# The effect of perceived self-orientation on the perception of visually induced self-motion

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Abstract

In certain environments the direction of "up" indicated by vision and gravity can be in conflict where these directions do not agree. Some people resolve this conflict by relying on their visual cues. In this case, when a participant and the room in which they are sitting are both tilted together, they would feel as if they were standing upright and would experience what is called a Visual Reorientation Illusion (VRI). A VRI on Earth might result from either (1) ignoring the gravity "up" in favour of the visual up, resulting in a higher visual weighting, or (2) misinterpreting the ambiguous vestibular acceleration cue not as a tilt but as a translation. In Chapter 2, I present evidence that during a VRI individuals require less visual motion to perceive that they have traveled through a specified distance: the move-to-target task. This might result from an enhancement of the visual cue due to a higher visual weighting while down-weighting the conflicting gravity cue, here referred to as my reweighting hypothesis. In Chapter 3, I find that people with VRIs actually have a lower visual weight and higher gravity weight when determining their perceived upright. This suggests that either the reweighting theory is incorrect or that the participants with a higher gravity weight might be more likely to detect, and then reweight, the conflicting visual and vestibular cues. In Chapter 4, I find that when the gravity cue is removed by moving into a 0g environment, initially there is no difference in performance on the move-to-target task compared to on Earth, but after adapting to microgravity and also upon return to 1g, participants need more visual motion to feel they have passed through a specified distance. Chapter 4 provides further evidence that my reweighting theory is incorrect. My research demonstrates that even within the same environment and while viewing the same stimuli, different people can have different interpretations of the environment which are related to changes in behaviour. Specifically, a person's perceived orientation can affect their self-motion perception. The findings are discussed in terms of sensory cue conflict and reweighting, as well as differences between how we perceive visual motion versus how we use it.

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# CHAPTER 1: General Introduction

During our day to day lives we use a variety of senses such as visual, auditory, proprioceptive, and vestibular to help us orient ourselves and to navigate through our environment. These cues provide both novel and redundant sources of information that can be combined together to help us safely and accurately move through our environment.

A fruitful and convenient way of studying the perception of self-motion is by looking at the response to using visual motion alone. Early studies on the illusion of visually induced self-motion (vection) hypothesized that tilting a person should affect the perception of visual self-motion due to the altered vestibular cue. The results of such studies (reviewed below) have been inconsistent. However, most previous studies ignored participants' perceived orientation and experience during assessment, even though a person's interpretation of their visual environment has been shown to impact visual self-motion perception (Preuss, Brynjarsdóttir, & Ehrsson, 2018; Guterman & Allison, 2019).

In this dissertation, I use virtual reality to create an ambiguous environment that causes some people when lying down to feel as if they are standing upright, while other people correctly perceive themselves as lying down. Using this environment, I investigate how the emphasis put on vision in order to arrive at a previously seen target distance is modulated by changing the perception of orientation.

In the first chapter, I review how visual and vestibular cues contribute to the sense of self-motion and orientation. Section 1.9 *Aims of this dissertation* outlines each of the following chapters as well as the main hypotheses in each experimental chapter. In Chapter 2, I look at how a participant's real and perceived orientation impacts their ability to visually move to previously seen target distances in the ambiguous virtual environment. Then, in Chapter 3, I investigate how differences in the weights given to visual and non-visual cues affect participants' perceived orientation and the amount of optic flow they need to perceive they have traveled through a given distance in the virtual environment. Finally, in Chapter 4, I look at how exposure to microgravity affects the use of optic flow in creating the perception of travelling through a virtual environment. Overall, this dissertation focuses on the contributions of the visual and vestibular cues to our perception of our orientation and self-motion and the interactions between them.

## 1.1 Visual cues to self-motion

As we move through an environment, the relative displacement of visual stimuli, including objects and geographic features, forms a pattern of motion that is referred to as optic flow (Gibson, 1950). Optic flow differs from retinal flow as optic flow is the pattern of motion generated by our environment and things in the environment as we move, while retinal flow is the pattern of motion generated on our retinae which may themselves be moving relative to the head (e.g., following an object in the scene) and is therefore more complex. Thus, if you translate forwards but track an earth-stationary object on, for example, the right, the patterns of optic flow and retinal flow differ. People are generally able to distinguish between the two (Cutting, Springer, Braren, & Johnson, 1992; Rushton, Bradshaw, & Warren, 2007) and extract optic flow from retinal flow but optic flow continues whether we have our eyes open or not..

Optic flow differs depending on the type of movement we are making (Gibson, 1950). For instance, linear motion evokes a different pattern than rotational motion, and side-to-side motion differs from forward-backward motion. Objects further away also provide a slower rate of optic flow than closer objects during translation since their angular position relative to the observer changes more rapidly than further objects; this relative motion of the images of objects in the environment provides motion parallax cues (Gibson, 1950).

The perceived direction of self-motion, or heading, provided from optic flow is heavily studied. Heading can be obtained from optic flow from the Focus of Expansion (FOE). When translating, optic flow radiates out from a single point (FOE) which is the direction in which you are heading and is independent of fixation (Gibson et al. 1955; Warren & Hannon, 1988a). If you move forward the FOE will be in front of you. If you were then to turn your head, the FOE is still ahead of you even though the pattern of retinal flow will differ (Gibson et al. 1955). People are quite accurate in estimating their heading during horizontal heading estimation using optic flow, particularly if the heading is close to straight ahead where they are accurate to about 1 degree of error (Warren et al. 1988b). Deviations away from straight ahead lead to an increase in error

(Crane 2012). There are also systematic biases away from straight ahead during horizontal (Crane 2012; de Winkel, Kurtz & Bülthoff 2018) and vertical heading estimation (Crane 2014a; Gibson, Kim, McManus & Harris, 2020).

Optic flow alone can induce an illusionary sensation of self-motion. For instance, if a person's entire visual surroundings are moved using virtual reality or a large computer screen and the person is kept stationary this tends to result in an illusory feeling of self-motion referred to as vection (Fischer & Kornmiiller, 1930, Brandt, Dichgans, & Koenig 1973). Much of the research on vection focuses on measuring the "qualia" or subjective experience of the vection, such as reports of the perceived speed (Palmisano, Allison, & Pekin, 2008) or magnitude (Palmisano, & Chan, 2004) of the sensation of vection, or the amount of time until the onset of the sensation (Palmisano, Gillam, & Blackburn, 2000).

Optic flow cues that generate vection are also informative enough that, even without any other cues to our motion, we can keep track of our location (Bremmer & Lappe, 1999; Redlick, Jenkin, & Harris, 2001; Ellmore, & McNaughton, 2004; Harris et al. 2012) as we experience visually-simulated motion through an environment. This differs from heading estimation as instead of simply knowing the direction in which you are heading (for example, forwards or laterally to the left), you are aware of your current location and have to keep track of your location as you move. However, during visually-induced self-motion people make systematic errors depending on the task, with differences occurring when participants are told to reproduce a previously experienced travel distance versus when they are asked to move to the location of a previously presented target (move-to-target task) (Lappe, Jenkin, & Harris, 2007). The motion profile can also affect visual self-motion processing: participants are more accurate during simulated constant acceleration motion compared to when experiencing simulated self-motion of a constant velocity. Lower acceleration or constant velocity optic flow results in a greater overestimation of the motion (participants perceived that they had traveled further) (Redlick, Jenkin, & Harris, 2001).

The location of the motion within the visual field visual field can also impact self-motion perception (McManus, D'Amour, & Harris, 2017). When motion is only provided in the far periphery (eccentricities greater than +-90 degrees) participants require less visual motion to reach a target distance than when it is applied across the full field or in other parts of the visual field. Lastly, the environment itself can influence optic flow, with “richer” or more detailed environments leading to more accurate walking trajectories (Wood, Harvey, Young, Beedie, & Wilson, 2000).

The distance participants need to travel when viewing optic flow to feel that they have passed through a given distance, that is the distance through which they perceive themselves to have traveled, is an indicator of the effectiveness of the visual stimulus in evoking self-motion. If the participant requires less optic flow to perceive that they have passed through a given distance, then the optic flow can be said to be more effective in generating the perception of self-motion than if they needed more optic flow to achieve the same percept. This effectiveness is separate from accuracy, as increased effectiveness of optic flow can lead to overestimating the distance traveled and generate errors in travel estimation.

Overall, the visual stimulus generated by natural self-motion in the real world contains a variety of information that can be used by people to inform self-motion perception. However, during natural self-motion the visual system is only one of several sensory sources of relevant information. Next, I will talk about a system that is specialized to respond to the physical forces generated by self-motion.

