Sensory Conflict: Effects on the Perceived Onset of Motion and Cybersickness in Virtual Reality

by

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Author's Declaration

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

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Abstract

The perception of self-motion involves the integration of multisensory information, however there are scenarios in which the sensory feedback we receive from these different sources can conflict with one another. For example, when inside the cabin of a ship at sea or playing a game in virtual reality (VR), sensory signals for self-motion from the visual and vestibular systems may not be congruent. It has been well documented that such scenarios are associated with feelings of discomfort and alterations in our perception of motion, but the mechanisms leading to these perceptual consequences remain uncertain. The goal of this dissertation is to explore the effect of sensory conflict between vestibular and visual signals on the perception of self-motion and implications for cybersickness. Chapter Two examined the effect of sensory conflict on the perceived timing of a passive whole-body rotation paired with both congruent and incongruent visual feedback using VR. It was found that the visual signal only influenced the perception of movement onset when the direction of the visual motion did not match the expected equal and opposite response relative to physical rotation. In Chapter Three, the effect of sensory conflict between visual, vestibular and body cues on the perceived timing of visual motion was explored. The results revealed that changing the orientation of the body relative to gravity to dissociate the relationship between vestibular and body cues of upright delays the perceived onset of visual yaw rotation in VR by an additional 30ms compared to an upright posture. Lastly, Chapter Four investigated the relationship between sensory conflict and sensory reweighting through measures of cybersickness and sensory perception after exposure to VR gameplay. The results indicated that the perception of subjective vertical was significantly influenced by an intense VR experience and that sensory reweighting may play a role in this effect, along with providing a potential explanation for individual differences for cybersickness severity. Altogether, this dissertation highlights some of the perceptual consequences of sensory conflict between vestibular and visual signals and provides insights for the potential mechanisms that determine the perception of self-motion and cybersickness in VR.

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Chapter 1

Introduction

Self-motion perception is an essential part of everyday life for navigating and interacting with our surroundings. To successfully do so, we need to form an accurate and precise representation of our environment and the events that occur within it. We also need to have a solid estimate of the position and orientation of our self in relation to the representation of the space around us. As we move, this relationship becomes more complex making our perception of self-motion crucial in maintaining and updating the representation of our self and the environment. Self-motion perception encompasses many aspects of motion including the direction, speed, estimates of distance or displacement and the time or length of the movement. These parameters can have functional roles in a wide range of applications such as the control of posture and gait, time-to-contact judgments to avoid obstacles, path integration and spatial orientation for navigation [40, 179].

Self-motion triggers an abundance of sensory feedback about motion that can be detected by the vestibular, visual, proprioceptive, somatosensory and even auditory system. The central nervous system is challenged with filtering through all the incoming sensory feedback to identify and process the information signalling the motion, among all the other sensory events that are occurring around us. Furthermore, the central nervous system (CNS) must complete this processing reliably and almost instantaneously such that we can function and operate smoothly. Among all the sources of sensory feedback, the vestibular and visual systems are the primary modalities that contribute to the perception of self-motion. For this dissertation, I will be focusing on these two sensory systems and exploring the relationship between them when experiencing motion. By examining how these sensory signals interact with one another, we can better understand how that information is integrated and processed in the formation of the many aspects of our perception of motion.

1.1 Vestibular System

The vestibular system is the structure of organs that are located within the inner ear known as the vestibular labyrinth. It is comprised of three tubes, the semicircular canals and two sacs, the utricle and saccule. The semicircular canals are primarily responsible for detecting rotational acceleration with two canals positioned vertically and one horizontally, with all three being orthogonal to eachother, to cover all the axes of rotation. The utricle and saccule detect linear acceleration in the horizontal and vertical plane, respectively. The vestibular labyrinth functions based on a mechanoelectrical framework: inertia from acceleration of the head and gravity causes the fluid found within the labyrinth to flow, which displaces the hair bundles (i.e., kinocilium and stereocilia) attached to the hair cells; this triggers the activation and firing of those cells, generating a signal that is transduced through the nervous system [104].

1.1.1 Cortical Regions

The processing of vestibular signals in the cerebral cortex is unique from other senses in that there is no specific region dedicated to vestibular information. After the signal from the vestibular afferents are integrated in the vestibular nuclei within the brain stem, the information appears to be broadly distributed to various regions of the cortex [49]. Studies involving extracellular recordings in primates have revealed several cortical regions that respond to both visual and vestibular signals during heading tasks including the medial superior temporal sulcus (MSTd; [95, 111]), ventral parietal area (VIP; [36, 48]), frontal eye fields (FEF; [112]) and visual posterior sylvian area (VPS; [47]). Interestingly, it has been shown that these areas contain populations of neurons that activate when the visual and vestibular cues signal either the same or opposite direction of self-motion. The reason for these two separate populations remains unclear, but these results provide evidence for the neural correlates in the integration of visual and vestibular signals and perhaps reveal the potential mechanism for deciding whether there is a discrepancy between the cues for determining self-motion.

More recent work has begun to try to explore these regions in human participants using non-invasive brain imaging techniques. The challenge with such techniques is that they require the observer to remain stationary to accurately capture the signal or image, limiting studies examining self-motion to artificial stimulation. Schindler and Bartels [202], were able to circumvent this limitation by taking advantage of the delayed onset of the blood oxygenation level dependent (BOLD) signal and only recording brain activity when the head was stabilized at the end of head movements. Using congruent and incongruent visual motion relative to the participants' voluntary head motion, they successfully found differential modulation of the anterior and posterior parieto-insular cortex (aPIC and pPIC) and parieto-insular-vestibular cortex (PIVC), as well as in area MSTd, dorsal VIP, the cingulate sulcus visual area (CSv) and a region in precuneus (Pc) as previously observed in the primate studies. These results are promising as brain imaging and immersive display technology advance, future research will be able to further explore and undoubtedly reveal more mechanisms and cortical regions involved in the integration of multimodal signals involved in self-motion perception.

1.1.2 Perceived Timing of Vestibular Stimulation

To maintain all the crucial functions of self-motion successfully, information from the vestibular organs must be processed rapidly. However, attempts to observe the perceived timing of vestibular signals has found that the perception of vestibular events is delayed. Barnett-Cowan and Harris [20] showed that the reaction times to a galvanic vestibular stimulation (GVS) is significantly slower in comparison to reaction times for a haptic, visual and auditory stimuli. Furthermore, the authors found that when paired together with a different sensory modality stimulus, the vestibular stimulation had to be consistently presented by about 160ms before the paired stimuli to be perceived as occurring simultaneously. One possibility for this delay could be the unnatural sensation evoked by GVS, however following studies using whole body rotations (19 to 91 ms) [44, 200] and head rotations (∼80ms) [21, 50] found similar delays. Despite the delay, the time that the vestibular event had to precede the paired stimuli was smaller compared to using GVS and additionally smaller when using head movements compared to whole body rotations. One potential difference that could explain this smaller delay between GVS and these later studies is that whole body and head rotations are more typically experienced vestibular events in natural settings, which may lead to them being better detected by the nervous system.

Another possible explanation is that the more natural vestibular stimulation also triggers other sensory feedback in the form of proprioception from the neck muscles and kinesthetic feedback from the limbs. In the studies with active head movements, there is also the presence of an efference copy signal, an internal copy of the motor command sent to signal the motion of the head, which is then compared to the resulting expected sensory outcome of that command to maintain proper control of the head movement. It was initially hypothesized that the additional signal would lead to improved perception of the timing, however Barnett-Cowan and Harris [21] found that the perceived timing of an active head movement was more delayed compared to a passive movement, suggesting that the re-afference signal instead suppressed the resulting sensory feedback. Similar findings have been found in neural recording studies in primates where it is found that there are specific populations of neurons that activate depending on whether the resulting sensory consequences match the initial motor signal [60, 61].

Chang et al. [44] found that the frequency and peak velocity of the body rotation can have a significant effect on the perceived timing as well, where a lower frequency and velocity were perceived as more delayed. More recently, Sachgau et al. [199] also showed that increasing head movement velocities resulted in smaller delays in perceived timing, although the head movement still had to occur significantly before the paired stimuli. Chung and Barnett-Cowan [50] measured the perceived timing of active head movements with and without vision while either maintaining an earth-stationary or head-stationary fixation. Vision provides significant information regarding self-motion (we will discuss this further in a later section) and with an earth-stationary fixation, the vestibulo-ocular reflex is active for maintaining the relatively stable visual environment with compensatory eye-in-head movements which is another source of signal for motion of the head. For a head-stationary fixation, the reflex is suppressed which can evoke strong sensations of visual motion where the entire visual image on the retina is moving. Despite these additional sources of feedback, there were no significant differences in the perceived timing of head movements from an active head movement without vision or eye movement signals.

Taken together, these studies show that more natural vestibular stimulation leads to better detection of movement onset and it can also be modulated by specific parameters of the movement. However, it has also been observed that not all additional sensory signals are necessarily useful, and that the delay in the perceived timing of self-motion can persist. It is unclear why certain signals can affect the perception of the motion onset while others do not and further research is also required to explore what aspects of these stimuli determine whether they are effective. In the following sections I will review some potential mechanisms to better understand how combining multiple sensory signals, specifically from the vestibular and visual systems can improve our perception of self-motion and what specific characteristics of these stimuli can influence our perception.

1.2 Multisensory Integration and Calibration

The detection and interpretation of sensory input is plagued by uncertainty, due to the noise present in both the physical nature of sensory stimuli (ex. thermodynamic or quantum mechanical properties of respective sensory energy sources) and the imperfect mapping of such stimuli through the noise present in our neurons and neural networks in the formation of the sensory representation of the events around us[91, 94]. It is something that is unavoidable and is only exacerbated as the environments and stimuli that humans interact with become more complex and dynamic. Signals from the environment are often noisy, ambiguous and varying in strength and we are challenged with understanding how the nervous system extracts the correct information related to signalling self-motion from these various sources [107]. A statistical approach to reducing uncertainty is to compound information from multiple sources both within and across sensory modalities to improve performance and minimize the amount of ambiguity to be able to efficiently interact with our environments and form an accurate representation. For example, forward motion of the head is an ambiguous signal for the otolith organs which is equivalent to backwards tilt of the head. However, signals from the semicircular canals (within) [11] or vision and neck proprioception (crossmodal) [151, 159] can be integrated with that signal to discern the orientation of the head and motion.

The nervous system uses two important strategies in combining redundant sensory information and using prior knowledge to reduce the noise of incoming signals and improve the reliability and accuracy of perceptual estimates [90]. The goal of multisensory integration and calibration are to improve precision and accuracy in the perception of events that are signalled by more than one sensory modality based on their individual reliabilities [9]. Integration using weighted averages and prior knowledge is useful for reducing ambiguity and noise in perceptual estimates, but it comes at the cost of introducing potential biases into those estimates if the most reliable source is not an accurate representation of the physical stimulus in the real world. Prior knowledge can also introduce biases if the prior probability is not accurate or conflict with the current environment, for example with many perceptual illusions because it contains scenarios that are opposite of what we are used to experiencing. The inaccuracy in the perception can only break down when there is enough evidence against it or if there is a large enough discrepancy beyond the window of spatial and temporal integration [90].

Deciding whether signals are discrepant also carries a lot of uncertainty because the perceptual system must decide based on estimates derived from the sensory signals themselves. The discrepancy in signals could be caused by a systematic difference in the signal or by random noise and since there is no way to know which possibility is true, the optimal behavior is to take both possibilities into account and weight them according to their relative certainties with the available evidence. If the discrepancy is large and consistent enough then we begin to remap or recalibrate the signals and the rate with which we adapt our perception largely varies depending on the sensory modality and the conditions of the task [90].

1.2.1 Multisensory Integration in Heading and Rotations

One area of motion perception where multisensory integration has been extensively studied is in heading perception, which is defined as one's ability to recognize the direction of self-motion. It is commonly measured using discrimination thresholds in the left or right direction of a forward translation. To observe the integration of visual and vestibular signals during self-motion, the reliability of the visual signal is altered such that the optic flow pattern ranges from clearly signalling a direction to being ambiguous or not representative of a coherent direction. By observing the discrimination thresholds of both visual and vestibular motion individually, the values can then be analyzed using a statistical model to predict how the signals are combined when both sources of information are available to the observer. This modelling approach describes the concept of a sensory reweighting mechanism, which involves the change in the relative contributions of those individual sensory thresholds in the final combined perceptual outcome. The sensory reweighting mechanism has been typically described following a Bayesian framework, where each individual sensory signal has a prior probability distribution based on previous knowledge and experience. This prior determines the weight of the given sensory signal involved in the perceptual estimate, however that weight of the prior can change based on the reliability of the signal through noise in that signal generated by the external environment or internally due to changes in the state of the central nervous system.

Using this method, research has shown that visual and vestibular self-motion cues are integrated following a statistically optimal model in which the final percept is determined by a weighted value based on the reliability of the individual signals [38, 39, 96]. However, when a discrepancy is introduced between the cues, such that they are signalling different directions from one another, it has been found that there is a tendency for the response to be biased to rely more on the vestibular cues [39, 76, 82, 96]. This bias most likely represents a predisposition to rely on vestibular information when determining self-motion as the primary source of sensory feedback. Results from Drugowitsch et al. [82] supports this idea, where they found that response times to visual self-motion were longer than in vestibular-only and visual-vestibular conditions while having improved thresholds when vision was available. This suggests that when making a heading judgment, there is a predisposition to rely more on the vestibular signals first and then using visual information to supplement and fine tune the estimate. It has also been shown that during heading, the visual system has difficulty dissociating object motion from self-motion and discrimination thresholds increase when visual reliability is low [80]. However, these detriments were alleviated when the visual stimuli are accompanied by vestibular signals [80].

Multisensory integration with visual and vestibular cues has also been explored with rotations in the yaw axis. Research in this area has been typically quantified using size or velocity estimations as the outcome measures. Contrary to heading discrimination where optimal integration is fairly robust [38, 72], results in this field indicate that the integration of visual and vestibular cues does not always follow the predictions of a statistical model [75, 103]. Instead, it appears that the integration of visual and vestibular cues during rotations can be undermined by prioritizing the ability to detect a discrepancy between the motion signalled by the two senses [103]. This follows the idea of the mandatory fusion or causal inference model where unisensory signals are converted into a combined bimodal signal when the sensory cues are redundant and the unimodal signals are discarded in favor of the combined signal for further processing [183].

Prsa et al. [183] showed that when two cues do not share a common cause, it is possible to still have access to the unimodal information to be combined with the posterior estimate to produce a weighted average. However, individual signals are often less reliable and there may be a cost for the brain to hold onto such similar neural representations in the case of self-motion information that may not be used at the perceptual level [183]. Thus, when the sensory signals are determined as originating from the same event, mandatory fusion of the visual and vestibular self-motion signals occurs allowing for more efficient encoding as a single bimodal signal rather than processed as separate senses. Findings from de Winkel et al. [73] also support this theory, where evidence for casual inference over optimal integration can occur in heading estimation, but is highly dependant on the dynamics and characteristics of both the visual and vestibular stimuli as to which multisensory processing strategy is chosen.

1.2.2 Multisensory Calibration

Despite the similar purposes for improving perceptual stability, little research has been conducted in examining the relationship between multisensory integration and multisensory calibration with visual and vestibular cues. Zaidel et al. [237] introduced a varying discrepancy in the heading angle between the visual and vestibular stimuli to assess the adaptation of the cues, in addition to varying visual coherence as previous integration literature has done. A single cue baseline condition was performed followed by a combined cue adaptation period and finally a post adaptation single cue block was completed to measure adaptation. It was found that both cues adapted towards one another as expected without external feedback for "internal consistency", however the extent of adaptation was not influenced by the relative reliability of the cues and were more aligned with predictions from a fixed ratio model with higher adaption ratio for vestibular signals[37]. Here, a higher adaptation ratio of vestibular cues suggests that visual signals are perceived to be more accurate in heading discrimination tasks, as they require less adaptation to reach what the system internally perceives to be accurate based on the available sensory feedback. More importantly, these results indicate a different mechanism for multisensory integration and multisensory calibration of visual and vestibular signals, which makes sense given that the goal of these processes is different (precision vs accuracy).

To further examine the multisensory calibration mechanism, Zaidel et al. [236] conducted a follow-up study where they included external feedback with the varying visual coherence and discrepancy between the visual and vestibular signals. Since there was a conflict between the cues, the external feedback indicated which cue was more accurate implying which direction the percept needed to shift to achieve calibration. They found an interaction between individual cue reliability and adaptation such that when the more reliable cue was accurate only the inaccurate cue shifted, however when the less reliable cue was accurate both cues were calibrated together causing the initially accurate cue to become inaccurate. These results were best explained by a suboptimal model that superimposes cue calibration in the presence of feedback with cue yoking and calibration without feedback that shifts the individual cues towards one another [236]. The model components shift when the accurate cue is more reliable or less reliable indicating that both cue accuracy and reliability are considered during multisensory calibration. When external feedback is available, the calibration relies on a combined cue to achieve external accuracy and when no feedback is present the cues are calibrated individually to maintain internal consistency [236]. This shows that external feedback from the environment can facilitate changes in perceptual and behavioural responses with multisensory plasticity, thus it is important to explore the interactions between cue reliability and accuracy in the presence and absence of feedback to better understand multisensory calibration [236].

1.3 Visual Stimuli

Vision is another important sensory modality responsible for signalling self-motion. The movement of the image that falls on the retinas generates optic flow patterns that are interpreted as either self-motion, object motion or a combination of both. Optic flow can induce strong sensations of motion even in the absence of physical movement known as vection. This is shown in the classic moving train example, where a passenger in a stationary train may experience a sudden illusory sensation of motion as adjacent vehicles begin to move. In multisensory self-motion research however, it is common for vision to be presented alongside real physical motion or other sources of sensory feedback indicating motion. It has been shown that visual adaptation can lead to biases in vestibular perception [65] and the opposite effect has been observed as well [122]. Vection can also be robust to conflicting visual and vestibular feedback and the sensation can improve when both sensory modalities are presented together [14, 15]. Thus, it is necessary to explore how vection is influenced by different visual characteristics and how vision can interact with other sensory signals to better understand how self-motion is integrated and perceived.

1.3.1 Vection

As previously described, vection has been traditionally defined as a visual illusion in a stationary observer. However, as vision is not the only sense found to be capable of generating perception of self-motion, it is now becoming more common for vection to be defined as illusory self-motion [179]. Research in self-motion has advanced to applying multiple sensory modalities in tandem, including actual movements of the head or body to investigate the integration of different self-motion signals and how these inputs can affect various aspects of self-motion. In these situations, it is more appropriate to describe them as mediated perceptions of self-motion as there are conditions that contain both real and illusory motion, as well as redundant multisensory information regarding the movement [179].

It is important to recognize the distinction between the conscious subjective feelings of self-motion, compared to simply aspects of motion without inducing the perception of self-motion. Although virtual reality (VR) and immersive media applications can provide remarkable visual realism, it is often inadequate in providing a compelling behavioural realism in the form of a believable sensation of self-motion. There is a difference in quality between showing observers a simulation of moving through an environment and for the observers to believe that they are experiencing it [195]. Ensuring that participants truly experience self-motion can have strong effects on experimental results, where vection is shown to have functional roles in heading, time-to-contact judgments, steering accuracy, navigation (path integration) and spatial orientation [179]. Vection being a subjective experience is measured using self-reports accordingly. However, this can introduce biases based on experimenter demands and individual differences in what constitutes onset or magnitude of vection [179]. Finding objective measures such as eye movements, EEG and even postural responses can allow for more precise and consistent measures of vection to reveal where, when and how these processes work to advance our understanding of self-motion.

1.3.2 Top-Down Influences

There are many known bottom-up factors that can affect vection that mostly have to do with the physical parameters of the stimuli (ex., field of view, velocity, density, spatial frequency and eccentricity, axis of movement, etc.). However, there is emerging research showing the importance of top-down influences as well and how one perceives and interprets the stimuli can also affect vection. Eye movements (fixation, retinal slip and gaze shifts) have been reported to modulate vection, as well as the perceived background motion or relative background motion compared to the foreground or stationary objects (separation) and stereoscopic depth cues [195]. This is similar to the reference frame hypothesis in which a background is typically perceived as stationary and provides an earth-stable reference relative to movement occurring in the scene. This is further connected to the naturalism and ecological validity and global consistency of the scene, as well as the inclusion of head-tracking which can further facilitate vection. Lastly, there are factors of attention in which attended stimuli are perceived to be closer or central to vision and also the possibility of actual motion or the belief of actual motion has been shown to modulate vection onset latencies and magnitudes [195].

Research on perception of self-motion heavily depends on the simulation of motion and the ability to make the perception of the movement as close to real and natural movements that are common behaviour. The challenge with this is that the main forms of motion, such as locomotion and vehicle transportation have limitations in research environments and equipment. As an alternative to changes to the technical aspects, research has started to investigate multisensory and top-down influences to improve motion simulation. Specifically, with the increasing popularity of VR applications, presence has been suggested to be an influential factor to make simulated self-motion more believable. The concept of presence is the ability of the virtual environment to make users truly believe or feel like they are actually in the virtual world and are not consciously aware of it as being a simulation [224]. It can be argued that some of the inconsistent findings in self-motion perception literature thus far may be attributed to a lack of controlled presence or similar high-level factors. At the same time, improving simulated self-motion perception can also have potential benefits in researching presence and the practical implications of improving presence in virtual applications [196]. Further analysis of previous experiments by Riecke and colleagues that included both top-down (realism of a scene) and bottom-up factors (intact compared to scrambled scenes) to explore the relationship between vection and presence found that overall, top-down influences had a significant role over lower level factors in various measures of vection suggesting that the believability or presence of the scene is a main contributing factor [196].

1.3.3 Realistic/Natural Stimuli

Most of the literature examining self-motion perception with vision has used minimal optic flow patterns (typically floating dots) to simulate movement. However, to get a better understanding of how visual motion is perceived in the real world, we must explore these mechanisms and perception using more natural visual stimuli. It has been observed that scene stability can enhance the perception of motion by providing a frame of reference which can be used to successfully distinguish self-motion from object motion [197]. As our natural surroundings are commonly earth-stationary, relative motion observed between oneself and the environment is more likely to be attributed to self-motion, whereas movement of independent objects are more likely to be seen as object motion [197]. Thus, using more complex and naturalistic visual stimuli which can enhance scene stability and create a more convincing frame of reference is more advantageous for producing a compelling sensation of self-motion perception. Riecke et al. [197] directly assessed this by comparing the effects of providing a photorealistic natural scene, a scrambled mosaic of the same scene, and a flipped version of the scene to preserve the visual dynamics while altering the familiarity. They observed that vection measures were higher when the scene was intact and presence measures were higher when the scene orientation was consistent with the orientation of the environment in the physical world. This study highlights the importance of both scene structure and properties for evoking the sensation of self-motion, as well as the global consistency of the scene for generating a sense of presence.

Different types of optic flow patterns can generate varying experiences of vection or perception of self-motion [29]. For example, Bonato and Bubka [29] found that increasing the chromaticity and spatial complexity of an optokinetic drum had a significant positive effect on vection onset latency and magnitude. Similarly, van der Steen and Brockhoff [219] found that using a flight simulator with a natural landscape scene produced saturated vection (instantaneous sensations of visual self-motion in tandem with a motion platform) much earlier compared to using an optokinetic drums. The authors believed that these findings can be attributed to the less ambiguous perception of scene and object motion with a natural scene layout, whereas an optokinetic drum may be perceived as an intermediate object between the observer and the natural environment. It has also been reported that higher frame rates in a display to generate smoother visual motion can enhance the perception of vection reflected in body sway [225]. These results provide further evidence in support of using more ecological visual environments or visual stimuli that share more visual features with what one would typically encounter to enhance scene stability and perceived vection.

