THE EFFECTS OF GRAVITY ON SELF-MOTION PERCEPTION

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Abstract

Gravity is the most pervasive force that we encounter. For instance, we observe a variety of objects being accelerated toward the Earth by gravity, but we also experience these forces when we are simply stationary—as gravity is a constant acceleration—or when we are ourselves in motion, such as when we are locomoting on foot, driving a vehicle, jumping or skiing. It follows that our ability to successfully navigate our environment must somehow take into account the effects of gravity on our body's motion-detecting senses—a dynamic relationship which changes with self-motion and self-orientation. The goal of this dissertation was to investigate how body orientation relative to gravity influences visual-vestibular interactions in visually-induced perception of self-motion (i.e., vection). Specifically, I examined this relationship by placing observers in varied postures and presenting visual displays simulating forward/backward self-motion with vertical/horizontal viewpoint oscillation, that mimics components produced by head-movements in real self-motion. I found that tilting observers reduced vection and the two viewpoint oscillations similarly enhanced vection, suggesting that current postural and oscillation-based vection findings are best explained by ecology. I also examined the influence of scene structure and alignment of the body and visual motion relative to gravity on vection. Observers in different postures viewed simulated translational self-motion displays consisting of either a single rigid structure or dots. The experimental data showed that vection depended on both posture and the perceived interpretation of the visual scene, indicating that self-motion perception is modulated by high-order cognitive processes. I also found that observers reported illusory tilt of the stimulus when they were not upright. I investigated these observer reports of a posture-dependent perceived stimulus tilt by presenting upright and tilted observers with static and motion stimuli that were tilted from the graviational vertical. Postural-dependent tilt effects were found for both these stimuli and were greater for motion experienced as self-motion than external motion. Taken together, the results of this dissertation demonstrate that our perception of self-motion is influenced by gravity, and by prior experiences and internal mental representations of our visual world.

Dedicated to the memory of my grandfather David Guterman, a Holocaust survivor whose strong will taught me to persevere. His love and support helped make this work possible.

Acknowledgements

This project was made possible with the support of many people. I would like to begin by thanking my family and friends whose love and support gave me the strength to complete my goals. Thanks to Jim Zacher for assistance with equipment materials and setup. Gratitude to my labmates for their support and contributions to this work. Thank you to Dr. Robert Allison, Dr. Laurence Harris, Dr. Laurie Wilcox, Dr. Richard Hornsey, Dr. Joel Goldberg, and Dr. Hongjin Sun, for serving on my dissertation committee. Finally, special thanks to my supervisor, Dr. Robert Allison, for his encouragement, patience, and guidance throughout this project. He has been my fountain of knowledge and mentor.

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General Introduction

1.1 Sensory cues to self-motion

When we move through the environment, either actively or passively, this movement is registered by multiple sensory systems that contribute to our sense of self-motion (e.g., direction and speed). Although our self-motion is predominately sensed by the visual and vestibular systems, other sensory sources also contribute.

In the natural world, all of our motions are constrained and defined by our interactions in our environment. The force of gravity influences our motions by acting on both the body and our visual environment. This review takes into consideration how gravity influences our perception of self-motion.

1.1.1 Visual cues

The importance of vision to self-motion perception is clearly evident when considering the effects of degraded or disrupted vision during self-motion. For instance, pilot who fly on a dark, moonless night or under poor weather conditions which deprive them of visual Earth-based orientation cues, could be prone to errors in orientation if it were not for aircraft gauges indicating the orientation of the aircraft. An example of this is a well-known somatogyral illusion called “The Leans”, in which a pilot banking an aircraft reaches a stable turning rate or bank angle such that the fluid in the vestibular organs of the inner ear stabilizes. The pilot may sense this lack of a vestibular signal as level-flight, and may “lean” their body or even aircraft to this new “level” attitude (Antunano & Mohler, 1992). There is also a climbing/descending illusion in which a pilot that is accelerating or decelerating, can experience the illusion that the aircraft is climbing or diving due to the resultant force being perceived as the force of gravity (Antunano & Mohler, 1992); as a result, an inexperienced pilot may attempt to make a correction by pitching the aircraft upward, or worse, downward toward the ground (i.e., “controlled flight into terrain”).

Of the sensory systems, the visual sense can inform us of all forms of self-motion (active/passive, translatory/rotational, constant velocity). It can be used to plan and independently predict the long-range consequences of our self-motion. Visual cues that help to support and maintain self-motion can be divided into two general categories: optostatic and optokinetic. Optostatic function includes natural and artificial features that indicate directionality (or polarity) in our environment, such as trees (trunk-side is “down”), buildings (roof is “up”), and the horizon as a reference to gravity. Also, visual frames and *a priori* knowledge that light typically comes from above, can also specify orientation. A demonstration of optostatic cues to orientation was conducted by Asch and Witkin (1948) who were the first to find that in a dark room, observers viewing a vertical, luminous rod in a tilted luminous frame perceived the rod to be tilted in the opposite direction of the frame tilt, in what is known as the rod-in-frame effect. Like other features in our environment, the frame—in a dark and visually impoverished—effectively served as a surrogate reference to the Earth horizontal/vertical, and altered the perceived tilt of the rod.

Optokinetic cues to self-motion are important for visually discriminating between rotation and translation during self-motion. The pattern of light that is structured by elements in our environment and reaches the eye can be thought of as an “optic array” (Gibson, 1950). Self-motion causes the visual direction of objects in the optic array to change producing what is called “optic flow”. These changes in the optic array provide information about the characteristics of self-motion, such as direction (e.g., radial flow indicates forward/backward motion) and speed. The point or region at which the optic flow originates is the “focus of expansion” and specifies the direction of self-motion or heading during translation. Figures 1.1 and 1.2 illustrate different types of optic flow that are associated with self-motion, showing the optic flow and flat-plane projections, respectively. Under natural settings, optic flow is generated by self-motion, with no flow indicating that the observer is not moving. It is also important to note that both horizontal translation and rotation about the yaw (or spinal) axis would produce a similar optic flow pattern, if it were not for motion parallax—a monocular depth cue in which closer elements of a scene generate more flow than objects that are further away.

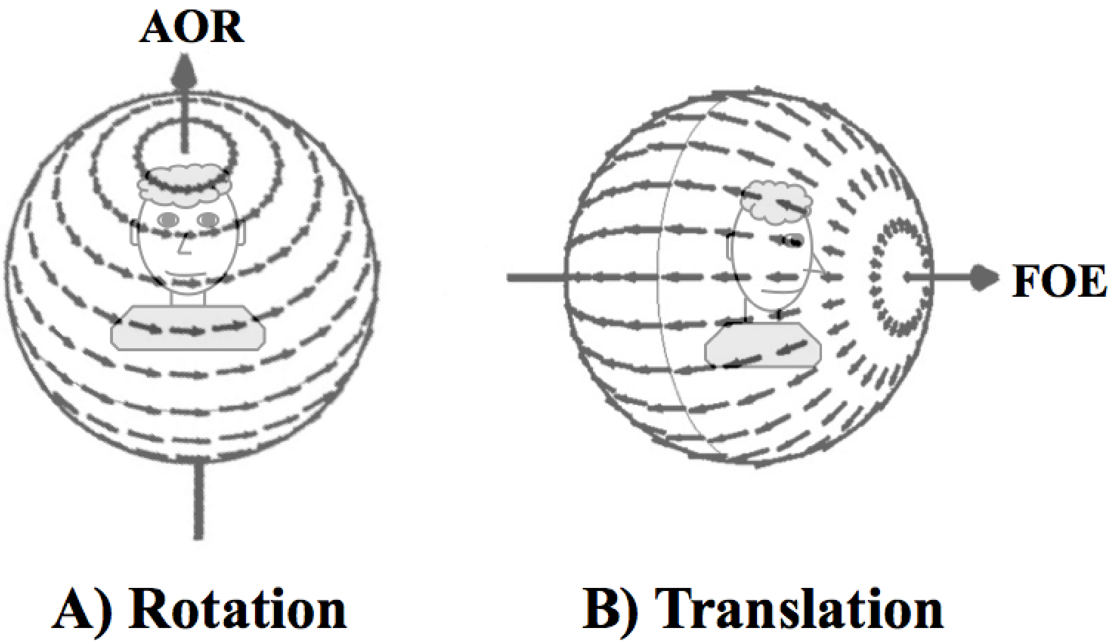

Figure 1.1: Spherical image models of the optic array for (A) rotational, and (B) translatory, motion. “AOR” and “FOE” indicate that axis of rotation, and focus of expansion, respectively (adapted by Karmeier et al. (2003).

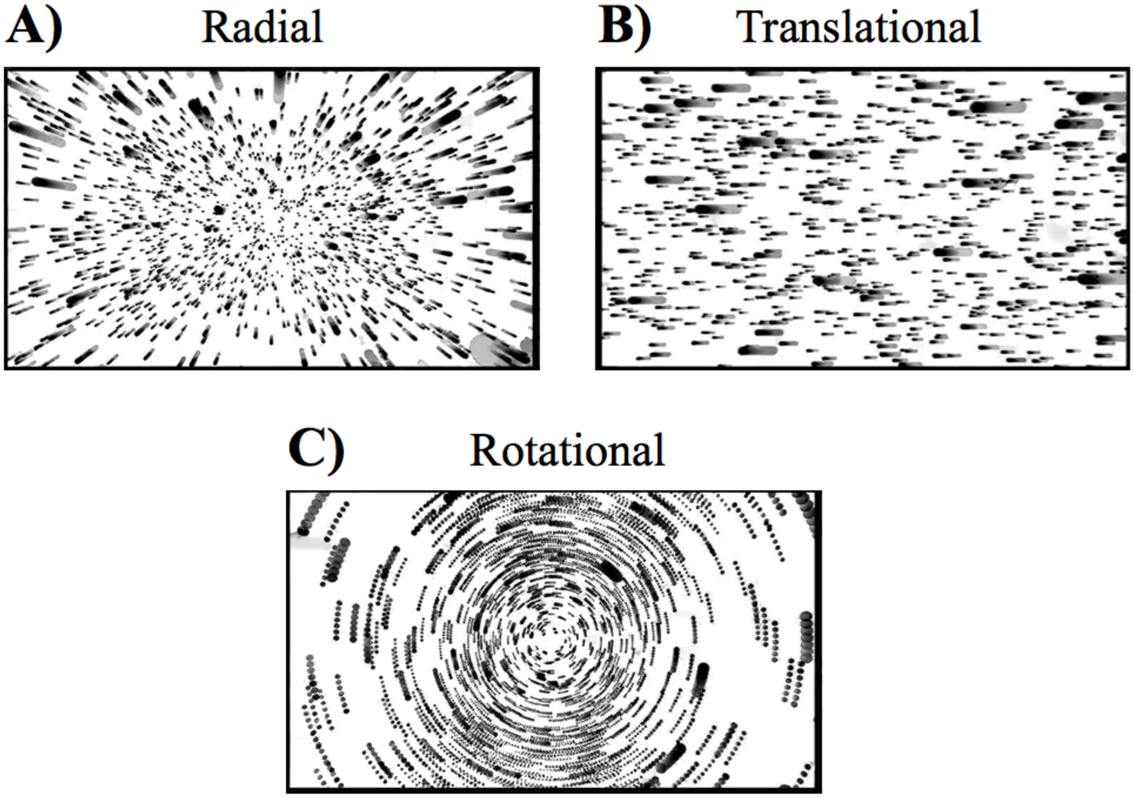

Figure 1.2: Representations of the types of optic flow associated with self-motion, for (A) radial, (B) translational, and (C) rotational, motion.

While optic flow can be a rich and dynamic source of information about self-motion, interpreting one's own motion from optic flow can be complicated by eye and head movements and the motion of objects in the external environment (Banks, Ehrlich, Backus, & Crowell, 1996; Regan & Beverley, 1982; Warren & Hannon, 1990). The brain is able to overcome these complications by using it's internal signals when executing motor actions.

Visual information is a powerful self-motion cue and optic flow generated by simulated visual scene motion in stationary observers, can induce the sensation of self-motion in an illusion known as vection (Mach, 1875); refer to Fig 1.2. Yet, we are still able to walk and perceive self-motion in the dark, suggesting that we also rely on non-visual cues for the perception of self-motion.

1.1.2 Vestibular cues

The vestibular system is the most influential of the non-visual senses for detecting information about active and passive, and linear and angular, self-accelerations (Benson, 1990). Its dominant role in the perception of self-motion was demonstrated by Walsh (1961) who measured vestibular sensitivity thresholds with a parallel swing, and found they were about ten times higher in subjects with vestibular lesions compared to normal subjects. Located within the inner ear, this sense organ detects mechanical stimulation of cilia within two structures filled with endolymph (fluid): (A) the three, roughly orthogonal semicircular canals that respond to three-dimensional angular accelerations, and (B) the utricle and saccule that respond to linear accelerations and head tilt relative to gravity.

The utricle and saccule are collectively called the otoliths—or ”ear stones” in Greek, due to the calcium carbonite crystals embedded in a gel-like membrane of the maculae. The semicircular canals and otoliths work synergistically to provide information about the magnitude and direction of acceleration of the head in space. Since this dissertation is primarily concerned with linear self-motion perception, further discussion on vestibular physiology will focus on the otolith organs. Figure 1.3 shows the anatomy of the vestibular system, with attention given to the motion sensitivities of the otolith sensory surfaces (epithelium) known as maculae.

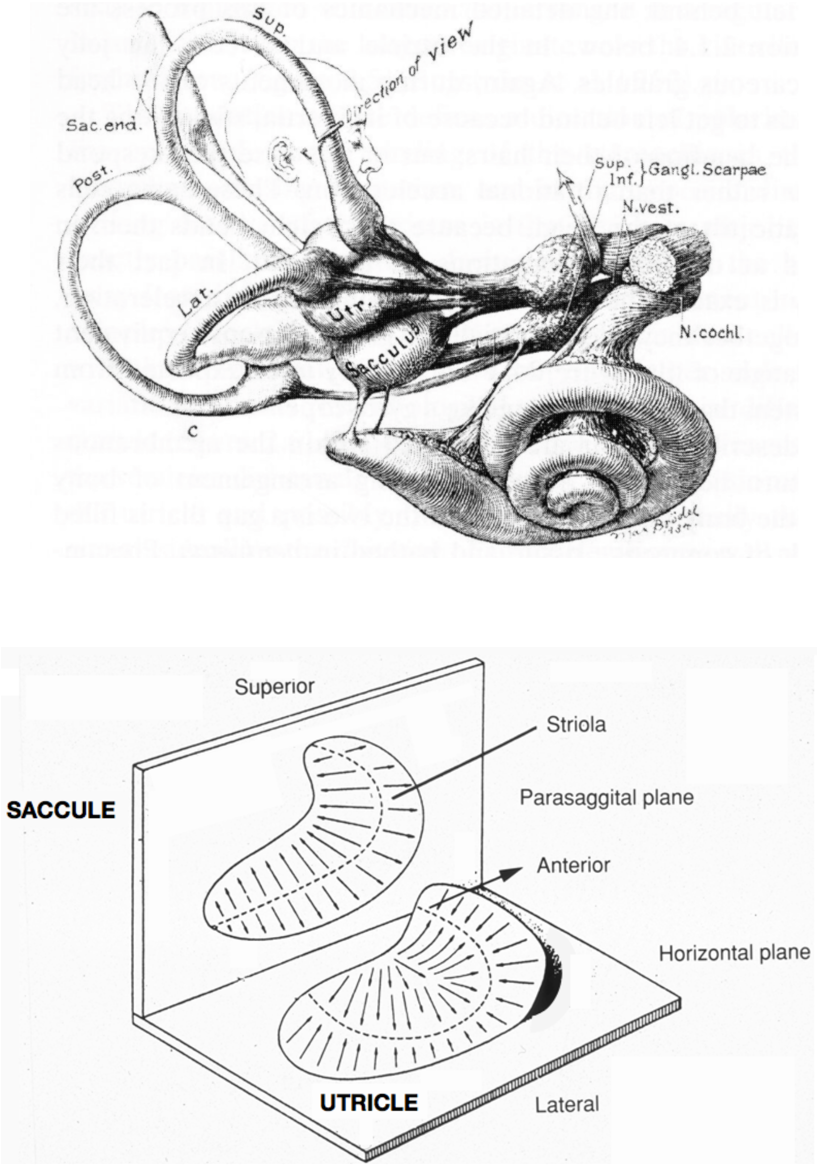

Figure 1.3: Diagram of the vestibular anatomy (top, from Hardy (1934)), and a schematic model of the otolith maculae (bottom, adapted from Barber and Stockwell (1976)) with the small arrows representing a map of the directional sensitivity of hair cells.

Due to the orientation and curvature of the maculae, the saccule is more sensitive to vertical acceleration (e.g., elevator-like motions), and the utricle to horizontal accelerations (e.g., moving walkway-like motion) and static/dynamic head tilt. The macular epithelium itself consists of a bundle of about 70 small hair-like structures called stereocilia, and one large hair-like structure called the kinocilium (Howard, 1982); altogether, the utricle and saccule contain roughly 33,000 and 19,000 hair cells, respectively. These cilia are embedded in a gelatinous layer that is topped by a heavier layer of calcium crystals (see Fig 1.4). Linear acceleration or head tilt results in a force that displaces the crystals relative to the macula, and deflects the underlying stereocilia in the opposite direction of that motion. A central parting of the macular surface known as the striola delineates sensitivity to motion in opposing directions—shown in the schematic model of the otolith in Fig. 1.4).

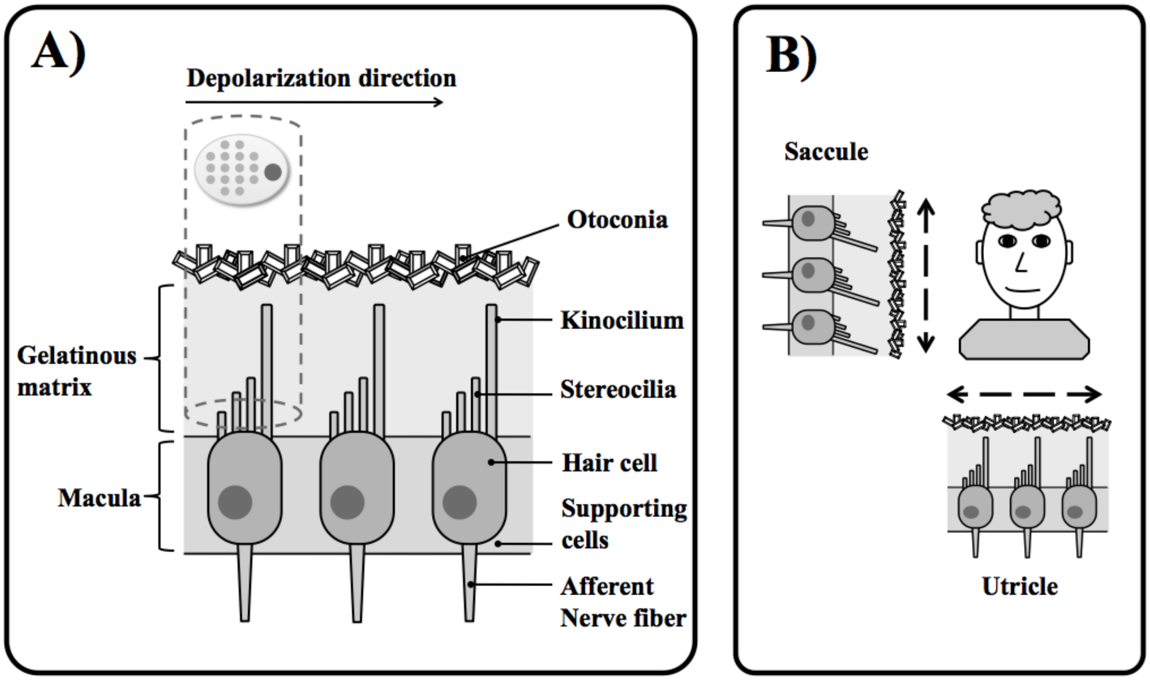

Figure 1.4: Schematic representation of (A) the macular epithelium, and (B) the differential sensitivity of the saccule and utricle to vertical and horizontal motion, respectively (adapted from De Vrijer (2009)).

As linear accelerometers, the otoliths provide signals that are inherently ambiguous. The mechanics of the otoliths respond similarly to force due to self-acceleration and gravity (Mach, 1875), and hence cannot distinguish between inertial and gravitational forces. As shown in Figure 1.5, linearly accelerating an observer through space or roll-tilting a stationary observer, would result in a similar otolith signal. However, this ambiguity can be resolved by considering concordance with signals of the semicircular canals and other non-visual senses. Furthermore, gravity is persistent and always 1-g, while acceleration due to self-motion is always limited in time. Consideration of the dynamics and magnitude of the otolith signals can also separate acceleration due to gravity from self-motion.

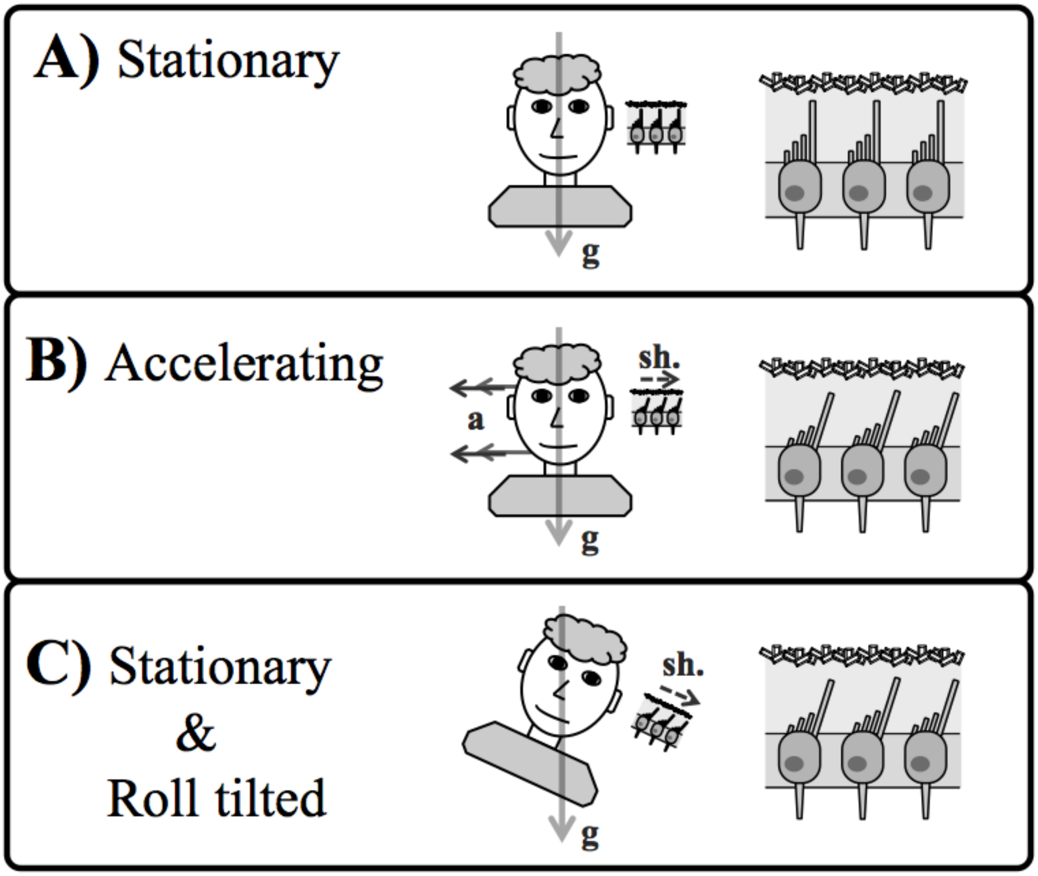

Figure 1.5: Response of the otoliths to linear acceleration due to self-motion and gravity. Self acceleration, gravity, and the shearing force, are indicated by “a”, “g”, and “sh”, respectively. The kinocilium are fairly rigid and may not bend so much as shown in the figure.

1.1.3 Other cues

Other non-visual senses that help us to resolve self-motion direction include the somatosensory and proprioceptive systems. Somatosensation, from the Greek "soma" for body, conveys information about the body's surface interaction with the environment (e.g., temperature and touch), and proprioception senses changes from mechanoreceptors in the muscles and joint and tendon receptors. There is also evidence from studies with paraplegic subjects (Mittelstaedt, 1996; Mittelsteadt & Fricke, 1988) to suggest that inertial forces might be sensed by gravity receptors in the trunk (truncal graviceptors) which mechanically support the kidneys and vascular system (Mittelsteadt & Fricke, 1988). According to this theory, linear motion might be sensed by changes in pressure due to the shifting of blood shifting in the body. Additional contributing signals are provided by baroceptors (Shimizu et al., 2002), the gut (Hunt, Knox, & Oginski, 1965), the auditory system (Benson, 1990; Lackner, 1977), and other sources.