## 1.2 The vestibular system

People can also keep track of their self-motion in the absence of vision (Roditi & Crane, 2012; Clark & Stewart, 1968). One sensory system that provides relevant information is the vestibular system (see Yoder & Taube, 2014 for a review of the vestibular system, heading direction, and self-motion/navigation). The vestibular organ is located in the inner ear and responds to accelerations of the head. It is made up of two sets of receptors, the semicircular canals and the otoliths. The semicircular canals are three canals where each respond to a rotational acceleration in one of three roughly orthogonal planes (Löwenstein & Sand, 1940). The otoliths consist of the saccule and utricle, which contain maculae covered in sensory hair cells that are displaced by linear accelerations (Fernandez, Goldberg, & Abend, 1972; Graybiel & Patterson 1955), such as when we accelerate or decelerate forwards or backwards. Of course, they cannot determine the source of this acceleration. This leads to an ambiguity: when the head is tilted back, the displacement of the hairs by gravity is the same as the displacement during translation forward and when the head is tilted forwards the otoliths are stimulated in the same way as by a deceleration.

Both the visual and vestibular system are usually active during self-motion, but each has its own weaknesses. Optic flow cues alone could indicate that we are moving or that the world is moving around us. The visual cue can also be influenced by the task (Lappe, Jenkin, & Harris, 2007), motion profile (Redlick, Jenkin, & Harris, 2001), the location on the visual field (McManus et al. 2017), and the richness of the environment (Wood, et al. 2000). The vestibular signal, specifically the otoliths, on the other hand always indicates accelerations of the self but is ambiguous as to the source of those accelerations which could be self-generated (by walking), passively created (by being carried), or correspond to the acceleration of gravity. A solution to the weaknesses of the visual and vestibular cues is to integrate them together.

## 1.3 Visual-vestibular integration

The ambiguity of the vestibular system poses a challenge when interpreting this system's signal. In order to disambiguate tilt from translation, one solution is to compare the otolith's signal with other information such as the information provided by the semi-circular canals (Merfeld, Zupan, & Peterka, 1999), or the visual system.

Vestibular cues from the semicircular canals can help to interpret ambiguous otolith cues (Merfeld, Zupan, & Peterka, 1999). The semicircular canals are 3 fluid filled canals located in each ear that are oriented such that they respond to dynamic rolls of the head in all directions. If you were to accelerate in a straight line (translate) there would be no activation of the canals, but you would have activation of the otoliths. On the other hand, if you were to pitch backwards there would be both the otolith and canal responses. Purkinje neurons, located in the cerebellar cortex, the outer layer of the cerebellum, respond strongly to translation acceleration but much less to tilt acceleration. This is achieved by using the semicircular canal signal to help interpret the otolith signal. If the semicircular canals are plugged and can no longer detect a rotation, then the Purkinje cells respond equally to tilt and translation (Angelaki & Yakusheva, 2009).

The presence of neurons in the brain that process both visual and vestibular signals (Fetsch, DeAngelis, & Angelaki, 2010; DeAngelis & Angelaki, 2012; Bremmer, Kubischik, Pekel, Lappe, & Hoffmann, 1999; Duffy, 1998; Daunton & Thomsen, 1979) suggests that visual information could be used to help interpret ambiguous acceleration information. Behavioral data also support this idea. For instance, when flying -- especially if there are poor visual cues to orientation -- an accelerating pilot can misinterpret the acceleration of their aircraft as tilt. This well-known effect is referred to as the somatogravic illusion (Tokumaru, Kaida, Ashida, Mizumoto, & Tatsuno, 1998; Clément, Moore, Raphan, & Cohen, 2001) (see Figure 1.1). However, informative visual cues, such as a view of the horizon, can reduce the occurrence of the somatogravic illusion (Tokumaru et al. 1998).

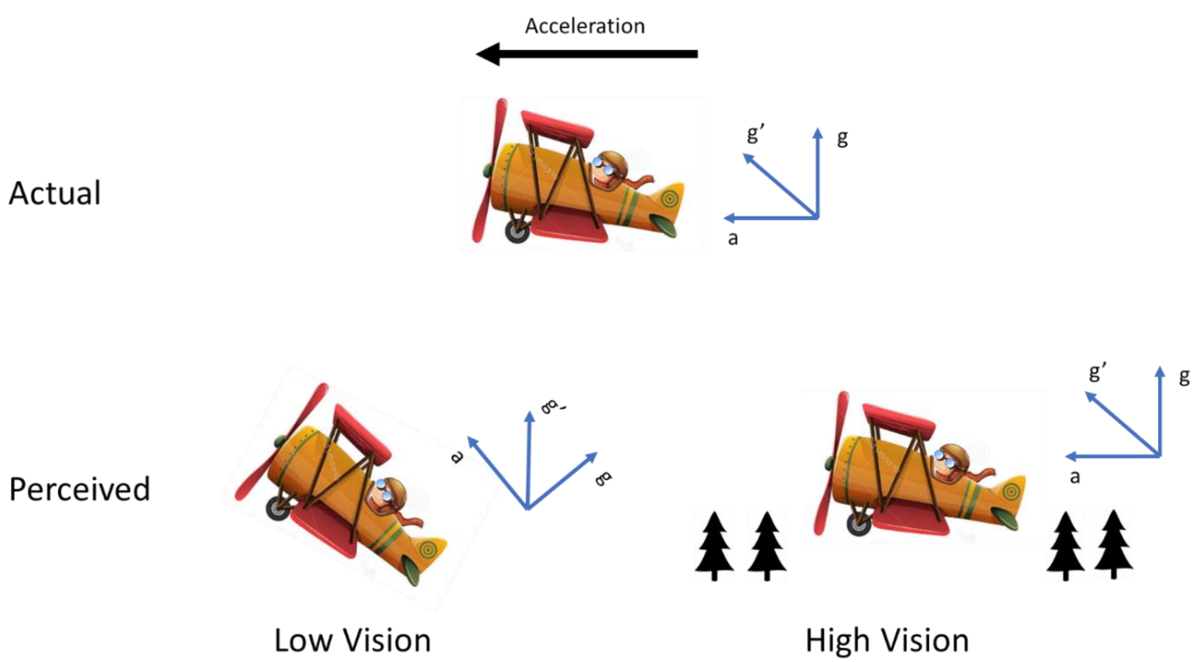



*Figure 1. 1* A diagram depicting the somatogravic illusion. The top row is the actual experience of the pilot who is accelerating forwards in their airplane. The second row shows the perceived tilt of the pilot in either a low vision condition, such as not being able to see the horizon or the ground below them, and a high vision condition where they have access to these visual cues.

When we move, we generate and take in potentially redundant information, all of which may be used together to process our experience. Combining multiple senses together into one coherent interpretation is referred to as multisensory integration (Laurienti, Burdette, Maldjian, & Wallace, 2006). One method that has often proved successful in modelling how the senses are combined is Bayesian integration where what we perceive is based on the average of the sensory cues after each cue is weighted by its reliability and any priors, or baseline assumptions, are taken into account (ter Horst, Koppen, Selen & Medendorp, 2015; Adams, Graf, & Ernst, 2004; Ernst, & Banks, 2002). The reliability is how precise (or noisy) our estimate from a particular cue is. Multisensory integration is often beneficial and can result in enhancements to behaviour (such as reaction time) and perception compared to responses to either of the two unimodal stimuli alone (Forster, Cavina-Pratesi, Aglioti, & Berlucchi, 2002; Laurienti, et al. 2006).

Combing different cues allows us to have a more accurate representation of our body in space as we move. Different models have been developed in an attempt to determine how we combine different sensory cues and planned motor commands (Laurens, & Angelaki, 2017; Merfeld, Zupan, & Peterka, 1999). It is believed that the brain, or more specifically, the cerebellum, uses information provided by the senses in order to dynamically estimate the consequences of our behaviour during an action (see Cullen, 2019 for a review). The difference between the predicted estimates and the actual experience results in an error signal that is used to recalibrate our perception or behaviour (Cullen, 2019; Laurens, & Angelaki, 2017; Merfeld, Zupan, & Peterka, 1999). For instance, during a rotation, the semicircular canals, being sensitive only to angular acceleration, only provide relative information -- changes to our current position or orientation. Integrating semicircular canal information with otolith information (Merfeld, Zupan, & Peterka, 1999) or extra-vestibular cues such as visual or somatosensory (Lackner, & DiZio, 2005), as well as prior information (such as from the hippocampus: Iaria, Petrides, Dagher, Pike, & Bohbot, 2003), allows us to more accurately predict the consequent changes to our orientation during a roll. The goal of our behaviour (Roy & Cullen, 1998), as well as the frame of reference also helps us to maintain an accurate representation of our orientation (Cullen, 2019). A reference frame is the system in which a particular sensory signal is coded, for instance the semicircular canals provide head-centered information. Goal-directed behaviour can be in various reference frames, for example, scratching an itch needs the stimulus and response to be coded in body coordinates, whereas throwing a baseball requires information to be coded in an external, allocentric frame.