Another aspect of providing ecological stimuli is the congruency of the visual and vestibular feedback being presented. Edwards et al. [86] observed that detection thresholds for both radial expanding and contracting optic flow patterns on a projector screen was lower when it was accompanied by a physical motion in a congruent direction to the optic flow compared to an incongruent motion. In a more novel top-down influence approach, Nigmatullina et al. [172] showed that participants asked to imagine a rotation before being physically rotated in the dark had higher detection thresholds when the imagined and actual rotation was in an incongruent direction. Ratings of vividness of the imagined rotation were also influenced retrospectively by the physical rotation that followed, in which congruent rotations led to higher ratings [172]. When studying the mechanisms of multisensory integration, the visual and vestibular cues are often presented in conflict with one another to observe the relative sensory weightings. However, it is important to consider how the difference between presenting the stimuli ecologically and non-ecologically can affect the participants' perception of self-motion.

Presenting observers with more ecological visual stimuli has also been shown to have a positive influence on the updating of spatial orientation and potential implications for navigation. In one study by Lathrop and Kaiser [153], participants were able to more accurately point to a remembered target that they physically rotated to with idiothetic cues compared to targets that they rotated to using a controller. Participants' performances were also influenced by interface fidelity, with conditions performed in a head-mounted display (HMD) being more consistent and closer to performance in the real world than using a desktop display viewing a virtual recreation of the physical environment [153]. In another study, Riecke et al. [193] found that when presented with a projection of a familiar and natural scene on a large curved screen covering one's entire field of view, participants were able to automatically and obligatorily spatially update their orientation in a pointing task in comparison to viewing an optic flow pattern which was not sufficient for any spatial updating to occur. Physical motion had no effect on automatic and obligatory spatial updating for both visual conditions. The takeaway here is that in studies where spatial updating or orientation matters, it may be important to consider natural scenes instead of optic flow patterns to assess and how that interacts with the vestibular signals which are known to influence vection [193].

1.4 Virtual Reality and Cybersickness

As VR technology becomes more accessible as a training and rehabilitation tool, as well as for mainstream media and entertainment, cybersickness is a prevalent issue for most people that experience it [188, 201]. Similar to simulator sickness, cybersickness is seen as a subset of motion sickness in the literature that is induced by exposure to visual motion through VR. Previous research has shown that visual motion can lead to sickness known as visually induced motion sickness (VIMS) [33, 139], however VIMS is classified as occurring when the observer is stationary while in VR there can now be scenarios that allow for movement of the body or even physical locomotion as VR systems and simulator technology advances. Thus, cybersickness can be viewed as an intersect between simulator sickness and VIMS.

1.4.1 Symptoms and Identification

Cybersickness is commonly compared to motion sickness and simulator sickness due to the nearly identical etiology. Symptoms of cybersickness can include, but are not limited to nausea, vomiting, pallor, sweating, disorientation, vertigo, headaches and eye strain [156]. Symptoms of cybersickness are polysymptomatic and polygenic, as they manifest differently between individuals making it difficult to characterize and understand [188]. The symptoms of cybersickness are commonly categorized in the literature based on the area of influence in nausea (e.g., stomach awareness, vomiting, etc.), oculomotor (e.g., headache, eyestrain, etc.), and disorientation (e.g., vertigo, dizziness, etc.), abbreviated as N, O and D, respectively [188]. It is believed that the main difference between cybersickness, motion sickness and simulator sickness is the symptom profile in which the subjective ratings of symptoms of these three categories differ based on the highly cited simulator sickness questionnaire (SSQ) by Kennedy et al. [140]. It has been shown that cybersickness has a profile of D $>$ N $>$ O, where disorientation ratings are higher than nausea and then oculomotor ratings, whereas sea sickness has a N $>$ O $>$ D profile, space sickness has N $>$ D $>$ O and simulator sickness follows an O $>$ N $>$ D symptom profile [138]. It has also been observed that HMDs specifically follow a D $>$ O $>$ N symptom profile [201]. The difference in symptom profile can be mainly attributed to the difference between the sicknesses that are experienced. Motion sickness is commonly experienced while using a form of transportation, whereas simulator sickness and cybersickness occur while using immersive displays and VR technology which can lead to greater oculomotor and disorientation effects.

Identification of cybersickness symptoms have predominantly been measured using self reported questionnaires. Due to the similarity in etiology with motion and simulator sickness, most of the questionnaires used are the same or adapted from those reports. One of the most widely used and validated questionnaires used is the simulator sickness questionnaire by Kennedy et al. [140]. As mentioned previously, the questionnaire is composed of symptoms from three categories (nausea, oculomotor and disorientation) and the severity of each symptom is rated on a four-point scale. One of the main challenges of questionnaires for measuring cybersickness is that they can only be administered outside of the exposure period, thus the responses can be influenced by the individual's recollection of the experience. For example, in a recent study post test SSQ scores were significantly higher than pretest scores for all participants despite only 30% explicitly reporting feelings of motion sickness [57]. Additionally, there has been evidence that demand characteristics can prime sickness symptoms when administering a pre-exposure questionnaire [234].

To overcome this challenge, Keshavarz and Hetch [142] introduced the fast motion sickness scale (FMS), which is a verbal rating scale from zero to 20 of motion sickness severity to continuously capture motion sickness data during exposure. Similarly, Treleaven et al. [218] used a simulator sickness visual analogue scale (SS-VAS) measuring sickness severity on a scale of zero to 10 marked on a 100 mm line and were able to find that some individuals who reported symptoms on the SSQ did not report such symptoms using the scale during immersion. This suggests simple reports may be better used to avoid the demand characteristics phenomenon where the participant only reports the symptoms after being prompted to by the questionnaire [218]. Short simple reports also have the advantage of being able to be administered during immersion, however they lack the detailed breakdown of the various symptoms obtained with the questionnaire format [218].

Despite this, questionnaires are still susceptible to individual biases and how difficult it can be to standardize ratings across all individuals. Recent research has begun to focus on finding objective measures for cybersickness to overcome the potential biases of self-reported measures. The interest for finding objective measures have been focused on observing physiological signals such electrocardiogram (ECG), blood pressure, electrogastrogram (EGG), respiration (RSP) and skin temperature [188]. Neural activity monitoring with electroencephalograms (EEG) and functional magnetic resonance imaging (fMRI) have also shown some promise [188, 216], but are more limited in applications due to the movement restraints required of the techniques. The advantage of physiological measures is the ability to continuously monitor changes in the signals during exposure and without the need to remove the user from the immersive experience. Although more research needs to be conducted to validate and standardize these measures.

1.4.2 Sensory Conflict

One of the most widely accepted theories for explaining the occurrence of motion sickness is the sensory mismatch theory [177, 186, 187]. This theory posits that motion sickness occurs when there is a discrepancy between the visual, vestibular and kinesthetic sensory inputs signalling self-motion. For example, motion sickness from travelling in a vehicle may arise while reading because the visual information (from the reading material and the internal cabin of the vehicle) is static, while the sensory feedback from the vestibular system and proprioception of the body in contact with the vehicle senses the accelerating motion. Similarly, when experiencing VR there is minimal movement of the head and body, relative to the amount of visual motion that is signalled through the display. This is especially troublesome for the application of VR. While there have been attempts to simulate the physical motion that accompanies the visual motion (e.g. through motion platforms and stationary treadmills), the movement is limited in comparison to the expected motion that one would naturally experience in the real world [68].

As VR begins to incorporate more natural movements to match the visual motion, research following sensory conflict theory may need to shift from the traditional mismatch theory to a multisensory integration approach. The integration of multimodal information regarding self-motion has been extensively studied in the literature, revealing the importance of combining feedback from all sensory sources regarding self-motion in forming a stable perception of and navigating our surroundings. However, research in this area has only begun to extend into the field of VR and the implications of multisensory integration and self-motion perception in VR and cybersickness are unclear. One theory that incorporates the multisensory approach with VR suggests that dynamic reweighting of visual and vestibular cues needs to occur to alleviate the sensory conflict which is believed to be one of the primary causes leading to cybersickness [101]. This idea is supported by evidence that there is a reduction in sickness severity observed when vestibular noise is introduced [226, 229] or when vestibular stimulation that matches the visual motion is provided [42, 46, 63, 102, 144, 161, 170, 191]. These findings all indicate that the vestibular signals need to be down-weighted to match the conflicting source of visual flow from VR to alleviate cybersickness symptoms. This is contrary to the bias towards the vestibular signals typically found in the self-motion literature, suggesting that adaptation of the reweighting function would be required when entering VR if dynamic reweighting is indeed a common mechanism for the occurrence of cybersickness [101].

One of the major arguments against the sensory conflict theory is the inability to predict why some individuals experience sickness whereas others do not even when they are exposed to the same conflicting stimuli. In addition, even with the incorporation of head or full body motions with VR, which reduces the sensory conflict, cybersickness still persists for some individuals. The multisensory approach provides a potential explanation for this critique in that the difference stems from individual differences in reweighting the sensory signals to consolidate the mismatch. If cybersickness is indeed caused by the presence of sensory conflict, then the level of sickness experienced by an individual will be reflected by their ability to reweight the conflicting sensory information, whereas an individual who can successfully attenuate the mismatch will experience lower levels of sickness compared to a different individual who fails to reweight their sensory signals. Future research is needed to confirm whether this may be a potential mechanism on how the sensory conflict theory induces sickness in relation to the multisensory integration approach and this will be further explored in Chapter 4 of this thesis.

1.4.3 Postural Instability

Another popular theory for explaining motion sickness is the postural instability theory, which proposes that motion sickness occurs when one's postural stability is compromised and is unable to maintain or adapt to the instability [192]. A common example of this theory is the occurrence of sea sickness, where symptoms may develop when one is unable to adjust to the constant swaying of the boat. While the postural instability theory remains popular, the findings in the literature have been controversial thus far. Studies examining the occurrence and severity of cybersickness symptoms after exposure to VR while either standing or seated, or incorporating head movement have found both significant [13, 45, 190] and insignificant [2, 77] correlations between sickness and postural instability. A few potential reasons for the inconclusive findings may be due to non-standardized experimental designs and equipment, misinterpretation of correlations for causality (for example in [163, 168]), as well as potential individual differences in sensory weighting and postural control.

In a review by Bos [31], the author gave some examples of why it is more appropriate to describe the postural instability theory for cybersickness as a second order effect despite findings of a correlation between the two. This is mainly indicated by two scenarios in which postural instability can be experienced without getting sick and motion sickness can occur in the absence of postural instability. Examples include findings of increase in instability while adaptation to sickness occurs; labyrinthine patients no longer experiencing motion sickness while being more unstable than healthy controls; and sickness can occur almost instantaneously in certain scenarios whereas the theory states the prolonged instability triggers sickness (reviewed in [31]). Thus, although some research indicates a correlation between postural instability and cybersickness, it is difficult to conclude whether there is a causal relationship until better measures for observing the onset of symptoms are developed. Rather, the correlations between balance control and sickness appear to suggest that they may not be causally related but instead covary with one another as a result of a mechanism that is linked to both postural stability and sickness.

1.4.4 Eye Movements

Eye movements have also been considered as an indicator or predictor for cybersickness. When experiencing motion of the full visual field, a reflexive eye movement known as the optokinetic nystagmus (OKN) is generated to stabilize the visual image on the retina [174]. The OKN consists of a slow-moving phase where the eyes follow the direction of the visual stimulus and then are followed by a fast phase in the opposite direction to reset the image. When this OKN reflex is induced in darkness, it becomes the optokinetic afternystagmus (OKAN) in which the slow phase eye velocity (SPEV) drops and decays over time [174]. Together with the vestibulo-ocular reflex (VOR), which is another form of reflexive compensatory eye movement that stabilizes gaze during head movements, they are indicators of the velocity storage mechanism (VSM). The VSM is a central integrative network made up of vestibular neurons in the medial and superior vestibular nucleus that is believed to have an important role in the integration of vestibular and visual information to generate corresponding eye movements [174, 232].

Past literature has indicated that the VSM is related to the occurrence of motion sickness [85, 97, 127], specifically longer time constants reflected by prolonged VOR and OKN responses are associated with greater susceptibility to motion sickness [32, 54, 121]. With the similarities between motion sickness and cybersickness, recent work has begun to explore the relationship between the VSM and VIMS. Using a virtual optokinetic drum, Guo et al. [113] found significant correlations between the time constants of the OKAN and nausea ratings. Nooij and colleagues [175] on the other hand, found that VIMS was most strongly predicted by vection strength compared to the OKN parameters for visual yaw rotations using a panoramic virtual projection of a natural scene. In a follow up experiment, Nooij et al. [174] showed that the activity of the VMS was dependent on the vection inducing strength of the visual stimulus, whereas the time constant was not affected by the visual stimulus. This suggests that rather than being directly associated with VIMS, the VSM may have more of a modulating role on sickness through the properties of vection. Future research needs to be conducted to better characterize the complex relationship between these mechanisms.

1.4.5 Temporal Adaptation

The temporal aspect of cybersickness is an area of interest that is important for both research and the development of VR technology. Understanding the time course in which symptoms can develop, how long they can persist for, as well as the time it takes to recover from symptoms are all crucial components for improving the experience and accessibility of VR. Thus far, the main findings in this field of research has shown that symptomology increases over exposure time (with a possible plateau effect) and effects from symptoms can persist post exposure with time periods ranging from minutes up to hours depending on exposure time [83]. Although exposure duration can increase symptoms, exposure frequency has been found to attenuate susceptibility to cybersickness through adaptation effects [83]. Similar results have been found in studies for simulator sickness, which has been found to have a positive relationship with exposure duration and a negative relationship with repeated exposures for military personnel who are often exposed to simulators for training purposes [141].

However, there is also a potential downside to adaptation in that it can lead to maladaptation of the real world or aftereffects when coming out of VR [101]. In some cases, such as rehabilitation this can be beneficial where one wants the sensorimotor or behavioural changes to carry over, but for entertainment or media purposes this may be less desired. One possible detrimental effect is spatial disorientation, as well as the effects to cognitive abilities when the impairment is novel [108, 109]. This can occur even when the person is unaware of the impairment, however the effects are diminished over time as the user adapts or becomes aware of the disorientation. This effect is observed more during movement of the visual field as experienced in VR rather than movement of the body potentially due to the unexpectedness or novelty of the visual field moving by itself, whereas head and body movements are commonly experienced and executed [108, 109].

1.4.6 Neural Correlates

Limited research has been conducted that has examined the neural correlates of cybersickness, however with improving brain imaging and VR technology, researchers are now better able to explore this field. One area of interest for the neural basis for motion sickness is suggested to be the nodulus of the cerebellum [56]. The nodulus is highly interconnected with the vestibular nuclei being involved in controlling eye position and orientation and more specifically, it appears that motion sickness originates from the vestibular-only (VO) neurons that send and receive signals involving the maintenance of posture and orientation of the head and neck [56]. The nodulus and VO neurons have a velocity storage mechanism that monitors the earth-vertical orientation and gravitational signals and habituates the system to constant acceleration and velocity. It is strongly believed that the sensory conflict mechanism responsible for motion sickness is dependant on the time constant of the velocity storage and the deviation from earth-vertical position [56].

In a study by Miyazaki et al. [166], they found asynchronous bilateral activation in the medial temporal area (MT+) using functional magnetic resonance imaging (fMRI) during exposure to a VIMS-inducing movie compared to a control movie without VIMS in observers who reported feeling sick. As MT+ has been known to be involved in the modulation of eye movements, postural control, vection perception and sensory integration networks, these results suggests that the asymmetrical activity may be a reflection of malaise responses in response to the potential triggers of VIMS [166]. Similar results were found by Toschi et al. [216] using fMRI and nausea inducing visual stimuli, observed a greater reduction in inter-hemispheric connectivity between left and right V1, as well as increased functional activity between visual motion areas (MT+/V5) and nausea-associated brain regions (anterior insula (aIns) and mid-cingulate (MCC) cortices) in people who experienced VIMS. In another study by Takeuchi et al. [209], it was observed that anodal tDCS to increase the excitability of the right temporal parietal junction prior to entering VR helped alleviate disorientation symptoms and improved postural stability upon exiting VR, suggesting that inhibition or lack of recruitment of this area responsible for vestibular function and integration may be part of the reason for cybersickness and postural instability. Future studies could examine tDCS while in VR to observe whether the facilitation can provide immediate relief, as effectiveness of tDCS has been previously shown to be limited by the time of administration [209]. Taken together, these results indicate that motion sickness is reflected in the activity of cortical areas responsible for processing information regarding self-motion and coordination of eye movements and postural stability, providing evidence from a neurological perspective for the major theories of why motion sickness occurs.

1.4.7 Vection and Visually Induced Motion Sickness

The common origin of visual motion between both vection and VIMS raises the question about whether there is an association between the two phenomena. From what has been observed thus far, it appears that vection may be a necessary prerequisite for VIMS but experiencing vection does not always lead to the occurrence of VIMS, however there has been limited and mixed findings regarding the direction of the relationship between the two factors (see [144] for a review). The direction of the correlation between them can have important implications for both research and application purposes. While vection is desired in applications of VR for rehabilitation, training and entertainment to create a more realistic sense of motion, VIMS would typically not be desirable with vection [144].

Depending on the association between the two factors and potential characteristics of the visual stimuli that may influence both, it may become a challenge when trying to maximize vection while minimizing VIMS. One factor that may lead to the occurrence of VIMS without vection or vice versa may stem from multisensory integration theory which posits that in the case of a sensory mismatch, the perceptual weight shifts towards the more reliable sensory modality [144]. Depending on the magnitude of the conflict and the ability of the system to reconcile or ignore the mismatch, it may lead to scenarios in which either vection, VIMS or both can occur [144]. Thus, a sensory conflict and multisensory integration approach may help researchers better understand the complex relationship between vection and VIMS along with potential parameters that may influence both factors.

There can be different types of optic flow patterns, specifically steady and changing patterns, that can produce different types of vection [30]. This can also be associated with differences in sensory inputs, where visual and nonvisual inputs are likely to be inconsistent during changing vection and active self-motion compared to steady vection and passive motion [30]. With steady vection, sensory conflict should only occur at the onset and termination of the flow pattern, however with changing vection, there is conflict each time the pattern changes. Using a constant expanding flow pattern and an intermittently expanding and contracting pattern in an optokinetic drum, Bonato et al. [30] found that a steady pattern produced a stronger vection magnitude and lower simulator sickness ratings compared to the alternating pattern. This suggests that while vection alone can still lead to simulator sickness, changes in vection and the resultant increased occurrence of sensory conflict can lead to more sickness symptoms.

The integration of ecological head movements has been shown to enhance vection in an HMD signalling the significance of multisensory interactions for vection [145]. Palmisano et al. [180] tested vection and cybersickness together while incorporating head oscillations with optic flow patterns that were compensated, uncompensated and inversely compensated relative to the head movement. They found that vection was strongest when head movement was compensated for with a constrained aperture, but with full field exposure there was no difference, suggesting that vection is mostly influenced by the area of visual motion and then followed by the sustained visual and inertial conflict [180]. Cybersickness on the other hand was found to be significantly greater in the inversely compensated condition compared to the other two conditions [180]. The results agree with the sensory conflict theory, where the greater visual-inertial conflict generated increased cybersickness symptoms. These findings also provide additional evidence for a negative correlation between vection and cybersickness, as the condition with no visual-inertial conflict had the greatest vection magnitude.

In a recent study, Keshavarz et al. [143] examined the joint effects and interaction of different parameters of visual motion simulation (speed, density and axis) on the experience of both vection, VIMS and presence. They found that higher visual speed and density was associated with greater vection intensity and presence and the effects of the parameters were additive, meaning they increased these measures further when combined in comparison to previous literature which mostly examined these parameters individually [143]. There were no differences in VIMS ratings in relation to density or speed, however the authors believed that this may have been due to the ability of the visual stimulus to induce symptoms which was relatively weak across all conditions (floor affects for VIMS to avoid ceiling results in vection) [143]. For the rotation axis, there were no significant results in association with vection ratings between the axes and for VIMS, pitch rotations resulted in the highest FMS and SSQ disorientation scores contrary to previous results that found no differences in sickness regarding rotation axis [143]. Overall, the differential modulation of vection and VIMs by the visual parameters, rotation axis and stimulus used in this study suggests that there is not a strong association between the two factors [143]. More specifically, since vection was shown to be affected by the parameters and VIMs was not and remained relatively low, these findings agree with literature that vection can be experienced in the absence of VIMs.

1.4.8 Alleviating Cybersickness Symptoms

Active Control and Vestibular Stimulation

One of the most common and well-known methods of attenuating cybersickness in accordance with the sensory conflict theory is to introduce proprioceptive information by adding motion. The idea behind this notion is that the additional sensory input from the vestibular system and proprioceptive feedback may help reduce or consolidate the conflict between the stationary user and visual motion. Additionally, giving the user control of the motion and the generation of a motor command and expectation of the resulting sensory outcome from the motor event is another crucial aspect in consolidating the conflict. In a systematic review of cybersickness studies using an HMD it was observed that stationary users had the highest SSQ scores followed by controller based moving and then walking [201]. The lower end occurrence of cybersickness is found when using a neck (head-based) controlled HMD and lower severity levels than previous literature [218] and galvanic cutaneous stimulation admitted intermittently during a virtual driving simulator helped reduce subjective scores of simulator sickness [102].

Waltemate et al. [222] observed the relationship between perceptual judgements (simultaneity, agency and ownership) and motor performance when viewing a mirror of upper body movement of an avatar in a CAVE VR with varying latencies. They found that agency and ownership decline at a slower rate than simultaneity as latency increases (more tolerant to latencies) and never fully breaks down even at the highest latencies tested [222]. Perceptual judgements on the other hand appeared to be more related to motor performance than with latency, suggesting that participants only become perceptually aware of the delays and breaks the perceptual quality of the experience when they notice errors in their motor performance [222]. This study is different from previous literature in that it employs a complex full upper body motor task where error could be high compared to previous simple isolated motor tasks (ex. a button press) that have lower rates and degrees of error in which delays might go unnoticed. This has important implications as VR advances towards full body immersion and shows that latency needs to be taken into strong consideration when designing more complex motor tasks.

Scene Content/Complexity and Visual Flow Rate

Recent work has shown that the interaction between scene content and complexity along with navigation control has an important influence on the sensory mismatch of visual and actual movement leading to different levels of cybersickness [188]. Simulator sickness while performing active tasks using an HMD was shown to be affected by image scale (both minification and magnification) but was unaffected by time delay [81]. As with previous studies, visual-vestibular interaction is robust to a certain extent with delays between actual movement and updating of the visual scene, however the scale of the image which affects the size of the objects and more importantly the optic flow rate of the visual movement relative to the head movement appears to strongly affect sickness reports [81]. A systematic review on cybersickness when using HMDs revealed that out of four major content types, gaming content produced the most severe symptoms followed by 360-degree videos and then minimalist and scenic content [201]. Higher visual stimulation was also associated with higher oculomotor SSQ subscale scores, most likely due to the vergence-accommodation conflict present with HMDs [201]. One solution for this is a "head-locking" rotation technique which locks the visual scene during movement and updates the image to the resultant new location has been shown to drastically reduce cybersickness [137]. However, much more research is needed in this area, as a majority of literature has been conducted with minimal content and the rapid advancement of VR with more realistic content is created.