1.2 Visually-induced self-motion

As discussed in section 1.2.1, the visually-induced sense of self-motion known as vection, occurs despite the lack of appropriate vestibular signals that would normally occur during self-motion. Perhaps the earliest record of this was an observation by Helmholtz (1867), who while viewing a flowing body of water experienced illusory self-motion in the opposite direction. Later, this phenomenon was reported by Mach (1875) after sitting in a stationary train while viewing a train moving on an adjacent track, and came to be known as the “train illusion”. This was also demonstrated by Wood (1895) in an arguably less naturalistic setting in which observers sat on a stationary swing that was inside of a rotating, furnished room (see Fig. 1.6). Each of these examples describe conditions in which the vestibular system signalled no self-motion, yet observers experienced a typically stable and compelling illusory experience of self-motion. However, for some observers, sensory conflict among the visual, vestibular, and other senses, can result in disturbing experiences of a visually unstable world, eye strain, and nausea. Therefore, how we integrate information from the senses is important in our perception and experience of self-motion.

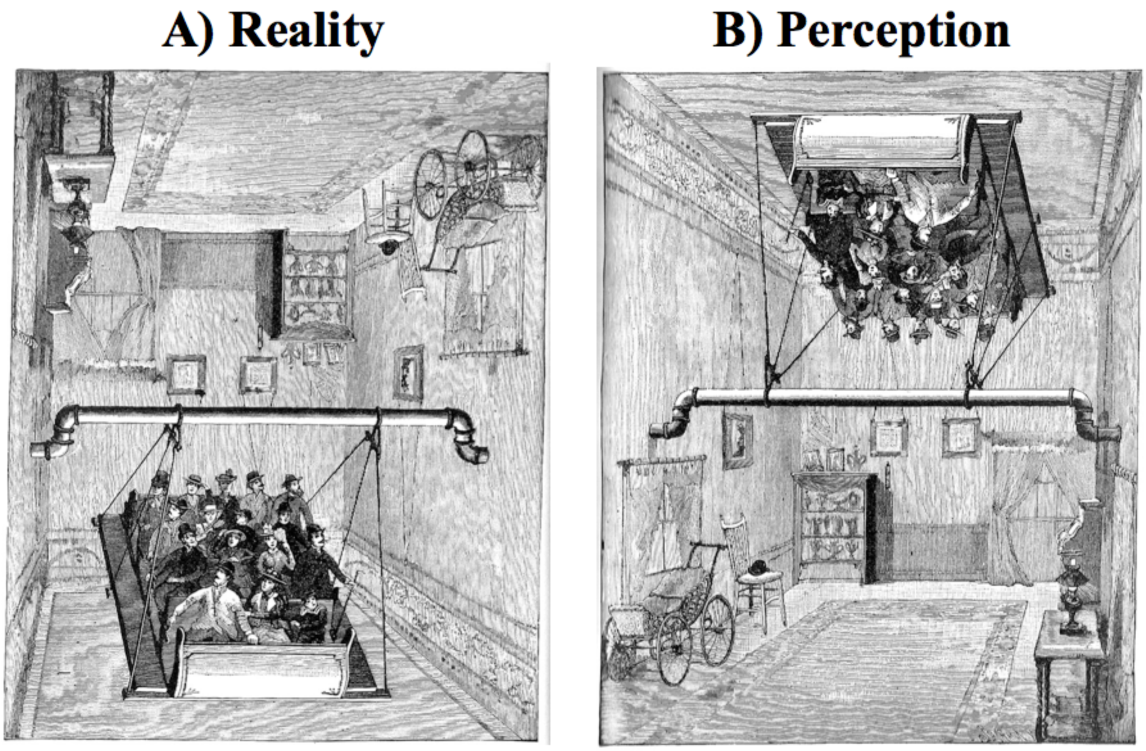

Figure 1.6: Illustration of the haunted swing apparatus (Wood, 1895) The left (A) shows the “True position of the swing” and right (B) shows the “Illusion produced by a ride in the swing.”

1.3 Multisensory integration in self-motion

The perception of self-motion relies on the integration of multiple sensory systems (Gibson, 1966). However, signals from these senses can be redundant, ambiguous, and even conflicting. These sensory conflicts can exist not only between senses, but as demonstrated in the previous section on the otoliths of the vestibular system, ambiguities can also occur within each sense (intrasensory ambiguity). There are several theories as to how these sensory signals might be integrated, by selectively weighting cues. In the following section, several theoretical models of multisensory integration in self-motion perception are discussed.

1.3.1 Sensory dominance theory

The sensory dominance theory of multisensory integration in self-motion perception explains why the sensation that one is moving can be solely induced by our visual sense (Johansson, 1977; D. N. Lee & Lishman, 1975; Lishman & Lee, 1973). According to Lishman and Lee (1973), the visual illusion of self-motion is due to visual information overriding input from vestibular, somatosensory, and other sensory systems indicating that the observer is stationary. A well-known demonstration of visual dominance in spatial tasks is the classic "ventriloquist effect" in which an auditory cue is localized to the closest visual cue. This theory and tendency towards visual dominance has also been extended to proprioceptive and tactile input in work by Gibson (1933) and later by Rock and Victor (1964), in which the wearing of prism or minimizing glasses distorted the perceived felt edge straightness and size, respectively, in favour of the optical perception. However, in many situations such as in poor visibility, our visual sense alone is not adequate to inform us about self-motion (Gibson & Mowrer, 1938), so we must also integrate information from other sensory systems.

1.3.2 Modality appropriateness hypothesis

According to the modality appropriateness hypothesis, the modality that dominates in the perception of self-motion would depend on the requirements of the task at-hand (Freides, 1974; Welch, 1999; Welch & Warren, 1999; Wood, 1980). This approach has been studied most extensively in audio-visual integration with the visual system thought to be better suited for spatial information (Bertelson, 1994; Bertelson & Radeau, 1981; Soto-Faraco, Spence, & Kingstone, 2004) and audition for temporal information (Bertelson & Radeau, 1981). Other factors may also play a role in determining the most appropriate sensory modality, such as the required accuracy, reaction time, and precision that the task requires. Studies which measured the gain of the response of the visual and vestibular systems as a function of temporal frequencies, have shown that these systems are well-tuned to low and high frequencies, respectively (Henn, Cohen, & Young, 1980; Young & Meiry, 1968; Zacharias & Young, 1981). Thus, one could suppose that the visual system is the appropriate sensory system for high frequency or transient movements and the visual system for low frequency movements. For instance, this property has been used in flight simulators to simulate changes in movements while keeping within the limits of the motion base. As shown in Figure 1.7, the displacement during the initial acceleration of a simulator closely follows the simulated motion. Since the vestibular organs act as accelerometers, this initial simulator motion or “kick” known as “acceleration-onset cueing”, corresponds well with simulated real motion. After this initial acceleration, the visual system should be the more appropriate modality and the simulator motion is gradually decreased or “washed out” at a rate that is below the vestibular threshold to ready the simulator for the next motion (Strachan, 2001). Thus, washout filter algorithms attempt to minimize the difference between the sensed motion of the simulator and real vehicle, by employing a variety of sensory motion cues when they are most appropriate—e.g., visual, vestibular, proprioception, etc. (Grant & Reid, 1997). However, the appropriate modality is not always clear (Asch & Witkin, 1948; Howard & Childerson, 1994; Mittelstaedt, 1986; Mittelsteadt & Fricke, 1988; Witkin & Asch, 1948), so it is not surprising that we often combine sensory information by additive or weighted averaging, or possibly in a probabilistic fashion.

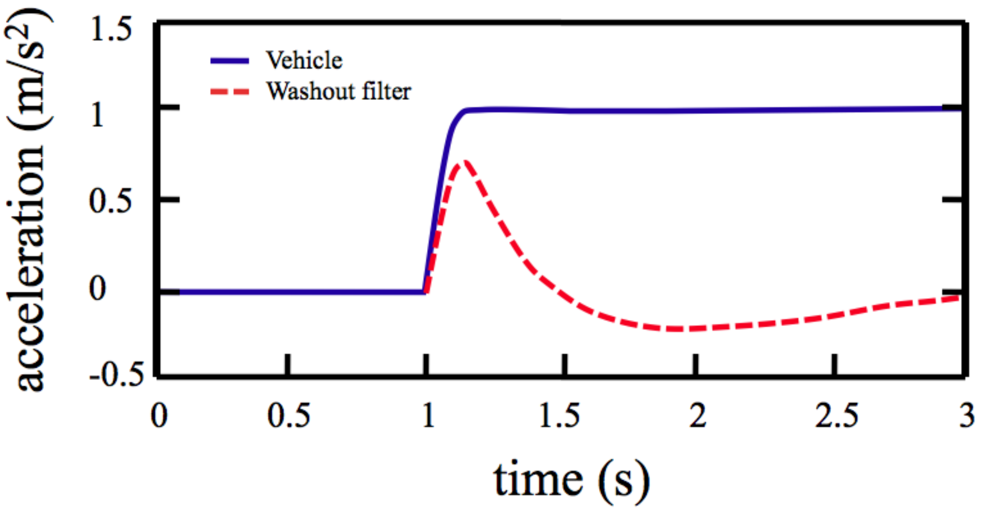

Figure 1.7: A comparison of real and simulator motion displacement for the initial acceleration, washout and re-set below the user's sensory threshold (adapted from Grant and Haycock (2008)).

1.3.3 Additive vector models

Another set of models which describes multisensory integration in the perception of self-motion are additive vector models. This is a quantitative approach which combines sensory motion vectors by either additive or weighted summation (Angelaki, McHenry, Dickman, Newlands, & Hess, 1999; Bos & Bles, 2002; Glasauer & Mittelstaedt, 1992; Merfeld, 1995; Zupan, Merfeld, & Darlot, 2002).

Originally proposed by Mittelstaedt (1983), this model attempts to account for known shifts in the subjective vertical due to head tilt (Aubert, 1861), by considering the orientation of the body relative to gravity. According to Mittelstaedt (1983) in the context of orientation, there is an internal representation of the body which he termed the “idiotropic vector”, which biases the subjective vertical toward the body’s longitudinal (or spinal) axis; he posited that this bias as well as poor updating of visual signals from vestibular and proprioceptive feedback could be responsible for shifts in the subjective visual vertical in tilted observers. Figure 1.8 shows a schematic of Mittelstaedt’s (1983) vector sum model.

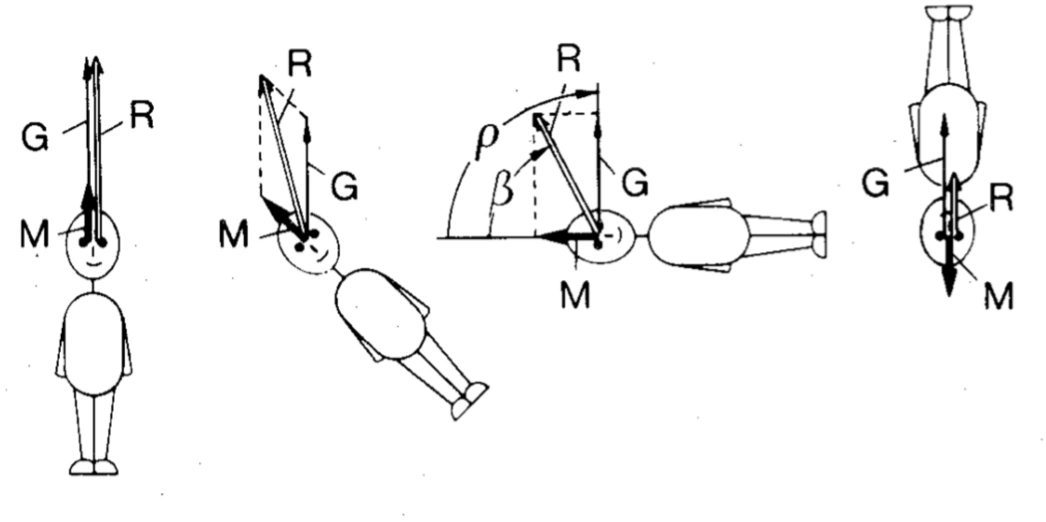

Figure 1.8: Mittelstaedt’s (1983) vector sum model showing the body in various orientations with respect to gravity. The vectors as presented above include the body vector (“M” with a thick arrow), gravity (“G” with a regular arrow), and the resultant (“R” with an unfilled arrow).

Additive models of sensory integration include simple and weighted vector models. Simple additive models represent information as the vector sum of signals from each sense. In self-motion, this model could involve a summation of the vectors of the visual and vestibular directions of self-acceleration. As a practical example, Figure 1.9 illustrates the vectors of a simple additive model and tilt-translation trading—for example, trading the gravity vector for acceleration by tilting the platform of a flight simulator. This approach has been useful in predicting the navigational behaviour of pigeons (Cheng, 1988, 1989, 1994; Cheng & Spetch, 1995), but is limited by its assumption that the relative contribution of each sense is more or less equal. However, as discussed in the aforementioned models, the balance of influence of each sense in the perception of self-motion can be "uneven" and depend on variety of factors. For instance, in the absence of an appropriate gravity signal in microgravity, otolith tilt-translation requires reinterpretation, as the otoliths are no longer stimulated by gravity and so the brain interprets head tilt as linear translation. Also, this interpretation is in conflict with neck proprioceptors signalling head tilt. Thus, astronauts tend to rely more on vision to help maintain spatial orientation (Harm & Parker, 1993; Harm, Parker, Reschke, & Skinner, 1998). The notion that the senses do not always contribute equally in self-motion perception is also supported by the findings of Wright, DiZio, and Lackner (2005), who presented vertical visual motion to observers seated on a vertically oscillating platform, and found that when these motions were temporally out-of-phase that the dominating input (visual/vestibular) depended on the oscillation amplitudes.

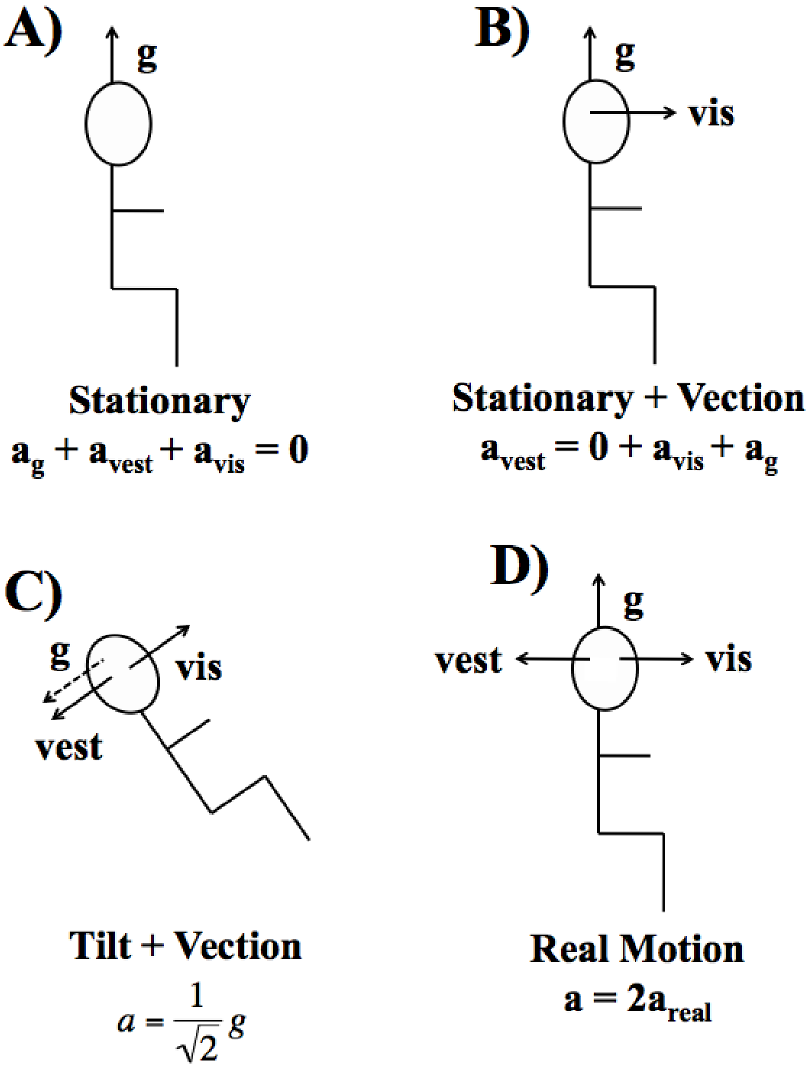

Figure 1.9: Illustration of vection responses for an observer that is (A) stationary and upright viewing no visual motion, (B) stationary and upright with vection, (C) stationary and tilted with vection, and (D) in-motion and upright. Since the otoliths are accelerometers, tilt and linear acceleration (C and D) signals are ambiguous, and both are perceived as translational self-motion.

An alternative model which might better describe sensory integration is a weighted vector sum model, which integrates sensory information by treating visual, gravity, and other body cues as vectors, with the weight modifying the vector length. However, simple additive or weighted vector sum models do not estimate the sensory signal noise which is invariably associated with sensory perception Green and Swets (1988).

1.3.4 Maxmimum likelihood estimation model

The maximum-likelihood estimation (MLE) model weighs each sensory input based on both the relative contribution and reliability of each sensory input, in order to produce a statistically optimal combination that reduces variance (noise) in the final multisensory percept (Alais & Burr, 2004; Edgeworth, 1908; Ernst & Banks, 2002; Ernst & Buülthoff, 2004; Landy, Maloney, Johnston, & Young, 1995). This model assumes that sensory inputs are combined linearly to produce a combined estimate that is maximally reliable (Fischer & Kornmüller, 1930). Accordingly, sensory signals which are more reliable (or less noisy) will be given more weight. The MLE has been applied to explain shifts in the subjective visual vertical (De Vrijer, Medendorp, & Van Gisbergen, 2008; Laurens & Droulez, 2007; MacNeilage, Banks, Berger, & Bülthoff, 2007), and has also been extended to include priors such as cognitive factors. More recently, MLE models of sensory integration have taken into account correlations between sensory modalities (Spence, 2011).

1.4 Explaining the time course of vection

The interplay among the many self-motion senses that has been discussed may explain the temporal features of visually-induced self-motion, such as the latency to vection onset and occurrences of vection dropout and decay. Consider the time course of vection induced by displays of radial or lamellar optic flow. Initially, a stationary observer viewing the moving display is confronted with two apparently conflicting signals: (1) the visual system registering self-motion from optic flow, and (2) vestibular signals indicating no self-acceleration; a state of visual-vestibular signal inconsistency which can explain the nausea associated with riding inside a moving vehicle (e.g., a car, train, boat, aircraft, and even space travel) or motion simulator (Oman, 1990; Reason, 1978; Reason & Brand, 1975). It is during this initial stage of vection that the observer correctly perceives the scene as moving and themself as stationary. However, as the vestibular organs do not respond to constant velocity but only to acceleration, the restraint that is initially imposed by the lack of vestibular inputs will no longer be a constraint (or "sensory conflict") and the observer will experience the sensation of self-motion.

Psychophysical studies of motion perception have shown that the vection time course depends on the type of optic flow, with heading perception for rotational displays having an onset latency of 3-14 s with “steady state” or exclusive self-rotation perceived around 8-12 s (Brandt, Dichgans, & Koenig, 1973) and linear vection requiring 1 s (Berthoz, Pavard, & Young, 1975). Observers are generally able to discriminate the direction of motion before experiencing self-motion (Berthoz, 1978). Interestingly, Brandt et al. (1973) found exclusively for rotational motion, that perceived self-rotation is consistent with the optic flow after 8-12 s, but may then reverse direction or gradually weaken or decay (Howard, 1986). These events are reflected in Figure 1.10 which shows an example time course of vection with a binary (yes/no) vection response, and onsets and dropouts (i.e., cessation of vection) indicated by the peaks and troughs of the blocks, respectively. It is unclear whether this habituation occurs at the point of vection saturation, since observers may also experience vection dropouts (i.e., the cessation of vection) and a return to vection throughout a viewing trial (Guterman, Allison, Palmisano, & Zacher, 2012), or other transient changes such as shearing or other distortions in the perceived direction of motion direction (Palmisano, Allison, & Howard, 2006), in their experience of self-motion.

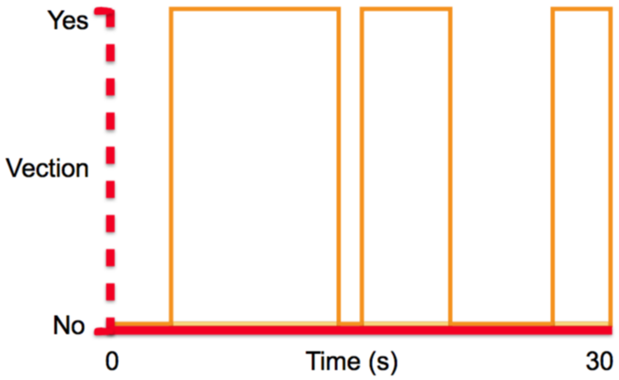

Figure 1.10: Illustration of vectors for an observer that is (A) stationary and upright viewing no visual motion, (B) stationary and upright with vection, (C) stationary and tilted with vection, and (D) in-motion and upright. Since the otoliths are accelerometers, tilt and linear acceleration (C and D) signals are ambiguous, and both are perceived as translational self-motion.

1.5 Overview of the dissertation

This dissertation explores how body orientation relative to gravity influences visual-vestibular interactions in the perception of self-motion. The relationship between these factors was investigated by positioning observers in upright and tilted body orientations viewed while viewing displays that induced the sensation of linear (radial and lamellar) self-motion.

In Chapter 2, I examined how modulating sensory conflict by adding viewpoint oscillation to vection displays and changing head orientation with respect to gravity, altered the likelihood and magnitude of forward and backward linear vection. I hypothesized that tilting observers would inhibit vection since the vestibular apparatus is particularly tuned for the dynamics of self-motion in upright observers (Hypothesis 2.1); vection would be promoted when the simulated direction of self-motion aligns with gravity (Hypothesis 2.2); and oscillating self-motion displays should enhance vection more than smooth optic flow as they mimic head movements that are common in walking and running (Hypothesis 2.3).

In Chapter 3, I further studied the effects of body orientation on vection, but also considered the influence of scene structure. I hypothesized that aligning the visual motion direction with gravity in upright observers would enhance vection (Hypothesis 3.1); when simulated self-motion is in a plane perpendicular to gravity, visual motion along the spinal axis would enhance vection (Hypothesis 3.2); and vection would be promoted by scene structure that is consistent with a stationary environment (Hypothesis 3.3).

In Chapter 3, I found that observers reported illusory tilt of the self-motion stimulus. In Chapter 4, I investigated this phenomenon and hypothesized that, there would be a consistent tilt effect for global motion (Hypothesis 4.1); this effect would be larger for motion stimuli than for static stimuli (Hypothesis 4.2); and the effect would be stronger for illusory self-motion compared to motion that is perceived as external to the self (Hypothesis 4.3).

Chapter 2

Influence of head orientation and viewpoint oscillation on linear vection

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2.1 Abstract

Sensory conflict theories predict that adding simulated viewpoint oscillation to self-motion displays should generate significant and sustained visual-vestibular conflict and reduce the likelihood of illusory self-motion (vection). However, research shows that viewpoint oscillation enhances vection in upright observers. This study examined whether the oscillation advantage for vection depends on head orientation with respect to gravity. Displays that simulated forward/backward self-motion with/without horizontal and vertical viewpoint oscillation were presented to observers in upright (seated and standing) and lying (supine, prone, and left side down) body postures. Viewpoint oscillation was found to enhance vection for all of the body postures tested. Vection also tended to be stronger in upright postures than in lying postures. Changing the orientation of the head with respect to gravity was expected to alter the degree/saliency of the sensory conflict, which may explain the overall posture-based differences in vection strength. However, this does not explain why the oscillation advantage for vection persisted for all postures. Thus, the current postural and oscillation based vection findings appear to be better explained by ecology: Upright postures and oscillating flow (that are the norm during self-motion) improved vection, whereas lying postures and smooth optic flows (which are less common) impaired vection.

