occurring by ensuring that (1) you will be lying down in the dark for the duration of the experiment to avoid any motion sickness caused by external visual cues or from standing, (2) trial times are short, (3) long breaks are provided between trials, and (4) the experimenter monitors your comfort level throughout the experiment. If, however, you begin to feel disoriented/nauseous/motion sick, please inform the researcher immediately, at which point the experiment will be paused or terminated depending on the severity of your discomfort and you will be asked to remain lying down for 10 minutes during which the disorientation/nausea/motion sickness should abate. If the disorientation/nausea/motion sickness persists beyond 30 minutes, you will be referred to Carleton University Health Counselling Services. You will be given full credit (1.0%) for your participation even if the experiment has not been completed.

Anonymity/Confidentiality: All data collected in this experiment will be kept strictly confidential through the assignment of a coded number and securely stored on a local computer for a maximum of ten years. Similarly, this Informed Consent form will be kept for a maximum of ten years before being destroyed. The information provided will be used for research purposes and may therefore be presented and/or published. You will not be identified by name in any reports produced from this study.

Benefits: The contribution of the balance system to visual-spatial orientation is poorly understood. The majority of research on this system pertains to applications in the clinical and medical field. However, with the emergence of high-fidelity simulators, driven by popularity and technical advancements in head-mounted display systems such as the Oculus Rift, understanding the contribution of the vestibular system will be important in integrating appropriate/corroborant visual displays to ensure high-quality simulation.

Right to Withdraw: You have the right to withdraw at any time during the experiment without academic penalty. Your participation in this experiment is completely voluntary.

I have read the above description of the study on using air caloric irrigation to induce illusory percepts of self-rotation. By signing below, this indicates that I agree to participate in the study, and this in no way constitutes a waiver of my rights.

Name: _____

Date: _____

Signature: _____

Witness: _____

Debriefing

Inducing a Spinning Sensation by Stimulating the Ear with Warm Airflow

Thank you for your participation! This study is designed to investigate illusions of self-motion when stimulating the vestibular system using warm air. Illusory self-motion is typically studied by stimulating the visual system, but in this study we sought to induce the feeling of self-motion by stimulating your balance system, which is in your inner ear. This is a foundational research study that will help us understand how illusory self-motion manifests itself in terms of magnitude, and duration. The characteristics of the type of self-motion induced in this experiment will be compared to those induced via the visual system. This research is fundamental to understanding immersion in virtual reality, which will inform how this technology is adopted for use in video games and simulated training. If you are interested in learning more about this study or the topic, please see the following:

Reference: Kassemi, M., Deserranno, D., & Oas, J. G. (2005). Fluid–structural interactions in the inner ear. *Computers & Structures*, 83(2), 181-189.

If you experience any disorientation/nausea/motion sickness following this experiment, then it is recommended that you find a comfortable place to sit down and close your eyes. Feelings of disorientation/nausea/motion sickness typically dissipate after 30 minutes. If any of these symptoms persist for longer than 30 minutes, the experimenter will escort you to the clinic on the Carleton campus for medical attention. This research was cleared by the Carleton University Research Ethics Board – B (Project Protocol Clearance # 104652) on June 23, 2016.

Should you have any ethical concerns regarding this study then please contact:

<u>Name</u>	<u>Contact Info.</u>
Dr. Shelly Brown, Chair, Carleton University Research Ethics Board - B	Shelley.Brown@carleton.ca 613-520-2600 ext. 1505
Andy Adler, Vice-Chair, Carleton University Research Ethics Board - B	ethics@carleton.ca

Should you have any other concerns about this study then please contact any of the following individuals:

<u>Name</u>	<u>Title</u>	<u>Department</u>	<u>Study Role</u>	<u>Contact Info.</u>
Ramy Kirollos	Ph.D. Student	Cog. Science	Principal Researcher	ramykirollos@email.carleton.

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Dr. Matthew Brown	Researcher	Psychology	Co-Investigator	matthew.brown@carleton.ca
Dr. Chris Herdman	Professor	Psychology	Faculty Advisor	chris_herdman@carleton.ca

Participant Demographic Questionnaire

Inducing a Spinning Sensation by Stimulating the Ear with Warm Airflow

Gender

Male ☐

Female ☐

Age _____

Handedness

Right ☐

Left