Technical Factors

Many technical aspects of early VR technology that were associated with cybersickness such as resolution, field of view, flicker, latency and refresh rate [156] are no longer relevant with the latest advancement in commercially available VR HMD technology. However, sickness symptoms continue to persist and are common among users. Rather than alleviating cybersickness, it is believed that improvements in technology have instead increased reports of cybersickness [188]. There are some recent reports that higher fidelity and more realistic graphics generate greater nausea ratings perhaps due to the greater levels of visual flow [69]. Cybersickness can be alleviated to a certain extent by reducing rather than increasing the FOV and it is now believed that it is better to dynamically adjust the FOV depending on the velocity of displacement to reduce symptoms of cybersickness without users noticing the change and affecting the quality of the experience [93].

One technical aspect that the technology has yet to overcome is the vergence-accommodation conflict that occurs when viewing VR through an HMD. The display places the screen at a constant distance from the eyes on one plane, preventing the eyes from performing the normal lateral vergence movements and adjusting the focal length of the pupil lens (accommodation) to change focus on various visual stimuli in the real world [188]. In addition, the lens of modern HMD models are still limited in adjustability and combined with equipment shifts makes the images not being correctly aligned with the eyes [188]. Taken together, this can lead to visual fatigue and may contribute to cybersickness, with oculomotor symptoms being one of the primary categorical symptoms, however, it has been shown that performing oculomotor exercises immediately prior to entering VR can reduce self-reported levels of cybersickness [182].

While there are many factors, such as individual variance and scene control to explain the emerging profiles of sickness symptoms based on the subscales of the SSQ, there is also evidence to suggest that despite the different magnitudes and severity of symptoms, the profile appears to be strongly based on the equipment being used [139]. However, examining the use of consumer grade VR systems in research applications shows overall end-to-end latency is relatively low, tracking is fast and noise levels for the tracker output is low [171]. There are also limited differences in cybersickness between HMD and CAVE setups [137], as well as with different types of displays such as projectors, 3D TVs, as well as research and consumer grade HMDs [194]. Changing the way VR is implemented rather than just improving the technology may be more important in preventing cybersickness.

Information that suggests a given regulatory behaviour or strategy needs to be able to be implemented or engaged with or else it creates a disruptive interaction where users may try to synchronize with the stimuli and more often fail to do so and preventing a true perception to action coupling [57].

1.4.9 Future Direction

One of the unique challenges of research involving cybersickness is that as VR advances, the implementation in experimental settings evolves along with the technology. The results observed from early VR studies where a lot of technical aspects were believed to be strongly involved in inducing sickness may be drastically different from those observed with modern VR HMDs. Even within contemporary studies it is becoming increasingly difficult to consolidate and replicate results due to the variety of equipment available and the vast amount of content that can be created and used. However, that is not to say all the research conducted thus far is irrelevant, but rather it is important to recognize the development of both the research and technology and attempt to create a form of standardization across the field.

1.5 Overview of the Dissertation

The following chapters of this dissertation explore the perception of vestibular and visual signals in the presence of sensory conflict. The close relationship between sensory conflict and cybersickness led to further investigation of whether sickness can influence or be influenced by vestibular-visual interactions.

Chapter 2 investigates the perceived timing of vestibular motion paired with congruent and incongruent visual motion using whole-body passive rotations in combination with VR. Participants judged the perceived onset of rotation while viewing a realistic virtual environment that moved relative to physical motion at different velocities. Additionally, cybersickness measures were recorded throughout the conditions to determine whether there was a correlation between the sickness severity, the degree of sensory conflict and the participants' ability to judge the perceived timing.

Chapter 3 explores the influence of gravity relative to body orientation on the perceived timing of visual motion. Participants reported the perceived onset of a visual scene simulating rotation around the yaw axis presented in VR while in different body positions, such that the gravitational vector on the vestibular labyrinth was either congruent or incongruent with the direction of the motion. This allowed us to observe whether vestibular input has an effect on the visual perception of self-motion.

Finally, Chapter 4 assesses the relationship between cybersickness and sensory reweighting by observing vestibular function after exposure to sensory conflict. Participants were exposed to different VR experiences to elicit varying levels of sickness and then performed a subjective vertical task to probe the individuals' weighting between the vestibular and proprioceptive signal. If cybersickness is associated with ones ability to resolve the sensory conflict, then this should be reflected in the perceptual weighting.

Chapter 2

Influence of Sensory Conflict on Perceived Timing of Passive Rotation in Virtual Reality

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2.1 Abstract

Integration of incoming sensory signals from multiple modalities is central in the determination of self-motion perception. With the emergence of consumer virtual reality (VR), it is becoming increasingly common to experience a mismatch in sensory feedback regarding motion when using immersive displays. In this study, we explored whether introducing various discrepancies between the vestibular and visual motion would influence the perceived timing of self-motion. Participants performed a series of temporal-order judgements between an auditory tone and a passive whole-body rotation on a motion platform accompanied by visual feedback using a virtual environment generated through a head-mounted display. Sensory conflict was induced by altering the speed and direction by which the movement of the visual scene updated relative to the observer's physical rotation. There were no differences in perceived timing of the rotation without vision, with congruent visual feedback and when the speed of the updating of the visual motion was slower. However, the

perceived timing was significantly further from zero when the direction of the visual motion was incongruent with the rotation. These findings demonstrate the potential interaction between visual and vestibular signals in the temporal perception of self-motion. Additionally, we recorded cybersickness ratings and found that sickness severity was significantly greater when visual motion was present and incongruent with the physical motion. This supports previous research regarding cybersickness and the sensory conflict theory, where a mismatch between the visual and vestibular signals may lead to a greater likelihood for the occurrence of sickness symptoms.

2.2 Introduction

Temporal integration of vestibular events with other sensory information is necessary for maintaining perceptual stability and to navigate our surroundings. However, signals from the environment are often noisy, ambiguous and can vary in strength [107]. Sensory stimuli are naturally in conflict with one another, in the sense that there is always a mismatch between the signals due the variation in sources, the time for the stimuli to reach us and transduction latencies within the central nervous system. The system is then further challenged with processing these discrepant signals and determining where these signals originated from and whether they belong to the same or separate events in the world to form an accurate perception of the environment. The sensory inputs that are being relayed can also carry an additional layer of uncertainty as they are being received and interpreted by a system of neurons that also contain a level of noise before the signals are formed into perceptual estimates [94]. Sensory conflict between vestibular and visual signals has been thoroughly investigated for self-motion perception in the spatial domain (e.g., [38, 39, 76, 75, 82, 96, 134, 183]). However, to our knowledge there have been no studies to date exploring the effects of sensory conflict between visuo-vestibular signals on the temporal processing of self-motion.

Previous findings in the temporal domain of vestibular signals have observed a delay in the perceived timing of vestibular stimuli relative to stimuli from other sensory modalities. It has been shown that a galvanic vestibular stimulation must precede a paired light, touch or sound stimulus in order to be perceived as occurring simultaneously [20]. Similar findings have been reported with passive head movements [21], passive whole-body rotations [44, 200] and active head movements [21, 23, 50, 199]. However, most of these findings were observed with the vestibular cues in isolation, whereas self-motion in a naturally occurring scenario that is typically accompanied by concurring visual feedback, as well as possible proprioception and auditory cues. Chung and Barnett-Cowan [50] found that providing vision did not affect the perceived timing of an active head movement, however the visual feedback provided was always congruent with the vestibular motion. Applying the sensory conflict approach from the spatial domain by introducing discrepancies between the visuo-vestibular signals may allow us to better understand the interaction between these signals in the perceived timing of self-motion.

In virtual reality (VR), the visual scene is updated relative to the users' head movement in the equal and opposite direction to maintain an earth-stationary environment [132, 167]. This relationship or ratio between visual scene motion and head motion is referred to as the "visual gain" or "gain factor" [15, 27, 130, 132, 152, 167]. By changing the visual gain, a discrepancy between the visual and vestibular cues signaling self-motion is introduced allowing us to investigate the integration and calibration of the conflicting signals. Interestingly, many studies using varying levels of visual gain have found that there is no significant difference in task performance and that participants do not notice that there is a discrepancy when the visual gain is not unity [15, 27, 152] or in a nonecological direction [123, 133, 147].

However, when an optic flow pattern is viewed in VR using a head-mounted display (HMD), vection magnitude ratings are significantly greater when the display movement was compensated for head movements in an ecological manner compared to when the direction of the display movement was inverted, resulting in non-ecological compensation of the head motion [145, 180]. In fact, it has been reported that when using an HMD, participants reported a higher gain factor as most stable and a wide range of higher gain factors were also accepted as earth stable [130]. However, in this study when the visual gain was in a nonecological direction it was not accepted as stable and it was also reported that there is a difference in gain tolerances for rotational and translational movements [130]. A similar finding was found when comparing gain amplification using an HMD or CAVE display, where participants were more tolerant to the amplification when using the CAVE display possibly due to the additional physical cues available [184]. These findings suggest that there is a different effect of perceived self-motion depending on the display type or certain characteristics of the visual stimuli.

It is surprising that people are unable to detect discrepancies between these signals that are so closely interconnected and redundant. There have been suggestions of a mandatory fusion model which states that the nervous system combines the signals into a single percept and discards the unisensory signals as it is inefficient for the system to hold onto to redundant signals [183]. This theory relates back to findings in conflict detection and multisensory integration studies, where the processing of visual and vestibular cues does not follow an optimal integration model when a discrepancy is detected where the signals are perceived as not having a common causality [38, 72, 73]. Similarly, recent reports have shown that observers adopt different causal inference strategies depending on whether they are performing an explicit or implicit heading discrimination task [1] and there is a trade-off between conflict detection and integration performance dependent on the observers' fixation strategy when integrating visual and vestibular self-motion signals [103, 167]. There have also been findings that when the visual gain is too large and a discrepancy is detected, then the integration of the signals breaks down and responses start to bias towards the more reliable cue [133, 152], providing further evidence to support this theory of sensory fusion and conflict detection.

With the emergence of consumer VR in recent years, it has become more pertinent to examine sensory conflict due to the discrepancy between visual and vestibular signals when exposed to VR, in which the observer is either stationary or limited in the space they can move around in. While there may be ongoing attempts to integrate other forms of sensory feedback to virtual experiences, the experience of motion in VR is primarily driven by visual feedback paired with limited vestibular and proprioceptive information, leading to sensory conflicts regarding self-motion information. In addition, there are latencies associated with the technology such as display lag, tracking latencies (with head-mounted display systems) and rendering speeds, that can all contribute to further discrepancies between the visual feedback and physical motion of the user. There is considerable interest with sensory conflict in VR and cybersickness [101], the malaise effects of VR exposure similar to symptoms found in motion sickness, such as nausea, vomiting, pallor, sweating, disorientation, vertigo, headaches and eye strain [156]. It is predicted that symptoms occur when there is a discrepancy between the visual and vestibular inputs signalling self-motion, known as the sensory conflict theory [177, 186, 187]. While it is important to determine the mechanism for alleviating cybersickness, it is also of interest to examine the role of sensory conflict and cybersickness on vestibular function. It has been shown that vestibular sensitivity and processing can be affected by exposure to vection and VR [99, 100] and prolonged exposure to optic flow can induce subsequent aftereffects in vestibular self-motion perception [65].

In this current experiment, our goal was to investigate the effect of manipulating the relationship between visual and vestibular motion on the perceived onset of a passive whole-body rotation. While previous reports have focused on the effects of modulating the visual gain for the perception of the visual aspects of self-motion and scene stability, here we seek to explore the novel effects of modulating the visuo-vestibular signal in the perception of self-motion relative to an auditory signal. With the presence of congruent visual feedback, we expect the delay in the perceived timing of the onset of motion to be reduced (closer to zero) due to the integration with the additional visual feedback compared to rotating in the dark. We explored the effects of modifying the gain of the visual scene by changing the speed and direction of the visual motion relative to the actual movement of the head and body making the visual and vestibular cues incongruent. We also set out to replicate previous findings that the delay in perceived timing of a passive rotation is lower at a higher rotational frequency [44] and whether this relationship is affected by the presence of visual feedback. With the use of VR and a motion platform in the current study, we also recognized the importance of monitoring and measuring cybersickness and it has also been previously shown that sickness symptoms are greater when optic flow patterns are inversely compensated relative to the direction of head motion [180]. Since we modified the gain of the virtual scene in the HMD to create a conflict between the visual and vestibular feedback, we expect there to be varying levels of cybersickness depending on the amount of discrepancy between the sensory cues.

2.3 Methods

2.3.1 Participants

Data was collected from twenty-seven participants (15 males and 12 females; mean age= 23.4, SD= 3.4) recruited from the University of Waterloo. An additional participant had been recruited but dropped out part way through the experiment due to sickness symptoms. Twelve of the participants were volunteers, while the remaining participants were remunerated $10/h for their participation. All participants reported having no auditory or vestibular disorders and had normal or corrected-to-normal vision. One participant dropped out part way through the experiment due to sickness symptoms. This experiment was reviewed and received ethics clearance through a University of Waterloo Research Ethics Committee and all participants gave their informed written consent in accordance with the guidelines from the committee.

2.3.2 Apparatus and Stimuli

Participants were seated in a racing seat (Corbeau FX1 Pro) and secured with a five-point harness. An extra layer of padded foam was added to the seat to minimize proprioceptive cues. A helmet was attached to the frame of the seat and over the center of the motion platform to ensure that the head maintained stable, upright and centered around the axis of rotation. The chair apparatus was mounted on top of a MOOG 6DOF motion platform (Figure 2.1a). Trajectories for passive whole-body rotations were generated using a custom

Python (ver3.6) script on Microsoft Visual Studio 2019 and sent through an ethernet controller to the motion base computer controlling the platform servers. The movements followed a raised-cosine velocity profile with a peak velocity of 20 deg/s presented at 1 and 0.5 Hz in the yaw axis. The total displacement of the platform was 10 and 20 degrees for the 1 and 0.5 Hz rotations, respectively.

The visual stimulus was a naturalistic virtual forest environment with a horizontal ground plane generated in Unreal Engine (ver. 4.16) (Figure 2.1b). However, areas further from the observer towards the horizon were randomly sloped to simulate a natural scene and to mask the outer bounds of the virtual environment. Ideally, the environment would be large enough where the observer could not see the boundaries and the slopes would not have to be as aggressive, but due to the technical limitations of rendering an environment with this level of detail while maintaining performance (frame rate) levels this feature was implemented as a solution. The virtual environment was presented through a head mounted display (Oculus Rift CV1). The Rift CV1 has an OLED display with a resolution of 2160x1200 (1080x1200 per eye) at a 90 Hz refresh rate. Previous work has shown that the visual scenes with more size and depth cues can lead to more accurate perceptual scaling between visual and inertial motion [58]. No visual fixation point or fixation instructions were provided to maintain a naturalistic experience and to prevent effects on self-motion perception [103, 195]. The ratio between the head and visual scene motion was manipulated such that speed and direction of the visual scene updated relative to the tracking of the headset was varied using a custom blueprint in the Unreal Engine software, referred to from here on as the "visual gain". This modification of visual gain also affected the resulting amplitude of the visual motion, where a larger or smaller gain resulted in a larger or smaller visual rotation angle, respectively, relative to the head rotation [27]. Tracking of the headset was performed by the Rift sensors and while we did not measure the end-to-end latency of our system, previous reports using the same headset model has measured extremely short baseline latencies (∼1.8 ms) [92].

Participants were presented with four visual gains (1, 2, 0.5 and -1; Figure 2.2) at both rotational frequencies in a block design. For the visual gain of 1, the visual scene moved at the same speed and in the opposite direction of the head rotation, simulating an earth-stationary environment. For the visual gains of 2 and 0.5, the visual scene moved in the opposite direction as well, but updated at twice and half the speed respectively, relative to the tracked head rotation. For a visual gain of -1, the visual scene updated at the same speed as the head rotation, but the direction of which the visual scene updated was reversed and moved in the same direction as the head motion instead of opposite (as it did in the visual gain 1 condition). This made the scene appear to move with the head motion in the same direction. In addition, there was a control condition in which participants performed the task with no visual stimuli by closing their eyes and the head mounted display was turned off acting as a blindfold. The presentation order of visual conditions was counterbalanced across participants.

Figure 2.1: **a** Screenshot of the naturalistic virtual forest environment used for the visual scene in the experiment. **b** Physical setup of the experiment with the 6DOF motion platform, the racing seat with added foam, helmet and Oculus Rift CV1 HMD.

In each trial, an 800 Hz tone was presented for 10 ms at nine stimulus onset asynchronies (SOAs) following a logarithmic scale: -600, -295, -145, -35, 0, 35, 145, 295, 600 ms, relative to the onset of the passive rotation (Figure 2.3a). A negative SOA indicates that the auditory stimuli was presented before the onset of movement, positive SOA indicates the auditory stimuli presented after the movement and zero indicates both stimuli occurring at the same time. The onset of the motion, auditory tone and subsequent SOA were validated using an external inertial measurement unit (IMU) placed at the center of the motion platform, along with a synchronized recording of the auditory signal. The onset of the movement was determined as occurring two samples (or 5 ms) before the signal exceed two standard deviations from the mean [50] sampled when the platform was held stationary for 10 s at the start of a simulated experiment run. Since the auditory tone generated a pronounced square wave in the auditory signal recording, the onset was determined as occurring when the signal exceeded the mean sampled during the initial 10 s at the start of the simulation. The order of SOAs was randomized among trials within each block.

There was a total of 54 trials within each block, so participants were presented with six repetitions of every SOA for each visual-frequency condition pair. Auditory stimuli were presented through in-ear headphones (Sony MDR-XB50AP), while participants also wore a pair of over-ear headphones (Sennheiser S1 Digital) at the same time playing white noise to mask any external auditory cues.

2.3.3 Measures

Cybersickness was assessed using the fast motion sickness scale (FMS) [142] to measure sickness levels immediately after each condition block was completed. The FMS is assessed by a verbal rating on a 20-point scale ranging from "0 (representing no sickness at all)" to "20 (representing severe or frank sickness)".

2.3.4 Procedures

At the beginning of the experiment, participants completed nine practice trials to familiarize themselves with the equipment and the task. The task was a two-alternative forced choice (2AFC) in the form of the temporal order judgment (TOJ) task, where participants had to indicate whether the onset of the self-motion stimuli (passive whole-body rotation) or the auditory tone occurred first. The trials were self-paced in that the next trial would not begin until participants' response with a button press on a gamepad (Logitech Gamepad F310) was recorded. In addition, there was a $\sim$1.6 ms delay (1 ms for the computer to communicate with the motion platform and 600 ms to allow the auditory tone to occur first) between the registration of the participants' response and the initiation of the movement of the following trial. Participants performed the TOJ task under the five visual conditions. Each condition was repeated with 1 Hz and 0.5 Hz rotations for a total of 10 conditions which were presented in a counterbalanced blocked design. At the end of each block participants were immediately gauged for sickness symptoms through the verbally administered FMS score. They were then given a minimum five-minute break or if they were experiencing sickness, then they would not continue until after their symptoms subsided. At the conclusion of all the conditions, participants completed the SSQ indicating any post-exposure symptoms.

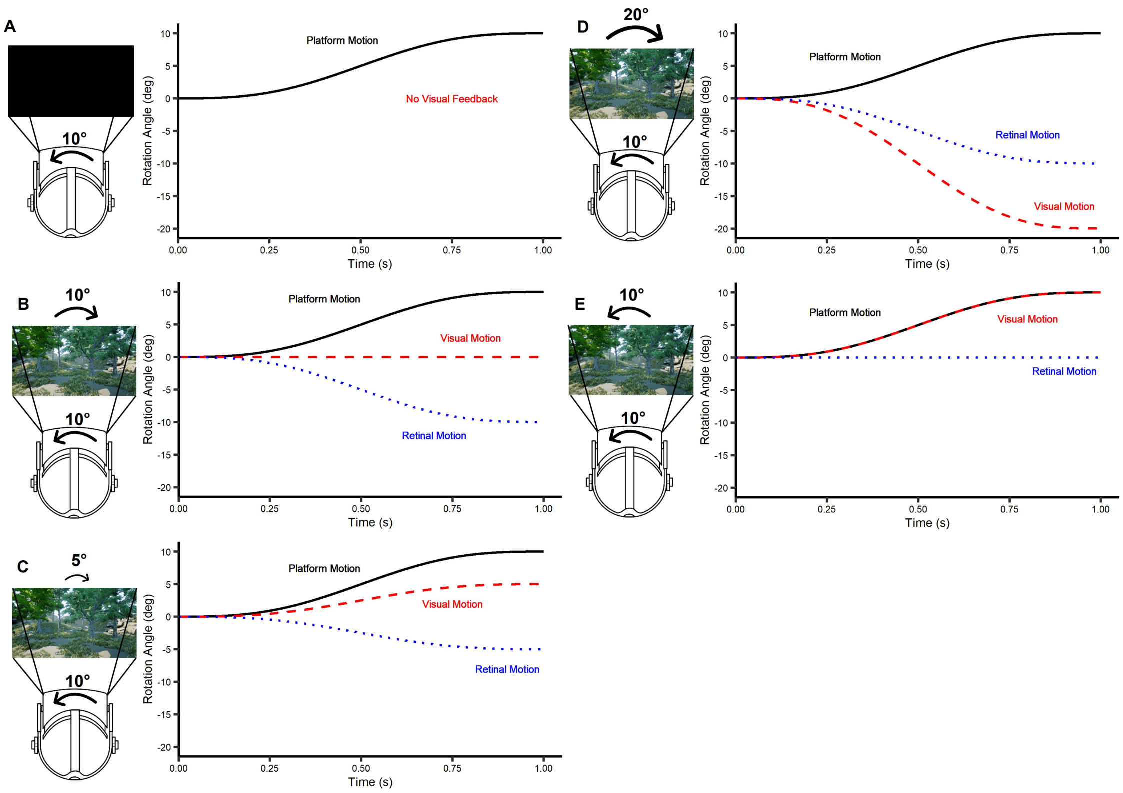

Figure 2.2: Schematic of the visual conditions for **a** eyes-closed, **b** visual gain 1, **c** visual gain 0.5, **d** visual gain 2 and **e** visual gain -1 conditions. The illustrations on the left depicts the updating of the visual scene relative to the observers' motion. The figures on the right displays the rotation angle of the motion platform, updating of the visual scene relative to the observers' motion and movement of the visual scene on the retina. Only rotational frequency of 1 Hz is shown here; the rotation angle doubled for the 0.5 Hz rotations. HMD graphic was modified from VR Headset created by Nicholas Frawley, from the Noun Project.

2.3.5 Data Analysis

Statistical analysis was conducted using R (version 4.0.5 using RStudio), SigmaPlot 12.5, IBM SPSS Statistics 25 and JASP (Version 0.14.1). A logistic function which accounted for lapses in participants' responses (Eq. 2.1) was fitted to the participants' percentage of "movement first" responses as a function of SOA using Sigma Plot, with the halfway (50%) inflection point of the sigmoid curve (x0) representing the point of subjective simultaneity

(PSS) and the slope of the function (b) as the just noticeable difference (JND) [21]. Thus, estimates of lapse rate, PSS and precision were derived from the three free-parameter equation to nine data points corresponding to the nine SOAs tested. In cases where the lapse function failed to appropriately fit the data ($R^2 < 0.2$), a 3-parameter logistic function (Eq. 2.2) was used instead. This substitution was resorted to nine times out of a total of 240 fits and it yielded better R^2 results that met the specified criteria in all the cases. For two participants, we were unable to fit either function to their responses ($R^2 < 0.2$) and thus these were excluded from subsequent analyses (14 males and 11 females; mean age= 23.4, SD= 3.6).

$$f = l + (1 - u - l)(\frac{1}{1 + e^{-(\frac{x-x_0}{b})}}) \tag{2.1}$$

$$y = \frac{a}{1 + e^{-(\frac{x-x_0}{b})}} \tag{2.2}$$

A positive PSS score indicates that the motion had to occur before the before the auditory tone by the value of the score (in ms) to be perceived as occurring simultaneously, while a negative PSS score indicates that the motion had to occur after (Figure 2.3 b). While the generated auditory stimuli are instantly above threshold, the vestibular stimuli require time to exceed the observers' detection threshold [44]. This threshold to perceived onset is further contingent on the rate of change of the movement, therefore the PSS values were adjusted by subtracting 72 and 144 ms for 0.5 and 1 Hz rotations respectively from each individuals' PSS based on the vestibular perceptual thresholds [106, 117] to ensure that the PSS score is representative of when the vestibular stimuli is detected [200]. Since the two different frequencies are adjusted unequally, we also analyzed the unadjusted data to confirm that any significant effects would not be due to the transformation of the data.