2.2 Introduction

As we move through the world, multiple sensory systems provide feedback about our self-motion, with vision and the vestibular system playing dominant roles in this process but providing complimentary information. Based on the optical/retinal flow, vision is sensitive to most self-motions, including constant velocity motion (Dichgans & Brandt, 1978; Warren, 1995). By contrast, the vestibular system of the inner ear only senses self-accelerations—with its otolith organs and semicircular canals being specialized for the detection of linear and angular accelerations respectively (Howard, 1986). When the body is upright, vertical acceleration is mainly sensed by the saccule, whereas horizontal acceleration is predominantly sensed by the utricle, although the maculae of both have some sensitivity to motion in all directions (Corvera, Hallpike, & Schuster, 1958; Curthoys et al., 1999; Rosenhall, 1972). Importantly, the vestibular system cannot distinguish between travelling at a constant linear velocity and remaining stationary (as these two conditions are indistinguishable to an inertial sensor (Howard, 1982; Lishman & Lee, 1973; Warren, 1995).

The visual and vestibular systems also provide information about the direction of gravity, the most pervasive linear acceleration we encounter (for review see Howard (1986). The visual perception of the gravitational“up/down” is derived by static and dynamic visual orientation cues which are available in our optic array (e.g. Allison, Howard, & Zacher, 1999; Howard & Hu, 2001). Similarly, since the otolith organs of the vestibular system register forces related to linear acceleration including gravity, they are also sensitive to static/dynamic head tilt (Hain & Helminski, 2007). However, since the force of gravity acts on all parts of the body, non-visual signals to its direction and magnitude are provided not only by the vestibular system, but also by the skin (Horak, Nasher, & Diener, 1990), gut (Hunt, Knox, & Oginski, 1965), baroreceptors (Shimizu et al., 2002), and other proprioceptive and somatosensory sources. Thus, in the case of these non-visual senses, ambiguity can sometimes arise on account of having two sources of linear acceleration (self-motion and gravity).

Many real world situations, such as walking or driving a car, provide consistent visual and vestibular information about our self-motion. However, fixed-based simulators, which display visual motion to physically stationary observers, can also evoke (sometimes compelling) sensations of self-motion. Such visually-induced illusions of self-motion are known as “vection” (Fischer & Kornmüller, 1930). Sensory conflict is often assumed to play a critical role in vection (Zacharias & Young, 1981). For instance, visual-vestibular conflicts should be transient when vection displays simulate constant velocity self-motion, since the vestibular system does not respond to this type of motion. However, the initial acceleration from a stationary position up to the constant speed represented by this display would normally be detected by the vestibular system during real (as opposed to simulated) self-motion. Thus, it has been proposed that this type of visual-vestibular conflict might be responsible for the observed latency of vection—with the vestibular system initially suppressing vection induction for a brief period after visual stimulus onset (Zacharias & Young, 1981).

Sensory-conflict based models of visual-vestibular interactions in vection typically posit that vection responses should be modulated by the degree and saliency of the conflict. For example, in Zacharias and Young's (1981) model, vestibular self-motion signals are compared with a visually-derived, high-pass filtered analogue to estimate inter-sensory conflict. The vestibular signal is proposed to be dominant during situations of significant sensory conflict since it is a more reliable indicator of high-frequency head motion. Consistent with this theory, Lepecq and his colleagues (1999) found that erect subjects' vection onset latencies to unidirectional upward or downward visual self-motion displays were significantly (but weakly) correlated with their vestibular detection thresholds for equivalent real self-motion stimuli.

Similarly, since physiological, anatomical and psychophysical evidence suggests that the human utricle is more sensitive than the saccule, Giannopulu and Lepecq (1998) predicted that vection along the naso-occipital axis (sensed more by the utricle) would generate greater sensory conflict than vection along the spinal axis (where the saccular response predominates) in erect observers. In agreement, they found that vection onset latencies were shorter for up or down motions along the spinal axis than for forward or backward motions along the naso-occipital axis. One complication in interpreting the data from this study arises from the fact that the translations along the naso-occipital and spinal axes—besides preferentially stimulating the utricles and saccules, respectively, of erect observers—also differed in orientation with respect to gravity; had observers been lying on their side (shoulder down), then both of the displays would have moved orthogonal to gravity.

This confound has several aspects worth considering including the facts that: 1) the vertical but not the horizontal acceleration signal is superimposed on a generally larger gravitational acceleration, 2) the saccular and utricular signal processing have evolved and developed to deal with a predominantly erect posture and thus a superimposed gravity signal and tilt sensitivity respectively, 3) gravity provides a constant acceleration signal in contrast to the limited periods of acceleration resulting from natural head movements, and 4) extended periods of horizontal motion are more ecologically relevant than vertical motion. By varying posture one can partially (but not completely) dissociate the direction of gravity with respect to the head, the direction of vection, and otolith sensitivity. For instance, in a supine posture the utricle becomes more vertical and thus sensitive to vertical acceleration but also becomes loaded by the superimposed gravitational acceleration.

Two previous studies have examined the roles that orientation with respect to gravity plays in linear vection. In the first of these studies, Kano (1991) used pairs of displays that presented 2-D optic flow simultaneously to the left and right visual fields of his stationary observers, who were either seated upright (Experiment 1) or lay supine (Experiment 2). These peripherally viewed (constant velocity) optic flow displays moved together in a direction that was either parallel or orthogonal (in a naso-occipital direction) to the observer's spinal axis in both postures. Like Giannopulu and Lepecq (1998), Kano found that for upright seated observers, the latencies for vertical self-motions (up and down) were significantly shorter than those for horizontal (forward and backward) self-motions. However, a different pattern of results was found when supine. In these conditions, vection latency was shorter when the self-motion was perceived to be either towards the feet or gravitationally downward towards the back (compared to when self-motion was perceived to be toward the head or gravitationally upward towards the front). Kano concluded that vection latency is not determined by egocentric or gravitational direction alone. Instead there was an interaction between gravitational and body-centric information.

Kano (1991) reported that overall vection onset latencies were shorter in supine compared to upright posture, but that this effect was not significant. Tovee (1999), however, analyzed Kano's results and noted that vection latency for simulated forward motion, along the naso-occipital axis, was shorter in supine than upright conditions (Kano did not comment on this comparison). Tovee argued that in the supine posture, the constant acceleration signal due to gravity should support rather than restrain this forward vection. To further investigate the influence of posture on forward vection, Tovee presented observers with simulated forward (along the naso-occipital axis) motion through a virtual hallway using a stereoscopic helmet-mounted display in both upright and supine postures. Contrary to expectations, subjects experienced vection more frequently and onset latencies were shorter (but only by about 500 ms on average for trials where vection occurred) for upright compared to supine conditions. Regardless of posture, the subjects tended to report feeling upright, travelling in the horizontal direction perpendicular to gravity through the hallway. Thus, visual and cognitive cues that promoted the percept of a hallway rather than an earth-vertical shaft seemed to overcome vestibular and proprioceptive signals indicating they were supine. The author argued that the conflict between visual and vestibular gravitational orientation cues might have caused the increased delay in the onset of vection in supine conditions.

As well as modifying vestibular sensitivity to assess the effects of sensory conflict and concordance on visual-vestibular interaction in vection, one can also vary the visual stimulus. Unlike constant velocity self-motion displays, optic flow indicating continuous variation in head velocity would normally be accompanied by significant and sustained vestibular activity. According to sensory conflict theories, the absence of this expected vestibular activity should generate visual-vestibular conflict, which in turn should continue to impair vection induction. However, this notion has been strongly challenged by recent findings that adding simulated viewpoint jitter or oscillation to patterns of radial optic flow simulating constant velocity motion can enhance vection—decreasing vection latency and increasing both vection durations and strength ratings (Palmisano et al.,2008; 2011; 2007; 2003; 2000). Viewpoint jitter or oscillation refers to perturbations of the viewpoint used to render the scene (virtual camera position) and hence the perspective image. The effect is similar to the flow resulting from the bob and sway of the head that typically accompanies locomotion or vehicular travel. These jitter and oscillation advantages for vection have always been tested when the observer was upright (typically seated) with the head and body aligned with the direction of gravity.

One goal of the present study was to see whether vection and the above mentioned simulated viewpoint oscillation advantage for vection change with observer posture and orientation with respect to gravity. Changing orientation with respect to gravity changes the dynamic response of the otoliths to gravity and linear acceleration. For instance, in a supine individual the saccular maculae should be more sensitive to oscillatory motion that is orthogonal to the gravitational axis than to motion parallel to gravity. By varying posture we can make the gravity vector congruent with or orthogonal to the main direction of simulated self-motion and/or to the oscillation component. Manipulation of these factors could modulate the effects of sensory conflict. Table 2.1 shows the relationship among postures, gravity, oscillation direction, and principal otolith sensitivity. The utricle is normally considered to be a more effective sensor of self-motion than the saccule (Malcolm & Melvill-Jones, 1974; Rosenhall, 1972). In prone and supine postures the utricle is sensitive to vertical acceleration; however, it is also loaded by the superimposed gravitational acceleration. Of the postures to be tested, the left side down position is unique in that the role of the utricle and saccule in sensing motion along the gravity axis is swapped compared to the erect posture. It is expected that these changes in sensitivity to gravity will inhibit vection since the vestibular apparatus may be particularly tuned for the dynamics of self-motion in upright observers.

		Display Oscillation Relative to Gravity		Otolith Sensitivity Bias to Gravity	
Posture	Gravity Relative to Self	x-axis	y-axis	Utricle	Saccule
Upright	y-axis	orthogonal	aligned	–	∗
Supine	z-axis (+)	orthogonal	orthogonal	–	–
Prone	z-axis (-)	orthogonal	orthogonal	–	–
Left Side	x-axis	aligned	orthogonal	∗	–

Table 2.1: A summary of the relationship between body-centric and gravito-centric frames of reference in the different posture and oscillation conditions. For each posture the table shows 1) the direction of gravity in body-centric terms, 2) the gravity-centric direction of x-axis and y-axis display oscillation, and 3) the gravity sensitivity of the utricle and saccule. In the last two columns an asterisk indicates that the given macula is oriented for high sensitivity in the direction of gravity.

Alternatively, an ecological account of vection would suggest that—apart from special situations such as swimming—traveling while supine, prone or lying on one's side are all unusual (i.e. non-ecological). Therefore, we might expect to find that vection is stronger when the observer is upright as opposed to lying down. Consistent with this ecological account, it has been suggested that the jitter/oscillation advantage for vection may be due to jittering/oscillating optic flow mimicking the bob, sway and lunge common to walking/running (Bubka & Bonato, 2010; Palmisano et al., 2011). Thus, it is possible that the oscillation advantage for vection may disappear when the observer is no longer upright if it is ecological in origin.

2.3 Methods

2.3.1 Participants

Ten graduate students and staff (Main experiment: 3 males, 7 females; mean age = 30, *SD* = 8.88; Control experiment: 4 males, 6 females; mean age = 30.5, *SD* = 8.64) from the York University community participated in this study. All had normal or corrected-to-normal vision and reported no vestibular impairment. Four of the participants had no prior experience with illusions of self-motion in a laboratory setting and underwent several practice sessions to ensure they were comfortable with the task. Written informed consent was obtained in accordance with a protocol approved by the York University Research Ethics Board.

2.3.2 Apparatus

The optic flow displays were generated on an IBM Lenovo T61p laptop with a 15.4 inch TFT display with a resolution of 1280 (horizontal) x 800 (vertical) pixels and refresh rate of 60 Hz. A custom Python program using the open-source libraries Visual Python (VPython) for the visual displays and Pygame for gamepad control was installed on each laptop. Each laptop was attached to a rigid frame to form a workstation that could be mounted and oriented to accommodate different body postures.

Posture was varied with respect to gravity. For the upright-seated posture, the observer's head was aligned with the display using the height adjustment of the chair or wood blocks beneath the workstation (see inset in Figure 2.1). For the upright-standing posture, subjects requiring height adjustment stood on appropriately sized, stable, wooden blocks (see Figure 2.1). For lying postures, the subject was appropriately positioned so that the head was centered on the screen. A massage table was used for the lying postures and the displays were mounted on steel stands. The "prone" display was mounted below the headrest of the table, the "supine" workstation was mounted above the table, and the "left side down" display at the side of the table. All displays were aligned with the orientation of the head (See Figure 2.1).

The viewing distance and visual angle were defined by a circular, black neoprene viewing tube that was fitted to the display. The tube had a length of 0.30 m (observer-to-screen distance) and subtended a visual angle of 39°. A secure fit of the tube prevented light leakage, and a matte interior limited reflections off the surface of the display.

Responses were recorded with a Logitech R Dual Action Gamepad. Observers wore earplugs to mute any environmental noise, which otherwise might have distracted them or provided orientation cues.

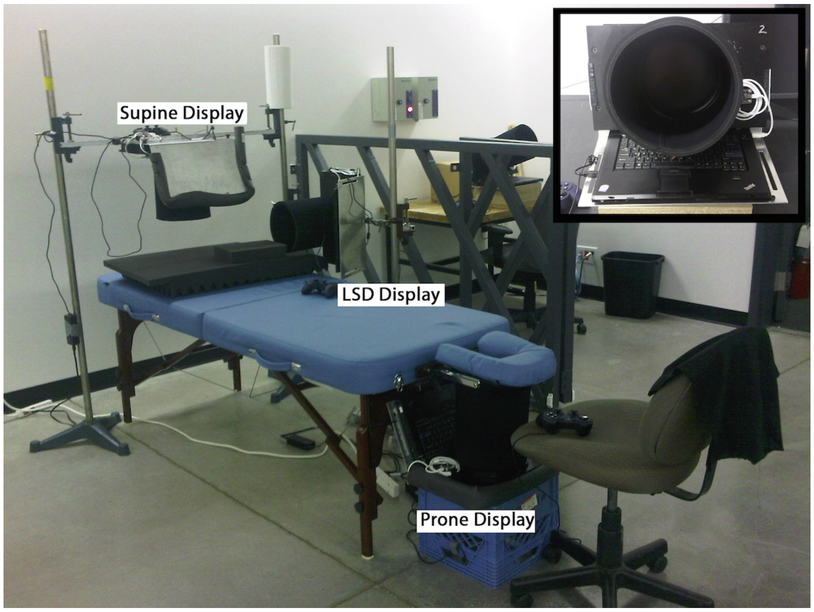

Figure 2.1: Photograph of the display and table for the lying down body postures. The inset shows the workstation containing the laptop with shroud. The workstations for prone, supine and left side down postures are mounted to the table and labelled. For the prone position the subject viewed the display through the open face rest of the massage table and, to account for the thickness of the pillow, the shroud was adjusted to maintain viewing distance.

2.3.3 Visual Displays

The self-motion displays were 3-D animations (frame rate of 60 Hz) of translation through a field of 600 randomly distributed, stationary, blue spheres (16.72 cd/m^2) on a black background (0.64 cd/m^2). The spheres had a simulated physical radius of

7.5 cm, and were randomly positioned in space to form a 3-D cloud of spheres that extended 30 m along the depth or visual axis and ±5 m horizontally and vertically along the motion path. Spheres were not drawn inside a small circular region (radius 5 cm) at the centre of the display, so as to avoid simulated collisions with the observer's head. Radially expanding or contracting flow was used to simulate smooth self-motion along the naso-occipital axis at 1.33 m/s through this stationary cloud. When simulated horizontal or vertical (with respect to the head) viewpoint oscillation was added to the display, this sinusoidal oscillation had an amplitude of 0.28 m/s peak velocity and a frequency of 2 Hz. Figure 2.2 illustrates the positional relationship of an upright body to self-motion with vertical oscillation. When any sphere moved beyond the field of view (off screen) it was redrawn at the same horizontal and vertical coordinates but at the maximum depth represented by the cloud.

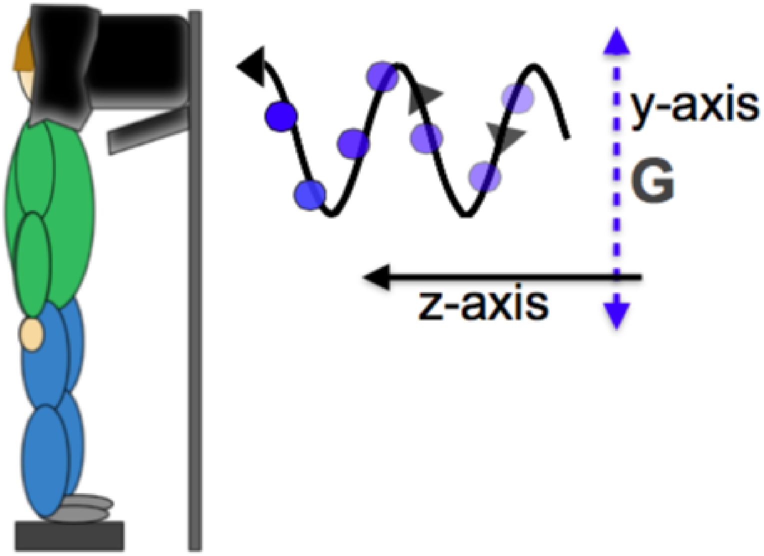

Figure 2.2: Illustration depicting an upright observer viewing a display simulating forward self-motion with vertical oscillation. Note: This figure is supplementary to the original article.

2.3.4 Design

There were three independent variables. (1) Body posture: upright (seated), and lying supine, prone, and left side down. (2) Optic flow type: smooth motion or motion with horizontal (x-axis) or vertical (y-axis) oscillation (with respect to the head). (3) Optic flow direction: forward (radial expansion) or backward (radial contraction) self-motion (with respect to the head). Each of the 24 factorial combinations of these conditions was repeated 4 times for a total of 96 trials. The trials were blocked by posture and, within each posture block, blocked again by flow direction. Within each posture-direction block, the 12 trials for all combinations of the remaining variables (flow type and repeat) were pseudo-randomly ordered. The blocks were ordered using a counterbalanced Latin-Square design. Experiment 2 (control study) used a similar design, comparing the seated (folded legs) and standing (extended legs) postures.

For each trial we obtained: 1) an overall vection strength rating, 2) the latency to vection onset, and 3) the total vection duration. Vection dropouts were identified by the release of the vection response button after the initial vection response on a trial (to count as a dropout, releases were required to last at least 250 ms to filter out accidental releases). We calculated four vection dropout measures for each trial: 1) number of dropouts in a trial, 2) time of the first dropout, 3) mean dropout duration, 4) total dropout duration, and additionally we calculated the proportion of trials with dropouts.

2.3.5 Procedure

Participants were informed that they would be viewing a series of movies of blue spherical objects in a computer-generated world. They were told to freely look around the display while attending to their feeling of self-motion. For each posture block, the participant was appropriately positioned. For all postures, the head was aligned with the trunk of the body, and the legs were extended in all but the upright posture. After approximately 60 s in that posture, the first display they were shown was a smooth radial flow pattern (expanding or contracting as appropriate for the block), which served as a standard stimulus (which they were told was to be assigned a vection magnitude of 50) to base their responses upon. During all of the subsequent trials in the block, participants pressed one of the shoulder buttons on the gamepad if they experienced vection (i.e. feeling of self-motion), and continued to hold this button down until the trial ended or the sense of vection disappeared.

Each experimental trial began with a 3-s inter-stimulus interval with the screen blank followed by the 30-s stimulus display. After each trial, observers rated their vection magnitude relative to the standard stimulus. If the feeling of self-motion was twice as strong (or more) than the standard, they were told to set the rating to 100. If the observer did not feel like they were moving, they were instructed to select a rating of 0. This rating scale had a resolution of 5 unit steps. The sequence of events are illustrated in Figure 2.3.

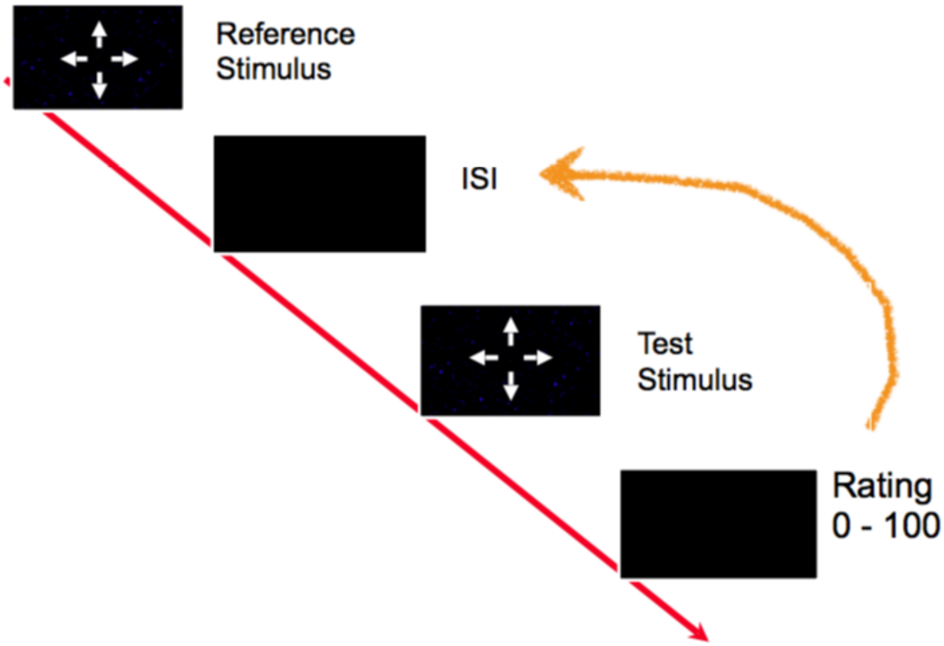

Figure 2.3: Diagram of the sequence of experiment events showing the 1) Reference stimulus, 2) Interstimulus interval (ISI), 3) Test stimulus, and 4) Response screen. After the rating screen, the sequence repeats starting with the ISI and ends when all of the trials have been rated. Note: Figure not in the original publication.

After the first block of 12 trials in one direction, observers were presented the standard and a set of 12 trials in the opposite self-motion direction. After blocks in both directions (24 trials) for a given posture, participants were placed into the next body posture and repeated the above procedure.

2.4 Results and analysis

One subject reported no self-motion (vection rating of 0) for 40% of the trials, particularly in the lying postures, and so was excluded from the dataset. In the remaining subjects, vection was reported for 861 of the 864 trials. Separate statistical models were fitted for each of the response measures.

Linear mixed effects (lme) regression models were fitted with fixed effects (namely body posture, 4 levels; optic flow type, 3 levels; and optic flow direction, 2 levels) and a random effect (to model inter-subject subject variability) using the R package nmle (http://cran.r-project.org/web/packages/nlme/). The response measures for vection onset, duration, dropout frequency, and mean and total dropout duration, were logarithmically transformed to reduce skew and improve normality. Normality of vection ratings was improved with a Box-Cox transformation. We adopted stepwise selection with Akaike's Information Criterion (Akaike, 1987) to select the final models. The final regression model varied for each response measure. For the vection ratings, body posture, optic flow type, and optic flow direction were selected for the model. For vection onset and duration, only optic flow type and body posture were selected. Of the vection dropout measures, we only found significant effects on the number of dropouts in a trial (only optic flow type selected), and the proportion of trials with dropouts (flow type and posture selected in a logistic regression). Although we were interested in whether the oscillation enhancement of vection was modulated by posture, the stepwise selection indicated that there were no significant interactions between optic flow type and body posture. Family-wise error was controlled for with Bonferroni correction and the adjusted p-values are shown for post-hoc analyses.

The results for vection ratings, onsets, and durations are shown in Figures 2.4 - 2.6. Oscillating radial flow displays produced significantly stronger vection ratings, shorter vection onsets, longer vection durations, and fewer trials with vection dropouts than smooth radial flow (main effect of optic flow for ratings: $F_{2,846} = 197.05$, $p < .0001$; onset: $F_{2,850} = 10.43$, $p < .0001$; duration: $F_{2,850} = 13.47$, $p < .0001$; proportion of trials with dropouts: ${\chi^2}_{2,861} = 6.51$, $p = .04$). Horizontal oscillation tended to result in more vection dropouts in a trial ($F_{2,850}=3.77$, $p=.02$), otherwise, there were no significant differences between mean vertical oscillation and horizontal oscillation data for any response measures (p's $> .05$).