Combining cues is an excellent strategy when all the cues provide an estimate of the same thing. However, there may be times when the cues conflict and provide very different estimates in which case, it might not be appropriate to average them. The next section deals with visual-vestibular conflict and how we might handle a conflict by reweighting or reinterpreting the cues.

## 1.4 Reweighting or Reinterpreting

Our senses are not always in agreement and sometimes the information provided by one cue conflicts with that signaled by another cue. In the cases of cue conflict, people are able to dynamically reweight the emphasis put on each cue based on a reliability estimation (Fetsch, Turner, DeAngelis and Angelaki, 2009). Fetsch et al. (2009) found that when making heading judgements with optic flow and vestibular cues mismatched, both people and monkeys could dynamically reweight visual and vestibular cues according to their reliability. However, they also found that in some cases the vestibular cue was given a higher weight than expected based on the predictions of a Bayesian model. Fetsch et al. (2009) argued that their participants might have resolved the mismatch between the visual and vestibular cue using causal inference: that is by deducing the cause of the various cues and integrating them based on the likelihood that they had the same cause (Körding, Beierholm, Ma, Quartz, Tenenbaum, & Shams, 2007; Shams, & Beierholm, 2010; Fetsch, Turner, DeAngelis, & Angelaki, 2009). While it is possible that visual motion came from a source other than the person's own motion, such as from external motion, the vestibular cue has no such ambiguity regarding its source – it can only come from physical acceleration of the head - making the vestibular cue the more reliable of the two. Fetsch et al. (2009) argue that the imbalance in the certainty between the two cues may have produced the vestibular over-weighting that they observed.

In some cases, such as with a large conflict in the sensory cues, a person may have to rely more on one cue, perhaps even to the point of completely suppressing or ignoring the other sense. With vection for example, vision indicates that you are moving, but the vestibular system indicates you are not. We might expect that during vection there would be a suppression of the vestibular cue, though this might depend on the motion profile used, with constant velocity (to which the vestibular system is insensitive) leading to a suppression of the now completely uninformative vestibular areas (Brandt et al. 1998), while acceleration (where both signals are active) might lead to co-activation (Nishiike et al. 2002). Adding a jitter – a constant random horizontal or vertical accelerations similar to a shaky camera (Palmisano, Gillam & Blackburn, 2000) -- to the motion also enhances visual self-motion which supports the suggestion that the perception of vection might be due to a co-activation of the visual and vestibular areas (Palmisano, Allison, Kim & Bonato, 2011).

The visual cues available to us could also lead to changes in the interpretation of the ambiguous vestibular cue, similar to the somatogravic illusion or an inverse somatogravic illusion where when tilted people may feel as if they are moving. In a paper by Crane (2014), participants' heads and bodies, or just their head, were tilted backwards or forwards by 10 degrees while they were on a motion platform (MOOG). For each trial, the platform would move them upwards or downwards and their task was to indicate the direction of motion that they experienced. When participants were tilted back, they perceived a movement backwards of 2.2 cm/s/s as stationary, indicating they might feel some forward motion that needed to be cancelled. Similarly, while tilted 10 degrees forwards, a motion of 3cm/s/s was more likely to be perceived as static, indicating they felt some backwards motion. In both cases, when standing upright on the motion platform with only their neck bent by 10degrees forwards or backwards the effects described above were not seen.

Crane (2014) suggested that when the head is in line with the body, vestibular cues may be interpreted as translation and not as tilt (the inverse somatogravic illusion). Providing additional cues to tilt through neck muscles could then minimize this misinterpretation by reinforcing the interpretation of tilt. Additionally, the body's other gravity sensors, such as those in the kidneys (Oman, 2007; Mittelstaedt, 1996), could also provide information regarding tilt or lack of tilt during neck bends. So, when only the neck is tilted, the body receptors will not respond, unlike when the body and head are tilted together. If only the head is indicating an acceleration this might suggest that the observer is not translating since your head cannot translate far without the rest of your body.

During a sensory conflict, such as during vection, cues may be dynamically reweighted to help resolve the conflict with one cue being down weighted or even ignored in favour of another cue. However, an ambiguous cue like the vestibular cue could also be reinterpreted. In the Crane (2014) paper a tilt relative to gravity lead to changes in physical self-motion perception. The next paragraph looks at how gravity can affect a person's visual self-motion perception.

### 1.5 Gravity and visual self-motion perception

Based on the literature reviewed above we might expect that tilting a person relative to the gravitational upright might affect the perception of vection, however findings have been inconsistent (Nakamura & Shimojo, 1998; Guterman, Allison, Palmisano & Zacher, 2012; Young & Shelhamer, 1990). Different aspects of vection appear to be differently affected by body tilt and by the direction of the visual motion. For instance, how long the sensation of vection lasts between dropouts (periods when vection sensation stops) differs depending on body position and direction of motion. Vection duration has been found to increase the greater the body tilt is from upright but only during vertical visual motion with no change for vection duration during horizontal visual motion during body tilt (Nakamura & Shimojo, 1998). The onset time for vection has been found to be increased while standing for forward linear motion relative to when tested prone (Guterman, Allison, Palmisano & Zacher, 2012) or reduced while standing relative to when supine (Tovee, 1999). Others have found no difference (Kano, 1991). Lastly the magnitude, or the strength of the sensation of vection also appears to be affected by body position. The magnitude of vection is weaker when prone versus sitting although no difference in magnitude was found between supine and sitting or supine and prone for forward vection (Guterman et al. 2012).

The ultimate test of whether gravity has an effect on visual self-motion is to remove gravity altogether. The loss of gravity results in dramatic changes to the functioning and responsiveness of the vestibular system. For instance, the otoliths no longer respond to head tilt when there is no gravity for the hair cells to be displaced relative to, but they will respond to acceleration induced by linear translation (Buckey & Homick, 2003).

Since the otoliths in space are now exclusively stimulated by linear acceleration, it has been proposed that following adaptation to this environment and return to Earth, a tilt of the head might be incorrectly interpreted as translation (Merfeld, 2003). While there has been little hard evidence to support this Otolith Tilt Translation Reinterpretation (OTTR) hypothesis, Parker, Reschke, Arrott, Homick and Lichtenberg (1985) found that participants who use a swing and then had to draw they path through which they moved drew their arc as expected before exposure to microgravity but post flight, two of the participants drew a mixture of an arc and translation. In addition to this, for approximately 3hrs after returning from 0g around 90% of astronauts report perceived self or world translation after making sinusoidal head movements (Harm & Parker, 1993).

If the OTTR hypothesis is correct, then, after adaptation to microgravity, and subsequent return to Earth, centrifugation should be interpreted as translation and not as a tilt like it is usually interpreted. As part of the Neurolab 1998 mission Clément, Moore, Raphan, and Cohen (2001) centrifuged four astronauts in the dark on Earth, several times during 16 days in microgravity, and again after returning to Earth. Centrifugation of 1g on Earth while upright and rotating with either the left or right ear out produced a sensation of roll of 45 degrees. This perceived 45-degree tilt is due to the gravity cue and the inertial force being vector summed, resulting in a tilt half-way between the two. In microgravity this roll tilt should feel closer to 90 degrees because of the low gravity vector. Clément et al. (2001) found that initially upon entry into 0g, the perceived tilt was closer to 45 degrees but by day 16 the tilt was perceived close to 90 degrees. They hypothesized that early in flight the body cue was still inhibiting the perceived tilt and that over time the body vector's weight was decreased and thus the perceived tilt angle was increased. The extent of the perceived tilt was quickly reduced upon returning to Earth and by the fourth day after return, the perceived tilt was back in line with the pre-flight perceived tilt levels. Clément et al. (2001) state that at no point did participants report perceived translation. The results in the Clément et al. (2001) paper do not support the OTTR hypothesis. However, Parker argued that long-duration microgravity experiments have found that after adaptation to microgravity astronauts do misperceive tilt as linear acceleration (Parker 2003).

While the interpretation of the vestibular cue post-flight is still somewhat debated, in microgravity there appears to be an increase in the sensitivity to linear visual motion (Oman, Howard, Smith, Beall, Natapoff, Zacher & Jenkin, 2003). Oman et al. (2003) looked at how the visual cue was affected by the removal of gravity by comparing how vection onset latency and the perceived velocity of vection were affected when gravity was removed. Even during constant velocity induced vection there is an initial acceleration of the stimulus from 0 (no visual motion) to the constant motion. On Earth, this results in a temporary conflict between the vestibular cue (indicating no acceleration) and the visual cue, which might delay the onset of vection. In microgravity, with the loss of gravity participants might have learned to rely more on the visual cue, which these authors argue should reduce this conflict leading to a reduced vection onset latency. The increased weight given to the visual cues should also result in vection being more compelling and being perceived as faster. Compared to on Earth the vection latency was indeed lower in 0g, and the perceived velocity was higher. They also collected verbal reports of the vection experience, where the reports seemed to strongly indicate an enhancement to vection in microgravity. This suggests that the removal of the gravity cue leads to an increased sensitivity to our perception of visual motion information.