The data violated the assumption of normality, thus an Aligned Rank Transform (ART) [230] was performed on the data to conduct a nonparametric repeated measures ANOVA to examine the effects of frequency and gain. Follow-up contrast tests were also conducted following the ART procedure [87, 136]. The FMS scores also violated normality, therefore the same procedure using the repeated measures ANOVA with the ART method was conducted on the sickness data. Furthermore, a Kendall's Tau correlation test was performed between the FMS scores with the PSS and JND measures to observe whether there was an association between the perceptual responses and sickness severity across all the conditions.

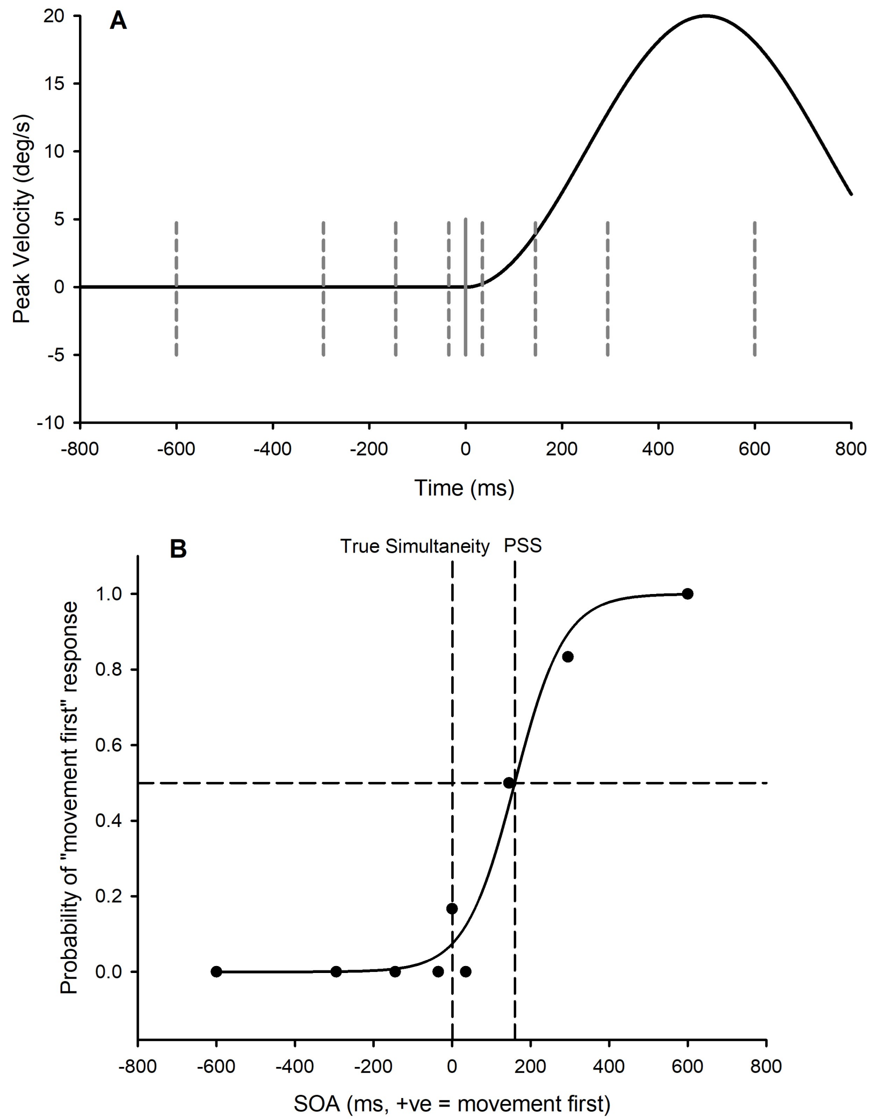

Figure 2.3: **a** Stimuli onset asynchronies (SOAs) of the auditory tone relative to the onset of the rotation. **b** Sample plot of how a single point of subjective simultaneity (PSS) is derived based on the participant's responses.

2.4 Results

2.4.1 Rotation Frequency

A repeated measures ANOVA on the ART data revealed a significant main effect of frequency [F(1,216) = 150.20, p < .001] on the unadjusted data. Since we observed a significant effect here, we performed the same analysis on the adjusted data and will report on those results going forward as a more accurate representation of the perceived threshold. A repeated measures ANOVA on the ART data of the adjusted data also revealed a significant main effect of frequency [F(1,216) = 12.80, p < .001, η_p^2 = 0.06], indicating that the PSS of passive whole-body rotations at 0.5 Hz were higher than 1 Hz rotations. No significant effect of rotation frequency was observed for the JND scores [F(1,216) = 0.40, p = 0.53, η_p^2 = 0.002]. See Figure 2.4 and Table 2.1 for a summary of the results.

2.4.2 Passive Rotation with Vision

The repeated measures ANOVA using the ART data also revealed a significant main effect of the visual gain F(4,216) = 3.28, p = 0.012, η_p^2 = 0.06], however there was no significant interaction between the rotation frequency and visual gain [F(4,216) = 1.91, p = 0.11, η_p^2 = 0.03]. Post-hoc contrast tests of the visual gain conditions collapsed across frequency (with Bonferroni p-value adjustments) revealed that the PSS was significantly higher in the visual gain -1 condition than the eyes-closed condition (t = -3.30, df = 216, p = 0.011). None of the other conditions were statistically significant from one another. For the JND, there was a significant effect of visual gain [F(4,216) = 3.12, p = 0.016, η_p^2 = 0.055] and no significant interaction [F(4,216) = 0.49, p = 0.74, η_p^2 = 0.010] was found in the repeated measures ANOVA. Post-hoc contrast tests revealed that that the JND was significantly higher in the visual gain 2 condition compared to the eyes-closed condition (t = -3.02, df = 216, p = 0.03).

2.4.3 Sickness Symptoms

For the FMS scores, a repeated measures ANOVA of the ART data revealed a significant effect of visual gain [F(4,216) = 12.36, p < .001, η_p^2 = 0.19]. However, there was no significant effect of frequency [F(1,216) = 2.80, p = 0.095, η_p^2 = 0.013] and no significant interaction between visual gain and frequency [F(4,216) = 0.71, p = 0.59, η_p^2 = 0.013]. Post-hoc contrast tests (with Bonferroni p-value adjustments) revealed that the FMS scores

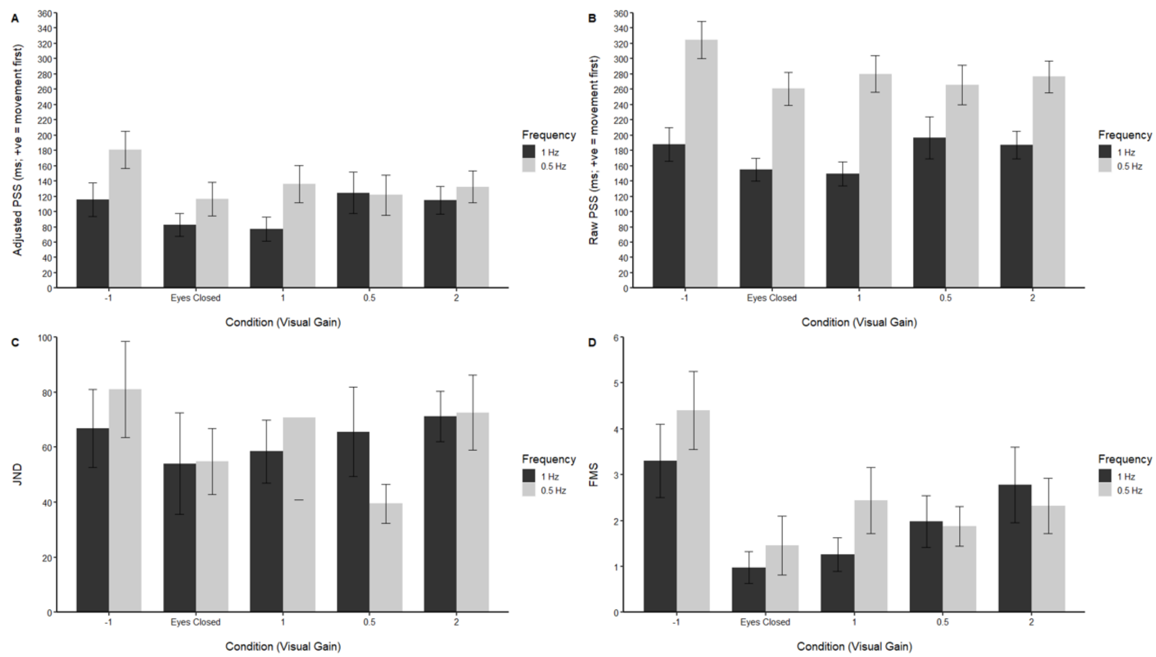

Figure 2.4: Summary of **a** adjusted point of subjective simultaneity (PSS), **b** raw PSS data **c** just-noticeable difference (JND) and **d** fast motion sickness (FMS) scores across the categorical visual gain conditions with the data from the two rotational frequencies plotted separately. Error bars are standard error

were significantly higher in the visual gain -1 (t = -6.93, df = 216, $p < 0.001$), visual gain 0.5 (t = -2.95, df = 216, p = 0.036) and visual gain 2 (t = -3.80, df = 216, p = 0.002) conditions compared to the eyes-closed condition. The FMS score in the visual gain -1 condition were also significantly higher than in the visual gain visual gain 1 (t = 4.18, df = 216, $p < 0.001$), 0.5 (t = 3.98, df = 216, $p < 0.001$) and visual gain 2 conditions (t = 3.12, df = 216, p = 0.021). See Figure 2.4 and Table 2.1 for a summary of these results.

Since there was no significant main effect of frequency for the FMS scores, the data was pooled together based on the gain condition. A Kendall's Tau correlation test revealed that there was no significant correlation between the FMS scores and both the PSS and JND measures across all the conditions (summarized in Table 2.2).

2.5 Discussion

In this experiment, we explored whether providing visual feedback using a virtual environment at various visual gains would affect the perceived onset of a passive whole-body rotation. The results showed that there was a significant effect of manipulating the visual gain on both the accuracy (PSS) and precision (JND) on the perceived timing of the motion. Specifically, the PSS was further from zero when in the visual gain -1 condition compared to when visual feedback was omitted. This suggests that when the visual scene updated in an equal and opposite movement relative to the physical rotation (visual gain 1), as well as changing the speed by which the visual scene updated (visual gain 2 and 0.5) had no significant effect on the perceived onset of the motion. However, when the direction of the visual updating was inverted relative to the accompanying rotation (visual gain -1), the perceived timing of the rotation was significantly further from zero. For the JND, the measure was significantly greater in the visual gain 2 condition compared to the eyes closed condition, meaning participants were less precise when the speed by which the visual scene updated was greater relative to the physical rotation. Furthermore, the PSS scores indicated that the onset of movement had to occur before the auditory tone to be perceived as occurring simultaneously across all the conditions, suggesting that the perceived onset of the motion is delayed [21]. The delay in perceived onset was also greater for slower rotations (0.5 Hz compared to 1 Hz), replicating previous findings in the literature [44].

The findings that the perceived timing was only affected when the direction of the visual gain was inverted agrees with previous findings related to the perceived stability of the visual environment, where a wide range of higher gain factors were accepted as earth stable, however when the gain factor was negative it was rarely accepted as stable [130]. Additionally, it has been shown that participants are unable to detect differences in positive gains [15, 27] and the perceived rotational gain of more detailed and naturalistic scenes is slowed down [181]. It appears that as long as the visual and vestibular signals are perceived as originating from the same sensory event, a certain level of discrepancy is accepted and the two signals can be consolidated or fused into a single percept [183]. The current results provide further evidence that changing the visual gain is within these acceptable limits and there is no perceived difference in timing with no visual gain factor. However, when the visual scene moves in a non-ecological direction is when the common causality between the visual-vestibular feedback breaks down. Another potential hypothesis for the observed effect is changing the direction of the relative visual motion led to partial attenuation of the vestibular signal. Since the individual visual and vestibular feedback were signalling motion in opposite directions, this may have caused the signals to partially cancel each other leading to the perceived delay.

Contrary to our predictions, providing an additional source of sensory information regarding self-motion in visual feedback did not improve the perceived timing of self-motion, indicated by no significant difference between the eyes closed and normal visual gain condition (gain 1). A possible explanation for this finding is that the task demands for the perception of self-motion onset is more reliant on the vestibular signal. Previous literature has demonstrated that the reweighting of visual and vestibular information can shift based on certain task demands or circumstances in which one source of information is regarded as more reliable, whether it be due to prior expectations or purposefully created cue conflicts [27, 37, 89, 96]. The presentation of visual information in the current experiment provided through a virtual reality headset, may have been regarded as unreliable or artificial, resulting in a shift towards a vestibular dominant percept of the event. In addition, any perceived display lag or latency with the rendering of the virtual environment may further contribute to the sense of unreliability of the visual feedback. Recent literature has begun to identify the importance of presence and the compelling sensation of behavioral realism to successfully simulate feelings of self-motion [195]. Thus, it is possible that with the current experimental setup and task demands, the visual information was perceived as redundant or unreliable and was either attenuated or discarded rather than integrated together with the vestibular signal. However, a limitation to the current design is the lack of a visual-only condition where the perceived onset of motion would be solely determined by visual information. Without knowing the perceived onset of visual self-motion, we cannot confidently eliminate the possible role and integration of vision.

Another possible explanation for the absence of contribution from the visual feedback may be the differing role of vision and vestibular information for signalling self-motion. Drugowitsch et al. [82] found that under certain conditions, there is a speed and accuracy trade-off between visual and vestibular information that needs to be accounted for depending on the task or when trying to model or relate to more ecological scenarios. In their study, the response times to a heading task in the combined visual-vestibular conditions mirrored that of the vestibular condition, while the response times in the visual condition was longer, suggesting that there is a prior to rely more on vestibular signals first and then followed by the integration of visual cues to supplement and fine tune the estimate. In our study, the participants were asked to determine the onset of motion occurring at the beginning of each trial. This may have resulted in task demands where the system relied more on the vestibular signal and since it was such a specific and narrow time point, there was no time or role for the visual signal to adjust the perception. Future work examining different aspects of the motion may find different results or contributions from the visual feedback.

We were also interested in cybersickness due to the introduction of a sensory conflict while being exposed to VR, we expected participants to experience varying levels of symptom severity. Using the FMS scale, we found that the overall sickness magnitude was greater when participants were exposed to VR compared to having their eyes closed. The current results provide evidence in support of the sensory conflict theory, where sickness ratings were significantly higher when the visual gain was inverted which provided the greatest level of discrepancy between the visual and vestibular signals. There was also a significant difference in sickness scores for the two modified visual gain conditions (gain 2 and gain 0.5), further supporting the idea that greater discrepancies are related to higher sickness ratings. These findings are contrary to previous studies that found no significant difference in cybersickness ratings between ecological (gain of 1) and nonecological (gain $\neq 1$) compensated head movement conditions with an HMD [13, 180]. However, in these studies active head movements were used instead of passive-whole body rotations and the visual stimuli consisted of optic flow patterns, whereas we used a natural scenic environment in the current experiment. The lack of neck proprioceptive signals and a motor efferent copy could have led to the greater cybersickness ratings observed in our experiment. Recent findings also suggest that higher fidelity virtual environments with more realistic graphics may lead to higher sickness ratings [69] and display lags introduced to a virtual environment with a ground and ceiling plane can increase cybersickness severity [146]. Future work is needed to explore the difference in cybersickness severity between active and passive motion when presented with conflicting stimuli and to determine specific parameters of the virtual environment that may lead to greater sickness symptoms.

An interesting observation in our findings is that the nonecological inverted gain condition resulted in both the highest cybersickness rating and PSS score. This suggested a possible association between cybersickness and the perceived timing of self-motion, however the correlation analysis between the PSS and FMS scores were not significant. There is clear evidence that vection is involved in simulator sickness but is not necessarily the primary driver, as experiencing vection alone does not always lead to sickness and appears to require a combination of other accompanying factors to trigger sickness [144]. One such factor is sensory conflict and the integration of visual and vestibular information, which has been commonly examined across cybersickness and motion perception research. One potential theory is the occurrence of cybersickness may be predicted by the sensory reweighting of discrepant visual and vestibular signals that has been observed in the multisensory integration literature [101]. Following this idea, a potential explanation of our current findings is that the conflict in the inverted gain condition was too large to be consolidated by the central nervous system leading to a break down in the perceived timing of the motion and the occurrence of greater cybersickness symptoms. A follow up experiment focusing on the possible relationship between the occurrence of sickness and difference aspects of motion perception during sensory conflict would be beneficial for understanding both cybersickness and motion perception.

2.6 Conclusion

In this study, we confirmed findings from past literature that the perceived timing of the onset of self-motion is delayed and is dependent on the frequency of the motion, such that a lower frequency leads to a further delay from zero in the perception of the motion. We also investigated whether providing visual feedback using a virtual environment would influence the perceived timing of the physical motion. While there was no reduction in the delay in perceived timing of motion onset when visual feedback was available, the perceived timing was significantly further from zero when the direction of the visual motion was incongruent with the observers' movement compared to having no visual feedback. This suggests that vision only contributes to the perceived timing of motion when it does not match the expected outcome of the corresponding physical movement. Results from the cybersickness scores support the sensory conflict theory in which the observers reported greater levels of sickness severity when the visual feedback was incongruent with the vestibular signals and appear to follow a similar trend with the perceived timing across the varying levels of visual-vestibular conflict. However, it is beyond the scope of the current study to assess the interaction between cybersickness and visual-vestibular perception and future research could aim to directly investigate the relationship.

Table 2.1: Summary of data across the visual conditions separated by rotational frequency

		Gain -1		Eyes Closed		Gain 1		Gain 0.5		Gain 2	
		1 Hz	0.5 Hz	1 Hz	0.5 Hz	1 Hz	0.5 Hz	1 Hz	0.5 Hz	1 Hz	0.5 Hz
PSS	Mean	115.58	180.79	83.10	116.66	77.42	136.13	124.63	121.73	115.02	132.49
	SE	21.99	24.42	14.96	21.81	15.76	24.24	27.28	26.03	17.92	20.90
JND	Mean	66.83	80.97	54.04	54.93	58.43	70.74	65.54	39.53	71.13	72.54
	SE	14.18	17.46	18.49	11.99	11.35	29.90	16.26	7.07	9.15	13.68
FMS	Mean	3.71	4.33	1.02	1.44	1.29	2.46	2.29	1.90	3.02	2.39
	SE	0.87	0.82	0.34	0.62	0.36	0.70	0.63	0.41	0.82	0.58

Table 2.2: Kendall Tau's correlation coefficient for timing measures and sickness scores

		Gain -1	Eyes Closed	Gain 0.5	Gain 1	Gain 2
PSS	Kendall's Tau B	0.106	-0.144	0.055	0.069	-0.019
	p	0.298	0.190	0.609	0.514	0.857
JND	Kendall's Tau B	-0.131	-0.031	-0.088	-0.081	-0.205
	p	0.201	0.780	0.408	0.443	0.051

Chapter 3

Off-Vertical Body Orientation Delays the Perceived Onset of Visual Motion

3.1 Introduction

Sensory conflict occurs when there is a discrepancy between multisensory signals. The mismatch of signals can arise due to differences in transduction and processing latencies between different sensory modalities. One such scenario where sensory conflict has been of interest is within the self-motion literature, where a mismatch between vestibular, visual and proprioceptive signals can commonly occur while using different vehicles of transportation and more recently with the application of virtual reality (VR). The vestibular system, responsible for detecting changes in acceleration of the head, is essential for providing us with information regarding our position and orientation in space and generates an internal sensation of self-motion [10, 49]. While vision provides similarly redundant information about self-motion through optic flow and vection [179], it additionally supplies us with information regarding the movement of objects in our environment. The integration of these cues usually creates a stable representation of self-motion, however when there is a mismatch between these signals there can be potential perceptual consequences such as disorientation, illusory self-motion, errors in decision making and in performing coordinated actions.

One of the primary reasons for the occurrence of conflict between visual and vestibular cues is that the vestibular signal is constantly providing feedback to the central nervous system. For example, when exposed to motion in VR while being physically stationary, visual feedback from the display signals self-motion while the vestibular system does not sense and signal any self-motion, leading to a mismatch. An additional source of conflict arising from the vestibular system is from the constant force of gravity on the hair-like structures found within the vestibular system known as stereocilia [104]. The anatomy of the stereocilia enables the vestibular system to detect acceleration or changes in motion of the head, however the hair cells of the otolith organs of the vestibular system will detect not only translational acceleration but also the signal of acceleration related to the constant force of gravity. The influence of gravity can lead to ambiguous otolith signals from the vestibular system, where the acceleration feedback resulting from a head tilt can be the same as from a translational or rotational movement along the same axis (the tilt-translation ambiguity; [59]). To differentiate the signals arising from these distinct events, the integration of otolith and semicircular canal signals (which detect rotational acceleration), along with visual and proprioceptive information is necessary to resolve the ambiguity of the vestibular signal. It has been shown there is a population of Purkinje cells in the macaque cerebellar cortex that are only selectively sensitive to head tilts and not translations [155] and these cells can also receive signals from the semicircular canals [12], suggesting that the cerebellum is an important neural structure for encoding gravity.

A common method that has been used to explore the effect of gravity is through manipulating the orientation of the body. By changing the position of the body, the direction in which the gravitational vector affects the vestibular system is shifted accordingly since gravity is constant on Earth. Researchers have used this relationship between gravity and ambiguous vestibular signals in combination with visual motion to examine the influence of gravity on the perception of vection, the illusion of self-motion when the body is stationary. Much of the literature has focused on the difference in vection measures, such has magnitude and onset latencies, in an upright compared to supine, prone or recumbent position. When paired with different visual flow patterns, the gravitational vector can either support or conflict with the direction of vection depending on the pairing of sensory signals. Some findings in the literature have suggested that vection ratings improve when the gravitational vector is congruent with the direction of the visual motion in a supine posture [135, 233]. However, there have also been reports showing that regardless of whether the direction of vection was with or against gravity, vection measures are higher in an upright posture [115, 124, 217, 223].

Based on the current evidence, it appears to be more appropriate to describe the conflict between body orientation relative to gravity and visual motion not only in terms of the physical mismatch of the stimuli, but also considering the ecological aspect of being in a non-upright posture. The ecological view is a top-down approach based around what observers are accustomed to experiencing rather than focusing on the conflict that is physically present in the stimuli. In normal circumstances, people are typically exposed to motion when they are in an upright posture, thus the system is better tuned for perceiving specific types of motion along certain axes or planes. This ecological advantage of aligning the motion with its typical axis or plane has also been previously observed in studies for rotational vection [124, 210], vertical and horizontal vection [114, 169], vection onset latencies [135, 217] and heading discrimination [160]. It has also been shown that adding an oscillating effect to the visual display to simulate the bob and sway of natural locomotion increases vection strength regardless of body orientation and the resulting gravitational conflict [115].