Body posture also significantly affected vection strength ratings ($F_{3,846} = 10.66$, $p < .0001$), onsets ($F_{3,850} = 3.70$, $p = .0116$), durations ($F_{3,850} = 6.21$, $p = .0004$), the number of vection dropouts in a trial ($F_{3,850} = 8.71$, $p < .0001$), and the proportion of trials with dropouts (${\chi^2}_{3,858} = 22.77$, $p < .0001$). Subjects generally experienced less compelling vection when lying down than the sitting upright. The left side down condition—which oriented the head so that otolith sensitivity was reversed (utricle rather than saccule sensitive to motion along the gravity vector)—resulted in the weakest sensations of self-motion. Compared to erect posture data, when lying left side down, vection had a smaller magnitude (z = 5.50, p = .003), took longer to develop (z = -3.15, p = .01), had a shorter duration (z = -4.20, p < .003) and produced more trials with dropouts (z = -4.81, p < .0003). Similarly, vection had smaller magnitudes (z = 3.48, p = .004) when lying prone versus sitting upright. These effects were weaker for the supine posture, and vection magnitude did not significantly differ from upright when supine (z = 2.15, p = .2). Although no interaction between optic flow type and body posture was selected with AIC, we observed that in the prone posture, subjects viewing smooth radial flow tended to have shorter vection onsets and longer vection durations than when upright.

While there was no significant main effect of optic flow direction (forward or backward), there was a significant interaction between optic flow direction and body posture but only for observers' ratings of vection strength ($F_{3,846} = 2.65$, p < .048). This effect was marginally significant and post-hoc analysis did not provide any clear pattern except a trend that simulated backwards self-motion produced higher average vection ratings than simulated forwards self-motion in the prone posture (z=-2.09, p=.07). There was no difference between the supine and prone posture in mean vection magnitude for forward self-motion (z=-1.06, p=.9).

Although there was no interaction between optic flow type (smooth or horizontal/vertical oscillation) and body posture, we observed that prone subjects viewing smooth optic flow had shorter vection onsets and longer vection durations.

A control experiment compared upright seated with the upright standing posture to see if the above findings showing improved vection when upright compared to lying down, could be explained by differences in sensitivity to vection when the legs were extended (lying) compared to bent (seated upright). The results were mixed—compared to sitting, standing produced lower vection ratings ($F_{1,417} = 5.00$, $p = .03$), but significantly longer vection durations ($F_{1,419} = 26.08$, $p < .0001$) and fewer dropouts ($F_{1,419} = 8.56$, $p = .004$), with no difference in latency ($p > .05$). Furthermore, the magnitudes of the effects were much smaller than the postural effects reported in the main experiment. Unlike the main experiment, optic flow direction had a significant effect with forward vection displays producing higher vection estimates ($F_{1,417} = 5.19$, $p < .02$), shorter latencies ($F_{1,422} = 7.52$, $p < .006$) and slightly longer durations ($F_{1,419} = 3.68$, $p < .06$) compared to backwards vection (generated by radially contracting flow), but conversely more frequent vection dropouts in a trial ($F_{1,419} = 14.79$, $p = .0001$) and a greater proportion of trials with dropouts ($F_{1,427} = 6.05$, $p = .01$) than backward vection. Some observers reported awareness of body sway and that vertical oscillation felt more natural while standing.

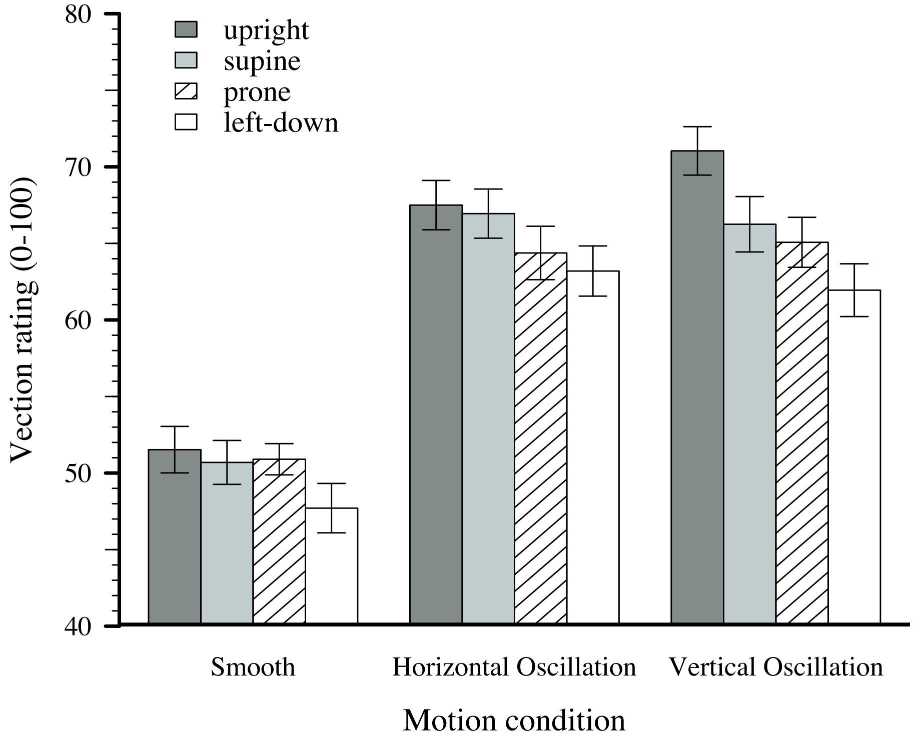

Figure 2.4: Mean vection strength rating (±1 standard error of the mean (SEM), 9 observers). The three motion conditions were smooth radial flow with no oscillation, or with horizontal or vertical oscillation (in display-centric coordinates). Observers based their magnitude estimates on a sample stimulus of smooth radial flow presented before each block of trials. Since the smooth radial flow displays were the same as the sample stimulus, it was expected that the ratings would have an approximate mean rating of 50.

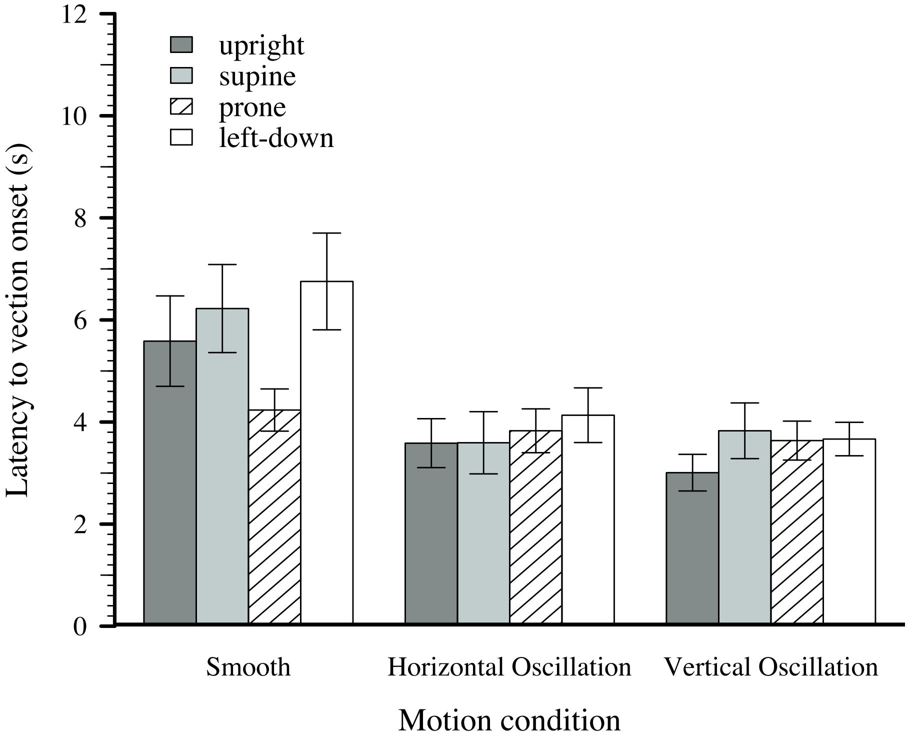

Figure 2.5: Mean vection onsets (±1 SEM, 9 observers). The three motion conditions were smooth radial flow with no oscillation, or with horizontal or vertical oscillation (in display-centric coordinates).

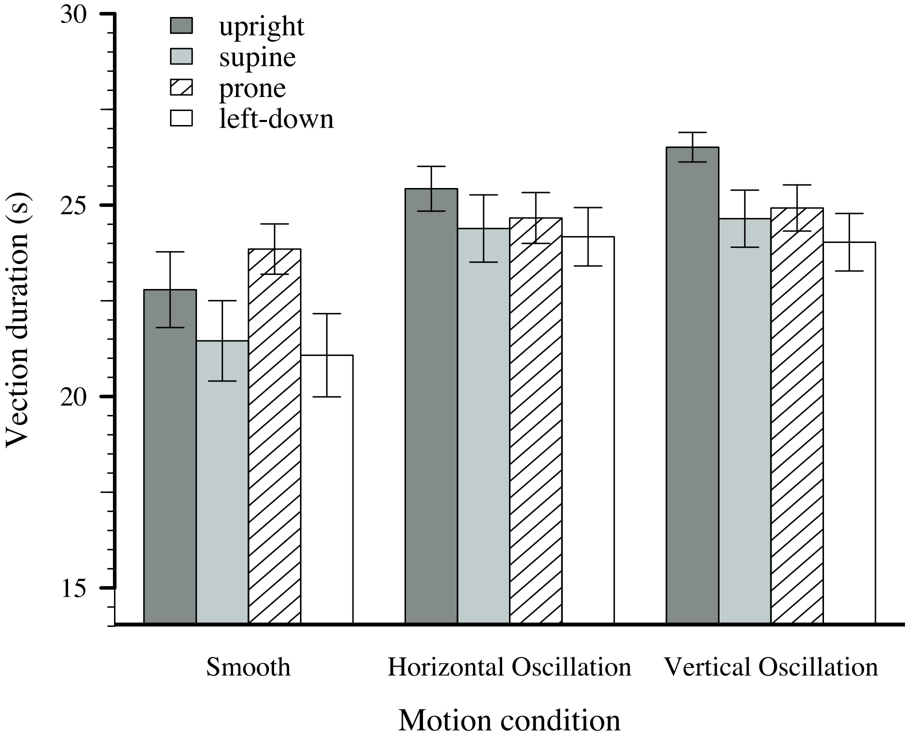

Figure 2.6: Mean vection durations (±1 SEM, 9 observers). The three motion conditions were smooth radial flow with no oscillation, or with horizontal or vertical oscillation (in display-centric coordinates).

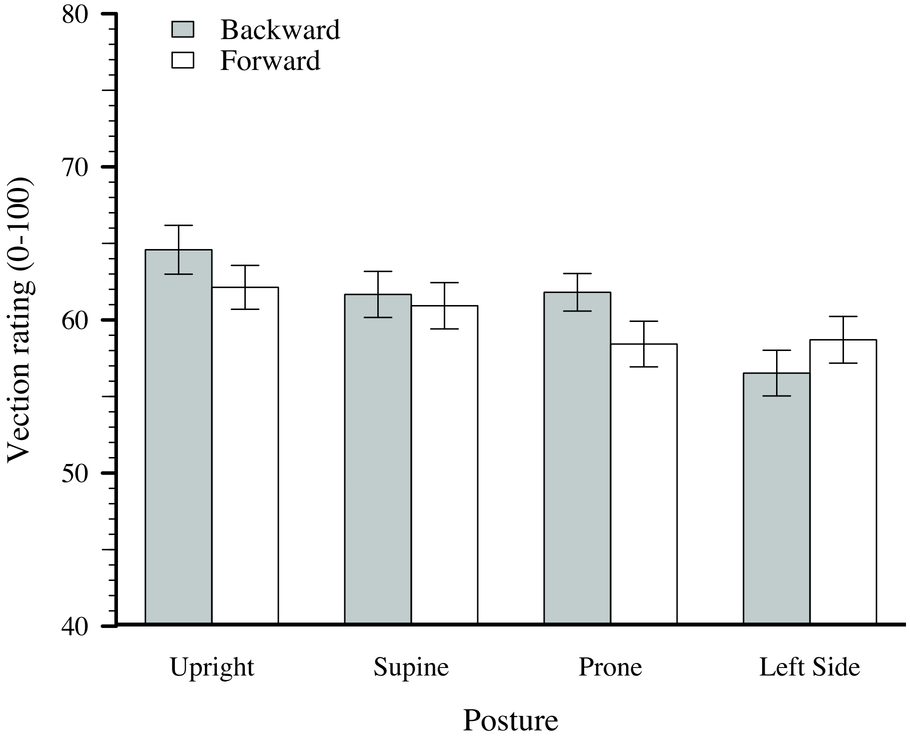

Figure 2.7: Mean vection strength rating as a function of body posture and motion direction (±1 standard error of the mean (SEM), 9 observers).

2.5 Discussion

We investigated whether vection, and the enhancement of vection by simulated viewpoint oscillation, were affected by head orientation with respect to gravity. Contrary to the predictions of sensory conflict theories, our results demonstrated that oscillating radial displays produced more provocative sensations of self-motion than smooth radial flow displays. Adding viewpoint oscillation to radial optic flow increased vection ratings for all postures. Viewpoint oscillation also increased vection duration and decreased vection latency compared to smooth radial flow for all postures. However, Figures 2.5 and 2.6 appear to show that oscillation advantage was noticeably weaker in terms of the vection time course for the prone posture. It is interesting to note that of all the postures tested, the prone posture produced the shortest vection latency and the longest vection duration when smooth radial flow was shown. These observations may reflect changes in sensitivity due to the orientation of the otolith maculae, which would be angled downward (membrane side down) and toward the resultant force of gravity. Alternatively it may reflect sensitivity to the pressure placed on the front of the body, which is more sensitive than the back of the body (Weber, 1834). Overall, the finding of an oscillation enhancement is consistent with Palmisano et al. (2000, 2007, 2008), who first showed jitter and oscillation advantages for vection in upright observers. The persistence of this viewpoint oscillation advantage for vection, across all the postures and orientations tested here, further strengthens the challenge that these effects pose for sensory conflict theories.

In principle, one might expect differences in the vection advantages produced by horizontal and vertical oscillation, since upright observers have differential vestibular sensitivities to head motions along these vectors (Malcolm

& Melvill-Jones, 1974). However, we found no significant differences in the vection magnitudes, latencies or durations induced by vertical and horizontal oscillation. Vestibular sensitivities to horizontal and vertical head motions should have been reversed in the left side down posture. This posture was also the only condition in which the horizontal oscillation was orthogonal to the visual direction of self-motion but aligned with the gravity vector. If the perception of self-motion depends more on head orientation with respect to gravity, it might be posited that a swap in otolith sensitivity would result in both different responses to horizontal and vertical viewpoint oscillation, and reduced vection when left side down, compared to the upright posture. While we found lying left side down resulted in the weakest vection there were no differences in sensitivity to horizontal and vertical viewpoint oscillation. It is possible that this role reversal may have simply exceeded the tolerance for sensory conflict.

Consistent with prior studies, the erect posture produced vection with shorter latencies, longer durations, and larger reported magnitudes than most of the lying postures. Recall, that in discussing Kano (1991), Tovee (1999) suggested that in the supine posture, the constant acceleration signal due to gravity should support rather than restrain forward vection (and by logical extension the prone posture should promote backward vection). However, contrary to this proposal we found no difference in the strength of the forward vection induced in supine and prone postures. Although there was a trend that backwards vection was improved when prone, this effect was not significant. Ecologically, there is little reason to expect that a constant acceleration due to gravity should support the perception of constant velocity motion in the same direction. Such an arrangement is not consistent with a real constant velocity translation along the naso-occipital direction, which would be accompanied by a transient otolith signal—a sustained otolith signal that is constant before, during and after the vection stimulus would indicate continuous acceleration which is most likely to be due to gravity. An erect observer should experience a transient change in the orientation of the resultant gravito-inertial vector at the start of motion and the utricle should be better positioned to sense the horizontal component of this change (Malcolm & Melvill-Jones, 1974).

Our results share some similarities with Kano (1991), reinforcing the notion that both gravitational and body centric information play an important role in the perception of self-motion. Based on cross-experimental comparisons, Kano concluded that vection was determined by an interaction between gravitational and body centric information. However, there was not strong support for this proposal from the current results—the upright posture consistently produced more compelling vection, and the effects of optic flow type remained relatively constant. As our vection always simulated self-motion along a naso-occipital direction, our results cannot be directly compared to Kano's. It is however possible to compare postural effects with previous work by Tovee (1999) who directly compared vection in upright and supine observers. Apparently in contradiction to our finding of weakened vection in lying postures (and to a degree, Kano), she found no appreciable difference in the perceived vection magnitude between seated upright and supine subjects. This can be reconciled by noting that, in both the present study and that of Tovee, the reference stimulus was presented prior to each block. Any effect of posture should also apply to the reference stimulus and, therefore, while vection magnitude is a useful measure of the effects of various parameters on vection strength within a block (posture), it does not permit meaningful direct cross-posture comparisons of vection magnitude. On the other hand, Tovee did report that the proportion of trials eliciting a vection response was lower in supine compared to upright postures. This measure does allow for cross posture comparisons and is consistent with our finding that vection dropouts were more frequent, vection latency longer and vection duration shorter in supine (and other lying postures) compared to the seated posture. Given that the method used to estimate magnitude should not allow for establishing inter-posture differences in vection magnitude, our finding that it significantly affected the perceived magnitude requires discussion. It is likely that the variation in absolute vection strength influenced vection ratings despite presentation of a standard in each posture, or that subjects simply rated their experience relative to the previous postures.

Additionally, changing the orientation of the head with respect to gravity affects vestibular sensitivity and can be used to modulate visual-vestibular conflict. Young, Oman, and Dichgans (1975) reasoned that tilting the head away from upright reduces the sensitivity of the otoliths (Graybiel, Johnson, Money, Malcolm, & Jennings, 1979; Graybiel & Patterson, 1954) making them less effective in suppressing visual tilt information. However, if tilting or pitching the head with respect to gravity makes the vestibular signal a less reliable indicator of self-motion, then we would have expected increased rather than reduced vection when lying down. Furthermore, it is possible that the weighing of the otolith signals is calibrated for the upright head.

Our pattern of results indicate that orientation with respect to gravity has a significant influence on linear vection. Oman et al. (2003) investigated the role of gravity in looming linear vection while space shuttle astronauts were free-floating or restrained in micro-g levels during orbital flight, as well as when placed in the supine and upright posture during pre and post-flight (one-g) tests. Contrary to our findings, they reported that pre-flight latencies did not differ reliably between supine and upright postures. However, they did find that vection responses were significantly affected by micro-g with both latencies reduced and magnitude estimates increased in free-floating micro-g, compared to 1-g tests. This was consistent with a hypothesis of increased weight on visual cues after adaptation to micro-g conditions. Anchoring the subjects firmly to the floor of the spacelab with constant force springs to partially simulate loading of gravity on the lower limbs reduced vection in two of the three astronaut observers. Similarly, in the present study a control experiment to examine the possible effects of lower body extension showed that standing observers (body extended condition) experienced longer vection durations, but had an overall lower quality of vection than seated observers (reflected by weaker ratings and more vection dropouts)—although, it is possible that postural sway could account for the reduced vection while standing.

Several ecological factors could account for the erect posture and oscillation advantages for vection. For example, we are typically in an upright posture when translating naturally through the world when walking or driving. Also, it may be that oscillation mimicked the head bob, sway or other motion that occurs while walking (Macadar, Wolfe, O'Leary, & Segundo, 1975). The general lack of difference between horizontal and vertical oscillation may simply reflect that the body in motion moves (bobs and sways) along several axes of motion. Oscillation also enhanced vection in lying postures, supporting the notion that visually induced self-motion is dependent on the egocentric direction of motion in the stimulus regardless of posture.

Postural effects are also consistent with an ecological account of vection.

Lying postures are less common during self-motion and were found to impair vection. An observation of stronger vection (in terms of onset and duration) for smooth radial flow in the prone posture than in the upright or other lying postures, may simply reflect that naso-occipital self-motion along the gravity axis typically occurs when falling, and it is possible that this association could have elicited a heightened response in our observers particularly for vection latencies (Lepecq, Giannopulu, Mertz, & Baudonnière, 1999).

Changing the orientation of the head with respect to gravity was expected to alter the degree/saliency of the sensory conflict, which may explain why vection tended to be stronger in upright postures than in lying postures. However, sensory conflict cannot explain why the oscillation advantage for vection persisted for both upright and lying postures. Furthermore, contrary to the notion that vection might vary based on the vestibular sensitivity to the type of self-motion being simulated, horizontal and vertical oscillation were both found to improve vection induced by to our radial motion displays in a remarkably similar fashion. We conclude that the current postural and oscillation based vection findings are best explained by ecology. According to this view, the upright posture and oscillating flow display both facilitated vection because these are the norm during real self-motions. By contrast, lying postures and smooth optic flows reduced vection because they are unusual/atypical in our experience of self-motion.

Chapter 3

Higher-order cognitive processes moderate body tilt effects in vection

3.1 Introduction

The act of moving in an environment generates a pattern of optical flow that can indicate the direction and magnitude of self-motion. As well, a stationary observer viewing a similar flow pattern can experience compelling illusions of self-motion. This illusory percept of self-motion and has been termed "vection" (Mach, 1875). A common experience of vection is the "train illusion," in which a passenger in a stationary train observes another train moving on an adjacent track and experiences a strong sense of self-motion in a direction opposite to the moving train. Both of these cases of self-motion (real and illusory) result in a similar percept. Determining self-motion depends on feedback from multiple sensory cues, including visual, vestibular, proprioceptive, tactile (Horak et al., 1990), and interoceptive (Hunt et al., 1965; Shimizu et al., 2002). Of these self-motion senses, vision and the vestibular system play dominant but complementary roles.

In natural surroundings, it would be unusual for a stationary observer to see a large portion of their surroundings move (Dichgans & Brandt, 1978)—i.e, to be presented with global optic flow. Accordingly, when a large segment of our viewable surroundings are moving, we tend to attribute this motion to self-motion (Riecke, Schulte-Pelkum, Avraamides, von der Heyde, & Bülthoff, 2006).

The vestibular system also signals self-motion. The otolith organs and semicircular canals sense self-acceleration, including linear and angular self-accelerations, respectively (Howard, 1986). In the case of an upright and translating observer, vertical self-translation is predominantly sensed by the saccules and horizontal translation by the utricles– though both are sensitive to motion in all directions (Corvera et al., 1958; Curthoys et al., 1999; Rosenhall, 1972). Additionally, the vestibular organs are mechanical inertial sensors, and therefore cannot distinguish between being stationary and constant velocity motion (Howard, 1982; Lishman & Lee, 1973; Warren, 1995).

Together, the visual and vestibular systems inform us about self-motion, and the direction of gravity—a constantly imposed acceleration (Howard, 1982). The visual system is able to estimate the gravitational "up/down" by static and dynamic orientation cues, which are grounded in assumptions about the physical world–e.g., a tree trunk is rooted in the ground, and a tossed object falls toward the earth. Likewise, the otolith organs detect linear acceleration due to gravity, and hence signal the direction of gravity. Varying posture has been shown to modulate experiences of visually-induced self-motion (Guterman et al., 2012; Kano, 1991). This may be due to tilt dissociating the direction of gravity with respect to the head, the direction of vection, and otolith sensitivity. This last dissociation is because the otoliths are particularly selective for motion along certain directions including the vertical, the normal direction of gravity. Otolith sensitivity to head tilt was examined by Young et al. (1975) who found that tilting the head tilt influenced visually induced sensations of self-pitch and roll, and attributed this to reorientation of the macular planes relative to gravity. These tilt effects on illusory self-motion suggest that the vestibular apparatus might be particularly tuned for self-motion in upright individuals. If the vestibular organs' response to accelerations from self-motion and gravity is most precise with an upright head, this could explain the potential for errors in self-motion estimates in tilted observers. However, by superimposing the direction of a visual motion signal on the larger gravitational signal by tilting the head, we may examine the effects of gravity on self-motion perception.

Information about head orientation relative to gravity is important for extracting self-acceleration from the gravito-inertial vector—the sum of the acceleration vectors due to self-motion and gravity (Mittelstaedt, 1983). When these vectors are parallel, the resulting gravito-inertial vector only changes in magnitude, but when self-acceleration is orthogonal to gravity it affects the direction and the magnitude of the gravito-inertial vector. For instance, if one moves vertically then an earth-vertical acceleration signal would be superimposed on a larger gravitational acceleration (Guterman et al. (2012)–see Chapter 2). Evidence of gravitational effects on self-motion were reported by Kornilova, Mueller, and Chernobylskii (1995), who found asymmetries and inversions in vertical linear vection when observers were in microgravity. Our perceptual orientation with respect to gravity is complex, and studies have shown that the interpretation of acceleration signals in the perception of self-motion can be influenced by higher-order cognitive factors.