From the literature reviewed, gravity affects how we perceive self-motion where tilting people on Earth leads to changes in the perception of visual self-motion depending on posture, direction of motion, and what is being measured. Removing gravity appears to lead to an increased sensitivity to visual self-motion, perhaps suggesting an increase in the visual weight. The next section looks at how participants' interpretation of the visual scene and representations of gravity might also play a role in self-motion perception.

## 1.6 Participants perceived experience during self-motion tasks

Much of the research on tilt vection reviewed above finds that any potential effects of the vestibular cue on vection differ based on posture, direction of motion, and what is being measured. However, few studies take into account how the participant actually perceives themselves within their environment. Differences in participants' interpretation of the visual scene might affect how they interpret visual and/or vestibular cues. For instance, viewing optic flow toward the face while supine is consistent with moving gravitationally upwards, whereas viewing motion towards the face while prone is consistent with moving gravitationally downwards. We know that people incorporate a representation of gravity when interpreting object motion. While standing people remember the final location of a moving target as further down when the movement was gravitationally downwards but show no biases for upwards motion (Hubbard & Bharucha, 1988; Nagai, Kazai, & Yagi, 2002), or for motion towards or away from the face (Nagai et al. 2002). This displacement in remembered object location is also found while prone and viewing an object with receding motion (away from the face) but not for approaching motion or for motion along the longitudinal body axis (Nagai et al. 2002). Nagai et al. (2002) concluded that the displacement from accurate perception occurs along the environmental axis (gravitationally down) as opposed to an egocentric axis (towards the feet). If people were to incorporate a representation of gravity when judging object motion, then it might also be the case that similar biases might exist with self-motion perception. A participant who views their self-motion as "falling" may experience self-motion differently than someone who feels they are moving forwards. These higher-level cognitive expectations or representations could potentially lead to changes in the perception of the magnitude of displacement caused by vection.

In fact, Guterman and Allison (2019) found that when upright and viewing vertical vection in a tubular environment, the perception of vection was enhanced compared to when upright in a bubble environment. There was no difference while tilted. While upright in the tube environment the authors state that participants reported an experience like being in elevator but did not experience this while tilted or in the bubble environment. This suggests that the participants' experience, or their interpretation of the environment effected their experience of vection.

How we perceive or interpret our environment and the motion cues within it, plays a role in how we might use visual and vestibular cues, or at least how we might perceive our self-motion. The next section looks at how our perception of ourselves within an environment might affect our use of visual and vestibular cues.

## 1.7 Perceived orientation

How we perceive our orientation is dependent on how we perceive our self, relative to our environment. In our day-to-day life we use a variety of cues provided by our environment to determine which way is up. The direction of gravity- sensed through the vestibular system - provides a constant up. Our body provides another up in which the top of the head is taken as being at the top (the "idiothetic vector", Mittelstaedt, 1996), and pressure on the body at the support surface can also inform us to our orientation (Horak, Nashner, & Diener, 1990). Vision provides an obvious cue to up through polarized cues, objects that have a visually defined up such as trees or dogs, or through contextual cue like a book lying on a table (see Howard 1982 for a review).

The potentially different directions of up provided by these cues are fused together to help us determine where "up" is, with the relative contributions of the senses differing depending on what kind of "up" we are measuring. For instance, our perceived direction of gravity, which might be measured with a task like "which way a ball would fall" is referred to as the Subjective Visual Vertical (SVV). Another measure of "up" is the Perceptual Upright (PU), which is the orientation at which things look upright or are most recognizable (Dyde, et al. 2009). The directions of both the SVV and the PU are well modeled as a weighted average of the directions of the body, the visual environment, and gravity. The SVV relies more on gravity compared to the other senses, while the contributions to the PU are more evenly balanced in comparison and, importantly, can still be measured without gravity present (Dyde et al. 2006).

An experiment by Harris, Jenkin, Jenkin, Zacher & Dyde (2017) looked at the contributions of vision, the body, and gravity in determining PU while on Earth compared to the ratio given to vision and body cues during the 0g phase of a parabolic flight. They found that the weighting of the visual cue did not seem to increase upon entry to 0g, instead, it appears that the idiotropic vector (body) becomes more important relative to vision (Harris, Jenkin, Jenkin, Zacher, & Dyde, 2017). However, static and dynamic cues to orientation may differ in their effectiveness. When a dynamic background environment (such as people walking around an office) was used instead of a static background (a still frame of the dynamic background) the contribution of vision was higher compared to the static background on Earth. With the dynamic background there was a tendency towards a higher visual weight during the 0g phase of the parabolic flight (Cheung, Howard, & Money, 1990; Jenkin, Zacher, Dyde, Harris, & Jenkin, 2011).

In environments that do not have independent ‘down’ cues, such as in 0g, “up” becomes subjective. Visual Reorientation Illusions (VRIs) can occur where the subjective identity of surfaces such as ‘floor’ vary based on where the viewer’s attention is focused (Oman, 2007). For instance, if a person is oriented such that they perceive the ground as below their feet they will feel upright, however if another person floats in sideways in Space a VRI can occur in which they suddenly reorient based on the orientation of the new person. The original person can then feel that they are now tilted sideways and that the other person is upright (Oman, 2007).

On Earth VRI experiences can occur when the “visual up” differs from the “gravity up”. People who have a VRI on Earth could be lying on their backs but feel as if they are standing upright. Howard and Hu (2001) found that people tend to reorient themselves based on the visual cues in the environment though VRIs are most likely to occur when the body and visual upright are aligned and inconsistent with gravity. They argued that on Earth, VRIs occur by ignoring the conflicting gravity cues in favour of visual cues (Howard & Hu, 2001) suggesting that the VRI on Earth is a resolution to visual and vestibular conflict in which the visual cues are prioritized. With an increased emphasis on vision, we might expect changes in our experience of visual self-motion similar to the enhancement seen in microgravity environments (Oman et al. 2003).

## 1.8 Main Arguments

How we interpret our environment, or ourselves within our environment, might lead to changes in our use of visual and vestibular cues, such as cues to self-motion, however few studies have taken higher level cognition into consideration. I argue in this dissertation that the presence of VRIs on Earth may provide an explanation for some of the discrepancies in the past literature on the effect of tilt on self-motion perception.

In vection experiments done on Earth, if no VRI occurs, this would indicate that the person has an accurate perception of their simulated motion through an environment. For instance, if a person were supine and viewing a plane surface passing through their feet then movement along this surface could be interpreted as going up relative to gravity, perhaps similar to feeling like Spiderman walking up a wall. However, with a VRI where a person is supine but perceives themselves as standing, they would interpret motion along this surface as forwards motion such as moving along a road (see Figure 1.2).

On Earth when there is a conflict between the gravity up and the direction of up indicated by visual information based on the studies reviewed above, this might result in changes in the use of visual information relative to other cues and could lead to the experience of a VRI. I argue that when VRI's are deliberately induced in tilt experiments, we will see differences in a person's processing of visual self-motion consistent with an increased weighting of vision (e.g., increased perceived velocity, increased perceived distance travelled etc..), compared to situations in which no VRI is induced and the direction of gravity is correctly perceived. However, it could also be the case that a VRI would not result from a higher visual weighting but could instead result from misinterpretations of the vestibular cue, similar to an inverse somatogravic illusion like in Crane (2014). If a person were tilted and the visual environment indicated that they were standing they would still have a vestibular signal. The presence of a VRI would indicate that they have not interpreted the vestibular cue as a tilt, in which case they might have misinterpreted the tilt cue as translation. We would expect that while supine the reinterpreted acceleration would aid self-motion perception, while when prone it would hinder self-motion perception.