Another important ecological aspect for the integration of visual motion and body orientation is the congruency of the signals. As previously mentioned, the tilt-translation ambiguity of the vestibular system requires additional sensory feedback to be resolved and under common circumstances those additional sensory cues are typically consistent with the vestibular signal. For example, a forward translation is accompanied by an expanding optic flow, or alternatively a backwards head tilt is accompanied by an upwards tilt of the visual scene. However, in certain scenarios such as riding a vehicle or experiencing VR, the visual and vestibular signals can become incongruent and researchers have been interested in exploring whether the change in this relationship between source of sensory information can affect our perception. In terms of body orientation, it has been reported that the perception of self-tilt is mainly processed in body coordinates [59], however the presence of visual scene tilt can improve or modulate that perception, but only when it is congruent with the tilt of the body [79, 119]. Furthermore, it has also been shown that body tilt can influence the perception of visual motion, including the perceived direction of an optic flow pattern [34], the estimated distance travelled in VR [150] and the perceived realism of linear self-motion [110]. These findings indicate that there is a reciprocal relationship between visual and vestibular integration and highlight the importance of the congruence between the two signals.

To the best of our knowledge there has yet to be a study exploring the effects of body orientation on the perceived timing of visual motion. In the current experiment, we examine the effects of sensory conflict on the perceived timing of visual motion during optic flow in the head-centered yaw rotation axis. The conflict is introduced by altering the orientation of the head and body, such that the observer experiences the motion in an ecological upright posture and when the vestibular and body orientation signal is dissociated in an off-vertical tilt orientation. For the off-vertical orientation, we chose to use the supine posture that has been commonly used in previous literature [115, 124, 135, 217, 223, 233]. However, there are also substantially different non-vestibular cues in somatosensory and proprioception signals when in a supine compared to upright orientation. Thus, we included lateral recumbent orientations to account for the potential influence of these additional non-vestibular signals and both left and right lateral positions were used as previous research has found asymmetries between left and right biases in the perception of body orientation [22]. Since yaw rotations are invariant to the effects of gravity in all four body orientations, any differences found between them could then be attributed to the potential non-gravitational sources of feedback. Following this, our main hypothesis is that the perceived timing of visual motion should be less accurate and precise when the visual flow presented in an off-vertical body orientations compared to the ecological upright orientation. We also explore whether there is a bias in the perceived timing for the direction of the visual motion in each of the body orientations. While the ambiguous tilt-translation signal is not in the axis of yaw rotations, the direction of gravity and visual motion are partially aligned in the lateral recumbent orientations (ex. rotations to the left are in the direction of gravity when in a left recumbent position). Thus, we hypothesize that there may be a difference between left and right rotations in the lateral recumbent positions compared to the upright and supine orientations due to the direction of gravity. Furthermore, we investigate whether there are asymmetries in the body tilt bias between the left compared to the right recumbent positions and also whether there are any differences in the off-vertical axes between the lateral recumbent positions compared to the supine orientation.

3.2 Methods

3.2.1 Participants

Data was collected from twenty-four participants (11 males and 13 females; mean age = 26.9, SD = 3.7) recruited from the University of Waterloo. Five of the participants were volunteers, while the remaining participants were remunerated $10/h for their participation. All participants reported having no auditory or vestibular disorders and had normal or corrected-to-normal vision. This experiment was reviewed and received ethics clearance through a University of Waterloo Research Ethics Committee and all participants gave their informed written consent in accordance with the guidelines from the committee.

3.2.2 Apparatus and Stimuli

The Oculus Quest system was used to provide the visual stimuli in this experiment. The Oculus Quest has a dual OLED display with a resolution of 1600x1440 (per eye) at 72 Hz refresh rate and a 93° field of view. The visual stimuli was a virtual starfield (Figure

3.1b) with 10000 particles each with a radius of 10cm randomly generated in a 100m^2 area starting from a 50cm radius sphere from the location of the observer using the particle system built in Unity. Visual motion was a 10° angular rotation in the yaw axis in both left and right directions (Figure 3.1a), following a raised-sine profile with a peak velocity of 20 deg/s [51] (Figure 3.2). No visual fixation point or fixation instructions were provided to maintain a naturalistic experience and to prevent effects on self-motion perception [103, 195].Auditory stimuli were presented through in-ear headphones (Sennheiser CX 1.00). The experimental control (trial randomization, recording of responses, graphical interface for monitoring progress of the experiment, etc.) programmed using the BiomotionLab Toolkit for Unity Experiments (bmlTUX) [25].

In each trial, an 800 Hz tone was presented for 10 ms at nine stimulus onset asynchronies (SOAs) following a logarithmic scale: -600, -295, -145, -35, 0, 35, 145, 295, 600 ms, relative to the onset of the visual motion (Figure 3.2). A negative SOA indicates that the auditory stimuli was presented before the onset of visual motion, positive SOA indicates the auditory stimuli presented after the visual motion and zero indicates both stimuli occurring at the same time. The order of SOAs was randomized among trials and each SOA was presented nine times for both directions of visual motion for a total of 162 trials (9 SOAs x 9 repetitions x 2 rotation directions). Participants reported whether they perceived the onset of the visual motion occurring before or after the onset of the auditory tone using the buttons on a gamepad (Logitech Gamepad F310).

3.2.3 Procedures

Participants were fitted with the Oculus Quest VR system before being positioned in one of four body orientations: upright, supine, left recumbent or right recumbent (Figure 3.1c). All participants experienced every body orientation in a block design and the order of orientations were counterbalanced across participants. In the upright orientation, participants were seated on an office chair and in the remaining orientations an examination table was used with a foam pillow to keep participant's head aligned with the body. The participants completed a temporal order judgment (TOJ) task in all four body positions, in which they had to indicate whether the onset of a visual motion stimuli (rotation of a starfield) or an auditory tone occurred first. The trials were self-paced in that the next trial would not begin until participants' response with a button press on a gamepad was recorded. Participants were given a brief break (2 to 3 min) at the half way point of each block and a longer break (5 min) in between blocks to minimize fatigue and maintain attention on the task.

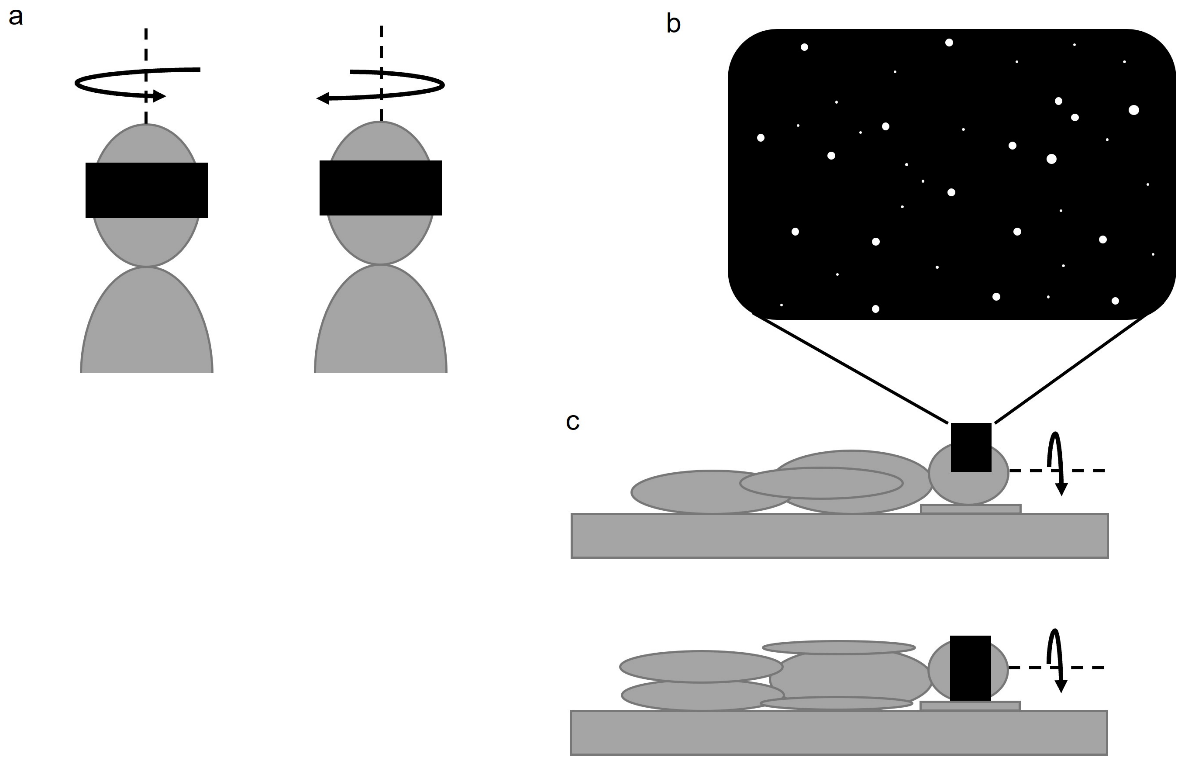

Figure 3.1: **a** Schematic depiction of an upright observer wearing an Oculus Quest VR HMD. Right and left rotations of the visual environment relative to the stationary observer were around the yaw axis indicated by the dotted line. **b** Starfield visual stimuli viewed using the VR HMD. **c** Schematic depiction of an observer wearing the VR HMD while either laying supine (above), or left side recumbent (below). Similar to the upright condition, right and left rotations of the visual environment relative to the stationary observer were around the yaw axis indicated by the dotted line.

3.2.4 Data Analysis

Statistical analysis was conducted using SigmaPlot 12.5 and IBM SPSS Statistics 25. A logistic function which accounted for lapses in participants' responses (Eq. 3.1) was fitted to the participants' percentage of "visual motion first" responses as a function of the SOAs. Estimates of lapse rate, PSE and precision were derived from the three free-parameter equation to nine data points corresponding to the nine SOAs tested. The halfway (50%) inflection point of the sigmoid curve (x0) represents the point of subjective simultaneity (PSS) and the standard deviation of the function (b) as the just noticeable difference

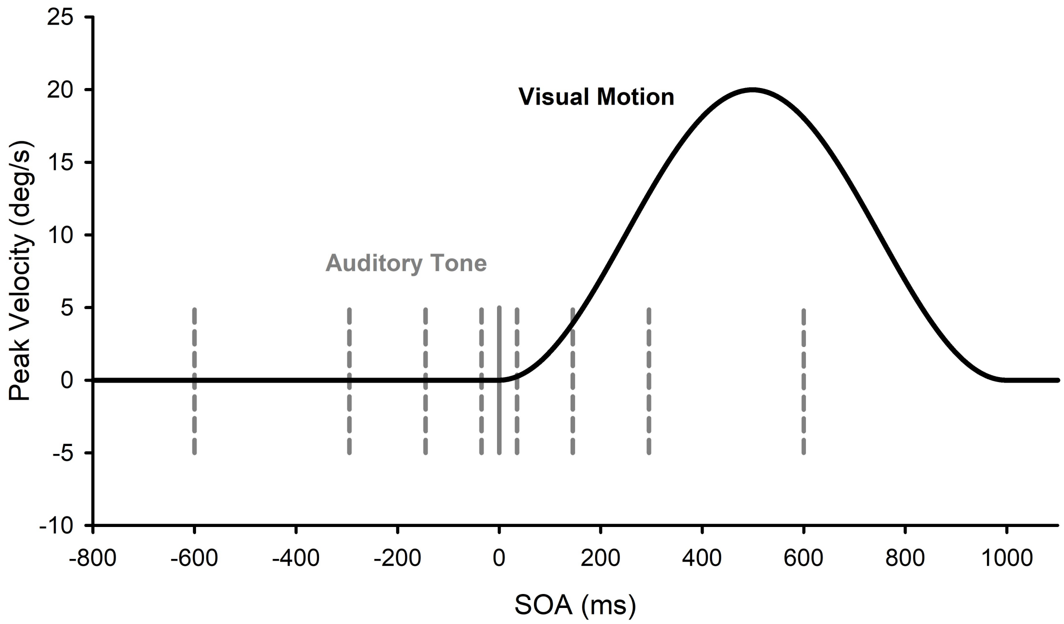

Figure 3.2: Plot of the visual motion profile in the black line with a peak velocity of 20 deg/s and the stimulus onset asynchronies of the reference auditory tone in the grey lines.

(JND; [21]). A positive PSS score indicates that the visual motion had to occur before the auditory tone by the value of the score (in ms) to be perceived as occurring simultaneously, while a negative PSS score indicates that the motion had to occur after. In cases where the lapse function failed to appropriately fit the data ($R^2 < 0.2$), an alternative 3-parameter logistic function (Eq. 3.2) was used instead. This substitution was resorted to 12 times out of a total of 192 fits and it yielded better R^2 results that met the specified criteria in all the cases. We were unable to fit either function to the responses of three participants ($R^2 < 0.2$ or $p < 0.05$) and were thus removed from the subsequent analysis.

$$f = l + (1 - u - l)\left(\frac{1}{1 + e^{-(\frac{x - x_0}{b})}}\right) \tag{3.1}$$

$$y = \frac{a}{1 + e^{-(\frac{x - x_0}{b})}} \tag{3.2}$$

3.3 Results

To observe whether there were any significant differences in the direction of the visual motion, paired t-tests were conducted between left and right rotations and revealed that there were no significant differences in the PSS between left and right rotations for all body orientations [upright (t = 0.80, df = 20, p = 0.44); supine (t = 1.40, df = 20, p = 0.18); left recumbent (t = 0.24, df = 20, p = 0.81); right recumbent (t = -0.20, df = 20, p = 0.84)]. Thus, the data for each participant was collapsed across rotation direction and re-fitted with the logistic functions (Eq. 3.1, 3.2) using the same methods as before. With the additional data points, we were able to fit the functions to all participants with seven substitutions using Eq. 3.2 out of 96 total fits that yielded better R^2 results meeting the specified criteria ($R^2 < 0.2$). All subsequent data analyses were performed using the collapsed data, with two participants removed due to the fit of their responses failing to meet our criteria ($R^2 < 0.2$ and $p < 0.05$) and an additional participant identified as a statistical outlier (over three times the interquartile range) (final sample n = 21; 9 males, 12 females; mean age = 27.5, SD = 3.3).

The average and standard error for the PSS and JND values are summarized in Table 3.1. One-sample t-tests were conducted to confirm that the PSS scores were significantly different from zero [Upright: ($t(20)$ = 7.18, p < .001); Supine ($t(20)$ = 7.59, p < .001); Left Recumbent ($t(20)$ = 6.21, p < .001); Right Recumbent ($t(20)$ = 5.99, p < .001)]. A paired t-test was conducted between the left and right recumbent orientations to determine whether there was an effect of the direction of the side lateral orientation on the participants' response. The results showed that there were no significant differences between left and right recumbent orientations for both the PSS [$t(20)$ = 0.29, p = 0.777, d = 0.063] and JND [$t(20)$ = -0.18, p = 0.861, d = -0.039]. Since they were not significantly different, the values were then collapsed by taking the average of the individual PSS and JND values across the left and right recumbent orientations for each participant [PSS(M = 156.72, SE = 24.34); JND (M= 77.62, SE = 10.18)]. A subsequent Wilcoxon Signed-Rank Test between the collapsed lateral recumbent and supine orientation found no significant difference in PSS (Z = -0.82, p = 0.424, r = -0.203) and JND (Z = -1.20, p = 0.237, r = 0.299). Thus, the PSS and JND data for the lateral recumbent and supine orientations were consolidated into a single "Off-Vertical" orientation by averaging the lateral recumbent and supine data for each individual participant [PSS(M = 157.94, SE = 21.24); JND(M = 74.16, SE = 9.93)]. A final Wilcoxon Signed-Rank Test between the upright and off-vertical orientations revealed a significant difference in the PSS (Z = 2.42, p = 0.016, r = -0.602), indicating that off-vertically oriented participants required visual motion onset to precede the onset of an auditory reference tone significantly earlier (30ms earlier) than when they were upright. No significant difference for the JND was found (Z = -1.10, p = 0.281, r = 0.273) (Figure 3.3).

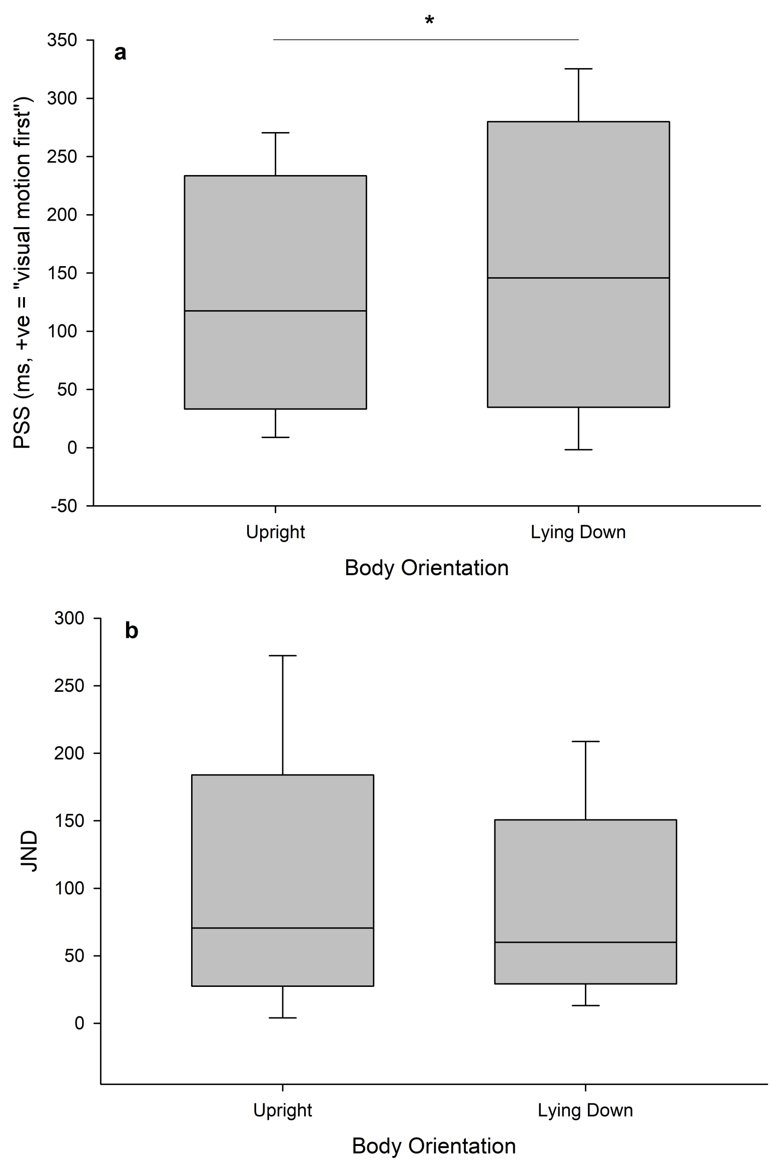

Figure 3.3: Summary of **a** point of subjective simultaneity (PSS), **b** just-noticeable difference (JND) between upright and lying down body orientation. Error bars are standard error.

		Upright	Supine	Left Recumbent	Right Recumbent
PSS(ms)	Mean	127.37	159.16	159.09	154.35
	SE	17.74	20.98	25.64	25.78
JND	Mean	85.70	70.70	76.69	78.54
	SE	15.44	13.78	10.94	11.93

Table 3.1: Summary of PSS and JND data across body orientations. Positive PSS values indicate that the visual motion needed to move prior to the auditory tone onset to be perceived as occurring simultaneously.

3.4 Discussion

The purpose of this study was to explore the effects of varying body orientation on the perceived timing of visual motion. Changing the orientation of the body from upright dissociates the gravitational vector from the idiotropic vector or longitudinal body axis [164] in signalling the direction of upright and we were interested in whether changes in this relationship would influence the perceived onset of visual rotation around the yaw axis presented in VR. The results showed that there were no significant differences in the direction of motion (left or right rotation), as well as between the various lying down orientations (left recumbent, right recumbent and supine). However, when all the lying down orientations were consolidated and compared to the upright orientation, the point of subjective simultaneity (PSS) was found to be significantly further from zero. The onset of the visual motion had to be presented an average of 158ms before the auditory tone for both stimuli to be perceived as occurring at the same time in the lying down orientations compared to only 127ms when upright. This suggests that there is a general attenuation effect on the ability to detect the onset of visual motion when the body is tilted relative to gravity resulting in sensory conflict between the vestibular and body signals. Contrary to previous findings that showed the precision in the perception of upright decreases when the body is tilted [53, 71], there was no significant difference in the just-noticeable difference (JND) in the perceived onset of visual motion across all of the body orientations.

When in an upright posture, gravity and the longitudinal body axis are aligned and changes in the vestibular apparatus due to inertia signals the presence of self-motion. Motion is also commonly experienced in an upright posture, for example when walking or riding in a vehicle, and previous research has found that there is an ecological advantage for various aspects of visual motion in the direction of gravity and an upright orientation

[114, 115, 124, 135, 160, 169, 210, 217, 223]. In our study, we found a significant difference in the perceived onset of visual motion when in an upright orientation compared to all the off-vertical orientations in which the timing estimate of visual motion was further then zero when the body was tilted in agreement with the ecological advantage hypothesis. Following this, we did not observe any differences between the supine and lateral recumbent orientations and a potential reason why may be due to the reference frame that the visual motion we presented was processed in. Our sensory systems encode information relative to different egocentric reference frames which need to be transformed into an allocentric representation that is gravity-centered to achieve a stable and upright representation of the world [67]. For example, the visual system encodes the image on the retina in eye-centered coordinates, but when you change orientations your perception of verticality still remains intact to a certain a degree (i.e. a tree or building is still perceived as pointing up instead of sideways or down). Being in an off-vertical orientation may have also distracted or pulled the observers' attention away from the task, which may affect their ability to perceive the visual motion [185].

MacNeilage et al. [160] compared visual and vestibular heading discrimination and found no effects of movement in head or world coordinates for visual heading in contrast to vestibular heading where thresholds were lower for horizontal translations when upright and also both visual and vestibular heading thresholds were consistently lower in the upright orientation compared to side-down for both horizontal and vertical plane movements. This suggests that vestibular heading is strongly dependent on movement in head coordinates and not world coordinates, meaning it is not influenced by or can compensate for the effects of gravity. However, vision appears to be even more specifically tuned to the upright orientation, suggesting that it may rely more on the longitudinal body axis as the preferred frame of reference. Claassen et al. [52] had participants conduct a visual motion coherence task for vertical and horizontal motion while upright and when on their left side. In both body orientations, lower thresholds were found when the direction of the visual motion was congruent with the direction of gravity, but in different frames of reference - downwards motion while upright and rightward motion while left-side down. Although the second finding did not reach statistical significance, it suggests a potential difference in the frame of reference for the same task between the two body orientations. In the upright position, the visual motion may have been viewed as object motion in an earth-centered reference frame, whereas the left side down position was viewed as an egocentric reference frame (left side down produces otolith input analogous to rightward motion) [52]. In the current design, the yaw visual rotation was invariant to the gravity and idiotropic vector for the different body orientations used. Thus, the perceived timing of the visual motion may have been processed within an egocentric frame, relying primarily on the longitudinal axis signal and unable to account for the effect of gravity in an allocentric frame. This may potentially explain why the timing estimates were further from zero when the body was tilted from vertical compared to the upright orientation because gravity and the longitudinal axis are aligned in an upright posture, but mismatched when the body was in all of the off-vertical orientations.