While much of the research on self-motion perception has taken a "bottom-up" approach and focused on the roles of the visual and vestibular system, vection and other self-motion studies using virtual reality have demonstrated that cognitive or "top-down" mechanisms can affect the intensity, onset, and realism, of visually-induced self-motion. These findings are in line with Wann and Rushton's (1994) stress on the use of naturalistic or more ecologically relevant visual stimuli, in the study of self-motion perception. Accordingly, Steen and Brockhoff (2000) used a flight simulator simulating linear and circular self-motion and found that vection saturation was enhanced when the motion in the scene was more naturalisitic. Similarly, Riecke et al. (2006) presented observers with naturalistic (coherent and incoherent/scrambled) and unnaturalistic 3D scenes of simulated self-motion using a dome projection setup, and found that scenes that were both coherent and naturalistic enhanced vection and "convincingness" of the illusory sensation of self-motion. Riecke et al. posited that such scenes provide the viewer the impression of a more stable visual environment, and thus the visual motion is more likely to be attributed to self-motion than external motion.

In this chapter, we show that vertical optic flow produces stronger vection than horizontal optic flow in upright observers. We also examined whether this gravity alignment effect is due to gravitational alignment or to alignment to the spine or trunk of the body. Observers viewed the same stimuli in various body orientations, including positions in which visual motion was along an axis in a plane that was orthogonal to gravity. In Experiment 3.1, we show that vection is influenced by both gravity-centric and body-centric direction. We then show in Experiment 3.2 that gravity and spinal effects in vection may be modulated by scene structure that influences the perceived context of a scene.

3.2 General Methods

3.2.1 Subjects

Participants included eight observers (four males, four females; mean age = 30.88, SD = 9.96) in Experiment 3.1, and six observers (three males, three females; mean age = 26.5, SD = 3.56) in Experiment 3.2. All subjects had normal or corrected-to-normal vision and reported no vestibular impairment. Participants had prior experience with illusions of self-motion in a laboratory setting. Written informed consent was obtained in accordance with a protocol approved by the York University Research Ethics Board.

3.2.2 Apparatus

Subjects stood upright on stable foot blocks or lay on a foam mattress with a headrest to appropriately orient and centre the head with a computer screen. The mattress enabled observers to maintain a full-body tilt of ±90° (left and right side down) about the naso-occipital (roll) axis, or to lay prone or supine. The stimuli were displayed on an IBM Lenovo T61p 15.4-inch TFT laptop with a resolution of 1280 (horizontal) x 800 (vertical) and refresh rate of 60 Hz. The laptop was mounted to a rigid frame with the screen frontal-parallel to the subject. Extraneous stimuli were masked using a circular viewing tube, cloth shroud, and a matt-black opaque aperture panel offset 1.5 cm from the screen. This aperture system set the observer-to-screen distance of 30 cm and the field of view of 39°. Responses were recorded using a Logitech R Dual Action Gamepad (see Fig. 3.1). Subjects wore earplugs (model 1100, 3M) to mute extraneous auditory orientation cues.

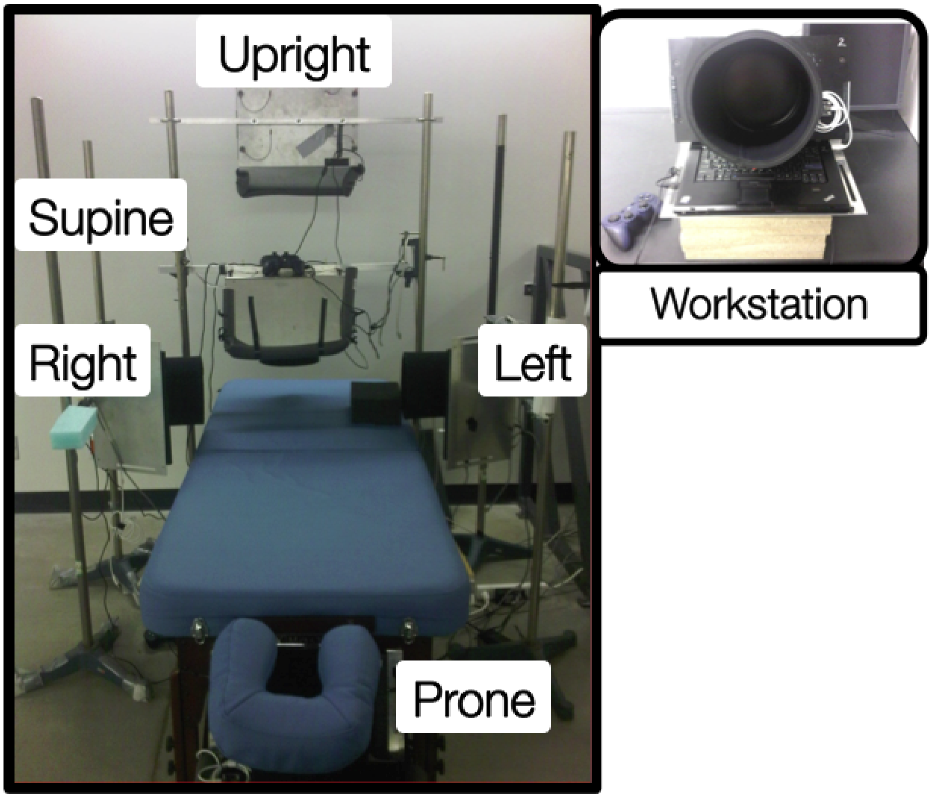

Figure 3.1: Photograph of the apparatus for the upright (standing), tilted (lying on the left and right side), supine and prone postures. Foot blocks and a foam headrest were used for height adjustment and support.

3.2.3 Stimuli

The self-motion displays were generated using custom Python software with open-source Pyglet libraries (Experiment 1), Autodesk Maya and Adobe Media Encoder (Experiment 2). Stimuli were 3-D animations of vertical and horizontal translation through a computer-generated scene. The virtual camera for the experiments had a vertical field of view of 39° to match the display.

In Experiment 3.1, the scenes consisted of a volumetric (3-D) optic flow field of 8500 randomly distributed blue dots (16.72 cd/m^2) on a black background (0.64 cd/m^2). The cloud of dots extended 30 m along the depth or visual axis. The dots had a simulated radius of 7.5 cm and were uniformly translated in 3-D space at 1.33 m/s to produce a lamellar flow pattern. The dots moved vertically and horizontally with respect to the display. When any dot moved beyond the field of view (off screen), it was redrawn at the same original vertical and depth coordinates on the opposite side of the virtual scene.

In Experiment 3.2, the scenes contained the same 3-D dot scene as in Experiment 3.1, or a blue, rigid 3-D pipe structure of randomly distributed and intersecting virtual pipes in a volume of black space (See Fig. 3.2). The pipes were oriented vertically and horizontally with respect to the display. Self-motion was simulated by translating a virtual camera through the pipe structure. The rendered animation frames were rotated to produce the stimuli for both the vertical and horizontal translation. The motion sequences were rendered with a frame rate of 30 frames per second as in Experiment 3.1, and the translation speed was 1.33 m/s.

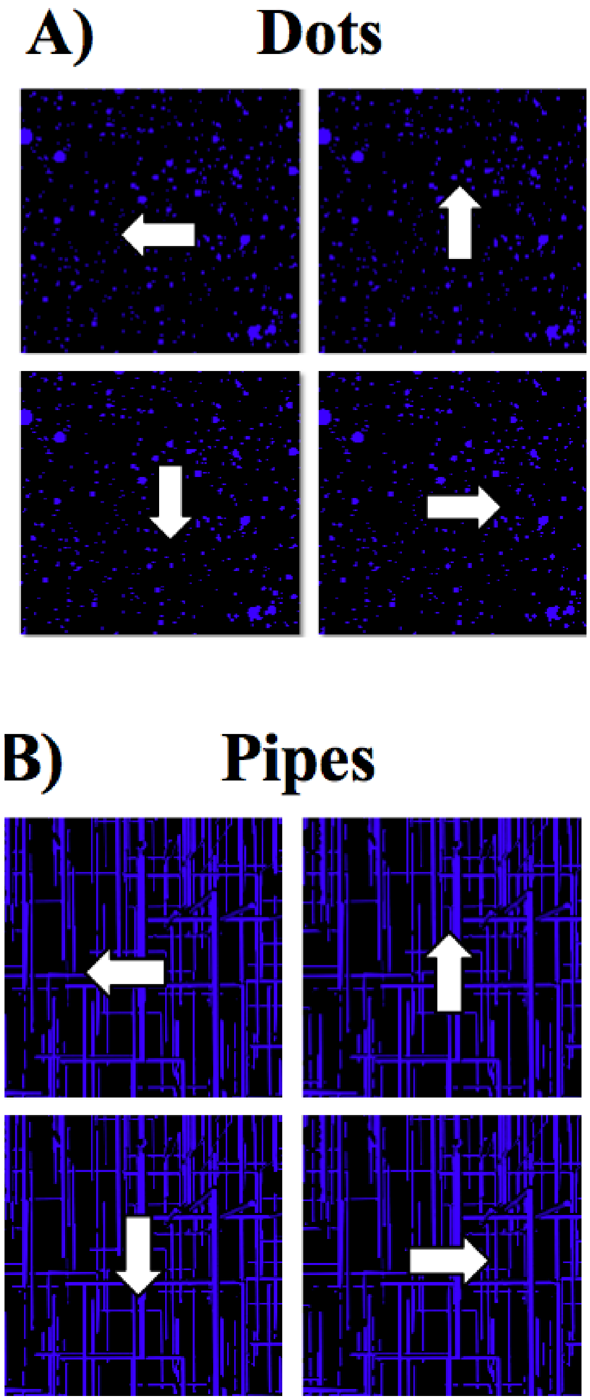

Figure 3.2: Screenshots of the dot (A) and pipe (B) stimuli and directions.

3.2.4 Posture Conditioning

While viewing the displays in the upright and lying postures, the head was aligned with the trunk of the body and the legs were extended. Only in the upright, left and right side down postures, was one of either the spinal or interaural body axes aligned with the direction of gravity; these body axes were orthogonal to gravity in the supine or prone postures. Figure 3.3 shows the direction of the body axes relative to the direction of gravity. The trials began after approximately 60 s in the given posture.

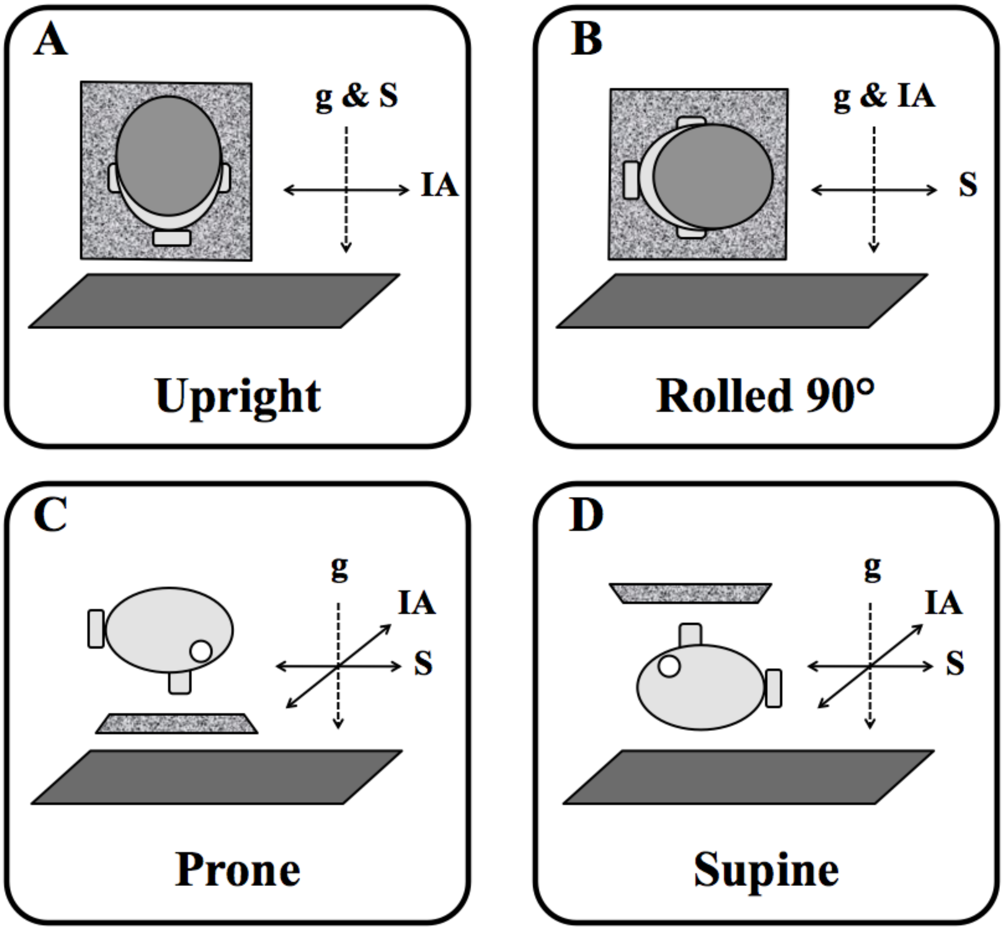

Figure 3.3: Visual schematic of the spinal (S) and interaural (IA) stimuli directions relative to gravity (g), for the upright (A), tilted (B), prone (C), and supine (D) postures. The solid gray and textured polygons represent the ground plane and display, respectively. For each posture, visual motion was presented along the spinal or interaural axes. As shown above, the direction of the stimulus motion and gravity could be aligned when participants were upright (g & S) or roll-tilted (g & IA), but not when lying supine or prone.

3.2.5 Procedure

The procedure was similar for the two experiments. Observers viewed a series of self-motion displays while casually looking about the display and attending to their perception of self-motion. In Experiment 3.1, observers first tested in the standing posture followed by testing in lying postures, which included lying left and right side down, supine and prone. In each session, they first stood upright and viewed a 30 s lamellar dot motion display (vertical or horizontal motion as appropriate for the block) while attending to their sensation of self-motion. Observers were told to assign a vection magnitude of 50 to the vection sensation produced, which served as a reference stimulus for subsequent trials.

During each trial, observers viewed the dot displays and pressed one of the shoulder buttons on a gamepad as soon as they experienced vection, and continued to hold the button until that sensation or trial ended. If vection ceased and reoccurred during a trial, the shoulder button was to be pressed again. Each trial was followed by a response screen prompting observers to use the gamepad to indicate their overall sensation of self-motion on a rating scale of 0-100 relative to the reference stimulus. The rating scale had a resolution of 5 units. If the observer's feeling of self-motion was twice as strong (or more) than the reference stimulus, they were told to give a rating of 100. If observers did not experience self-motion, they were asked to provide a rating of 0.

In Experiment 3.2, observers stood and lay left side down, while viewing 20 s lamellar motion displays consisting of either the same dot motion as in Experiment 3.1, or motion across a scene of pipes. Each display was followed by a black, blank screen, during which observers verbally reported their sensation of self-motion on a rating scale of 0-100. Observers were told to give a rating of 100 for maximal/saturated vection (i.e., they perceived themselves as moving in a world of stationary dots/pipes), and 0 if they did not experience vection (i.e., they perceived themselves as stationary with dots or the pipe structure moving past them).

For each trial, the motion direction (vertical or horizontal) and stimulus type (dots or pipes for Experiment 2) were randomly selected and blocked by posture. Within each posture block, trials were randomly ordered. The blocks were ordered using a counterbalanced design.

Qualitative reports of observers' vection experiences were collected during the experiment debriefing. Participants were asked the open-ended question "How would you describe your experience of self-motion?" to potentially reveal any unintended or unexpected perceptions or sensations during or following the experiment.

3.2.6 Data analysis

Data analyses were performed using the R packages nmle (http://cran.rproject.org/web/packages/nlme/) with RStudio. Outlying points were identified through regression diagnostics and visual inspection of the response measures. We adopted stepwise selection using Akaikes Information Criterion (AIC) to select the final regression models. Separate statistical models were fitted for each of the response measures, which were vection onset, duration, magnitude (Experiment 1 only) and saturation (Experiment 2 only). A goodness-of-fit test based on the analysis of deviance was used to evaluate the fit the model. Family-wise error was controlled for with Bonferroni correction and the adjusted p-values are shown for the post-hoc analyses. Trials in which vection was not reported were excluded from the analysis.

3.3 Experiment 1

In the first experiment, we examined how aligning the direction of head tilt and simulated self-motion modulates sensory conflict. We dissociated these body and display vectors from gravity by varying body posture with respect to gravity. In the upright posture, the display-vertical (and spinal axis) was aligned with the direction of gravity. As shown in Figure 3.4, the visual motion and gravity do not align at all in the prone and supine display.

3.3.1 Methods

Trials were sessioned and blocked by the direction of the reference stimulus and posture (20 blocks of 4 ref. x 5 postures). Prior to a testing block, subjects stood and viewed a reference stimulus moving in one of the four motion directions (up, down, left, and right). They then moved to the appropriate posture for the block and viewed one test stimulus for each of the four motion directions. Following each trial, they rated their vection relative to the reference stimulus. After these four trials, they moved to the next posture for the block. Each of the 20 blocks consisted of 16 trials, with 1 or 4 replicates for the standing and lying session, respectively.

3.3.2 Results and Discussion

Vection was reported for nearly all of the trials (approximately 97% of the total responses). Data points that were identified as outlying or where vection was not obtained were removed included, 33 data points (across response measures).

As shown in Figure 3.4A, there were no significant vection differences between the opposing motion directions for vertical (up/down) or horizontal (left/right) motion for the reference and stimulus directions (p's $>$ .05), so these levels were collapsed into the two head-centric reference directions "Interaural" and

“Spinal.” There were also no significant differences between laying left and right side down (p’s $>$ .05), or supine and prone (p’s $>$ .05), so these conditions were combined and noted as “Rolled 90°” and “Pitched 90°” postures, respectively (see 3.4B). The results shown are from data collapsed across the motion directions and postures. Figure 3.4A shows the vection ratings averaged across all subjects.

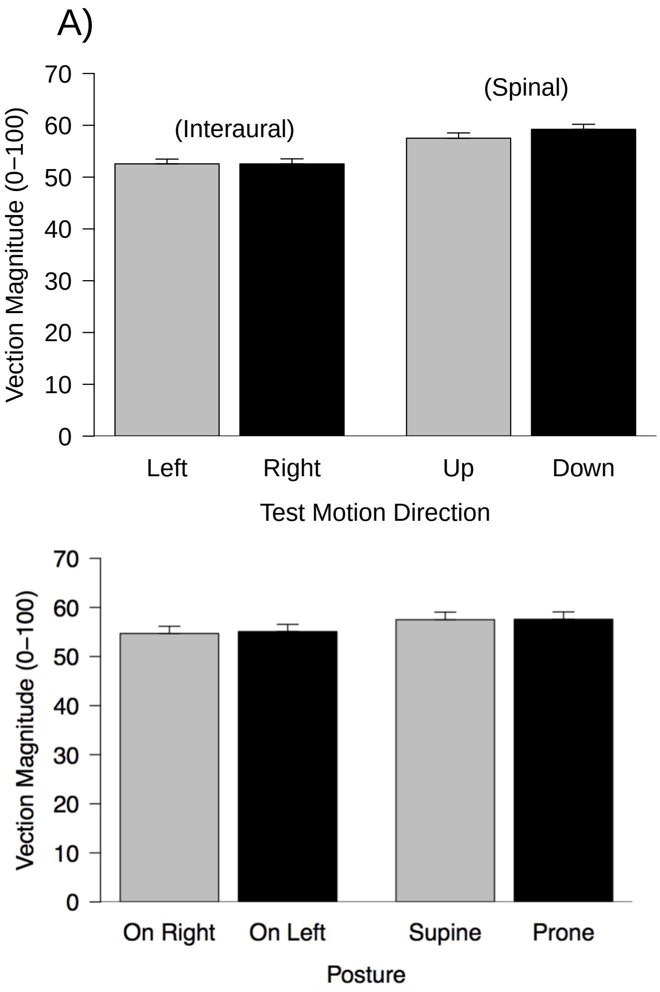

Figure 3.4: Mean vection magnitude ratings (±1 standard error of the mean (SEM), 8 observers) for (A) opposing motion directions across postures, and (B) opposing body tilts. Ratings for both types of opposing conditions were not significantly different (p's $>$ .05). Observers based their magnitude estimates on a reference stimulus with a given vection rating of 50, corresponding to one of the four reference motion directions before each block of trials.

Consistent with predictions, visual motion that was aligned with gravity enhanced vection. However, when the motion axis was orthogonal with gravity (in the pitched postures), motion along the spinal axis resulted in more compelling vection than interaural motion. Figures 3.5-3.7 show the mean vection ratings, onsets, and durations across all subjects. Specifically, body orientation significantly influenced vection ratings, $F(2, 947) = 10.33$, $p < .0001$; onset, $F(2, 947) = 3.31$, $p = .0370$; and duration, $F(2, 947) = 11.04$, $p < .0001$. The test motion axis also had a significant impact on vection ratings, $F(1, 947) = 64.51$, $p < .0001$; onset, $F(1, 947) = 4.57$, $p = .0328$; and duration, $F(1, 947) = 12.16$, $p = .0005$. While there was a significant posture x motion axis interaction for observer vection ratings, $F(2, 947) = 16.42$, $p < .0001$, this was not the case for vection onsets or durations (p's $> .05$).

In directly comparing interaural and spinal motion by posture, we found that when observers were upright, vection ratings were significantly higher for visual motion that was presented along the spinal axis compared to interaural motion ($t(947) = 14.77$, $p < .0001$, $d = .74$), with short onsets ($t(947) = 3.75$, $p = .0002$, $d = .11$) and longer durations ($t(947) = 7.66$, $p < .0001$, $d = .14$). In contrast, when observers lay on the side (rolled 90°), interaural motion resulted in significantly stronger vection ratings than spinal motion ($t(947) = -5.45$, $p < .0001$), though the effect size was small ($d = .17$) and no difference was found for vection onset or duration (p's > .05). However, when observers were supine or prone (pitched 90°), visual motion along the spinal axis resulted in significantly higher vection ratings ($t(947) = 5.94$, $p < .0001$, $d = .34$), with no significant differences in vection onset and duration (p's > .05).

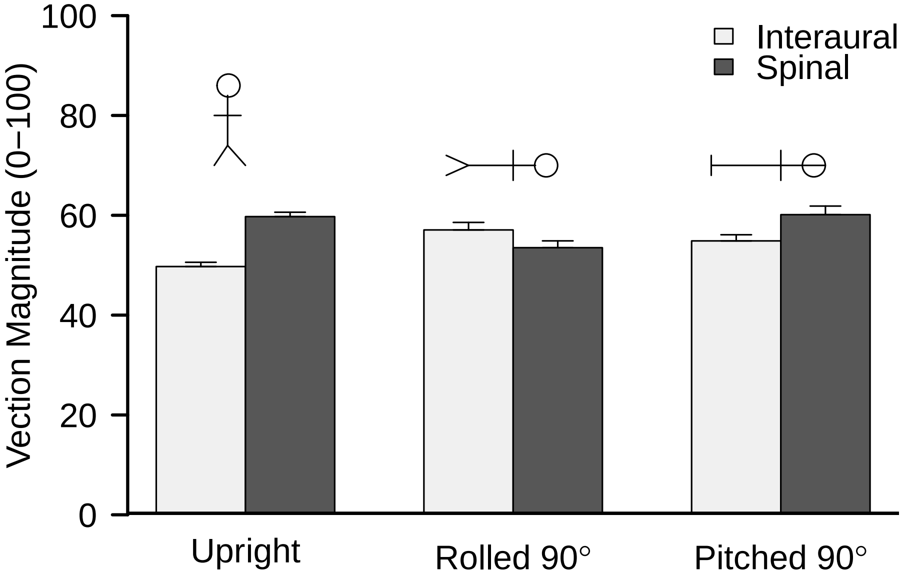

Figure 3.5: Mean vection magnitude ratings for the upright posture (Experiment 1, far left) compared with the tilted, prone, and supine postures (±1 SEM, 8 observers). Ratings for the opposing motion directions for vertical (up/down) and horizontal (left/right) test and reference stimuli were not significantly different (p > .05) and so were collapsed and coded into the two head-centric reference frames Interaural and Spinal. The vection magnitude ratings for the left and right side down, and supine and prone postures, were also not significantly different ($p > .05$) and so were collapsed into the “Rolled”and ”Pitched” body orientation conditions.