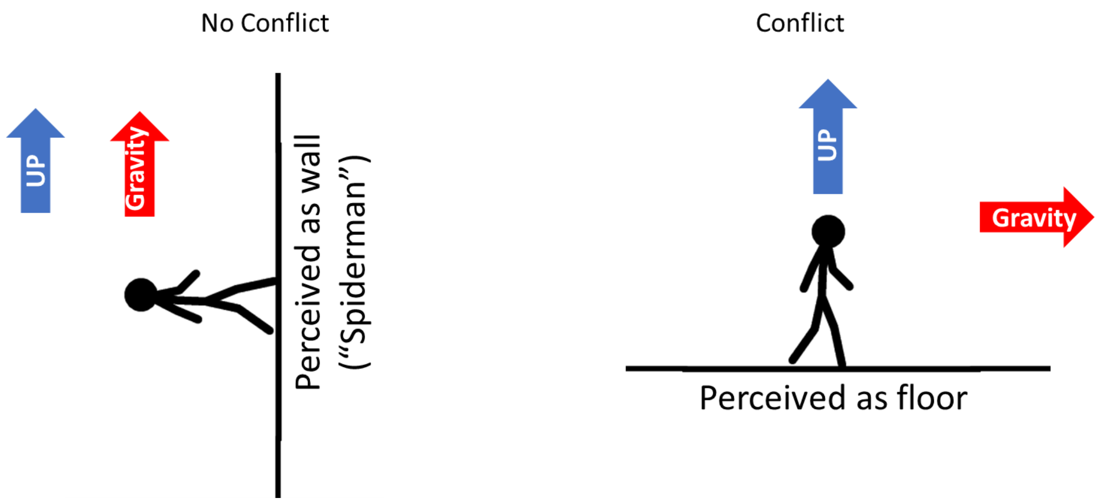



*Figure 1. 2* This image compares the perception of a person tilted supine looking forwards with a surface beneath their feet without a VRI (left image) or with a VRI (right image). Blue arrows are the visual upright and red arrows are the gravity upright. In the no VRI image the person's visual up is not in conflict with gravity up and they would perceive themselves with their feet on a wall. In the VRI condition the person perceives themselves as upright and standing on a floor. In this case the visual upright would be in conflict with the gravity upright

## 1.9 Aims of this dissertation

This dissertation explores how changes in our use of gravity might potentially affect changes in the emphasis put on vision and aims to help explain some of the previous conflicting literature on vection. If a VRI were to be induced in virtual reality on Earth, it might be caused by people ignoring non-visual cues to true gravity (Howard & Hu, 2001). Changes in the relative use of visual and non-visual information and an increased sensitivity to visual information may then result in changes in self-motion perception.

To investigate this, I performed a series of experiments where I compared the effectiveness of processing optic flow while manipulating either the perceived visual upright (relative to gravity) and/or the gravitational upright (relative to the body).

Chapter 2 describes three experiments that compare the effectiveness of optic flow when visually simulating moving to the location of previously seen targets presented at different distances in virtual reality (the move-to-target task) while the head and body, or just head are tilted, with the effectiveness of optic flow when standing upright. I compared the effect of a polarized hallway environment to that of a less polarized starfield environment.

In Experiment 1, I compared optic flow effectiveness while supine and prone compared to standing in a VR hallway that induced a high rate of VRI. I hypothesized that:

(1) a VRI will lead to partially reinterpreting gravity as linear translation, where a supine posture would support the visual motion (leading to enhancement compared to standing)

(2) a prone posture would oppose the visual motion and would lead to a deficit compared in the use of visual motion compared to standing.

In Experiment 2, I reduced the level of conflict between the visual, body, and gravity "up" by tilting the head, which should reduce the amount of VRI experienced. I hypothesized:

(3) There will be a reduction in any optic flow enhancement or deficit seen in Experiment 1.

In Experiment 3, I compared the effectiveness of a polarized environment (hallway) with that of a non-polarized environment (starfield). I hypothesized:

(4) The hallway will lead to a high rate of VRI and the enhancement seen in Experiment 1 and

(5) the starfield should not.

From the experiments in Chapter 2 I found that, generally, as the likelihood of experiencing a VRI increased the effectiveness of optic flow increases in both a supine and prone posture relative to standing. This suggests that in situations where there is a conflict between the visual up and the gravity vector, people might ignore the gravity vector in favour of vision, leading to higher visual weightings. Individuals with an increased visual weight would require less visual motion in order to feel they had passed through an indicated target distance. In the next 2 chapters I investigated how the visual weight might be affected during a VRI and if similar results were obtained on a move-to-target task when gravity is removed instead of just ignored.

In Chapter 3 I looked at relative weightings provided by vision, the body, and gravity when determining the perceptual upright and compare between VRI sensitive people and VRI insensitive people. Since a VRI on Earth results from a dominance of visual cues over gravity cues and based on the results of Chapter 2, VRI sensitive people should have a perceptual upright that is more influenced by vision compared to VRI insensitive people. I hypothesize that

(6) individuals who report a VRI will require less visual motion to perceive that they have passed through a previously seen target distance in virtual reality than those who do not report a VRI and

(7) that individuals who report a VRI will have a higher visual weight contributing to their PU than those who do not report a VRI.

Chapter 4 compared the effectiveness of optic flow during a move-to-target task on Earth and in microgravity. If a VRI results in reweighting the visual cue due to ignoring the gravity vector we might then expect that removing gravity should similarly impact optic flow use. I hypothesize that

(8) compared to on Earth, early exposure to microgravity will lead to participants needing less visual motion to perceive that they have passed through a previously seen target distance, suggesting an increased visual weight in 0g compared to on Earth.

# CHAPTER 2: When gravity is not where it should be: How perceived orientation affects visual self-motion processing

*This chapter has been submitted to the journal Plos One where it is currently under review. I am the first author on the paper and Dr. Harris is the second author.*

*My contributions to the paper include designing the experiments, programing the tasks, writing up the ethics forms, running pilot tests, testing participants, analysing and interpreting the data, and writing up the paper.*

*Dr. Harris's contributions include helping with the design of the experiments (such as discussing the background literature and discussing the rational of the tasks), providing feedback on the experimental tasks, providing feedback on the interpretations of the results, editing and providing feedback on all written work, and updating the ethics forms. Dr. Harris also designed Figure 2.3.*

## 2.1 Abstract

Human perception is based on expectations. We expect visual upright and gravity upright, sensed through vision, vestibular and other sensory systems, to agree. Equally, we expect that visual and vestibular information about self-motion will correspond. What happens when these assumptions are violated? Tilting a person from upright so that gravity is not where it should be impacts both visually induced self-motion (vection) and the perception of upright. How might the two be connected? Using virtual reality, we varied the strength of visual orientation cues, and hence the probability of participants experiencing a visual reorientation illusion (VRI) in which visual cues to orientation dominate gravity, using an oriented corridor and a starfield while also varying head-on-trunk orientation and body posture. The effectiveness of the optic flow in simulating self-motion was assessed by how much visual motion was required to evoke the perception that the participant had reached the position of a previously presented target. VRI was assessed by questionnaire. When participants reported higher levels of VRI they also required less visual motion to evoke the sense of traveling through a given distance, regardless of head or body posture, or the type of visual environment. We conclude that experiencing a VRI, in which visual-vestibular conflict is resolved and the direction of upright is reinterpreted, affects the effectiveness of optic flow at simulating motion through the environment. We discuss potential mechanisms for this such as reinterpreting gravity information or altering the weighting of orientation cues.

## 2.2 Introduction

As we move about the world our senses keep track of our body's location and orientation in space. One of these senses is our vestibular system, which helps determine our head's orientation and movement. Within our vestibular system are the otoliths, which indicate linear acceleration. Tilting the head backwards or forwards relative to gravity displaces the hairs on the macula of the utricle of the otolith system in the same way as forward or backwards acceleration, respectively. This tilt-translation ambiguity poses a challenge to the brain to resolve the otolith's signal into components due to gravity and to self-motion. One way it might be resolved is to compare the otolith's signal with other information such as visual (Tokumaru, Kaida, Ashida, Mizumoto, & Tatsuno, 1998), vestibular canals (Angelaki & Dickman, 2003) or somatosensory cues (such as pressure on the feet while standing) (Horak, Nashner, & Diener, 1990; Hunt, Knox, & Oginski, 1965). Additionally, motion sensitive neurons in the brainstem and cerebellum (with information provided by the otoliths and semicircular canals) may also help to disambiguate tilt and translation by using their patterns of activity to construct an internal model of our movement (Angelaki, Shaikh, Green, & Dickman, 2004). Additionally, there is also an assumption, or prior, that the top of the head is "up" (Mittelstaedt, 1983) which may also contribute. Without such additional information, tilt and self-motion acceleration can be confused. For instance, when pilots accelerate, the plane's acceleration can be misinterpreted as tilt: a perception known as the somatogravic illusion (Clément, Moore, Raphan, & Cohen, 2001; Tokumaru et al. 1998). The presence of visual information, such as a view of the horizon and the visible relative motion of the ground, can reduce the occurrence of this illusion (Tokumaru et al. 1998) by disambiguating the vestibular cue. Such observations illustrate the interaction between visual and vestibular cues that is necessary to interpret self-motion and orientation cues. Here, we investigate how visual cues to orientation such as a view of the horizon, might affect the perception of visually induced self-motion.

In microgravity environments, astronauts' perceived orientation is necessarily based exclusively on visual and body cues. Astronauts might orient themselves by regarding the area below their feet as the floor, or by using landmarks. However, when faced with a polarized object such as a co-worker in a different orientation, or when moving into a new cabin, astronauts can experience a shift in their perceived orientation in which they reinterpret where they perceive up to be. This reinterpretation of "up" -- based on visual cues -- is called a visual reorientation illusion (VRI) (Oman, 2007).