Why might the visual stimuli be processed in an egocentric frame and not combined into an allocentric representation to include the orientation of the body when vestibular and body signals are unreliable? Part of the reason may be from top-down influences and the context of the visual stimuli. In a study by Vidal et al. [221], participants had to estimate the perceived angle of the bend of a curved virtual corridor presented using optic flow in the pitch and yaw axes while upright and lying right side down. In the upright position, forward pitch turns had significantly greater overestimation errors than backwards pitch and in the right side down position, estimation of yaw rightward turns were being overestimated more than left turns. This combination of rotation direction along with the respective body orientations represented the context equivalent to the direction of falling forward. This suggests that top-down influences from scene navigability and fear of falling with the direction of gravity may have led to the enhanced processing of visual motion resulting in the overestimation of the visually derived curve [221]. In a similar study using the same task, it was reported that the overestimation of downwards pitch turns were diminished when the task was performed while free floating in space compared to on earth [70]. In support of the top-down influence hypothesis, this reduction in asymmetry could have been explained by the absence of risk of falling due to the weightlessness from free floating. In the current results, we did not find a significant difference for the direction of the visual yaw rotation for both right and left recumbent positions. This could be explained by the lack of orientation in the starfield environment that was used for the visual motion. Future work using more visually enriched content (such as was used in Chapter 2 of this dissertation) could be used to assess the effect of visual polarity cues.

Visual context has also been reported to influence the temporal perception of visual motion. Estimations of time-to-passage (TTP) are overestimated when accelerating in a vertical downwards direction (free fall) compared to acceleration vertical upwards and in an earth-horizontal direction [129]. Precision was also lower during constant acceleration in the vertical downward compared to acceleration suggesting that there is an expectation or anticipatory effect due to the presence of visual gravity [129]. Another top-down influence is a phenomenon called the visual reorientation illusion (VRI), which is when a person's perception of upright is recalibrated based on the visual context [176]. McManus et al. [162] hypothesized that experiencing a VRI would lead to different perception of visual motion for prone and supine orientations due to reinterpretation of the gravity vector in an active visual distance estimation task. A VRI while supine would lead to gravity being ambiguous with a forward translation, therefore increasing visual gain or require less visual motion to reach a target and vice versa with prone orientation. However, this hypothesis was not supported by their findings that visual gain increased in both lying down orientations. Instead, they found that an increase in visual gain was correlated with the level of VRI which was largely dependent on whether the visual environment had orientation cues (a hallway vs. a starfield) [162]. These results support a cognitive (top-down) hypothesis where the interpretation of the environment is more important with the level of VRI being correlated with the visual gain regardless of body orientation.

In addition to visual context, other characteristics of visual stimuli, such as field of view (FOV), disparity and scene layout, have also been reported to explain some of the differences observed in the bias of visual heading discrimination moderated through vection [74]. Tanahashi et al. [210] also found that increasing visual stimulus size increases vection strength induced by circular rotation around the pitch, yaw and roll axes. In the current study, visual stimuli was presented using a relatively new head mounted display (HMD) model with a limited FOV (Oculus Quest). It is possible that a larger display providing a more expansive FOV could generate more compelling and effective visual motion stimuli. The findings discussed so far have also been from a variety of apparatuses such as different models of HMDs, shrouded displays, as well as projector screens. Whether this interacts with how the visual context is perceived and the effectiveness of the visual motion can potentially explain some of the differences found across studies.

While these findings have demonstrated the varying contributions of vision, gravity and vestibular cues, as well as body orientation cues in the perception of upright align with previous reports [131]. The question that remains is what are the mechanisms that govern the role of these factors in determining upright relative to the perception of motion? One potential mechanism that has been suggested that could explain these findings is the Bayesian optimal cue integration and sensory reweighting theory [96, 149]. The idea behind the optimal integration and reweighting concept is that multiple sensory cues are combined based the relative reliability of the unisensory signal to determine the "weight" or contribution of that signal to the final representation. Miwa et al. [165] reported that the longitudinal body axis dominates the perception of subjective uniform motion of a circle stimulus in the fronto-parallel plane when the direction of the visual motion matched the gravitational cue (upright position) without much consideration for visual polarity cues. Only when the body orientation cue was dissociated from gravity did visual polarity have an effect, supporting a Bayesian framework of shifting the representation of upright to rely more on the visual cues when the reliability of the gravity and body orientation cues were reduced due to conflict.

Interestingly, when the body orientation cue was dissociated from gravity and no visual cues were present, the perception still followed the longitudinal axis even when gravity cues (from vestibular input) were in conflict, suggesting a prior effect of relying on the longitudinal axis when no other cues of upright are available. This may explain our finding of why the perceived timing of visual motion was further from zero in the off-vertical orientations because no visual orientation cues were present, the timing estimate relied on the vestibular and longitudinal axis which were aligned in the upright orientation, but unreliable due to the mismatch when the body was tilted. Similar findings have been reported between the interaction of body and visual orientation cues, in which there is no influence of vision when upright and only when body orientation and gravity do not align, providing further support of the reweighting hypothesis [70, 128, 162]. Review of brain imaging studies on the reciprocal inhibitory interaction between visual and vestibular stimulation provides potential physiological evidence for the sensory reweighting mechanism when there is a sensory mismatch or incongruent sensory signals (see Brandt et al. [35] for a review). Future research should include visual orientation cues, to determine whether the perceptual timing estimate will shift towards the visual signal when the vestibular and body cues are unreliable.

3.5 Conclusion

In this study, we explored whether the presence of a mismatch in body orientation and vestibular cues due to gravity would influence the perceived onset of a visual yaw rotation. In all conditions we found that the onset of visual motion had to be presented before an auditory tone in order to be perceived as simultaneous (127-159ms). We also found that visual motion had to be presented approximately 30ms earlier when an observer was in an off-vertical orientation compared to when they were upright for the stimuli to be perceived as occurring simultaneously. This suggests that the perception of upright signalled by the vestibular and body cues relative to gravity had a significant influence on the accuracy of responses in which there is a delay in the ability to detect visual motion when the body is tilted from upright. This additional delay may be attributed to the uncommon experience of motion when in a non upright posture or from the sensory conflict resulting from the dissociation between the vestibular and body cues relative to gravity, leading to a decrease in the reliability of these signals. Future work will need to include orientation cues in the visual stimuli and further control for the reliability of the gravity, body orientation and visual cues to further explore the interaction between the perception of upright and motion.

Chapter 4

Sensory Reweighting: A Common Mechanism for Subjective Visual Vertical and Cybersickness Susceptibility

4.1 Introduction

Virtual reality (VR) technology has grown immensely and become widely available for both consumer entertainment and for applications in research and therapy [28]. Despite the advancement in VR displays and systems, cybersickness still remains a concern and a barrier to using VR technology for most users. Cybersickness consists of a variety of unpleasant symptoms related to nausea, disorientation, eye strain and fatigue and these symptoms can manifest differently depending on the individual [156, 188]. This has made it challenging for researchers to accurately quantify and predict the occurrence of sickness. Recent work using physiological and neuroimaging techniques have provided better insights into the neural basis of cybersickness [56, 188, 216]. However, more research is still needed to understand the mechanisms by which cybersickness is triggered along with any interactions with the virtual content that the user is experiencing. Researchers have been able to predict between 34 to 55% of the incidence of cybersickness using various modelling approaches between sickness ratings and physiological measures, sensory perception and behaviours, demographic information, as well as hardware and software factors [43, 78, 148, 175, 189, 228].

One of the prevalent explanations of cybersickness is the sensory mismatch theory [177, 187, 186], which describes how sickness is induced when there is a discrepancy in feedback from the sensory inputs signaling self-motion. This conflict is notably evident when immersed in most virtual reality experiences in which there is an abundance of visual motion, but minimal movement signalled by the vestibular and proprioceptive systems leading to discomfort and sickness [55, 126, 144, 146]. While there have been arguments against the sensory conflict theory [206] regarding the inconsistencies in predicting the occurrence and severity of sickness and how sensory mismatch is defined. The fundamental basis of cybersickness still appears to be centered around the integration of sensory cues responsible for self-motion and perhaps a multisensory perspective may be able to better describe the neural mechanisms leading to sickness [101].

To alleviate cybersickness based on sensory mismatch, a direct solution would be to provide vestibular feedback to consolidate the conflict. One such approach has been to incorporate real movement with the VR system by allowing the observer to physically move [46, 161] or by using a motion platform [144, 170]. However, there are practical and technical limitations with motion systems and the possible repercussions of different navigation techniques in VR have yet to be thoroughly explored [68, 120, 173]. Another approach is to generate an artificial sensation of movement by sending an electrical current to the mastoid process known as galvanic vestibular stimulation (GVS) [63, 157]. Studies have shown that synchronizing the stimulation with the speed and direction of visual motion [42] or applying the stimulation intermittently and during changes in visual motion (e.g., sharp turns and curves in a driving simulation) [102, 191] can reduce experiences of sickness symptoms.

More recently, it has been observed that the vestibular stimulation does not necessarily need to be mimicking a real motion or synchronized to match the visual motion to reduce sickness. Noisy vestibular stimulation using bone-conducted vibrations to the mastoid process [226], or using bilateral random noisy GVS [229] have both been shown to be effective at reducing sickness symptoms. This effect may be attributed to a sensory reweighting mechanism, in which the noisy vestibular stimulation leads the central nervous system (CNS) to down weight the unreliable vestibular signal and rely more on the visual system, hence reducing the apparent sensory conflict [101, 229]. It has also been reported that vection latencies are reduced in the presence of noisy vestibular stimulation [227] and that exposure to optic flow in VR can modulate sensitivity to vestibular input and vestibular processing [99, 100]. This further supports the notion of a shift in sensory weighting and the consequences for motion perception. Sensory reweighting has been predominantly observed in multisensory perception and postural control based on optimal integration around the reliability and functional significance of the sensory signals [16, 41, 88, 89]. However, whether this mechanism has any relationship with cybersickness and sensory conflict has yet to be established. Barrett and Thornton [24] found that observers who were more sensitive to bodily as opposed to visual cues were more likely to experience sickness in an active driving simulator, suggesting that an individuals' "perceptual style", a tendency to rely on one sensory modality over another, can be a possible predictor of sickness.

To assess this, however we also need to better understand how the CNS responds to VR and to determine what are some of the potential aftereffects of being exposed to VR. Most research in the field of VR primarily focuses on the mechanisms and factors responsible for inducing cybersickness and how to mitigate them, while research using psychophysical techniques has predominantly used VR as a tool to generate and present highly controlled stimuli. It is known that cybersickness symptoms can persist well after the VR exposure (see [83] for a review), however the consequences of this persistence for sensory perception and behaviour have not been thoroughly explored. It has been reported that while experiencing a typical VR game (i.e., commercially available) does not affect reaction times across response activation or inhibition [203], it may impede learning in other cognitive tasks such as spatial orientation and the ability to visualize or mentally rotate objects, as well as sustained attention [220]. It has also been shown that after experiencing a VR game, decision-making in a choice reaction time is slower and is likely driven by a decrease in attention [208]. Furthermore, the accommodation reflex of the eyes which is responsible for changing focus in depth is affected by VR and is correlated with ratings of sickness [208]. Here, we aim to directly examine the effect of a typical experience of a VR game not only in regard to cybersickness, but also for sensory perception.

The subjective visual vertical (SVV) is a perceptual measure of verticality consisting of orienting a line presented visually towards the perceived direction of gravity or upright. This task has been shown to represent the integration of multisensory signals involving visual, vestibular and body cues [84]. The vestibular system signals the direction of upright through the mechanical properties of the hair cells within the otolith organs and inertia from gravity, while the orientation of the body axis also provides a reference to the direction of upright known as the idiotropic vector [164]. When in an upright orientation, the vestibular and body signals of vertical are aligned and the perception of upright measured using the SVV task is relatively accurate to true vertical [71, 84]. However, when the vestibular and body cues are dissociated by tilting the head and body from upright, the SVV estimate shifts towards the longitudinal body axis indicating a bias in the perception of upright (A-effect) [4, 17, 53, 71, 84]. This bias has been shown to depend on the level of the head tilt from upright, where larger tilts beyond 60° have been shown to demonstrate the A-effect, while smaller tilts have been found to result in a shift in the subjective vertical in the direction opposite to the head tilt known as the E-effect due to ocular counter torsion [71]. It has been shown that this shift in the estimate of the perceived vertical is representative the relative changes in the contributions of the vestibular and body cues and can be modelled by a reweighting or Bayesian model [4, 53, 71, 84]. There have also been reports that the SVV is sensitive to differences between gender, expert observers such as dancers and astronauts who have highly trained vestibular sensitivities and patients with vestibular deficits or loss [6, 19, 26, 116]. This suggests that the SVV task can be used as a reliable measure to observe the sensory reweighting mechanism between vestibular and body signals.

The purpose of this experiment is to investigate the aftereffects of VR on sensory perception and to determine whether the occurrence of cybersickness is associated with the sensory reweighting mechanism. Using the SVV task, we plan to observe whether exposure to varying intensity levels of virtual content will lead to changes in the contributions of the vestibular and body cues in the perception of upright. Following the sensory conflict theory, if the vestibular signals need to be down weighted to consolidate the conflict induced by exposure to VR, then we expect the estimate of the SVV to shift further towards to longitudinal body axis. Furthermore, if cybersickness is indeed dependent on an individuals' ability to dynamically reweight their sensory signals, then we should expect to be able to observe a change estimate of upright representing the change in the relative contributions of these sensory signals based on the severity of symptoms experienced. We hypothesize that there will be a larger shift in the estimate of the SVV after exposure to a high intensity VR experience compared to a lower intensity experience and we also hypothesize that this change in the perception of upright will be related to severity of cybersickness symptoms. We predict that an observer who experiences a smaller or no difference in sickness severity between the two experiences should display a larger shift in the SVV estimate compared to an observer who experiences more severe symptoms of sickness. Lastly, we aim to explore whether there are gender or other demographic differences on the perceived estimate of upright and cybersickness.

4.2 Methods

4.2.1 Participants

Data was collected from thirty-one participants (16 males and 15 females; mean age = 25.6, SD = 3.9) recruited from the University of Waterloo. Seven of the participants were volunteers, while the remaining participants were remunerated \$10/h for their participation. All participants reported having no auditory or vestibular disorders and had normal or corrected-to-normal vision. This experiment was reviewed and received ethics clearance through a University of Waterloo Research Ethics Committee and all participants gave their informed written consent in accordance with the guidelines from the committee.

4.2.2 Apparatus and Stimuli

The Oculus Quest system was used to provide the VR content in this experiment. The Oculus Quest has a dual OLED display with a resolution of 1600x1440 (per eye) at 72 Hz refresh rate. It is a completely wireless system featuring 6 degrees-of-freedom (6DOF) inside out tracking allowing the user to freely move around. Here we allowed participants to move within a 2.4x2.4m designated play area. Two commercially available VR games were selected for the VR content - Sports Scramble (Figure 4.1a) and Echo VR (Figure 4.1b). These games were chosen to elicit different levels of sickness severity based on user reviews on the Oculus Quest store and because they share comparable gameplay aspects with both games belonging to the sports genre. Sports Scramble was chosen as the low-intensity experience and consists of three main sports (baseball, tennis and bowling) where the user is predominantly stationary both within the game and in the physical world and mainly involves to use of arm movements to catch, throw and hit a ball in each respective sport. Echo VR was designated for the high-intensity experience and puts the user in a zero-gravity arena in which they must navigate using the provided controllers in combination with rotation of their physical body to catch and throw a disc into an opposing team's goal.

The subjective visual vertical (SVV) task was used to measure participant's weighting of vestibular cues using the "luminous line" technique [19] and the method of constant stimuli. A line (3 x 0.5°) was presented for 500 ms on a neutral grey background with a central fixation point (0.45°of visual arc) of the same mean luminance on a laptop (Macbook Pro). A shroud was mounted to the display of the laptop in which participants viewed the screen through to block out peripheral vision. With this shroud, the screen subtended a 35°diameter circle at a distance of 25 cm. There were 21 line orientations from -50°to +50°in 5°increments (Figure 4.1c). Each line orientation was presented seven times for a total of 147 trials, which took approximately 5 minutes to complete. Participants reported whether they perceived the line was orientated clockwise or counterclockwise relative to their perceived vertical upright using the buttons on a gamepad (Logitech Gamepad F310).

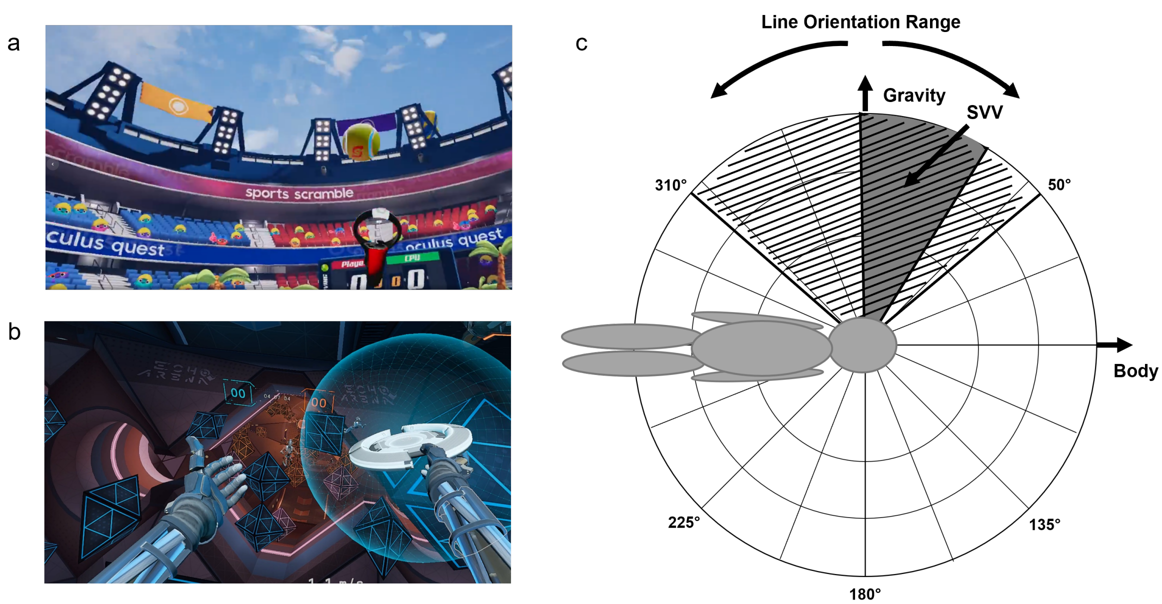

Figure 4.1: Screen capture of VR environment of the games used in the VR exposures **a** Sports Scramble and **b** Echo VR. **c** Polar illustration in earth coordinates relative to the right side down orientation. The range of the line orientations presented is highlighted by the hatched area and the shaded area indicates the range of the SVV estimates reported in the current study. The direction of upright signalled by the vestibular (gravity) and body axis cues are depicted.

4.2.3 Measures

Cybersickness was assessed using the fast motion sickness scale (FMS) [142] to measure sickness levels immediately after each VR session was completed. The FMS is assessed by a verbal rating on a 20-point scale ranging from "0 (representing no sickness at all)" to "20 (representing severe or frank sickness)". Participant's gaming experience was also measured at the beginning of the experiment using a questionnaire including the following questions: "Do you have any experience with video games?", "Do you play video games regularly?", "On average, how many hours a week do you spend playing video games?", "How would you describe your current level of gaming expertise?".

4.2.4 Procedures

Participants laid on their right side on an examination table with a foam pillow headrest to align their head with a circular shroud mounted on the screen of a laptop. The laptop was oriented 90°clockwise and mounted on a custom built stand. They completed a baseline SVV task in which they had to indicate whether a series of lines presented was oriented clockwise or counterclockwise from gravity ("the direction in which a ball would fall") via a 2-alternative forced choice task by button press on a gamepad. This took approximately 5 minutes. After completing the SVV task, the participants were guided to the VR play area where they were fitted with the Oculus Quest system. Participants played either Sports Scramble or Echo VR for 30 minutes. This was conducted using a within-subjects design, so participants completed both VR games in the same experimental session in a counterbalanced order. At the end of the VR session, participants' sickness level was verbally assessed using the FMS scale and then participants immediately completed another SVV task for approximately 5 minutes. Participants were then given a 15-minute break and after ensuring that any sickness symptoms had subsided, they began the second VR session with the alternative game that they did not experience in the first session. After the end of the second VR session, participant's sickness severity was measured again and followed by a final SVV assessment that again took approximately 5 minutes. (Figure 4.2). To rule out the potential confound of practice effects from repeated administering of the SVV task, a subset of participants (n = 11) conducted a second baseline test after completing the first baseline task, before entering the first VR session.

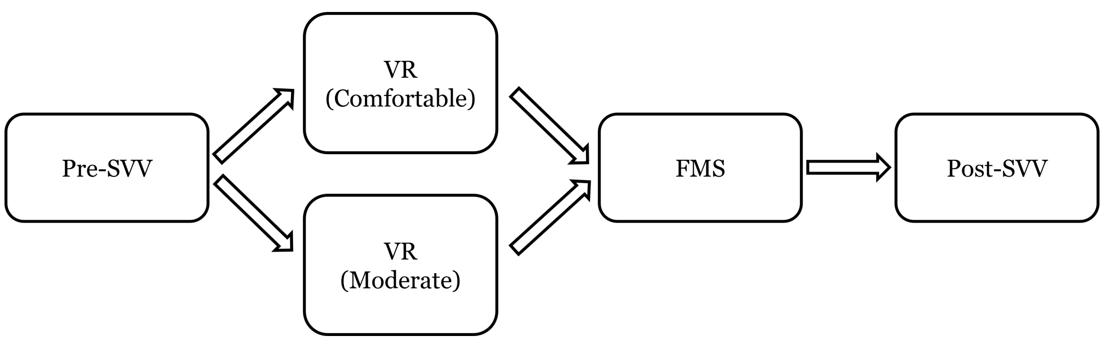

Figure 4.2: Schematic of experiment pipeline.

4.2.5 Data Analysis

Statistical analysis was conducted using SigmaPlot 12.5 and IBM SPSS Statistics 25. A logistic function which accounted for lapses in participants' responses (Eq. 4.1) was fitted to the participants' percentage of "clockwise" responses as a function of the line orientation. Estimates of lapse rate, bias and precision were derived from the three free-parameter equation to 21 data points corresponding to the 21 line orientations tested. The halfway (50%) inflection point of the sigmoid curve (x0) represents the point of subjective equality (PSE) which here represents the SVV estimate and the standard deviation of the function (b) as the just noticeable difference (JND) [19]. A positive SVV value indicates that the line was perceived as vertically upright when it was orientated clockwise from true vertical, while a negative SVV score indicates that the line was perceived as vertically upright when it was oriented counterclockwise from true vertical. For one participant, we were unable to fit the lapse function to their responses ($R^2 < 0.2$) and they were excluded from subsequent analyses (final sample: 15 males and 15 females; mean age = 25.5, SD = 3.9).

$$f = l + (1 - u - l)(\frac{1}{1 + e^{-(\frac{x - x_0}{b})}}) \tag{4.1}$$

For the gaming experience survey, participants were categorized into two groups of "low" and "high" gaming experience based on their responses in the survey. Participants who had no experience with video games, did not play video games regularly or only played video games regularly for less than one hour a week were categorized into the "low" gaming experience group. Participants who played video games regularly for more than one hour a week were categorized into the "high" gaming experience group. In total, 15 participants were assigned to the "low" gaming experience group and 15 participants were assigned to the "high" gaming experience group.