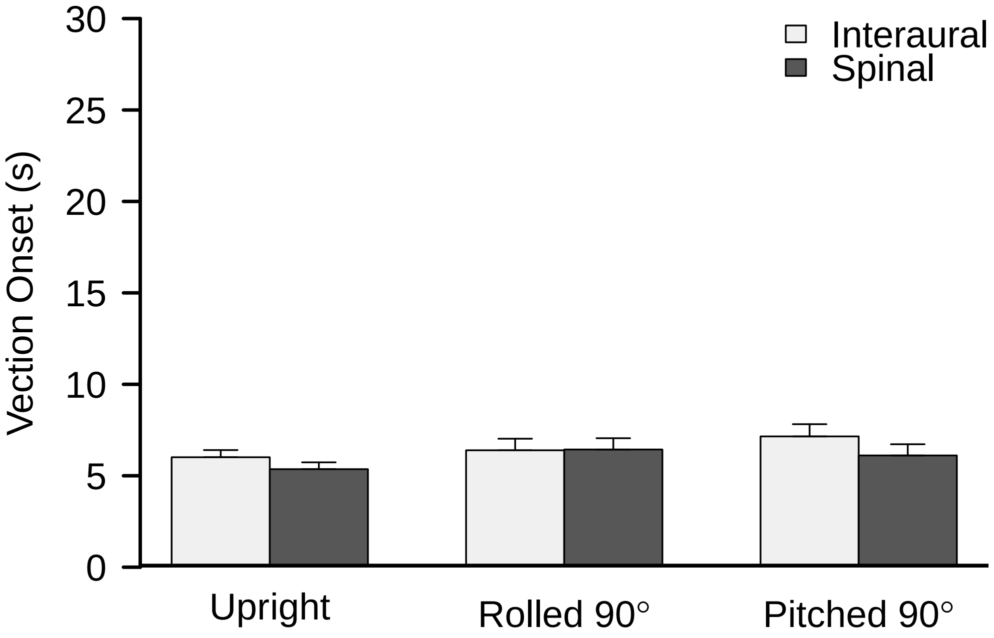

Figure 3.6: Mean vection onset (±1 SEM, 8 observers). Onsets for the opposing motion directions for vertical (up/down) and horizontal (left/right) motion were collapsed into the head-centric axis directions Interaural and Spinal.

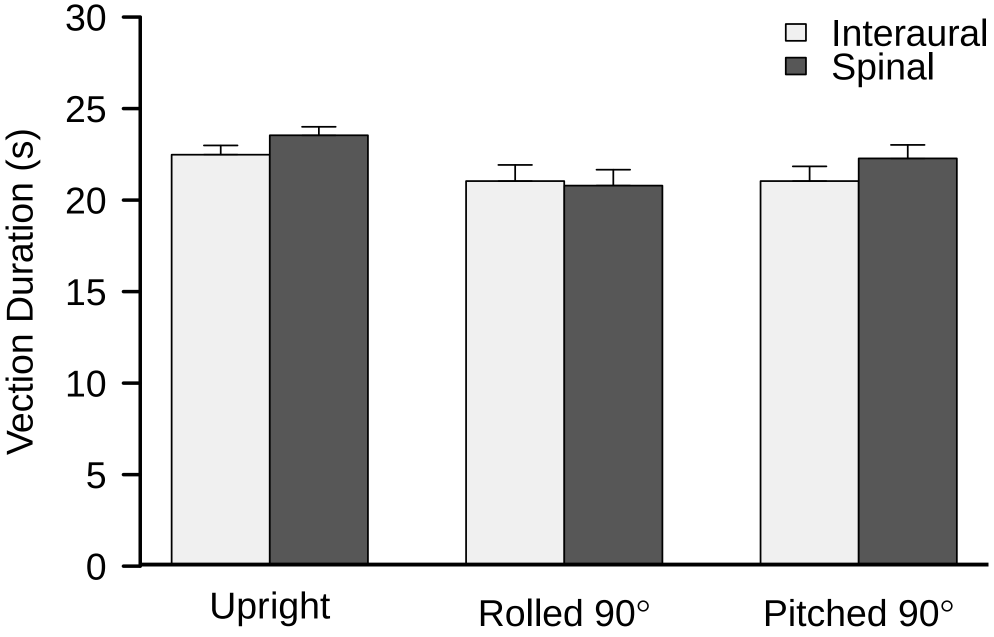

Figure 3.7: Mean vection duration (±1 SEM, 8 observers). Durations for the opposing motion directions for vertical (up/down) and horizontal (left/right) motion were collapsed into the head-centric stimulus axis directions Interaural and Spinal.

Our finding that the relative direction of the body and visual motion axis significantly influenced vection, is consistent with that of previous vection studies in which these factors enhanced the feeling of illusory self-motion in observers (Giannopulu & Lepecq, 1998; Kano, 1991). However, consider that in the upright posture, the head-centric vertical/up was the same as gravity, so it is unclear whether the vection advantage for vertical motion with respect to the display was due to alignment with the spinal axis or the gravity axis. Thus, from the data for the upright posture, it may be argued that (a) gravity reinforced the visual signal in vertical vection, (b) there is a preference for motion along the trunk of the body, or (c) both the gravity and body vectors influence vection. The results from the rolled and pitched postures suggest that the latter conclusion is most correct, that both gravity and body influence vection. In other words, the strength of visually-induced self-motion depends on the axis of visual motion relative to both gravity and the body. In particular, this is evident in our finding of enhanced vection for interaural motion in roll-tilted (motion is gravity-aligned), and spinal motion for pitched, observers. This pattern was found for all of the response measures, but to a lesser degree for vection onset and duration than magnitude.

The similarity of responses for vection from flow in opposing motion directions (vertical up/down and horizontal left/right), suggests that these alignment effects are not due to a simple vector summation of the visual and gravity signals. Furthermore, the lack of a significant vection difference between the supine and prone postures is consistent with the similar pressure sensitivies of the chest and back of the body (Weinstein, 1834).

During the session debriefing, three observers spontaneously reported that when they were roll-tilted, the stimulus motion appeared to be moving along a tilted axis with respect to the vertical and horizontal axis of the display—a possible A-effect (for a review see Aubert (1861); Müller (1916); Van Pelt, Van Gisbergen, and Mendendorp (2005)). One of these observers also reported illusory scene shearing/distortion during the perceived self-motion.

Additionally, some observers reported that the dots stimulus looked like stars and that this resulted in sensations of flying through outerspace. For other observers, the dots sometimes appeared as moving bubbles or snowfall, and this created the impression that they were stationary and viewing a moving stimulus.

The afforementioned stimulus percepts varied by both posture and motion direction. As these phenomena were brought to light during the debrief, it was unclear as to the role that the perceived scene context or scene structure might have in influencing the effects of motion-gravity alignment in vection.

3.4 Experiment 2

In the second experiment, we examined whether the influence of body orientation and motion direction with respect to gravity might depend on scene structure. To explore how the structure of a scene influences the perception of self-motion, observer posture was varied relative to gravity while they viewed motion along the spinal and interaural axis. The displays simulated self-motion across a 3-D volume of dots as in Experiment 3.1, or a 3-D scene that contained a single, solid pipe-like structure; we refer to these stimuli as “dots” and “pipes” respectively.

3.4.1 Methods

The procedure was the same as Experiment 2, except observers viewed lamellar global optic flow displays while standing upright and lying down. There were three independent variables: (1) Body posture: standing (upright) and lying left side down (roll-tilted 90°); (2) Simulated self-motion direction: up, down, left, and right (relative to the display); and (3) Scene type: dots and pipes. Trials were divided into two blocks by posture. For each of the two postures, the 8 factorial combinations (4 motion directions x 2 scene types) were repeated 4 times for a total of 32 trials per block an overall total of 64 trials per subject. For each trial, we recorded the vection saturation (rating of 0-100), to limit the number of postural changes required given the four motion directions and differently-structured stimuli. A vection saturation response of 0 meant the scene was perceived as moving and the self as fully stationary, and 100 meant that the scene was perceived as stationary and the self as fully moving.

3.4.2 Results and Discussion

Figure 3.8 shows the mean vection ratings across subjects. There were no significant differences between the opposing motion directions for vertical (up/down) or horizontal (left/right) motion, so these levels were collapsed into the two head-centric motion directions Interaural and Spinal. As in Experiment 3.1, body orientation had a significant effect on vection, $F(1, 367) = 10.50$, $p =$ .0013, and so did the direction of visual motion, F(1, 367) = 4.29, $p = .0390$. The stimulus type (dots or pipes) did not have a significant main effect on vection, $F(1, 367) = 0.43$, $p = .5090$; however, interactions indicated that the effect of stimulus type depended significantly on body orientation, $F(1, 367) = 5.32$, $p = .0217$, but not on visual motion direction ($p = .76$). There was also an interaction between body orientation and motion direction, $F(1, 367) = 12.84$, $p = .0004$; however, in tilted observers, there was no significant difference in vection between interaural and spinal motion, $p > .05$, but rather, a trend towards stronger vection for motion along the spinal axis. Additionally, upright observers experienced stronger vection when viewing the pipes, both when motion was along the interaural axis, $t(367) =$ -3.11, $p = .0020$, $d = .66$, and the spinal axis, $t(367) = -2.63$, $p = .0088$, $d = .39$. When participants were roll-tilted left side down, vection strength for the dots and pipes stimuli were not significantly different for both interaural motion, $t(367) =$

.67, $p = .5050$, and spinal motion, $t(367) = 1.28$, $p = .2016$.

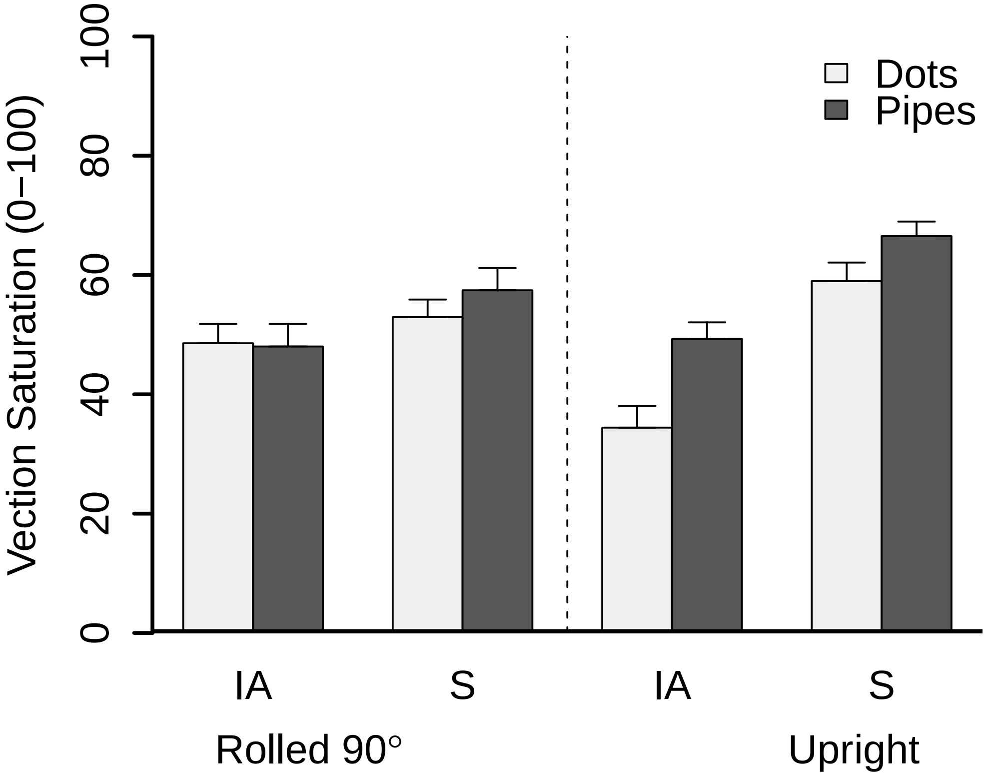

Figure 3.8: Mean vection saturation rating (±1 SEM, 6 observers). Ratings for the opposing motion directions for vertical (up/down) and horizontal (left/right) motion were not significantly different ($p > .05$) and so were collapsed into two motion directions (vertical and horizontal) and coded into the head-centric reference frames Interaural and Spinal. Here, the "Rolled 90°" posture represents the left side down body orientation.

In sum, while aligning the direction of visual motion with gravity promoted vection in Experiment 3.1, this was not always the case in the present experiment. Here, we found that vection tended to be stronger when motion was along the spinal axis for both the upright and tilted body orientation, suggesting that vection is largely trunk-centric for those observers.

Interestingly, in the debriefing observers reported that the pipes stimulus gave the impression of being in a moving elevator and this effect tended to enhance vection; however, this "elevator effect" was reduced when observers lay tilted, as some felt that this effect seemed less natural when they lay on the side given the atypical posture for that perceived context. Therefore, the perceived context and naturalness of the scene had the potential to both enhance and inhibit vection. Such observer anecdotes demonstrate the effects of scene interpretation on illusory self-motion, and suggest that higher-order cognitive processes may be involved in vection.

3.5 General Discussion

Varying head orientation allowed us to partially dissociate the effects of the direction of gravity with respect to the head, visual motion direction, and otolith sensitivity, on vection.

In line with the gravitational effects on vection reported by Kano (1991) and Kornilova et al. (1995), we hypothesized that superimposing the direction of gravity and illusory self-motion might influence sensitivity to vection. In agreement with the findings of those studies, we found that vection was enhanced in upright observers viewing vertical flow. Observers reported increases in magnitude, shorter onsets and longer durations, for vection that was parallel to gravity compared to vection that was orthogonal to gravity. This effect was also examined in observers laying roll-tilted and pitch-tilted 90°. In Experiment 3.1, gravity appeared to influence the visual signal in vection in roll-tilted observers, but in the prone and supine postures, motion along the spinal axis enhanced vection. This finding of a spinal effect for vection with the prone and supine postures—in which gravity was perpendicular to the stimulus motion plane—suggested that visually-induced self-motion is also influenced by the head or trunk of the body. In Experiment 3.2, the spinal alignment effect seemed to dominate even in tilted observers. Although this finding that posture played a greater role in vection than gravity appears to contradict our earlier findings in Experiment 3.1, it is consistent considering that, if gravity played a role we would have expected differences for up versus down vection (in upright observers) and left versus right vection (in roll-tilted observers), and the very small effect size when comparing spinal and interaural motion in roll-tilted observers in Experiment 3.1.

The vection advantage for lamellar motion along the spinal axis when roll-tilted (in Experiment 3.2) and particularly so for the supine and prone postures, may be because in an upright observer, this axis would also be along the "up/down" direction of the body, which is typically aligned (during real locomotion) with both the visual and gravitational up. Our finding that self-motion depends on body orientation, also falls in line with those of MacNeilage, Banks, DeAngelis, and Angelaki (2010) who measured visual and vestibular thresholds for heading discrimination in upright and roll-tilted observers and found that these thresholds depended on direction with respect to the head and not the world. If, as suggested by MacNeilage et al., we somehow compensate for gravity in making self-heading judgments, then this may also translate to making judgments of the magnitude of visually-induced self-motion and provide some explanation for our vection enhancement for spinal motion in the tilted postures. Using the trunk of the body or a head-based reference system would also be consistent with an ecological account of vection, given that we evolved to deal with a predominantly upright posture for self-motion. Additionally, the body is laterally symmetric and we use our legs to locomote.

There have been many models proposing how linear self-motion perception might be determined by a weighted summation of visual and vestibular (and other) sensory signals. Evidence for weighted models has been presented by Berthoz et al. (1975), who found lower vestibular detection thresholds when the direction of visual motion was concordant with real fore-aft accelerations. Alternatively, Ohmi (1996) found that when visual and inertial vestibular stimulations were misaligned, that the visual cue determined the perceived self-motion direction. Based on their findings, Berthoz et al. and Ohmi proposed that self-motion perception might be based on (1) the summation of visual and vestibular (and other sensory) signals, and (2) discrepancies causing visual dominance of the apparent self-motion. However, our lack of significant direction effects for opposing visual motion and body tilt is evidence against a simple additive model. Furthermore, our finding that the perceived context of the visual motion also had an impact on vection, suggests that a simple weighted sum is not a complete model, but that these dynamics include higher-level cognitive processes.

More recent studies have shown that, contrary to simple summation models, cognitive factors can influence perceived self-motion. Wright et al. (2005) conducted a similar study to Berthoz et al. (1975) and Ohmi (1996) but used simulated, naturalistic visual displays that were either spatially or temporally in or out-of-phase with the motion of an oscillating seat. They found that visual scenes that were consistent with the physical surroundings tended to dominate the vestibular inputs in the perceived self-motion. They also found that oppositely directed visual and vestibular motion did not reduce or cancel out the perceived self-motion.

The role of naturalism/realism in vection has also been reported by Ogawa and Seno (2014) who reported that holding of an umbrella while perceiving moving stimuli as rain or snow inhibited vection. Interestingly, our finding of enhanced vection for the pipes stimuli in the upright postures—for which observers reported feeling like they were riding an elevator—provides further evidence that cognitive factors not only help shape our perceptual experience of self-motion, but may also depend on other ecological factors.

In the present study, the perceived context of the visual scene varied with head orientation and motion direction relative to gravity. The resulting interpretation of the scene reported enhanced or inhibited vection. For instance, observers reported "flying" through the dots defining the space (i.e., the dots perceived as stars) and that this enhanced their vection experience, whereas viewing the dots as bubbles or snow falling tended to reduce their sensation of self-motion. With the pipes scene, observers who reported that they felt like they were riding an elevator also added that they experienced stronger vection. However, the lack of a main effect for stimulus type (i.e., dots versus pipes) but rather, an interaction of stimulus type with head orientation, suggests that both cognitive and ecological factors may be determinants in perceived self-motion.

Our varied interpretations of our stimuli might be explained by the fact that, unlike in the studies by Wright et al. (2005) and Riecke et al. (2006), our pipes stimulus was not a real image or virtual simulation of a naturalistic scene, but rather was more abstract. Interestingly, the interpretations of the dots stimulus varied more and seemed to influence vection both positively and negatively, while the pipes scene provided a more consistent and positive effect on vection. We predicted and found that the rigid pipe structure might be more comparable to real scenes—which consisted of mostly geometric objects and frame-like structures—tended to be compared more to real scenes and from observer reports seemed to contribute to greater sense of presence and enhanced vection. Notably, most of our observers in their debrief reports related their experience of the pipes stimulus to that of riding in an elevator. It is possible that this elevator interpretation was due to expectations of being upright based on everyday experiences with elevators. This might partially explain the increased influence of spinal orientation on vection for the pipes stimulus. Furthermore, lying on the side places pressure on the side of body and therefore may not only be less comfortable than being postured upright, but could also draw further attention to the unnatural condition and percept of riding an elevator while roll-tilted. Thus, the significant interaction between the scene and body orientation seems to indicate both higher-order cognitive processes and ecological factors in the perception of self-motion.

Here, we have demonstrated that the perception of self-motion can be influenced by the alignment of visual motion with gravity and the body, and is also dependent on the perceived context of the scene. In Experiments 3.1 and 3.2, aligning the direction of visual motion with the gravitational vertical in upright observers resulted in vection enhancement. Yet, in postures in which the visual motion was orthogonal with the gravity vector, observers experienced improved vection when motion was along their spinal axis, suggesting that the preference for the vertical direction may be based more on the trunk of the body or a head-based coordinate system, rather than the orientation of the body relative to gravity. The illusory self-motion also depended on the perceived context of the visual scene, which was found to be influenced by posture. Finally, when we changed the structure of the visual scene, this too impacted their experience of self-motion. Taken together, these findings support earlier findings that gravity, body orientation, and cognitive ("top-down") processes are involved in the perception of self-motion. Finally, observers real-world interpretations of our more abstract moving pipe scene, also indicates that these higher-order process may extend to more basic spatial representations of a scene.

Chapter 4

The A-effect and global motion: Vection is processed differently

4.1 Introduction

Many activities in our daily life such as walking, riding a bike, and even sitting still, rely on our ability to control our equilibrium. Our sense of orientation relative to gravity helps us maintain both static equilibrium (postural balance) when we are still and dynamic equilibrium when we are in motion (Dichgans & Brandt, 1978; Howard, 1982). Verticality or the direction of 'up' can be derived from visual cues in our environment such as the polarity of an object (Allison et al., 1999)—e.g., knowing that a tree trunk is rooted in the ground—and from internal, non-visual cues which relay information about our body orientation in space. Non-visual self-orientation cues include those from the vestibular system, which is sensitive to angular and linear accelerations (including gravity), and thus senses static or dynamic head tilt (Hain & Helminski, 2007; Howard, 1986), as well as somaesthetic cues from proprioception, interoception (e.g., the gut and baroreceptors–Hunt et al. (1965); Shimizu et al. (2002)), and exteroception (e.g., touch and pressure—Horak et al. (1990). However, while we are very good at estimating our body orientation relative to gravity (Kaptein & Van Gisbergen, 2004; Mast & Jarchow, 1996; Mittelstaedt, 1983), we do not always have a veridical percept.

Observers lying on their side (roll-tilted) in the dark make appreciable systematic errors when asked to estimate the orientation of a line or other elements relative to gravitational vertical (Kaptein & Van Gisbergen, 2004; Tarnutzer, Bockisch, Olasagasti, & Straumann, 2012; Van Beuzekom & Van Gisbergen, 2000). Aubert (1861) was the first to observe that a vertical luminous line appears tilted when the head is roll-tilted in the dark. Müller (1916) examined this effect and found that a vertical line appears tilted in the same direction as the head for head tilts greater than 60° ("A-effect") and in the opposite direction for smaller head tilts ("E-effect"). While A and E effects could be explained by an over and underestimation of self-tilt, respectively, observers with a nearly veridical percept of self-tilt (relative to gravity) still tend to make gross systematic errors in judging external object tilt (Kaptein & Van Gisbergen, 2004). Given that both world and head-based reference frames are used in determining object and self-orientation, it is possible that errors in estimating object tilt could be due to the mistranslation of these estimates to an egocentric representation (Eggert, 1998; Kaptein & Van Gisbergen, 2004; Mittelstaedt, 1983). We hypothesized that if tilt judgments in egocentric and allocentric space are independent then the perceived direction of self-motion percepts relative to gravity may exhibit different biases than judgments of the motion of external objects.

Guterman et al. (2012) examined the effect of posture with respect to gravity on the latency to onset, duration and magnitude of vection. Vection was more immediate, lasted longer, and was stronger when observers viewed radial flow while upright (seated and standing) compared to lying (supine, prone, and left side down) postures. Furthermore, observers standing in upright postures and viewing radial flow with simulated viewpoint oscillation—both of which were consistent with ego-motion compared to lying down and smooth flow—enhanced vection. Although the postural and oscillation effects may simply reflect ecological components of natural self-motion through the world when walking, it is also possible that gravity played a role in this oscillation advantage (Allison, Zacher, Kirollos, Guterman, & Palmisano, 2012).

It is unclear if motion along the cardinal directions (i.e., vertical and horizontal with respect to the head)—perceived as either object or self-motion—may be subject to the same A-effect observed with static lines. De Vrijer et al. (2008) compared tilt perceived in planar motion with that in static line displays. They found a similar pattern of systematic errors for the line and motion displays and so concluded that orientation judgments of both static tilt and motion involved a common spatial reference frame and a shared computational strategy. Their brief motion displays contained random visual noise to minimize local directional cues. It is unknown whether a similar tilt estimation strategy might be used when presented with coherent motion and additional visual cues such as motion parallax.

In the present experiments, we compared the influence of whole body tilt on the perceived orientation of a line with the apparent tilt in the direction of various types of global motion. We also compared perceived motion direction when the motion was perceived as external scene motion (Experiment 1), and during vection (Experiment 2) in which the scene appears stationary and visual motion is attributed to the self.

4.2 Experiment 1

Upright and tilted observers judged the tilt of a static line, and the direction of both coherent planar and volumetric flow to examine whether systematic errors in tilt were affected by the presence of motion parallax.

4.2.1 Methods

4.2.1.1 Subjects

Twenty observers (eight males, twelve females; mean age = 26.7, SD = 5.5) participated. All subjects had normal or corrected-to-normal vision and no reported vestibular impairment. Written informed consent was obtained in accordance with a protocol approved by the York University Research Ethics Board and that conformed to the 1964 Declaration of Helsinki.

4.2.2 Apparatus

Subjects stood upright on stable foot blocks or were supported on a foam mattress with a headrest at a full-body tilt of -90° (left side down) about the naso-occipital (roll) axis. Care was taken to align and centre the head with the computer screen. The stimuli were generated on an IBM Lenovo T61p 15.4-in. TFT laptop using custom Python software and open-source Pyglet 1.1.4 libraries (http://pyglet.org). Visual displays were generated with a resolution of 1280 (horizontal) x 800 (vertical) pixels and refresh rate of 60 Hz. The laptop was mounted to a rigid frame with the screen frontal-parallel to the subject. Extraneous stimuli were masked using a viewing tube, cloth shroud, and a matt-black opaque aperture panel offset 1.5 cm from the screen. This aperture system set the observer-to-screen distance of 30 cm and the visual angle of 39°. Responses were recorded using a Logitech R Dual Action Gamepad (see Fig. 4.1). Subjects wore 3M 1100 earplugs to attenuate extraneous auditory orientation cues.