VRI's can also be experienced on Earth in a specially constructed tilted room, using a mirror bed (Howard, Hu, Saxe, & James, 2005) or in virtual reality. If a person lies supine in a 90-degree-tilted room, such that the polarity of the objects and decorations of the room indicate that they are actually upright, 84% of people will experience a VRI and feel that they are upright (Howard & Hu, 2001) even though gravity is providing cues that they are horizontal (Figure 2.1). A mirror bed, with a cleverly arranged mirror at 45°, achieves the same thing (Howard et al. 2005).

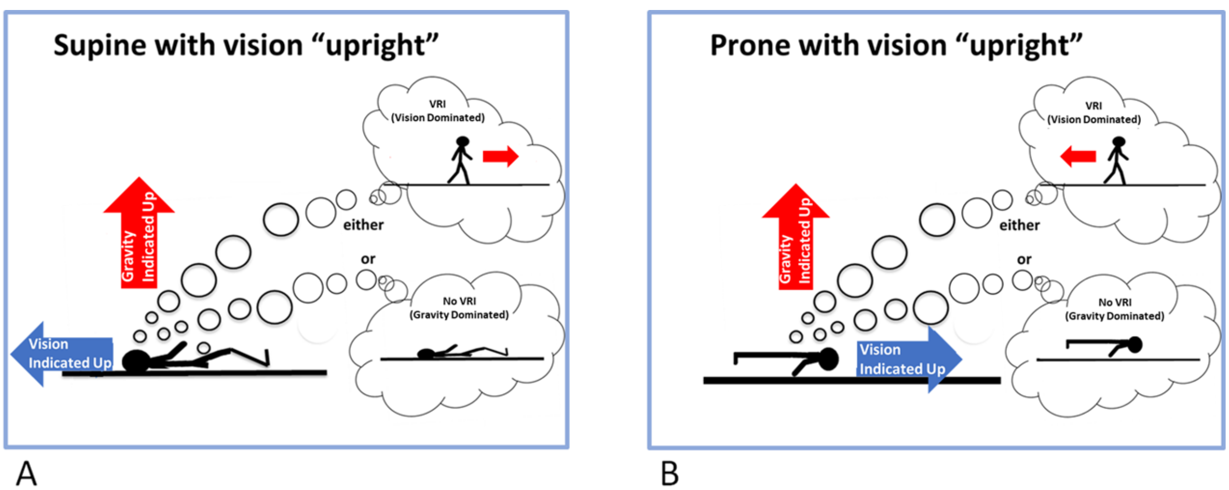



*Figure 2. 1* A person lying down in an environment that has visual cues indicating one upright (blue arrow) and gravity cues indicating another upright (red arrow). The arrows point in the direction of up signaled by each cue. In (A) the person is supine and in (B) they are prone. If the visually-indicated upright were to dominate, the person would experience a visual reorientation illusion (VRI) and perceive themselves as upright (top thought clouds). If gravity cues were to dominate, they would perceive themselves supine or prone (bottom thought clouds). During a VRI (top clouds) the acceleration of gravity would be parallel to the perceived support surface.

If a person were tilted but believed that they were upright – that is, they were experiencing a VRI -- how might they interpret the still-present vestibular and somatosensory cues consistent with a different body orientation? If the person were to correctly perceive themselves as supine, they should simply interpret the vestibular signal as confirming this. However, with a VRI it is clear the person is not interpreting the vestibular cue as indicating tilt. One possibility is that under some conditions the vestibular acceleration cue might be at least partially reinterpreted as translation (Figure 2.1, top thought clouds). Crane (2014) found that tilting a person's head and body by 10 degrees forwards or backwards affected how they perceived a physical motion stimulus. The participants in Crane (2014)'s study were seated on a moving platform and were moved in the fore-aft direction, with a control condition in which there was no movement. The participants had to indicate in which direction they thought they had moved. When a participant's head and body were tilted back and they were translated at a velocity of 1.4 ± 0.7 cm/s backwards, they perceived themselves as stationary. Similarly, when tilted forwards and translating at 1.9 ± 0.5cm/s forwards they again interpreted the motion as corresponding to them being static. Then, when participants were tilted backward, they perceived a static condition as forwards motion and vice versa when tilted forward. These results suggest a possible misinterpretation of the gravity cue while tilted as indicating translation. However, tilting only the head did not bias their perception of motion. Crane (2014) suggested that the neck muscles that were activated during head tilt might help to minimize any tilt-translation confusion so that only when the head and body were tilted together would the person interpret the vestibular signal as translation.

When upright, seeing visual cues consistent with forwards self-motion can be enough to evoke the sensation of self-motion, a phenomenon known as vection (Brandt, Dichgans, & Koenig, 1973; Mach, 1875) even though the vestibular signal indicates no physical acceleration. People are able to use the visual cues alone to update their sense of location as they experience simulated motion through an environment (Harris et al. 2012; Lappe, Jenkin, & Harris, 2007; McManus, D'Amour, & Harris, 2017; Redlick, Jenkin, & Harris, 2001). However, while supine and viewing visual motion consistent with forwards self-motion (relative to the body), the acceleration of gravity is now in a direction aligned with the visual motion. If gravity were to be interpreted as a physical acceleration, we might expect an enhancement of the visual motion cues in simulating the experience of movement through the environment, in which a given amount of visual motion might make them feel they were going faster and further (Figure 2.1A). Similarly, while prone the acceleration of gravity would oppose the visual motion which might make them feel they had travelled less far (Figure 2.1B). We will refer to this as the “additive hypothesis”. Previous studies have found conflicting evidence as to whether tilting a person affects the perception of vection (Guterman, Allison, Palmisano, & Zacher, 2012; Nakamura & Shimojo, 1998; Tovee, 1999). It appears that changing body orientation (upright, prone, supine relative to gravity) and the direction of visual motion (forwards, backwards, upwards or downwards relative to the viewer) impacts the interpretation of motion that depends on which aspect of vection is being measured (e.g., onset, duration, or magnitude), but even for a single metric, results differ across experiments (see Kano, 1991).

Additionally, cognitive factors such as the perceived context of the visual motion might influence the interpretation of self-motion (e.g., Riecke, 2009; Seno, Ito, & Sunaga, 2011; Seno, Abe, & Kiyokawa, 2012; Seno, Palmisano, Riecke, & Nakamura, 2014). For instance, Guterman and Allison (2019) found that vertical vection in an environment made of tubular pipes enhanced vection compared to when participants were in a bubble environment, but only if participants were upright: no difference in vection was found when the participants were tilted. The authors state that during debriefing their participants reported that while upright in the pipe environment they felt as if they were in an elevator but did not experience this while lying down or in the bubble environment. This suggests that it was not posture per se that led to the changes in vection experience, but instead the participants’ “experience” of the environment which lead to changes in vection. We will refer to this as the “cognitive hypothesis” which makes no explicit prediction about the effect of having a VRI on the effectiveness of visual motion, merely that an effect will occur. Guterman and Allison’s (2019) study was unusual in asking their participants about their perceived experience. Most previous studies have not allowed for the possibility that participants may be interpreting the presented visual environments differently. This could explain some of the conflicting findings in the literature.

In order to address these issues, we manipulated people’s physical and perceived body orientation while they completed a move-to-target task (MTT). The MTT provides a way of quantifying the perceived motion relative to the environment induced by optic flow. Performance on the MTT was compared in three separate experiments using two visual environments (see Figure 2.2). In Experiment 1 participants were standing, or lying supine or prone, and were placed in a virtual reality environment with cues indicating that upright was always towards the top of the head (Figure 2.2 A, B), for instance the light always came from above the participants head, the target and walls rested on a floor surface which was positioned beneath the participants’ feet, and there was a horizon. We expected this environment to induce a VRI while tilted. We hypothesized that a participant experiencing a VRI may then at least partially reinterpret gravity as linear translation. Within this virtual world, participants were visually accelerated at 9.8m/$s^2$ (1g) forwards. The visual motion profile was chosen to match the gravitational cue in magnitude to make the visual and gravitational cues more likely to be confused and thus to increase the likelihood that participants might misinterpret the vestibular cue as visual motion.