To assess the relationship between the SVV estimate and FMS scores, a three free-parameter Gaussian nonlinear regression model was fit to the FMS scores as a function of change in SVV from baseline after each VR exposure (Eq 4.2). Note that this regression equation was fit once to the SVV and FMS ratings from both the low and high intense VR sessions in a single model to explain the change in the relationship between the two outcome measures.

$$f = ae^{-0.5(\frac{(x - x0)}{b})^2} \tag{4.2}$$

4.3 Results

4.3.1 Subjective Visual Vertical

The results showed that the SVV was shifted in a positive direction towards the body axis at all three measurement times [Baseline ($M = 10.94$, SE = 1.59); Low Intensity ($M = 8.87$, SE = 1.52); High Intensity ($M = 8.07$, SE = 1.68)] (Figure 4.3a). To determine whether there was an effect of the VR exposure on the performance in the SVV task, a one-way repeated measures ANOVA was conducted on the SVV and JND data. Mauchly's test of sphericity was violated for the SVV scores [$\chi^2(2) = 7.72$, $p < 0.021$] and the Greenhouse-Geisser corrected test revealed a significant main effect for the SVV scores across exposures [$F(1.61,46.74) = 3.63$, $p = 0.043$, $\eta_p^2 = 0.11$]. Post hoc tests with Bonferonni adjustments for multiple comparisons indicated that the SVV scores were significantly lower after the high intensity VR exposure compared to baseline ($t = 2.61$, $p = 0.035$), indicating that the SVV was set closer to gravity and farther from the body. No significant difference was found after the low intensity VR compared to baseline ($t = 1.88$, $p = 0.129$) and the high intensity VR ($t = 0.73$, $p = 1.00$) (Figure 4.3a). For the JND scores, the Friedman test was performed and there was no significant main effect across exposures [$\chi^2(2) = 3.20$, $p = 0.202$] [baseline ($M = 4.68$, SE = 0.59); low intensity ($M = 4.22$, SE = 0.49); high intensity ($M = 5.18$, SE = 0.74)] (Figure 4.3b).

4.3.2 Cybersickness

To confirm that the low and high intensity VR experiences induced different levels of sickness severity, a Wilcoxon Signed Rank Test revealed a significant different in FMS scores ($Z = 4.55$, $p < .001$) [low intensity ($M = 1.87$, SE = 0.42); high intensity ($M = 7.90$, SE = 0.94)] (Figure 4.4).

4.3.3 Subjective Visual Vertical and Cybersickness

For our main hypothesis, we wanted to examine whether a change in the perceptual weighting of gravity versus bodily cues is correlated with a change in sickness severity, represented by the SVV and FMS scores, respectively. To examine this relationship, we took the absolute values of the difference in SVV scores after the high and low intensity sessions, as well as the difference in the FMS scores (note that we did not have to take the absolute values of the FMS scores because all participants reported either the same or higher ratings after

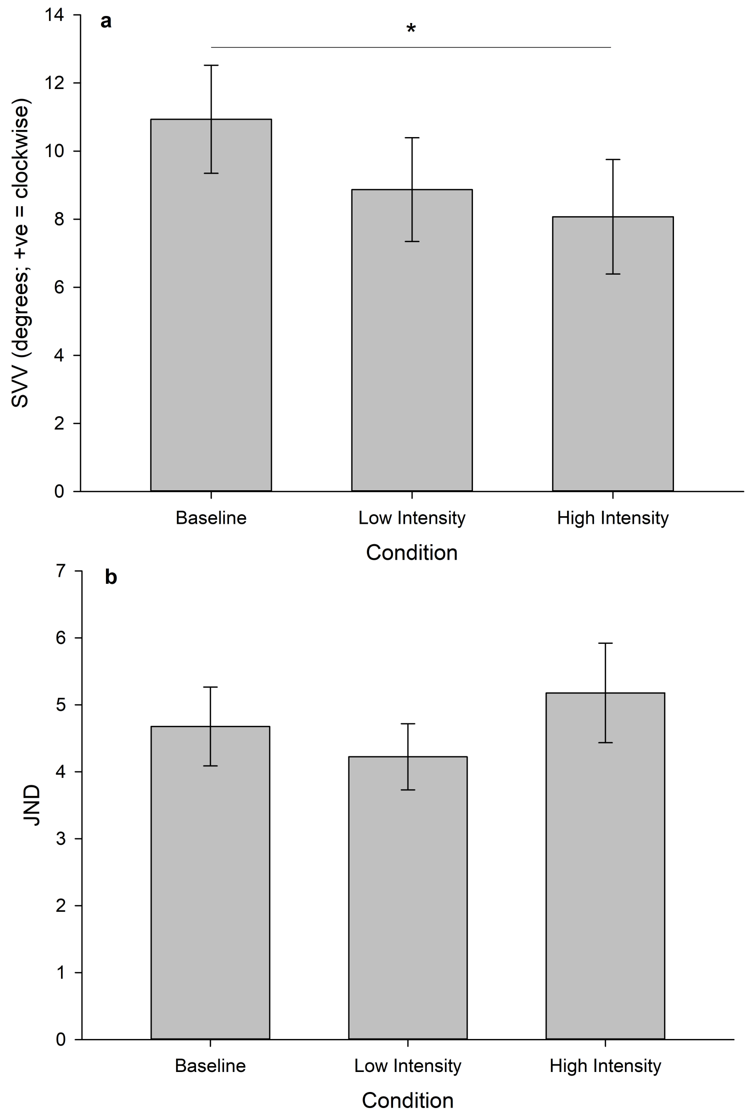

Figure 4.3: Summary of **a** subjective visual vertical (SVV) estimate and **b** just-noticeable difference (JND) between low and high intense VR exposures. Error bars are standard error.

the high intensity session). As cybersickness scores are not normally distributed [189] confirmed by a Shaprio-Wilk test [$W(30) = 0.90$, $p = 0.008$], we conducted a Spearman's rho correlation and found that there was no significant correlation between the absolute SVV difference and FMS difference between the low and high intensity sessions [$r(30)$ = -0.198, p = 0.294] (Figure 4.5). To further investigate the relationship between cybersickness and change in the SVV, a Gaussian regression model was fit to the FMS ratings as a function of change in SVV from baseline after each VR exposure. The results of the regression revealed that the change in SVV significantly predicted 49.5% of the variance in the FMS ratings [($R^2 = 0.49$), $F(5,54) = 10.58$, $p < 0.0001$] (Figure 4.6).

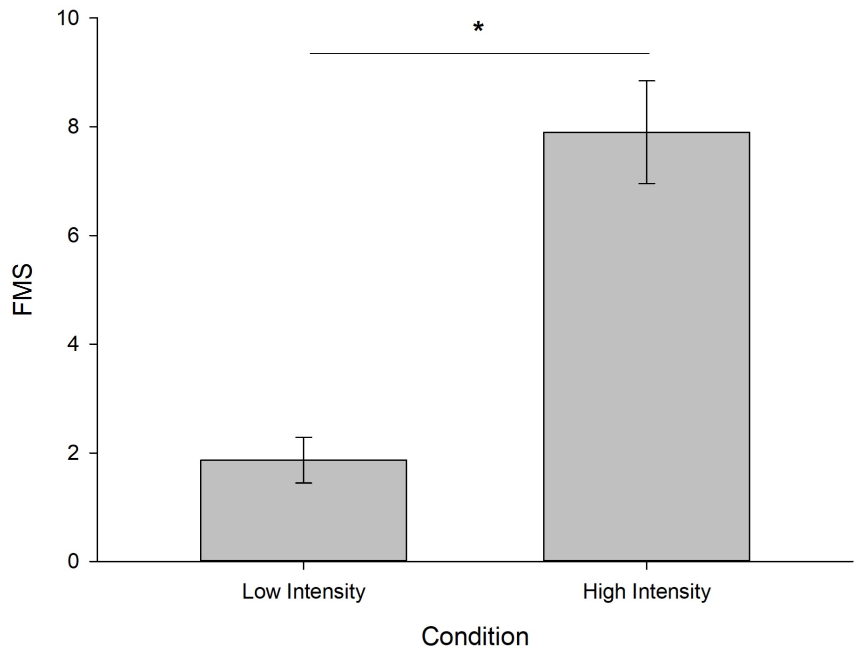

Figure 4.4: Summary of fast motion sickness (FMS) ratings between low and high intense VR exposures. Error bars are standard error.

4.3.4 Individual Factors

To determine if there were any gender differences in the SVV estimates and FMS scores, the data was split between males and females (summarized in Table 4.1). A series of independent samples t-tests with Bonferroni-adjusted significance criteria were conducted to compare the SVV and FMS scores across the different measurement points. The results showed that there were no significant differences between males and females in the SVV

[Baseline ($t(28)$ = -0.195, p = 0.847); Low Intensity VR ($t(28)$ = 0.392, p = 0.698); High Intensity VR ($t(28)$ = -0.317 , p = 0.754)] and FMS scores [Low Intensity VR (U = 89.0, p = 0.312); High Intensity VR ($t(28)$ = -1.099 , p = 0.281)]. The same procedure was performed to examine the effects of gaming experience between participants with low and high gaming experience (summarized in Table 4.1). The results revealed no significant differences in the SVV [Baseline ($t(28)$ = -0.195, p = 0.772); Low Intensity VR ($t(28)$ = -0.943, p = 0.354); High Intensity VR ($t(28)$ = -1.005, p = 0.323)] and FMS scores [Low Intensity VR (U = 72.0, p = 0.079); High Intensity VR ($t(28)$ = 0.383 , p = 0.705)].

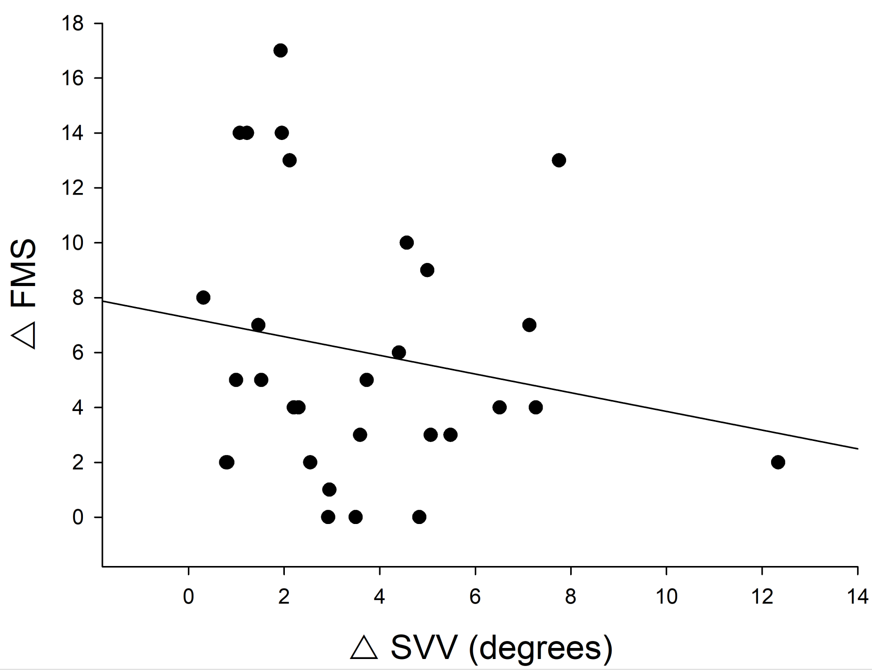

Figure 4.5: Correlation between the change in FMS score and change in absolute SVV value between the high and low intense VR exposures. The black line represents the line of best fit (R = -0.198).

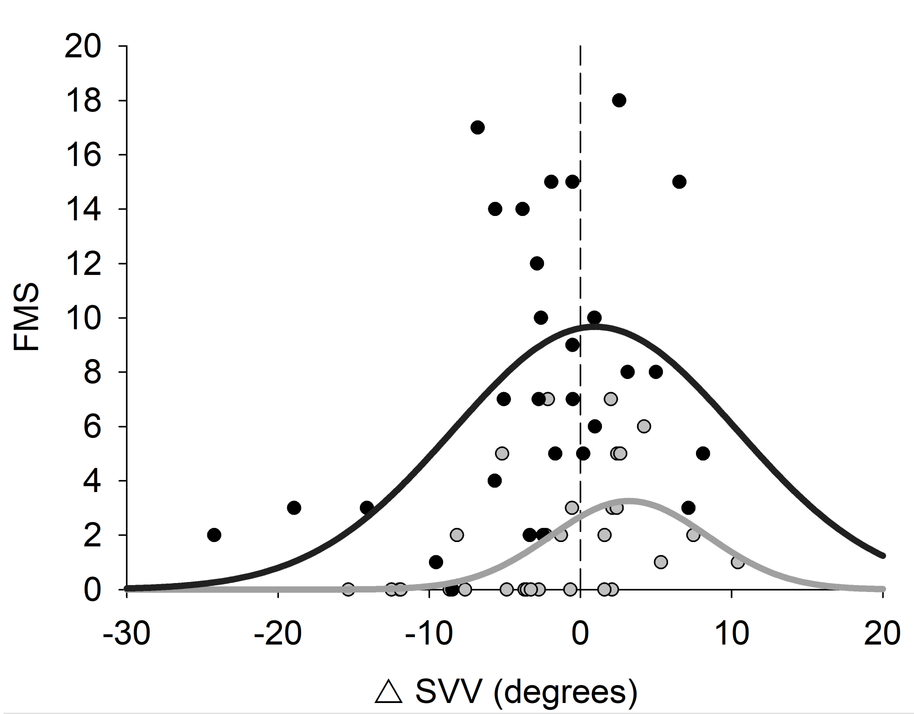

Figure 4.6: Gaussian model of FMS ratings relative to the change in SVV for both low and high intensity VR exposures from baseline. The grey-filled dots represent the data points from the low intensity VR exposure and the black-filled dots from the high intensity VR. The grey line is the Gaussian model prediction for the low intensity VR and the black line for the high intensity VR. The dashed line indicates the upper specification of the regression of no difference in the SVV from baseline.

			Baseline	Low Intensity VR	High Intensity VR
SVV	Male	Mean	10.62	9.48	7.53
		SE	2.05	1.76	2.32
	Female	Mean	11.25	8.26	8.61
		SE	2.49	2.54	2.51
	Low Gaming	Mean	11.41	7.43	6.38
		SE	2.11	2.23	2.29
	High Gaming	Mean	10.46	10.31	9.76
		SE	2.44	2.08	2.46
FMS	Male	Mean		2.20	6.87
		SE		0.62	1.19
	Female	Mean		1.53	8.93
		SE		0.58	1.46
	Low Gaming	Mean		1.20	8.27
		SE		0.49	1.54
	High Gaming	Mean		2.53	7.53
		SE		0.65	1.14

Table 4.1: Summary SVV and FMS split by gender and gaming experience measured at baseline and after the low and high intensity VR exposures. Positive SVV scores indicate that the perceived upright was rotated clockwise towards the body axis. FMS scores are rated on a scale from 0 to 20.

4.4 Discussion

The purpose of this experiment was to investigate the effects of different VR exposures on sensory reweighting and whether there is a relationship between sensory reweighting and cybersickness severity. Sensory reweighting was observed through the systematic bias in subjective visual vertical (SVV) task towards the axis of the body when performed in a 90°clockwise roll tilt orientation [4, 6, 53, 71, 84]. We found that after participants were exposed to 30 minutes of an intense VR experience there was a significant shift in the bias of the SVV away from the body axis towards the gravitational upright indicated by a significant decrease in the PSE. This finding suggests that either the contribution of the vestibular cue increased, the contribution of the idiotropic body cue [164] decreased or a combination of both occurred in subjective vertical after the VR experience. Participants also reported significantly higher sickness ratings in the high intensity experience and although the correlation between the change in SVV and difference in sickness severity between the two VR experiences was not significant, there appears to be a trend for participants who experience a lower difference in ratings of sickness to have a larger shift in their estimate of the SVV compared to those who experience a greater difference in sickness. This shift in sensory weighting was as predicted in our original hypothesis, however the direction of the shift was opposite to our expectations of down-weighting of the vestibular signal.

Our results for the SVV being biased towards the body axis agrees with previous findings for the A-effect or under compensation for roll tilt on the perceived upright based on the line orientation [4, 6, 17, 53, 71, 84]. This bias is based on the idea that body tilt introduces noise into the vestibular system [53], presumably from the mismatch between the vestibular (otolith) cues and gravity. According to the Bayesian reweighting model, the decreased reliability of the vestibular cue leads to an increased reliance on the body cue of upright and along with the influence of a prior for each sensory modality, produces an estimate of upright based on a combination between the two signals [53, 67, 71, 84]. In addition to the bias in the SVV, we also found that there was a significant shift in the SVV towards the vestibular cue after exposure to high intensity VR. Previous reports of a shift in the bias of the SVV have been found with changes in the degree of roll tilt orientation [71] or bilateral vestibular loss [6] leading to a shift in sensory reweighting, however in the present study the orientation of the observers remained consistent and only healthy participants were recruited. Another potential explanation could have been practice effects from completing the same SVV task repeatedly, however we had a subset of participants ($n = 11$) perform a second baseline task and found no significant difference from the initial baseline. Furthermore, the order of the two different VR experiences were counterbalanced across participants and no significant differences were observed for the SVV after the low intensity VR experience. This suggests that the significant shift in the SVV found was likely due to the exposure to the high intensity VR experience.

Following the Bayesian framework, the current results could be described as either an increase in vestibular cue weighting, a decrease in body cue weighting or a combination of both based on the change in reliability of each individual sensory signal. The current design with whole body roll tilts does not allow for us to investigate or model the contributions of each individual sensory cue in the estimate of upright. However, previous studies have found an increased reliance of the SVV on vestibular signals when dissociating the contributions of vestibular and body cues using comparisons with estimates of subjective body tilt (SBT) and head-on-body tilts. The SBT is thought to be mainly represented by body-in-space sensors, but can also be derived through an indirect pathway from head-in-space coordinates modulated by the head-on-body representation and vice versa for the SVV [53]. It has been reported that the relative contributions of the sensory signals for upright differ for each of these task [53] and while body cues through indirect pathway previously described can make up for the estimate of upright when the vestibular function is compromised, it cannot completely make up for the missing vestibular cues [6]. In another study by Alberts et al. [4] vestibular and somatosensory contributions to the SVV was dissociated by examining performance in the task with body tilt compared to head-only tilt. There was an increased biased with both body and head tilts, however the systematic error in SVV was found to be a function of head-on-body tilt rather than body tilt. This suggests a larger contribution of head sensors through the vestibular and otolith signals and possibly neck proprioception on the SVV over the body cues like previous reports of SVV operating in a head-fixed reference frame [211]. Taken together, these findings provide some evidence to suggest that the shift in SVV observed in the current study is likely a result of an increase in vestibular weighting rather than a decrease in reliance on body cues.

Why is the SVV shifted after exposure to VR and more specifically why is the weighting of vestibular cues increased? Harris et al. [116] measured the SVV and perceptual upright in astronauts pre-flight and after returning from long term exposure to microgravity in space. There were no significant differences between the astronauts and a control group for the shift in SVV pre- and post-flight, however variance in the SVV without visual orientation cues were significantly increased in astronauts post-flight. While we cannot directly compare the current results with these findings, this study showed that the SVV is sensitive to the balance between vestibular and body cues in the representation of upright and can reflect the changes in sensory reweighting between these sensory signals. It is plausible then that the shift in SVV found in the present study stems from potential sensory reweighting that occurred when observers were exposed to VR. It has been shown that VR can modulate vestibular sensitivity and processing [99, 101] and our results agree with these findings that the reliance on vestibular signals were altered after exposure to VR. Although the direction of the reweighting of the vestibular signal increased instead of decreasing like we had hypothesized, this finding is not necessarily surprising. We know that sensory conflict between vestibular and visual cues in VR is a potential cause of cybersickness [55, 126, 144, 146] and minimizing or consolidating this mismatch can alleviate symptoms [170, 213, 226, 229]. While previous strategies have focused on down-weighting the vestibular signal to rely more on the visual motion signals present in VR, it is also possible that the vestibular signals could be up-weighted to promote physical stability. According to the postural instability theory in cybersickness, sickness is correlated with postural instability or when people are naturally unstable or unable to maintain control of their posture when exposed to VR [13, 16, 66, 190, 198]. While we did not observe a significant correlation between the difference in sickness rating and difference in SVV, there was a trend towards lower difference in sickness with greater changes in SVV and sickness severity was significantly greater in the high intensity VR experience. Thus, the weighting of vestibular cues may have increased to promote postural stability modulated by cybersickness from the VR exposure, however future work including a measure of posture control during the VR experience is needed to explore this hypothesis.

To further investigate the relationship between cybersickness and the SVV, a regression model was used to explore whether cybersickness ratings could be predicted by the change in performance in the perceptual task. A recent review modelling the severity and incidence of cybersickness in the literature found that demographic information can explain 44.2% and hardware and software factors can explain up to 55% of the variance in cybersickness [189]. Previous research has also attempted to predict cybersickness using a similar regression approach with various factors. Kim et al. [148] used a stepwise regression model and a battery of physiological measures to determine that a combination of autonomous variable (heart period), electroencephalogram (EEG) activity representative of an increase in cognitive demand and stress response and past motion sickness susceptibility was able to predict 46% of the variance in the severity of cybersickness symptoms measured using the Simulator Sickness Questionnaire (SSQ). A similar report using the same modelling approach and a different range of physiological measures found that stomach activity, blinking and breathing rates can explain 37.4% of the variance in cybersickness measured by the SSQ [78]. In addition to physiological factors, it has also been shown that vection strength [175] and eye movement behaviours [43] can be strong predictors of sickness (48% and 34.8% respectively). However, all of these studies the participants were limited in their ability to interact with the virtual environment due to restrictions from the measurement devices or just passively viewing a virtual environment without user control. In a study more comparable to the current design by Weech et al. [228], balance control, vection and vestibular measures were taken before completing two different VR tasks of varying intensities and found that their model predicted 37% of the variability in cybersickness measured by the SSQ with a strong contribution (16%) from postural stability. In the present results, 49.5% of the variance in cybersickness measured using the FMS scale was predicted by the change in SVV performance alone. It should be noted that previous models used the SSQ as the primary sickness measures which calculates a weighted score based across multiple symptoms, while here the FMS score on a 21-point Likert rating scale was used. This indicates that the interaction between visual, vestibular and body cues in the perception of upright is a strong predictor of cybersickness and suggests that sensory reweighting may be an important underlying mechanism.

Both the SVV and cybersickness are subjective measures that can greatly vary between individuals as indicated by the magnitude of the variance observed in the results. As previously mentioned, a model of existing data in the literature showed that demographic information can explain 44.2% of the variance in cybersickness [189]. For these reasons, it is important to consider demographic and individual factors when investigating cybersickness to try to account for these potential individual differences. For the SVV, gender differences have been previously reported in which females are more likely to be influenced by the orientation of a visual background when upright [19] and mixed results have been found with expert observers, where dancers were found to be more susceptible to the vestibular noise generated by head tilts [26] and astronauts performed no different than a control group on earth [116]. Recent reviews have also highlighted various factors related to individual, hardware, content and experimental paradigm differences leading to the vast differences observed for susceptibility to cybersickness in the literature [125, 214]. There have been contrasting reports regarding gender differences with females being more susceptible to cybersickness, but recent findings have begun to suggest that this may have been due to improper fitting of the HMDs to the inter-pupillary distance (IPD) of females, as well as differences in sensitivity to motion parallax and 3D visual acuity [8, 98, 205]. Another interesting factor is gaming experience, in which it appears that people with more gaming experience may be less susceptible and recover faster from sickness [62, 66]. The genre or content of video games can also influence the occurrence of cybersickness with action and first-person shooter games being more likely to induce sickness than adventure games, possibly due to the greater amount of fast angular motions in those genres [66, 189]. This may be related to video game experience, as users with more experience may have reduced susceptibility to cybersickness due habituation or familiarity with the characteristics of the game content or improved visuospatial skills [204]. In the present study, we did not find any significant gender differences in SVV or cybersickness as we used a more recent HMD model with IPD adjustments (Oculus Quest) and anecdotally, no participants reported adjustments issues with the lens. We also did not find a significant effect of gaming experience, although it is interesting to note that most of the participants that reported "low" gaming experience were female (11 out of 15) and a majority of the "high" gaming experience were male (11 out of 15). Future work with a larger and balanced sample size is needed to properly examine these demographic factors.