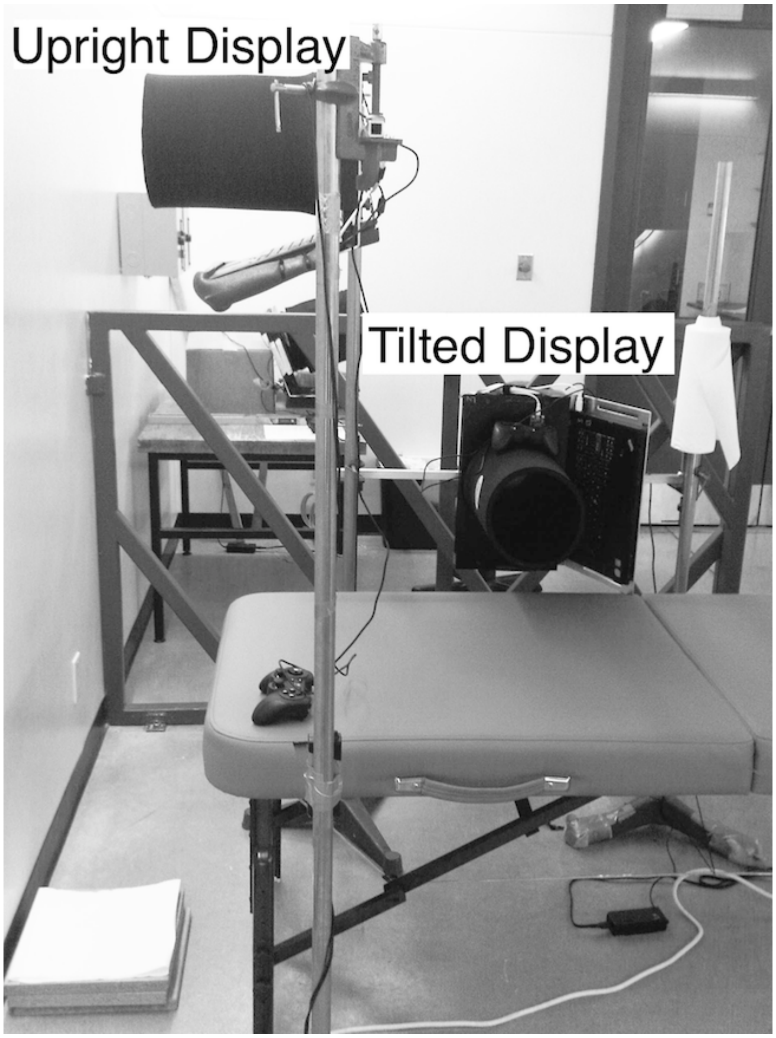

Figure 4.1: Photograph of the apparatus for the upright (standing) and tilted (lying on side) posture. Foot blocks (bottom left) and a foam headrest (not pictured) were used for height adjustment and support.

4.2.2.1 Visual displays

The displays were a static line that spanned the display (39° x 0.2°) and two types of global motion dot stimuli. Both the line and dots were blue (16.72 cd/m^2) on a black background (0.64 cd/m^2). The motion conditions included planar (2-D) and volumetric (3-D) optic flow. The motion displays contained randomly distributed dots in a computer-generated world. The dots modelled spheres in the rendered scene with a simulated radius of 7.5 cm. The motion was produced by translating the virtual camera parallel to the screen to produce a lamellar flow pattern that moved upward (for 0° tilt conditions) with a simulated speed of 1.33 m/s. When any dot moved beyond the field of view (off screen), it was redrawn at the same original horizontal and depth coordinates on the opposite side of the virtual scene. The line and motion axes were tilted by rotating the virtual camera, which produced the viewpoint used to render the scene.

For the volumetric flow displays, there was a simulated cloud of dots that extended 30 m along the depth or visual axis. The apparent velocity of these dots was a function of the distance and relative angular displacement at the camera viewpoint, providing the depth cue of motion parallax. For the planar flow displays, the dots were sized to appear to be at depths ranging from 0.1 (the near clipping plane) to 30 m, but were actually drawn at the middle of the depth range (at 15

m) to form a single moving plane of dots. Due to these different depth projections, the volumetric and planar stimuli had the same appearance when static, but not while in motion. Effectively, the volumetric displays simulated a linear flow field that would be consistent with real observer translation, whereas the planar displays produced the impression of motion relative to a wall with dot wallpaper. Figure 4.2 shows a schematic of the stimuli and the depth of the objects in the scene space. Figure 4.3 illustrates the orientation of the static line, and the direction of lamellar flow and perceived self-motion, relative to the direction of gravity, for the upright and tilted postures.

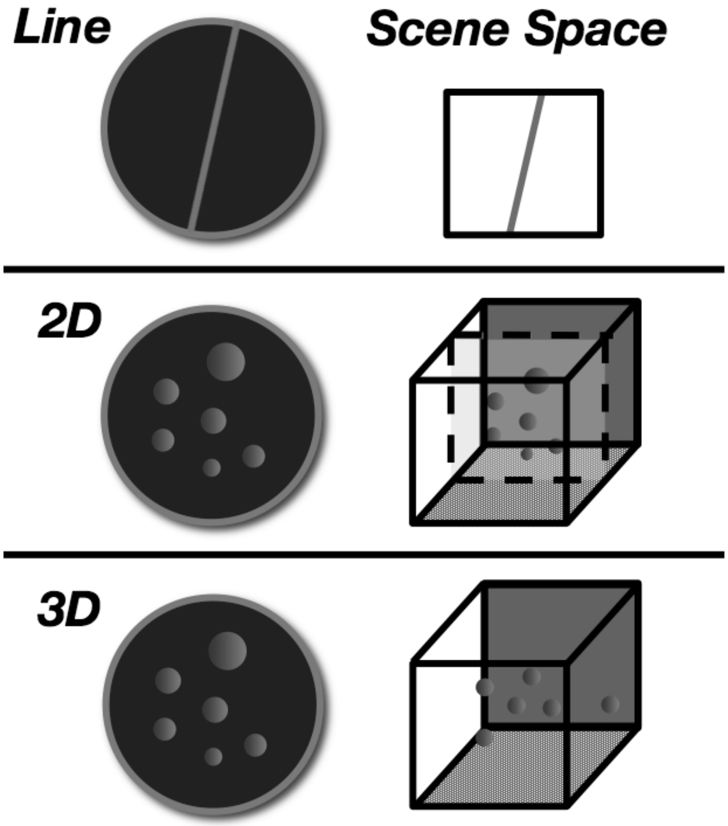

Figure 4.2: Illustration depicting the virtual depth of the line segment and dots in the virtual scene space shown on the displays. The top of the image shows the line segment that was drawn in 2-D space and extended across the entire display. The middle depicts the 2-D lamellar flow. The dots were drawn in different sizes on a plane positioned at the middle of the depth range (15 m) and therefore had no motion parallax. The bottom image shows the 3-D lamellar flow stimulus with dots drawn along the full virtual depth range (0.1 - 30 m). Static images of the 2-D and 3-D stimuli looked the same, but in motion only the 3-D stimulus provided the visual cue of motion parallax.

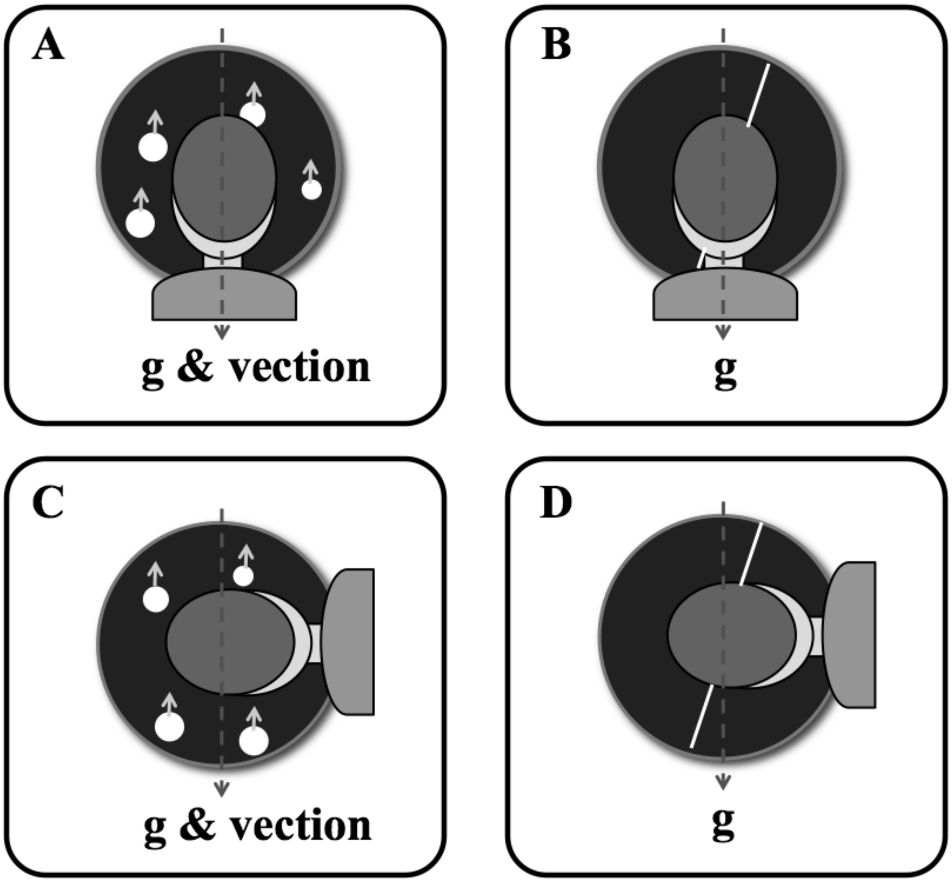

Figure 4.3: Visual representation of the head orientations, object and perceived self-motion (vection) relative to the direction of gravity. The dot and line stimuli are shown as presented to upright (A and B) and tilted participants with the body left side down (C and D). The arrows attached to the dots represent the upward motion direction of the dots, which in the self-motion condition (in Experiment 2) would be perceived as downward self-motion (if the direction were perceived veridically).

4.2.2.2 Design

There were three independent variables: body orientation (0° or -90° tilt), stimulus type (line, planar or volumetric lamellar flow) and stimulus tilt. Each stimulus was presented for 500 ms. The static line or direction of motion was tilted 0°, ±10°, ±20°, and ±30° from the gravitational vertical. Each of the 42 factorial combinations (2 body tilts x 3 stimulus types x 7 stimulus tilts) was repeated 20 times for a total of 840 trials per subject. Trials were blocked by posture and pseudo-randomly ordered to avoid immediate repetition of the same condition. The blocks were ordered using a counterbalanced design.

4.2.2.3 Procedure

Observers were told to look casually about the screen while attending to the direction of line or dot motion. While viewing the displays in the upright and tilted postures, the head was aligned with the trunk of the body and the legs were extended. The trials began after at least 60 s in the given posture.

All of the displays were followed by a black, blank screen, during which observers pressed one of two shoulder buttons on a gamepad to indicate whether the stimulus (or its direction of motion) appeared to be tilted clockwise or counter-clockwise from the gravitational vertical. As this was a two-alternative forced choice (2-AFC) procedure, observers were instructed to select one of these button options, even if the line or motion axis did not appear to be tilted.

4.2.2.4 Data analysis

Data analyses were performed using the R packages nmle (http://cran.rproject.org/web/packages/nlme/) with RStudio (version 0.98.1103). The proportion of clockwise responses were computed for each tilt angle and fitted to a psychometric curve. The subjective visual vertical was defined by the Point of Subjective Verticality (PSV), and is the fitted angle at which the proportion of clockwise responses was .5 (or 50%). The slope of the psychometric function was used to determine the discrimination threshold or just noticeable difference (JND).

The resulting PSV and JND data were analysed using linear mixed effects (lme) regression models, with fixed effects (posture, stimulus type) and a random effect to model inter-subject variability. Outlying points were identified through regression diagnostics and visual inspection of the response measures. Based on these tests, there were 3 subjects and 5 data points identified as outlying and they were removed from the dataset. The final regression models were selected by adopting stepwise selection using Akaikes Information Criterion (AIC). A goodness-of-fit test based on the analysis of deviance was used to evaluate the fit of the model. Post-hoc comparisons were performed using Wald t-tests. Family-wise error was controlled for with Bonferroni correction and the adjusted p-values are shown for the post-hoc analyses.

4.2.3 Results and Discussion

Psychometric functions were obtained by fitting the proportion of clockwise responses as a function of body and stimulus tilt. Figure 4 shows the responses for the line and global motion in the upright and tilted body orientation. When the body was upright the responses were close to veridical. Tilting the body resulted in significant shifts in the perceived vertical in the direction of the body tilt compared to the upright condition, $F(1,80) = 95.23$, $p < .0001$. The stimulus type also had a significant influence on tilt judgments, $F(2,80) = 26.38$, $p < .0001$, and an interaction with body tilt, $F(2,80) = 5.48$, $p = .0059$. The shifts in the PSV when observers were tilted were smaller for the motion conditions than for the line, with a significantly smaller shift for planar flow, compared to volumetric flow, $t(80) = -5.17$, $p =.0001$ and the line, $t(80) = -7.27$, $p < .0001$. There was also a significant PSV difference between the volumetric flow and the line condition, $t(80) = -2.10$, $p = .0388$. Figures 4B, 4C, and 5A show the psychometric functions and mean PSV in degrees for the tilted and upright body orientations when observers viewed the line, planar and volumetric flow.

The mean just noticeable differences (JNDs) are shown in figure 5B. Overall, observers had significantly higher tilt discrimination thresholds when they were tilted than when upright, $F(1,82) = 60.58$, $p < .0001$. These thresholds were found to differ across the stimulus types, $F(2,82) = 14.89$, $p < .0001$; the interaction term was not significant ($p > .05$). Observers had higher discrimination thresholds for the planar flow stimulus than for both volumetric flow, $t(82) = -3.75$, $p = .0003$, and the line, $t(82) = -5.43$, $p < .0001$, regardless of body tilt. There was no significant difference in the JNDs between the volumetric flow and line stimulus, $t(82) = -1.66$, $p = .1008$.

Given the differences in discrimination thresholds, we considered that the shifts in the PSV might reflect the choice of psychometric procedure. That is, the differences between conditions might have reflected an increasing regression toward the mean of the stimulus set with more imprecise stimuli. Therefore we repeated the PSV estimates using an adaptive staircase procedure (N = 7, mean age = 26.0, SD = 6.82). The results were qualitatively and quantitatively consistent with the findings from the method of constants data in the main experiment.

In another control experiment (N = 16, mean age = 26.75, SD = 5.13), we compared observer tilt judgments for single and multiple line (see Fig. 6A) displays that had the same mean luminance as the dot displays. We found no significant differences between these conditions, suggesting that the difference in body tilt-induced bias between the line and motion stimuli was not due to differences in element number, density, eccentricity, or luminance.

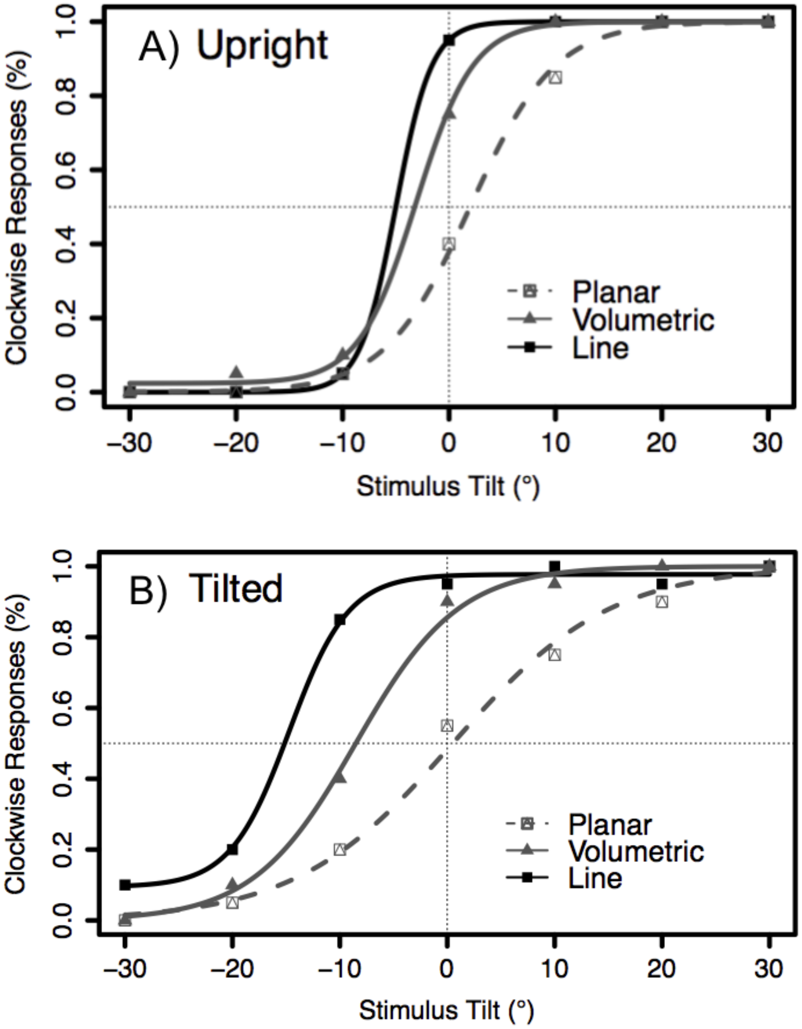

Figure 4.4: Psychometric functions showing the percentage of times that the stimulus was perceived as tilted in the clockwise direction relative to the gravity vector. The fitted psychometric functions from one subject for the "Upright" (A) and "Tilted" (B) head orientations. Planar flow, volumetric flow, and the line are represented by a triangle-filled square, filled triangle, and filled square, respectively.

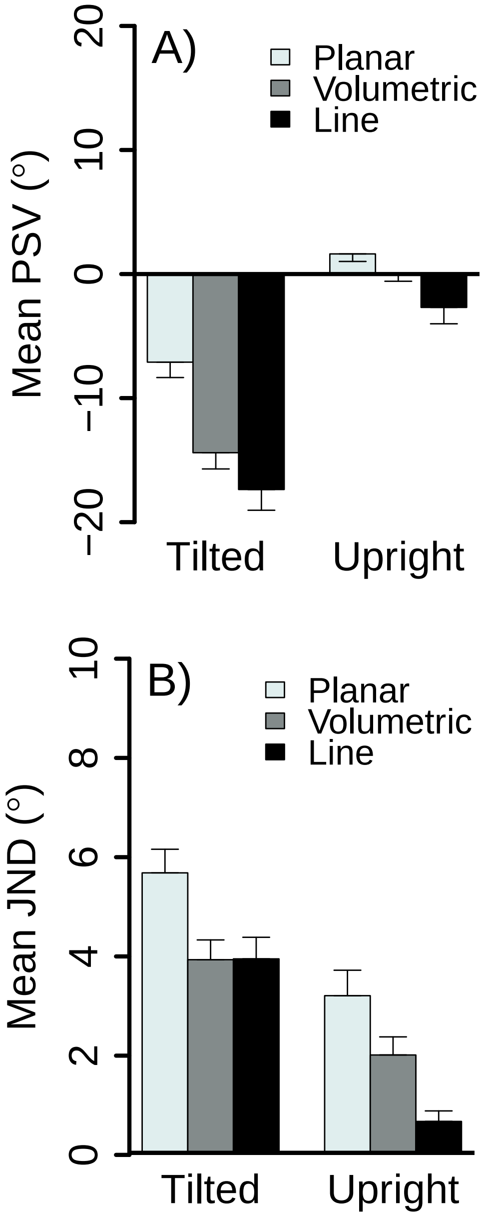

Figure 4.5: The mean PSV (A) and JND (B) averaged across observers as a function of head tilt and stimulus type (±1 standard error of the mean (SEM)). A lower JND represents greater certainty or precision in judging the stimulus tilt.

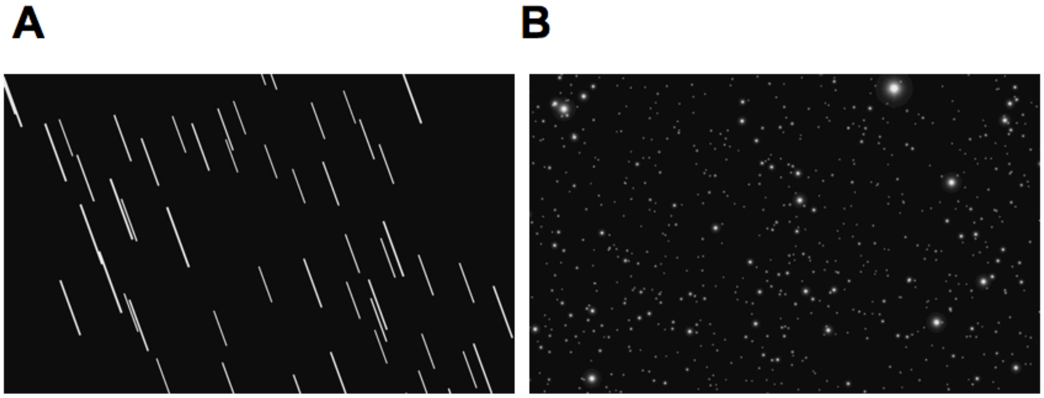

Figure 4.6: Screenshots of the multiple-line stimulus (A) and dot stimulus (B).

Our finding of a stimulus-dependent A-effect seem inconsistent with the proposal that systematic errors in visual tilt judgments are due to misestimates of self-tilt since errors in estimating body tilt should affect the frame of reference for visual tilt estimates, and thus should affect all tilt judgments equally. Rather, we found significant differences in the tilt estimates for the two motion conditions of planar and volumetric flow; these stimuli were the same pictorially, and only differed by the addition of motion parallax in the volumetric flow condition. Thus, tilt estimates are not the same for motion in general and may reflect differences in processing different types of global motion. Furthermore, the tilt biases differed between motion orientation and line orientation judgments. A control experiment using an adaptive staircase procedure produced results that were consistent with these findings, and thus these conclusions are not dependent on choice of psychophysical procedure.

4.3 Experiment 2

An optic flow display like those used in Experiment 1 can be perceived as external scene motion or as vection, in which the scene appears stationary and the motion is attributed to the self. In vection the external world is typically perceived as stationary, constant and rigid, so it is possible that cues to the visual vertical are treated differently than when the visual world is perceived as changing and dynamic relative to a stable self. If so, differences in the point of subjective verticality (PSV) for perceived object and self-motion might reflect a change in sensory weighting for visual and vestibular signals during vection.

4.3.1 Methods

Eight observers (4 males, 4 females; mean age = 30.3, SD = 8.65) participated in Experiment 2. All subjects had normal or corrected-to-normal vision and no reported vestibular impairment. All had prior experience with judging illusions of self-motion in a laboratory setting.

The apparatus, stimuli and procedures were the same as in Experiment 1 with the following exceptions. First, the number of randomly-distributed dots portrayed was increased to 8500. Second, all stimuli were displays of volumetric flow. The duration of these displays was experimentally controlled to promote either the perception of “external” motion (0.5 s) or “self” motion (20 s). There were 28 factorial combinations (2 body tilts x 2 stimuli x 7 stimulus tilts), each repeated 8 times for a total of 224 trials.

Self-motion trials were preceded by an auditory bell prompt to notify observers that they should attend to their perception of self-motion. During these self-motion trials, observers indicated if and when they experienced their first sensation of self-motion (i.e., vection onset) by briefly pressing one of the shoulder buttons on the gamepad.

As in experiment 1, observers were required to report the tilt direction of the motion display; however, for the self-motion trials, if vection was not experienced observers were to press one of the front-facing circular buttons on the gamepad rather than indicating clockwise or counter-clockwise.

4.3.2 Results and Discussion

After regression diagnostics, there was one subject excluded from the analysis. All of the observers experienced vection during the self-motion trials. Vection occurred in 841 out of 896 self-motion trials, or approximately 93.86% of the total responses. Trials in which vection was not experienced were not included in the computation of the PSVs and JNDs. The vection responses from one observer indicated the perceived direction of self-motion rather than the tilt of motion axis, so their responses for those trials were appropriately reversed. Mean vection latency across observers during these trials was 5.78 ± 4.50 s.