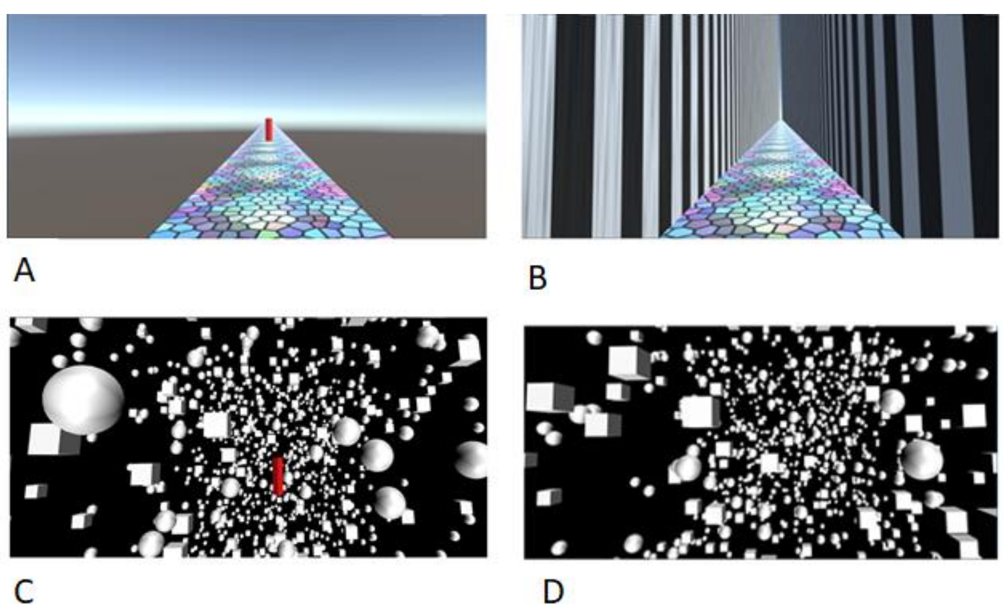



*Figure 2. 2* Screen captures of the hallway environment (A and B) and the starfield environment (C and D). A and C are what the scenes looked like before movement while the target (vertical red line) was visible and the walls were invisible, B and D are what the scenes looked like once the participant had clicked the left mouse button and the optic flow started to simulate motion

down the hallway. The hallway environment was used in Experiments 1, 2, and 3, the starfield environment was used only in Experiment 3.

If participants who had a VRI partially reinterpreted gravity as linear translation then, when the directions of visual acceleration and gravity were in the same direction (Figure 2.3 A, C, E), the stimuli should enhance each other, and the participant would need less visual motion to simulate that they had passed through a given distance compared to when not experiencing a VRI. Contrariwise, when the directions of the visual acceleration and gravity were opposed (Figure 2.3 B, D, F) the stimuli should oppose each other, and the participant would need more visual motion: the "additive hypothesis". In this case, the experience of gravity would be the reaction to the downward force of gravity such that when lying supine on a surface, our participants experienced pressure on their backs (or fronts while prone) equivalent to that produced if the bed were accelerating upwards at 9.8m/s/s; in physics this is referred to as the "normal force".

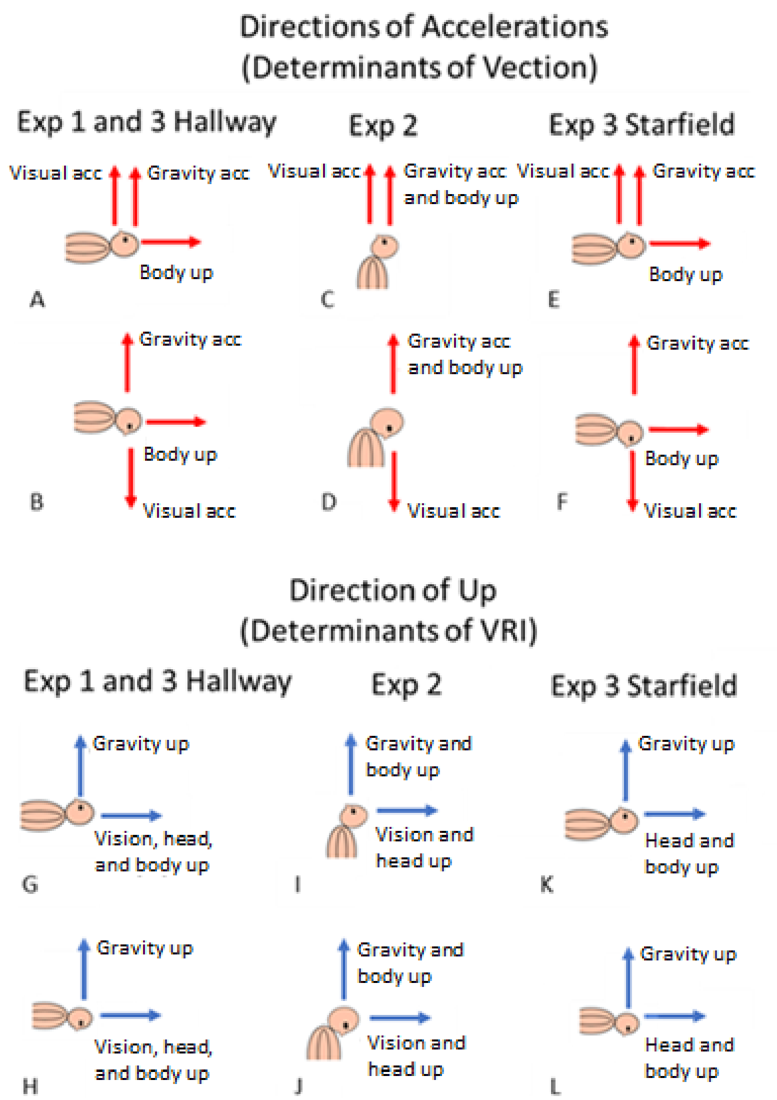



*Figure 2. 3* How gravity and vision (top panel) and perceived up (bottom panel) are affected by body and head posture. The red arrows in the top panel (A-F) show the visual and gravitational accelerations experienced by the participant in the same body postures as in the bottom panel G-L. When looking up (A, C, E) the direction of the visually simulated self-motion is in the same direction as the reaction to the gravitational acceleration; when looking down they are opposed (B, D, F). The bottom panel G-L shows the contributions to the cues to upright (blue arrows) while wearing a VR HMD with visual cues consistent with “up” being towards the top of the head (see Figure 2.2 A, B), and with the head, or head and body tilted. In the starfield environment (see Figure 2.2 C, D) there is no “visual up” (K, L).

The task used in this experiment differs from other measures of the sensation of vection (Guterman & Allison, 2019; Nakamura, Shimojo, 1998; Tovee, 1999; Kano, 1991) as it can be completed solely by using optic flow cues (visual motion). Participants do not need to experience a sensation of motion in order to perceive that they have passed through a particular target distance, in order words vection is not required. Instead the distances traveled by the participants in the environment reflect the effectiveness of the optic flow cues in simulating motion of the observer relative to the environment.

In the next two experiments, we varied the likelihood of experiencing a VRI: first by varying the alignment of the available orientation cues, and secondly by varying the orientation cues that were present in the visual environment. In Experiment 2, participants were in the same visual environment as in Experiment 1 where non-gravitational "up" was always towards the top of the head (Figure 2.2 A, B). Now, instead of being supine or prone, the participant was always upright with their head tilted forwards in a "prone similar" position (Figure 2.3 D, J), or backwards in a "supine similar" posture (Figure 2.2 C, I), by close to 90 degrees. In the supine (Figure 2.3 A, G) and prone (Figure 2.3 B, H) postures used in Experiment 1, the direction of gravity was supported by somatosensory cues, and the internal idiotropic body vector (Mittelstaedt, 1983) supported the direction indicated by vision. However, when the head was held at 90° to the body (Figure 2.3 I, J) there were fewer cues to support the visually indicated direction of "up" and therefore participants should be less likely to experience a VRI. As well, activation of the neck muscles might reduce vestibular ambiguity and support the perception of tilt over the perception of motion (Crane, 2014; Fraser, Makooie, & Harris, 2015) referred to as our "head-tilt hypothesis". Therefore, in experiment 2, when the head is tilted while the body remains in line with gravity and out of line with the visual upright, we expected participants to be less likely to have a VRI or that any VRI they did experience would be less compelling. Our head-tilt hypothesis is that a reduced VRI experience will then result in a reduction in any effect of tilt on the effectiveness of the optic flow cues found when the head is aligned with the body.

In Experiment 3, we varied the visual cues in the environment providing a direction of up. By comparing the effectiveness of an oriented environment (a hallway, Figure 2.2 A, B) with one with no orientation cues (a starfield, Figure 2.2 C, D) we expected only the oriented environment to be associated with a VRI and therefore gravity to only influence the effectiveness of the optic flow cues in this condition.

## 2.3 Materials and Methods

### 2.3.1 Overview

Under various conditions, participants judged how far they had moved within a simulated virtual environment. They were presented with a target at some distance away from them that then disappeared. They then experienced simulated visual motion towards the target's previous location and indicated when they had reached that location. The distance traveled through the environment was taken as a measure of the effectiveness of the visual motion. The experiments were conducted in agreement with the Declaration of Helsinki and were approved by the ethics committee of York University. All observers signed informed consent forms before taking part in the experiment and were naïve as to the purpose of the study at the time of testing. They had normal or corrected-to-normal vision and reported no vestibular, balance or depth perception problems. Undergraduate volunteers were awarded course credit for their participation.