Sensory conflict in VR primarily involves the visual, vestibular and proprioceptive systems, however in the present SVV paradigm, we did not include a measure for the contributions of vision. Visual feedback has been shown to have a significant influence on the perception of upright, with visual orientation cues in the form of a static scene or frame background when vestibular and body cues are not aligned [3, 5, 7, 19, 84, 116]. Since we did not provide any visual orientation cues, our interpretation of the current results is limited to the vestibular and body axis cues. Having the contributions of vision would have allowed us to model the reweighting of the sensory signals involved in the perception of upright [3, 84] and provide a more comprehensive understanding of what is occurring to the sensory systems after VR exposure. Another limitation of the current study is potential carry over effects between the VR exposures given the time that participants had to rest and recover from any sickness symptoms in between. We chose a 15-minute break following the guidelines of the Meta Quest Health & Safety Manual, however the persistence of sickness symptoms is not fully established and has been reported to last from anywhere between 10 minutes to up to 4 hours [83, 207]. A multitude of factors can contribute to the persistence of the symptoms such as the individual's susceptibility, the state of the user, exposure time, the VR content, the hardware used and along with relying on subjective reports on symptoms makes it extremely difficult to control for each participant. One solution could have been to have participants conduct the second VR exposure and associated SVV task on a different day, however this would prevent the comparison of the SVV between the two conditions. Lastly, the VR content used in the current study were commercially developed games and how each participant interacted with the game content could only be controlled to a certain extent across participants. This limits the depth of our interpretation of the findings regarding the specific aspects of the VR exposure beyond the sickness ratings that led to the observed results.

4.4.1 Conclusion

In the current study, the relative contributions of vestibular and body cues in the perception of upright were examined after exposure to two VR experiences of different intensity levels. Furthermore, we investigated whether the perception of upright and susceptibility to cybersickness were related based on a common sensory reweighting mechanism. The results showed that exposure to a high intensity VR experience resulted in a larger shift in the perception of upright towards the vestibular signal compared to a low intensity VR content. This finding suggests that the sensory weighting of the vestibular cue in perceiving upright increased after the high intensity VR exposure. However, there was no significant correlation between the change in perception of upright and susceptibility to cybersickness quantified as the change in sickness ratings between the two VR experiences. Despite this result, there still appeared to be a trend towards the hypothesis that there is a shared sensory reweighting mechanism for some participants and the change in performance in the perceptual task between the VR exposures was able to predict 49.5% of the variability in the sickness measure. Future research can try to better capture this relationship and the overall findings from this study provide important implications for potential aftereffects of general use of VR for entertainment in a more typical setting.

Chapter 5

General Discussion

In this dissertation, our primary goal was to explore the relationship between vestibular and visual signals regarding the perception of self-motion. These two sensory systems provide crucial information in the process of maintaining a stable representation of our surroundings and enabling us to successfully navigate and interact with the environment around us. However, sensory feedback from multiple sources that are sensed through different sensory modalities may not always be perfectly aligned and congruent with one another. How the central nervous system processes and integrates conflicting sensory information provides meaningful insights that allow us to infer how that information is perceived and shapes our decisions and behaviours. While previous research in the self-motion literature has well established the contributions of vestibular and visual information in the spatial domain, such as detecting the direction of self-motion or estimating the distance one has travelled, here we investigated the interaction between vestibular and visual signals of self-motion within the temporal domain. Specifically, we modulated the congruency of the feedback between vestibular and visual motion cues to examine the perceived timing of vestibular and visual motion events. Our results reveal that under certain conditions, incongruent sensory feedback regarding the direction of self-motion signaled by the vestibular and visual systems negatively impacts the accuracy of the perceived onset of both vestibular and visual motion.

A secondary goal of this dissertation was to investigate the implications of sensory conflict and self-motion perception in the application of virtual reality (VR) and cybersickness. The occurrence of cybersickness has persisted since the emergence of VR and has been problematic for the widespread adoption of the technology. One of the biggest questions that research has struggled to answer is why some individuals experience severe symptoms, while others may not experience any symptoms at all. There has also been limited research into any other potential negative aftereffects of VR exposure outside of cybersickness. In this dissertation, we hoped to address these concerns by examining whether a typical VR gaming experience could influence performance in a sensory perception task that has been used in the spatial perception literature to reflect the relative weighting of visual and vestibular cues. The findings revealed that exposure to an intense VR game altered the relative contribution of vestibular and body cues on the subjective visual vertical (SVV) and that this change in the SVV following VR exposure is a strong indicator for predicting whether cybersickness had occurred. These results suggest that there is a common mechanism between cybersickness and the processing of sensory signals that can be reflected in sensory perception after VR exposure, providing a novel metric for assessing cybersickness severity, which also further advances the theory that sensory reweighting may be a mechanism used by the central nervous system to combat sickness. These findings also may explain why some people do not get as sick in VR (i.e., they are able to reweight sensory cues) compared to those more prone to cybersickenss (i.e., they are less able to reweight sensory cues). In the following sections of this chapter, we will further discuss the importance and implications of the findings in this dissertation.

5.1 Summary of Findings

In Chapter 2, the influence of visual feedback on the perceived timing of vestibular stimulation in the form of a passive whole-body yaw rotation was measured in a virtual environment simulating a natural forest. The results showed that the perceived onset of passive rotation of the body using a motion platform was delayed relative to an auditory reference tone and there was no difference in this timing estimate when visual information was available or removed. It was also found that the delay in the perceived timing of the motion was further delayed from zero for a higher rotation frequency replicating previous reports in the literature [44]. In addition to presenting visual feedback congruent with the physical motion, the speed and direction by which the visual scene updated relative to the physical motion of the observer was varied to produce a sensory mismatch in self-motion signaled by the vestibular and visual cues. The results for conditions that used incongruent visual motion showed that neither decreasing nor increasing the speed of visual scene updating had any effects on the perceived onset of the passive rotation, however changing the direction of the visual updating significantly delayed the perceived timing further from the true point of simultaneity. Further, it was found that increasing the speed and changing the direction of the visual updating led to reports of increased cybersickness severity. These findings suggest that the interaction between vestibular and visual signals for the perceived timing of self-motion is contingent on the dissociation of specific parameters between the actual and expected outcome of self-motion. The similarities in the influence of sensory conflict between the timing estimates and cybersickness were beyond the scope of this chapter to further assess but they influenced design decisions for the experiment in Chapter 4.

While there appeared to be no significant improvement in the vestibular timing estimate with visual feedback, one condition missing to fully account for the effects of vision was the perceived timing of visual motion. In Chapter 3, the second study of this dissertation was designed to address this gap from the previous study, as well as in the literature as no research has previously been conducted to explore the reciprocal influence of vestibular signals on the perceived onset of visual motion. In this study, visual motion was presented in VR using a dot star-field in the yaw rotation axis. Sensory conflict with the vestibular signal was introduced by manipulating the orientation of the body, generating a mismatch between body and vestibular cues due to gravity in the perception of upright and creating an ambiguous vestibular signal of either head tilt or translation. The results revealed that the perceived onset of visual motion was further delayed from zero (i.e., true simultaneity between visual onset and a reference auditory tone) by approximately an additional 30ms when viewed in a supine or side recumbent orientation compared to an upright posture. There were also no significant differences in the timing estimates of the visual motion between all the non-upright orientations. Similar to the findings from Chapter 2, this indicates that the perceived timing of visual motion is negatively impacted by the presence of conflict in the vestibular and body signals, even despite the mismatch not being in the direct plane of the axis of rotation used in this design.

The purpose of the final study in Chapter 4 was to investigate the potential relationship between sensory perception and cybersickness. The subjective visual vertical (SVV) task was used to measure the relative sensory weighting between vestibular and body signals in the perception of upright. Varying levels of cybersickness severity were induced by having participants play two VR games rated by game users for different degrees of intensity. The SVV estimate taken at baseline and after each VR exposure showed a greater bias towards the direction of upright indicated by the vestibular cue than the body cue compared to baseline after experiencing the high intensity VR game for 30 minutes. Participants also reported higher ratings of sickness severity on the fast motion sickness (FMS) scale after experiencing the high intensity VR game compared to the low intensity game. This suggests there was a significant shift in the relative contributions of vestibular and body signals in the perception of upright after being exposed to an intense VR experience and that this sensory reweighting was captured in the estimate of the SVV. This finding also raises caution for the possibility of aftereffects from intense VR gameplay for sensory perception, which can have important implications involving decision making and behaviour. We found that while a simple linear correlation cannot capture the relationship between change in the SVV and cybersickness, a simple 3-parameter gaussian regression model fit to these data can account for 49.5% of the variance in fast motion sickness ratings based only on how much the SVV changed post VR exposure. As susceptibility to cybersickness has been repeatedly theorized to arise from sensory conflict, this finding highlights the relationship between cybersickness and the subjective visual vertical rooted in a possible common sensory reweighting mechanism.

5.2 Interaction Between Visual and Vestibular Signals

Previous studies have reported that a combined vestibular and visual signal can increase the precision of perceptual estimates in the spatial domain compared to the unisensory cues through multisensory integration [38, 39, 96]. However, in Chapter 2 of this dissertation we found no changes in the precision of the timing estimates for passive whole-body rotations with and without visual feedback. This suggests that the benefits of providing additional sensory cues may be limited within the spatial domain, or that there may have been properties of the motion in the tasks used in the previous studies that were not captured in the current paradigm. It has been reported that giving participants more time to accumulate evidence for self-motion can lead to improvements in vestibular and visual thresholds [82]. Here, we asked participants to determine the onset of a passive rotation relative to the onset of an auditory reference tone, which is a very specific window within the entire movement in comparison to heading estimates where participants have until the end of the movement to form their perception of the event. Perhaps a more comparable design in the temporal domain to properly assess the integration of vestibular and visual signals would be to examine the duration or speed of the movement. Unfortunately, we were unable to examine this relationship regarding visual motion in Chapter 3, due to the manipulation of the vestibular stimulation not being in the same plane of motion as the visual stimuli. However, due to the similarities in the following findings that we will discuss between Chapters 2 and 3, we suspect that the consequences for visual motion would follow a similar trend and require more comparable stimuli properties.

One of the common findings between Chapters 2 and 3 was that the precision of the timing estimates of both vestibular and visual motion were not influenced by the presence of conflicting sensory information from the other modality. This indicates to us that the additional sensory information provided by either the visual scene in Chapter 2 and body orientation and gravity in Chapter 3, was most likely disregarded in the decision of the perceived timing of the motion meaning that the perceptual estimate was comprised predominantly from the main modality of the motion. This is supported by the findings that responses to heading are more biased or rely more on the vestibular cues when the vestibular and visual cues signaling self-motion are incongruent cues [39, 76, 82, 96]. Similar findings have been reported in direction discrimination of yaw rotations where the detection of a conflict between vestibular and visual cues are prioritized over optimal integration when a discrepancy between the signals is detected [103]. These findings demonstrate that it is possible for the perceptual estimate to rely on just a single modality despite the availability of an additional source of sensory information from a different modality. This mechanism appears to be modulated by the mismatch identified in the signals, as Prsa et al. [183] have also reported that it is possible to access the unimodal information when the two signals are not perceived as sharing a common cause.

The main finding of Chapters 2 and 3 was that the perceived onset of both vestibular and visual motion was further delayed from true simultaneity when there was a sensory conflict with the accompanying sensory modality. This shift in the delay of the perceived timing is representative of a decrease in the accuracy of the perceptual estimate. It is theorized that there are two different strategies that govern the perception of redundant sensory information based on the reliability of the sensory signals and prior knowledge and expectations of the sensory outcomes of an event, with multisensory integration being responsible for improving precision and multisensory calibration for the accuracy of the perceptual estimates [9, 90]. While the mechanisms of multisensory integration have been thoroughly explored as discussed previously, less information is known regarding multisensory calibration. A few studies have shown that vestibular and visual signals in heading estimates can be calibrated to shift the perceived direction of motion based on the reliability of the cues and the availability of external feedback, providing evidence that there is indeed a sensory calibration strategy separate from integration [236, 237]. In this dissertation, we found that the accuracy of the perceived timing of vestibular and visual motion was shifted in the presence of sensory conflict while the precision of the timing estimates were unaffected. This further supports the view that there is a separate multisensory integration and calibration strategy and that the mechanism is based around the congruency of the sensory signals involved. The increase in delay of the perceived timings that we observed may have been a result of the mismatch between the sensory signals leading to a decrease in the reliability of the cues, thus causing the perception of the event to break down and adapt to a new calibration [90].

5.3 Sensory Reweighting as a Common Mechanism

In all three Chapters of this dissertation a shift was observed in each respective perceptual estimate when sensory conflict was present. In Chapters 2 and 3, the perceived timing of vestibular and visual motion shifted further away from true simultaneity and in Chapter 4 the perceived upright shifted away from the direction signaled by the body axis and towards the direction of the vestibular signal. While the conditions and tasks of each experiment were different from one another, a common theme that has the potential to explain the main findings from all three experiments is the sensory reweighting mechanism. The idea of sensory reweighting involves the change in the relative contributions of a sensory signal in the final perceptual outcome. This is typically described using a Bayesian framework, in which each sensory signal has a prior probability distribution of an expected outcome or sensory input for a specific event based on past knowledge and experience that gives the signal a certain weight in the perception of said event. However, the weight of the sensory signal can either increase or decrease based on the relative reliability of the signal given the circumstances around the sensory event, such as a change in the state of the central nervous system or the conditions of the environment surrounding the event. For example, in Chapter 2 the speed and direction of which the visual scene updated relative to the physical rotation was altered and in Chapters 3 and 4 the orientation of the body was varied. Previous reports have suggested that a shift in the weighting between vestibular and visual signals can shift based on task demands or the way in which an information source is regarded due to prior expectations or purposefully created cue conflicts [27, 37, 89, 96]. In other words, a situation that can trigger sensory conflict has the potential to lead to sensory reweighting.

Evidence of sensory reweighting has been observed in many studies within the multisensory integration literature. For instance the studies involving multisensory integration and heading described in the previous section has shown that vestibular and visual cues are combined in an optimal fashion based on the weighting value of the relative reliability of each individual signal [38, 39, 96]. The SVV task used in Chapter 4 has also been demonstrated to reflect sensory reweighting, with reports in which the perceptual estimate of upright can be modelled by a Bayesian reweighting framework between the relative contributions of the vestibular, body and visual cues involved [4, 53, 71, 84]. Essentially almost any study that has been conducted that involves examining a change in the perception of a sensory signal or the combination of multiple sensory from the same or different sensory modalities can be linked back to the sensory reweighting mechanism. Reports of short-term plasticity (STP) at the neuronal level provides further evidence of sensory reweighting, as this process may either facilitate or represent the mechanism by which sensory reweighting occurs. STP is the change in excitability of the synaptic connections between neurons and previous research has found dynamic short term changes in brain activity using neuroimaging techniques after sensorimotor spatial adaptation and training in discrimination of visual and auditory stimuli [154, 158]. Since we did not design our experiments to be able to directly model the changes in the weighting of the sensory signals involved, we can only conclude that the current findings from this dissertation provides indirect support for a common sensory reweighting mechanism.

The secondary goal of this dissertation was to investigate the potential implications of the relationship between sensory perception and sensory conflict for VR and cybersickness. Sensory conflict between vestibular and visual cues have been shown to be correlated with cybersickness [55, 126, 144, 146]. Following the notion that sensory conflict also leads to sensory reweighting, and sensory reweighting can be captured within the estimates of sensory perception tasks, it is then reasonable to hypothesize that perceptual estimates can reflect cybersickness, modulated by the relationship between sensory conflict and reweighting. This is supported by reports that minimizing or consolidating the mismatch between vestibular and visual cues, effectively changing the reliability and thus reweighting of the sensory signals can alleviate symptoms [170, 213, 226, 229]. In the results of Chapter 2, it was observed that sickness severity appeared to follow a similar trend to the estimate of the perceived timing across the varying levels of sensory conflict. Following this observation, in Chapter 4 we demonstrated that the change in the perceived estimate of upright can successfully predict up to 49.5% of the variance in the sickness ratings. This demonstrates that the sensory perception can be used as a metric for assessing cybersickness severity and sensory reweighting is a key modulating factor. Furthermore, this has the potential to address one of the weaknesses of the sensory conflict theory, that it fails to account for individual differences, since every individual experiencing the same VR content should theoretically be exposed to the same sensory mismatch, but the severity of symptoms can vary across those same individuals. However, if we consider a common sensory reweighting mechanism then we can account for those individual differences based on the individual's ability to sensory reweight. This is evident in findings that individuals who are more sensitive to certain sensory cues are more susceptible to sickness [8, 24, 98]. Thus, this suggests that those who are able to reweight sensory cues will experience less sickness symptoms than those who do not.

5.4 Limitations and Future Directions

In this section we will discuss some of the broader limitations across this dissertation and some directions for future research following the findings reported here. In all the Chapters of this dissertation, we compare our results to a lot of modelling approaches for both sensory integration and cybersickness between vestibular, visual and body signals. However, one of the main limitations of the design of our experiments was the inability to directly compare all the sensory systems involved together to evaluate these models within our own results. In Chapters 2 and 3, the goal was to explore the effect of visual-vestibular integration on the perceived timing of the motion, but the timing estimates in those experiments were based off of audio-vestibular and audio-visual stimuli instead of visual-vestibular judgements. Originally, Chapter 2 was designed with audio-vestibular judgements to replicate and extend the findings from previous timing literature [21, 44, 50] with the addition of visual input and then the intention from there was to transition the design to investigate visual-vestibular judgements and to model the integration of vestibular and visual signals when varying the reliability of each individual sensory cue in the perceived timing estimates. However, the development of these follow-up experiments were suspended due to COVID-19 restrictions and the designs of the following Chapters had to change to accommodate for potential testing outside of the lab environment or even remotely with virtual reality (VR) systems being delivered to the participants' homes. Regarding the limitation to properly examine all of the sensory signals of interests in Chapter 3, future work should explore combinations of visual motion in the same axes as the ambiguous motion resulting from the interaction between the vestibular signal and different body orientations with gravity.

In Chapter 4, we modelled the severity of sickness using the change in the SVV perceptual estimate and found that it was a strong predictor relative to previous models in the literature. However, as mentioned in the discussion of that chapter, the design of our experiment was quite different from what had previously been done and we also assessed sickness severity using the more simple FMS scale. While the validation of the FMS scale has shown it to be comparable to the SSQ in its ability to measure sickness severity [142], future research is needed to confirm the validity of our prediction model using different cybersickness and sensory perception measures. The addition of visual orientation cues was also missing from our design to fully model the sensory weightings between vestibular, body and visual signals. Thus, to follow up on this study future work will need to include the SSQ and possibly physiological measures for cybersickness severity and incorporate visual orientation cues in the perceptual task, such as using the rod-and-frame variant of the SVV or the Perceptual Upright task [84]. It would be also interesting to explore whether this finding extends beyond the perception of spatial orientation to other visual-vestibular integration tasks such as self-motion detection and discrimination. This work would have important implications for better understanding the underlying causes and mechanisms of cybersickness, providing new and possibly more efficient approaches to assessing susceptibility to sickness and developing new techniques to minimize or prevent the occurrence of sickness.

Another limitation common in all the Chapters of this dissertation is the use of a psychophysical task as the main outcome measure, such as the temporal order judgement (TOJ) and subjective visual vertical (SVV). These methods are limited to determining the measures of accuracy and precision of the perception of the stimuli specific to the task and do not directly quantify their underlying mechanisms on their own. However, the psychophysical estimates are very much informative and provide a lot of external validity into the understanding of how people are perceiving and respond to certain stimuli or sensory events. It should be noted that reports comparing the neurophysiological response from networks of neurons believed to be involved in the processing of vestibular and visual self-motion signals in primates with the behavioural responses in psychophysical tasks are closely correlated [60, 112, 111]. Thus, future work with brain imaging techniques or physiological measures are important to compliment these psychophysical measures and confirm the underlying mechanisms of the perceptual estimates. Since the TOJ and SVV tasks in our current designs involved minimal movement, it may be possible for future research to use functional near-infrared spectroscopy or electroencephalogram to measure the patterns of brain activation correlating with the regions found in the animal models to assess those findings of a functional link between certain neural networks and psychophysical responses in human participants.

A recent review of cybersickness incidence and severity reported that individual demographic differences, as well as the VR hardware and software used are major contributing factors of cybersickness occurrence [189]. While we did not observe any sex differences or differences based on gaming experience, our sample sizes were relatively small to properly investigate these factors. In terms of the experimental stimuli and apparatus, one limitation that arises is the use of VR exclusively to present the stimuli. VR as used here was presented using a head-mounted display (HMD), in which the lens of the device sits directly in front of the eyes at a fixed distance. It has been reported that VR-HMDs can evoke vergence responses of the coordinating eye movements to fixate on an object with both eyes, but it cannot account for the appropriate accommodation response for the lens of the eyes to adjust to the appropriate depth of the object, possibly leading to a blurry image, more visual fatigue and eye strain [208]. For this reason, future research using a different type of display is required to confirm the current findings of this dissertation to ensure that there were no interactions of the results with the VR hardware. Another limitation of VR is the realism factor or the ability to invoke presence in which the observer feels like they are truly in the virtual world or that the virtual environments is real to them. The level of presence has been found to have important implications for cybersickness [213, 224] and the perception of self-motion [195, 196]. We did not include any measures of presence or perceived realism in any of the current experiments, however we would recommend that future research involving perception and VR to include such measures to help identify whether there are top-down influences regarding the perception of the VR environment itself. VR is still a novel experience for a lot of individuals and the technology is also constantly evolving, thus it is important for researchers to consider the entire experience of VR when designing an experiment rather than just using it as a tool for displaying stimuli. More research needs to be conducted to uncover which factors play a role in both the sensory perception and cybersickness literature and a standard approach needs to be developed to allow for better comparisons between studies.

5.5 Conclusion

In this dissertation, the perceptual consequences of sensory conflict between vestibular and visual signals were investigated in the temporal domain of self-motion perception, as well as the implications of sensory reweighting for cybersickness in the application of virtual reality (VR). The results showed that the presence of sensory conflict negatively impacted the perceived timing of vestibular and visual motion and that individual differences of sickness severity could be successfully modelled using the change in the relative contributions of vestibular and body cues involved in the perception of the subjective vertical. Taken together, the findings from this dissertation provide novel findings for the interaction between vestibular and visual cues in the temporal dynamics of self-motion perception with important implications for VR and cybersickness with the potential relationship between sensory conflict and sensory perception through the sensory reweighting mechanism. Moving forward, VR developers need to continue to reduce the latency in motion tracking and visual updating since a mismatch or dissociation between them could have detrimental effects on sensory perception and decision making behaviour. Furthermore, if postural change relative to upright negatively effects motion perception then this will need to be factored into VR development for recreational applications with reclined viewing or for passengers susceptible to motion sickness or even in self-driving vehicles where passenger intervention may be required. Lastly, if perceptual differences capturing the effect of short-term plasticity and sensory reweighting are indeed related to cybersickness susceptibility, then sensory adaptation, pharmaceutical solutions or brain stimulation techniques could be developed to reduce sickness severity and mitigate symptoms in the future.

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