The mean PSV for the two postures when stimulus motion was perceived as object motion and self-motion are shown in Figure 4.7A. Head tilt resulted in a significant bias toward the direction of the body tilt, with greater biases when the head was tilted than upright, $F(1,15) = 20.92$, $p = .0004$. This result is an A-effect in that the tilt bias was in the direction of the head tilt. There was also a significant effect of stimulus type on tilt biases, $F(1,15) = 11.29$, $p = .0043$; shifts in the PSV were greater when the motion was perceived as self-motion compared to scene motion. The interaction between head tilt and stimulus type was significant, $F(1,15) = 7.98$, $p = .0128$, with greater PSV shifts between the condition types when observers were tilted, $t(15) = -3.36$, $p = .0043$.

The mean JNDs are shown in Figure 4.7B. There was a significant effect on the JND of posture, $F(1,15) = 11.18$, $p = .0044$, perceived motion type (object and self-motion), $F(1,15) = 23.60$, $p = .0002$, and an interaction between these factors, $F(1,15) = 7.50$, $p = .0152$. Tilted observers had significantly lower tilt thresholds when the motion was perceived as self-motion than external motion, $t(15) = -4.86$, $p = .0002$. As illustrated in Figs. 4.7, tilting observers resulted in larger systematic errors when observers judged the perceived direction of self-motion compared to object motion, despite greater precision in the former condition.

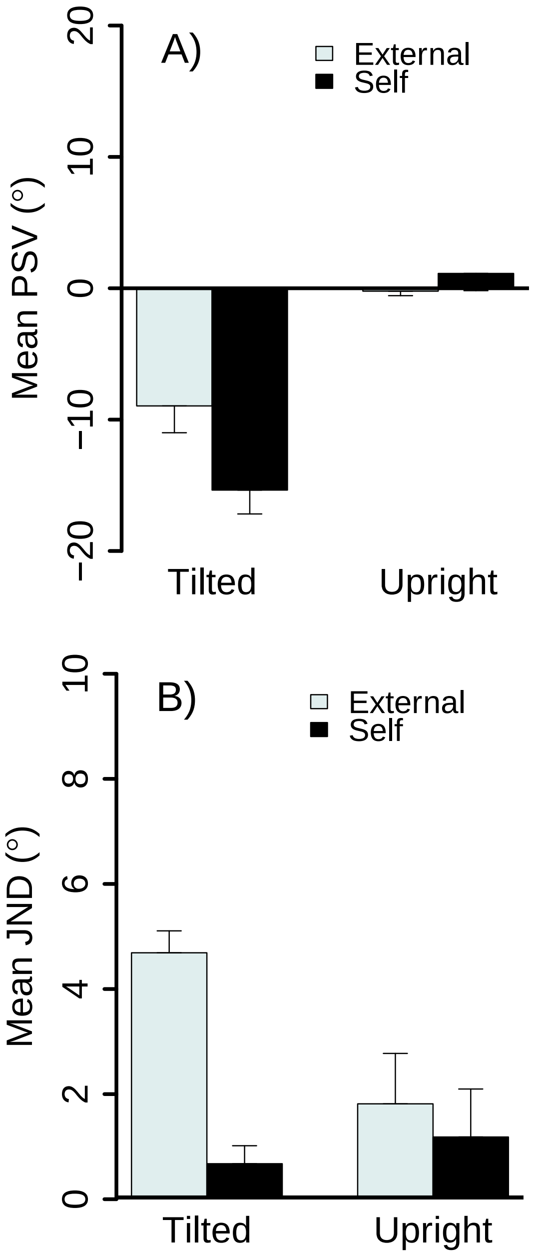

Figure 4.7: The mean PSV (A) and JND (B) as a function of body tilt and stimulus type (±1 SEM).

In sum, we report the novel finding of an A-effect for visually-induced self-motion. The bias in PSVs with head tilt significantly greater when global motion was perceived as self-motion than as external motion. We also found a significant difference in the JNDs for the perceived direction of external motion and self-motion relative to gravity. These results would be consistent with the position that idiothetic visual signals are more heavily weighted than vestibular cues to motion verticality. However, the JNDs indicated that tilted observers were less precise in their tilt judgments when perceiving external motion than self-motion. This finding may reflect greater sensitivity and reliability of the vestibular system for judging the direction of (self-) motion during self-tilt, than vision for external motion.

4.4 General Discussion

We investigated the effects of head tilt on the perceived direction of global motion relative to gravity, when the motion was experienced as external to the self (object motion) or induced the sensation of self-motion (vection). When subjects viewed a static line or motion displays while their body was tilted, the line or axis of motion—along which dots moved visually downward—were perceived to be tilted in the direction of the body tilt. These results are consistent with those of De Vrijer et al. (2008) and demonstrate that the A-effect can occur with both static and moving visual stimuli. In addition, we found significantly larger PSV shifts and greater precision in judging tilt of a static line than for the motion stimuli (shift for volumetric flow > planar flow). While we found that the difference in tilt bias toward the body between the line stimulus and volumetric global motion was negligible, in contrast to De Vrijer et al. (2008), there were significant differences between the planar flow and line condition in tilted subjects. Given that the perceived tilt depended on the type of stimulus motion, suggests that the perceived verticality of these stimuli might rely on another common underlying factor.

One possible explanation for the larger systematic errors but greater precision for the line and volumetric flow is that these stimuli contained more reliable visual cues—such as perspective projection—to better resolve the stimulus orientation than the planar flow. In the case of the line, subjects were presented with a salient tilt signal compared to the planar motion. Unlike the planar flow, the volumetric stimulus included the cue of motion parallax, which can also aid in determining the direction of the motion. If the reliability of a visual cue for judging scene orientation influences the relative weighting of visual and vestibular signals, it is possible that it may also affect the perceived self-tilt. The greater precision in orientation judgments for the line and volumetric flow may reflect an increase in the weighing of the visual signal, and the larger systematic errors indicating the perceived stimulus tilt relative to gravity, may reflect a decrease in weighting of the vestibular signal. It is also possible that the planar flow was simply perceived as a more ambiguous stimulus than the line and volumetric flow, as it did not contain motion parallax and could be perceived as rotation. Either case suggests that the perceived motion may rely on a computational strategy that takes into account a number of visual motion cues, including motion parallax. However, differences in verticality percepts for vection compared to object motion suggest that this explanation may not fully extend to perceptions of self-motion.

We also report that the A-effect occurs not only for motion perceived as external to the body, but also for motion perceived as self-motion. There were generally larger tilt-induced PSV shifts when subjects experienced vection compared to object (volumetric) motion. A lack of vestibular signals consistent with the presented visual motion—as in the self-motion condition—could result in the favouring of the visual input over the vestibular signal, as the more reliable directional signal. Sensory signals from the visual and vestibular system must be integrated into a common reference frame (Burns, Nashed, & Blohm, 2011; Harris et al., 2015), and it may be that the inconsistency of these signals in vection could introduce noise in that transformation. For instance, noise could potentially occur due to faulty estimates of the body's position in space and in spatial updating, due to vection itself. Somatosensory cues—such as pressure felt on the side of the body in the tilted posture—could also add further conflict and noise in resolving stimulus tilt relative to gravity. Furthermore, we also found significant differences in the discrimination thresholds between both of the motion conditions in tilted observers. The difference in these thresholds for tilted observers is a novel finding and runs somewhat contrary to Mittelstaedt (1983), who proposed that systematic errors in subjective tilt for roll-tilted subjects (at tilts greater than 60°) are due to the underestimation of body tilt. While such errors in tilt estimates also occurred for the vection condition in tilted subjects, the finding of significantly lower tilt thresholds seems to indicate that a different strategy is used in the estimation of self-motion direction, or is possibly affected by the inconsistency of the visual and vestibular signals that occurs during vection.

In summary, we have shown that when the whole body is tilted, both a static line and the direction of optic flow—whether it is planar or volumetricis typically perceived as tilted in the direction of the body tilt, demonstrating the A-effect. Additionally, tilting the body also typically results in visually—induced illusory self-motion to exhibit a similar but larger A-effect. Different magnitude A-effects for the line and motion conditions—and for object and self-motion—may be due to differences in processing or inconsistencies in the internal visual and vestibular signals, particularly so in the case of vection which occurs despite visual-vestibular conflict. We found systematic errors across most of the stimulus conditions and this is in-line with the notion that perceived line and motion axis tilt may be due to over or underestimations in self-tilt. This explanation would be consistent with our finding that our postural effects also depended on the stimulus. Further research into the integration of other visual cues such as lighting, could help provide insight into how noise might be reduced in the determination of tilt of external motion and perceived self-motion.

Chapter 5

General Discussion

5.1 Summary of major findings

The results presented in this dissertation have suggested that the perception of self-motion is not only influenced by gravity, but is also determined by higher-order cognitive and ecological factors. In Chapter 2, the data showed that tilting observers reduced vection (consistent with hypothesis 2.1) but aligning the direction of visual motion with gravity does not necessarily increase vection (inconsistent with hypothesis 2.2). Similarly, adding viewpoint oscillation increased vection but it did not matter if the oscillation was aligned with gravity (inconsistent with hypothesis 2.3). Chapter 3 had observers view random dot and pipe structure displays to examine the effects of aligning the direction of lamellar flow with gravity, and higher-level cognitive processes in vection. We found that the direction of visual motion with respect to both the head and gravity influenced vection, and thus could not simply be explained by the alignment with the head or gravity (consistent with hypotheses 3.1 and 3.2). Our results also showed stronger vection for the pipes than the dots which depended on posture and the perceived scene interpretation, indicating that self-motion perception is modulated by higher-level cognitive processes (consistent with hypothesis 3.3). In Chapter 4, I tested whether the observer reports of a perceived stimulus tilt in Chapter 3 was due to the same A-effect observed with static lines. I found an A-effect for all three stimuli (hypothesis I, correct), which was stronger for the line than for motion (hypothesis II, correct), and for motion perceived as self-motion than external motion (hypothesis III, correct), leading to the conclusion that gravity is an important factor in estimating the direction of visually perceived external and self-motion, and that these judgments may rely on different strategies. Together, these results suggest that gravity plays an important role in self-motion perception, although cognitive and ecological factors also play an important role. In the discussion that follows, I will provide the implications of these findings within the context of sensory conflict theories of vection.

5.2 Gravity does not always support vection

It was posited that varying head tilt might alter the perception of self-motion given that 1) the otolith organs are sensitive to acceleration due to gravity (and self-motion), and 2) we have expectations of motion in the world relative to gravity–for instance, as typically upright observers, we might expect things in the world to fall down towards the earth, with gravity. Also, the world and body up are usually consistent. This hypothesis was tested by having observers view smooth or oscillating motion displays in different postures, and indicate the magnitude, onset, and duration, of vection. Based on the data presented in Chapter 2 and 3, I concluded that gravity does not always influence our perception of self-motion. If, as Young et al. (1975) reasoned, tilting the head from upright reduces the sensitivity of the otoliths to motion, then we would have expected increased rather than reduced vection when lying down. For the simulated forward/backward self-motion in Chapter 2, we would have expected stronger vection in the supine and prone postures, since the radial flow in those conditions were aligned with gravity. Also, while there was an oscillation advantage for vection, it did not vary by posture or for vertical/horizontal oscillation. These findings run contrary to those of Kano (1991) and Tovee (1999), who suggested that the acceleration signal due to gravity should support or restrain vection.

The lack of differences between the vertical/horizontal and opposing motion conditions contradicts the findings of microgravity studies on perceived motion in regards to judging object and self-heading. In studies performed in parabolic flight, a 20-s micro-g or hypo-g phase (i.e., the period of apparent weightlessness or 0g) is preceeded and followed by a 20-s phase of hypergravity. Figure 5.1 shows the phases of gravity during parabolic flight. Consistent with this theory, Senot et al. (2012)

conducted a virtual target interception task in parabolic flight found a reversal in responses for the hypo and hypergravity phases of the flight. Similarly, Moscatelli and Lacquaniti (2011) had upright and tilted observers judge the duration of an accelerating target and found better performance when the object was moving downward in the direction of gravity than for objects moving upright or sideways. In self-motion studies, asymetries have also been found in the ability to discriminate pitch direction with a bias for motion along the gravity vector. Significant up/down asymetries were found by Vidal, Amorim, McIntyre, and Berthoz (2006) on Earth, and in a follow-up study by De Saedeleer et al. (2013) that was also conducted in free-floating cosmonauts during long-duration space flight. Yet in De Saedeleer et al.'s (2013) subsequent study, affixing the feet to the station floor resulted in a reduction of response asymetries. Thus, while gravity (or lack thereof) altered the visual perception of self-motion, both gravity and ecological factors such as proprioceptive cues (e.g., the feet touching a surface), may have influenced the perception of self-motion.

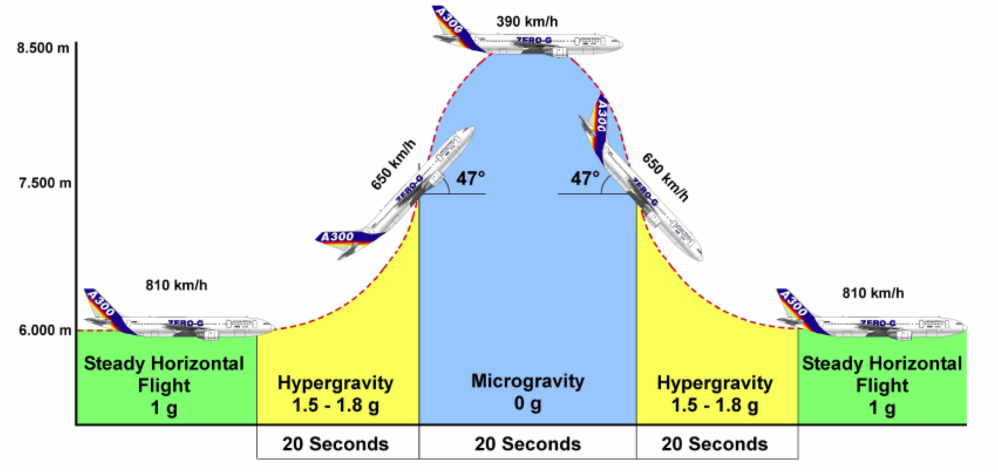

Figure 5.1: Illustration of parabolic flight characteristics showing the force and duration of gravity relative to aircraft pitch and altitude (from ESA (2015)).

Accordingly, in Chapter 3, I compared vection in upright and tilted observers viewing lamellar motion and the results showed that gravity-alignment enhanced vection when they were upright or roll-tilted (left/right side down). When they were pitch-tilted (supine/prone), neither the visual motion nor spinal axis aligns with the gravity vector. However, when observers were laying supine or prone, vection was stronger, started sooner and lasted longer, when motion was along the spinal axis. Thus, these vection effects depended on whether gravity was relevant in the given condition, and suggests that the perception of self-motion is not simply influenced by gravity, but is also largely head or trunk-centric. Thus, vection might be better explained by ecology, such as experience of the body and world in motion, and naturalness of the scene.

5.3 Naturalism and ecological validity

Vection occurs despite conflicting visual and vestibular information. According to sensory conflict models, increasing sensory conflict should inhibit visually-induced self-motion, but instead, it has been shown that increasing conflict by means of adding simulated viewpoint jitter or oscillation to optic flow displays tends to result in vection that is more compelling, with short onset latencies and longer durations (Guterman et al., 2012; Palmisano et al., 2011, 2000). A simple explanation for this oscillation advantage for vection is that it is more naturalistic or ecological since real self-motion generates head movements including rotations along multiple axes (Cutting, Springer, Braren, & Johnson, 1992; Grossman, Leigh, Bruce, Huebner, & Lanska, 1989; Hirasaki, Moore, Raphan, & Cohen, 1999; von Grünau, Pilgrim, & Zhou, 2007). Bubka and Bonato (2010) compared vection for motions from a handheld camera while walking and from a rolling cart, to test the notion that naturalistic optic flow should enhance vection. In agreement they found that the motion filmed while walking produced superior vection over that from the cart. This finding is consistent with my results showing enhanced vection with simulated viewpoint oscillation. Naturalism or an ecological account of vection could also explain why vection overall is reduced when lying down and is largely body or trunk-centric—considering that real world self-motion typically occurs when upright and restrained by gravity along the spinal axis. That is, it might be that more natural or ecologically plausible conditions for self-motion support vection.

Yet, an ecological account of vection does not explain the oscillation advantage for all postures. Nor does it explain the lack of a significant difference in vection in Chapter 3 between the pipes and dots displays in tilted observers, given that participants judged the pipes to be a more “naturalistic” scene than the dots stimulus. Palmisano, Allison, Ash, Nakamura, and Apthorp (2014) challenged the findings of Bubka and Bonato (2010) by assessing vection with simulated viewpoints that better matched the complexity of real head movements that occur during self-motion. They compared vection ratings of observers walking on a (motorized) treadmill and stepping-in-place, with simulated viewpoint jitter matching the observers head movements in real-time. It is important to note that treadmil walking tends to be considered more natural than stepping-in-place (S. J. Lee & Hidler, 2008; Pozzo, Berthoz, & Lefort, 1990; Templeman, Denbrook, & Sibert, 1999; Usoh et al., 1999), it has been found to be similar in its kinematics to overground (forward) walking (S. J. Lee & Hidler, 2008; Pozzo et al., 1990; Riley, Paolini, Della Croce, Paylo, & Kerrigan, 2007). Interestingly, while Palmisano et al. (2014) found marked differences in the head motion data between treadmill walking and stepping-in-place, the vection ratings between those conditions were not significantly different. Thus, the findings from the current study and that of Palmisano et al. (2014), do not entirely support an ecological account of vection. Rather, my findings and those showing equally compelling vection for more and less natural walking suggest that other factors such as cognitive processes, may also be influential in self-motion perception—or just that the "ecological" filter is not very selective.

5.4 Cognitive influences on vection

Besides sensory cues and ecological validity of the scene or posture which can indicate whether self-motion can occur, for vection we may also need to be "convinced" that self-motion is possible (Riecke, 2011). In Chapter 3, I showed that observers' pre-existing contexts for self-motion—e.g., perceiving the motion as an elevator ride, flying through space, bubbles, or as precipitation—influenced vection. Indeed, the contribution of higher-order cognitive processes in self-motion perception has been recognized by theme parks, where simulator riders are primed for the illusory self-motion by ushering them through environments that heighten the believability of the context of the motion; an example of this is Disney's *Star Wars* ride, in which riders are guided through an "intergalactic airport" prior to their "flight" through the galaxy.

Several other studies have also shown that users with a cognitive or perceptual framework for “moveability” (Riecke, 2011) can facilitate vection. One of the first studies to directly examine higher-level contributions to vection was by Lepecq, Giannopulu, and Baudonniere (1995), who showed reduced vection onsets for children seated on a chair with rollers (“moveable”) compared to a stationary chair (“unmovable”). The facilitation of vection through the power of suggestion has been demonstrated by seating observers on moveable carts or platforms that could be moved along a horizontal axis (Andersen & Braunstein, 1985; Berthoz et al., 1975; Lepecq et al., 1995; Pavard & Berthoz, 1977) or even vertical axis (Wright, DiZio, & Lackner, 2006), relative to gravity. In addition to enhancing vection by manipulating the perceptual framework for self-motion, it has also been found that cognitive manipulation by varing instructions for reporting the perceived motion can influence vection. Similar to Lepecq et al. (1995), Palmisano and Chan (2004) had observers viewing motion displays in a “moveable” chair report the onset and offset of self-motion (bias for self-motion), and in a separate group had observers in an “unmovable” chair report object motion (bias for object motion). Interestingly, they showed that those in the “moveable” or self-motion bias group experienced more vection than the “unmovable” object-motion group, but contrary to Lepecq et al. (1995) found no difference in motion onsets between the groups. The interpretation of the findings are complicated by the fact that in the latter instruction manipulation study, trials with partial vection were identified as vection trials. Nonetheless, the findings of my studies which were without observer (vection) priming showing that the spontaneously perceived context of the moving scene influences vection, indicate that higher-level, top-down cognitive processes are involved in the perception of self-motion. Given that these perceived contexts are based on prior experiences of self-motion, it may also be possible that conscious perceptions of the scene may also play an important role in other judgements of self-motion. Use of a more naturalistic scene may help to clarify the relationship between cognitive and postural effects on vection.

5.5 Vection in heading and path integration

When we physically travel through an environment, we are aware of our speed and direction so as to reach targets or avoid contact with obstables (Palmisano, Allison, Schira, & Barry, 2015). In theory, the pattern of optic flow which is seen in real or illusory self-motion, can be used in the guidance of self-motion. This notion was tested by Warren (1995), in which stationary observers judged their visual heading direction (left or right) from a virtual display; however, in that study it was not reported whether vection actually occured (Palmisano et al., 2015; Palmisano & Gillam, 2005). In a more recent study, Ito and Shibata (2005) found that heading judgments are in fact influenced by whether observers experience vection. Furthermore, Grigo and Lappe (1998) found that heading judgments of observers could be affected by reducing optic flow presentation durations below the typical minimum time needed for inducing vection. Adding visual elements to self-motion displays which promote vection (e.g., road signs on a virtual driving course), has also been shown to alter estimates of self-motion speed (Kawashima et al., 2011) and time to collision for virtual objects (Gray & Regan, 2000).

I found that not only did vection induction influence direction (or "heading") judgments, but that the orientation of the body relative to gravity also influences these judgments. Interestingly, in the experiments of Chapter 3, tilted observers reported that they perceived the lamellar motion—which was always aligned with the head/body and parallel with the display and gravity vector—to be moving along a tilted axis. In Chapter 4, I investigated this illusory tilt phenomenon to see whether the reported tilt differed when the motion was perceived as external motion or self-motion. In effect, this also addressed the question of how the (visual and vestibular) effects of gravity might be taken into account when making self (or object) heading judgments, during sensory conflict. The results indicated that not only was there an A-effect for both types of perceived motion (i.e., self and external global motion), but that the extent of the subjective stimulus tilt was greater when observers perceived the visual motion as self-motion. Thus, I not only found that vection influences perceived heading, but also depends on one's body orientation with respect to gravity. This finding has important implications for the development and use of both stationary and moveable self-motion simulators and of virtual environments (Palmisano et al., 2015), given that distortions in perceived self-motion direction is not only influenced by the optic flow in the displays and physical manipulations/movements of the simulator, but also by the relative direction/orientation of the body and motion to gravity.

5.6 General conclusion

Gravity is the most pervasive external force that acts on the body and objects in our environment on Earth. This dissertation examined and made significant contributions to the existing understanding of how gravity influences the perception of self-motion. In a series of vection experiments, the body and axes of visual motion were varied relative to gravity, to examine how the brain accounts for gravity in processing and integrating cues to self-motion. The data presented here demonstrates that the scope of this phenomenon of vection is exceptional, as it can be generated by external stimulation of the visual, vestibular, somatosensory and other senses; as well as shaped by prior physical experiences or ecological factors; and influenced by internal mental representations or higher-order cognitive processes. Therefore, I suggest that the perception of self-motion is both perceptual and cognitive in origin. The implication of this finding is that it provides supporting evidence that vection can also be a conscious subjective experience. This body of work also showed for the first time that the brain processes global motion differently based on whether it is perceived as external motion or self-motion, and highlights the complex balance among visual, vestibular, and higher-level cortical networks in self-motion perception. These insights into how gravity and other factors influence vection, could be used in the design of virtual reality simulators and microgravity environments; training and re/adaptation to and from Earth, micro or hypergravity environments; and potentially to better understand the effects of sensory disorders on the perception of self-motion.

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Appendix A

Author Contribution Statement

For all of the studies of this dissertation, I was the main contributor and lead author for papers that have been published or in preparation for publication. The scope of my contributions included developing most of the key ideas and experimental designs, programming the experimental software, setting up and running the experiments, and analysing and interpreting the data.

The contributions of co-authors primarily included discussions of the research literature and potential experimental directions, assistance in helping to build and accquire equipment, being a "second (or third) eye" in reviewing the experimental stimuli and parameters, and editing manuscripts in preparation for journal submission.

Robert Allison was involved at all levels of the project as my supervisor, and provided funding, guidance and critiques, and was the main editor of the manuscripts. This dissertation also incorporated joint research undertaken in collaboration with Stephen Palmisano and James Zacher under the supervision of Robert Allison. I developed theories to explain the results of the experiments, and drafted the first version of the manuscripts. Together, we decided which journals and conferences that this research was to be submitted.