### 2.3.2 Apparatus

In Experiments 1 and 2, stimuli were displayed using the Oculus Rift Developmental Kit 2 (DK2). The DK2 has a field of view that extends approximately 95°(horizontally) x 106° (vertically). The screen has a resolution of 920 x 1080 pixels and a 75hz refresh rate.

In Experiment 3, stimuli were presented in an Oculus Rift CV1 virtual headset. The CV1 has a field of view that extends approximately ±110° diagonally. The screen has a 1,080 x 1,200-pixel resolution per eye and a 90Hz refresh rate. For all three experiments the stimuli were created in Unity (Version 5.5.2f1, Unity Technologies SF, US) on an Alienware Area-51 R2 computer with an intel i7 core and a Nvidia GeForce GTX 980 graphics card. The projection was stereoscopic and was actively linked to the position of the participant's head. Therefore, distance cues were available from stereoscopic cues and motion parallax.

### 2.3.3 Oriented simulated environment: the hallway

The hallway had black and white vertically striped walls (each black or white stripe was approximately 1m wide) and a multicolored stained-glass floor. The simulated width of the hallway was 9m. The walls were 1000m high so the viewer could not see over the top of the walls (see Figure 2.2 B). The walls and the floor extended 10,000m in front of the viewer. There was no ceiling on the virtual hallway so participants could see a blue simulated sky along with a simulated sun that provided the light source. No shadows were added to the environment. There was also a horizon at eye level that participants could see down the hallway and also when the walls were not visible (Figure 2.2 A).

The target used with the hallway was a red 3D rectangular box that was 5m x 1m x 1m in size (see Figure 2.2 A) drawn with one edge towards the viewer. Participants' eye height was always set to the top of the pillar so that the viewing angle of the scene was the same for all participants. The hallway's walls were not visible at the same time as the target was presented to stop participants from using them as a marker of distance. The distance to the target was defined as being from the center of the participant (the location of the camera) to the center of the target shape.

### 2.3.4 Non-oriented simulated environment: the starfield

The starfield environment (Figure 2.2 C, D) was a simulated environment consisting of white spheres and cubes on a black background. The simulated width of each cube was 6m and the circumference of each sphere was 6m. The objects were randomly placed in a starfield that was 250 x 250 x 250m in size. The objects were illuminated from front, top, and bottom of the object Each object blinked on and off with its own pattern (on for between 5-10s; off for between 0-10s). This was done to reduce the likelihood that participants could fixate on one object and use it to track their location. The target was the same as used in the hallway and was aligned with the body with the top of the pillar at eye height. The pillar did not rest on a surface but instead appeared floating in the environment.

### 2.3.5 VRI assessment

#### 2.3.5.1 Experiment 1 and 2

The experimenter remained in the room with the participant for the first five trials. The experimenter was there to remind the participant of the instructions during the first trial and to answer any additional questions. They remained until the 5th trial at which point the participant was asked about their experience in the hallway. They were asked if they felt they were:

1. Moving horizontally, this might feel like being upright and moving down a hallway
2. Moving upwards, this might feel like flying towards the sky
3. Moving downwards, this might feel like falling towards the ground

The question was asked for each of the three body postures and the order of the three choices was varied. Participants were also given the option to report some combination for experience. The responses were recorded by the experimenter.

#### 2.3.5.2 Experiment 3

It was later felt that these questions could be improved. For instance, participants could perceive the motion as up or down while their posture reflected a different orientation. A participant who was actually prone might paradoxically feel that they were standing but that the motion simulated falling. Additionally, it was felt that the potential for a mixed experience should be stated more explicitly. Lastly, some participants had difficulty following the options, so the questionnaire was run at the end of each body posture once the participant had removed the HMD. However, the experimenter still remained in the room with the participant until after the 5th trial to ensure the participant understood the instructions.

The questionnaire was read in full after the first part of the experiment with the first body posture. For the 2nd and 3rd body postures, the first paragraph was omitted so that it would be less repetitive for the participant.

"I am going to describe three different ways you could have felt while you were in the virtual environment. It's important that you think about how you felt while you were in the virtual environment, while you were stationary and while you were moving.

Due to the nature of virtual reality people can have different experiences. All of these are normal, and I am interested in how you felt while you were in the virtual environment. While you were in the virtual environment you might have felt one of three things, or possibly a combination of them. So, did you feel like you were:

1. looking up, and when moving, moving upwards. You might think of this lying down while flying upwards towards the sky

2. looking forwards, and when moving, moving forwards. You might think of this as moving similar to how you regularly move when not in VR, such as standing upright and moving forwards

3. looking down and when moving, moving downwards. You might think of this as lying down and looking over an edge down a cliff or maybe like falling

4. Some combination or other experience"

The participant reported which of the four options best described how they felt. The presentation order of options 1-3 were randomized each time they were asked. Option 4 always came last. The participant's response was recorded, and they were then asked to elaborate on how their body's orientation felt during the experiment, which was also recorded. Unlike for experiments 1 and 2, this questionnaire was read after completing each posture, instead of during each posture. While this did mean that when answering the questions, the participants had to reflect back on their experience, it allowed for the experimenter to use props to demonstrate the perceived postures, for instance the experimenter oriented their hand in different ways to help clarify the orientation and motion being described (Figure 2.4).

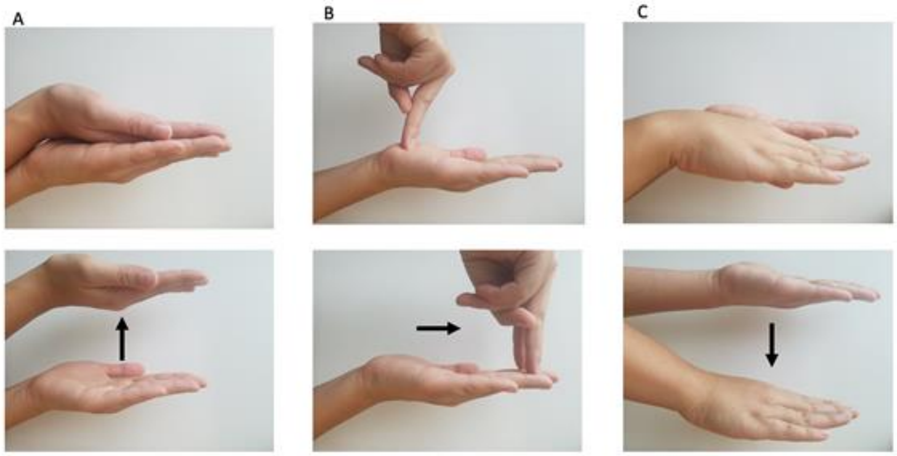



*Figure 2. 4* The hand postures used to help clarify the questionnaire. Column A demonstrates the hand posture shown for option 1 in the questionnaire. Column B demonstrates option 2, and Column C demonstrates option 3.

### 2.3.6 Methods specific to Experiment 1

#### 2.3.6.1 Participants for Experiment 1

The experiment had 18 participants (mean age 27.50 ± 7.68yrs, 9 females). Participants could not be varsity athletes or other high-level athletes.

#### 2.3.6.2 Body conditions for Experiment 1

There were three body conditions: (1) an upright viewing condition where the participant stood upright, (2) a supine condition where the participant lay on their back on a massage bed with their feet up against a wall, and (3) a prone condition where the participant lay on their stomach on the massage bed with their head hanging over the edge of the table and the underside of their chin resting on the side of the bed. A box was placed against the soles of their feet during the prone posture to simulate the wall against the feet during the supine posture. In all three body conditions the whole virtual environment was rotated relative to gravity so that the visual display appeared exactly the same, with up corresponding to the top of the head in all conditions.

#### 2.3.6.3 Procedure for Experiment 1

Participants wore the virtual reality headset and were positioned in one of the three body postures. At the beginning of every trial, participants saw the target shape projected at either 10, 20, 40, 60, or 80m sitting on the textured pavement (Figure 2.2 A). Participants were instructed to pay attention to how far away the target was from them and, when ready, to click the left mouse button. Immediately upon the click, the target disappeared, the hallway walls appeared, and the optic flow simulated an acceleration of $9.8m/s^2$ down the hallway. When the participant felt that they had reached the location of the previously visible target (that is, their head was inside where the target had been) they clicked the right mouse button. Once this button was clicked the next trial started with the participant repositioned at their original position in the hallway, the target appeared at a new distance, and the walls were again rendered invisible.

In each experiment and for each body condition the target distance was chosen pseudo-randomly. The order of the body conditions was determined using a Latin square method. Each target distance was presented to each participant 10 times resulting in 50 trials per participant per body condition. There were two additional trials, one at the beginning of the experiment and one at the end. These were not used in the analysis. The first was used to familiarize the participant with the environment and how the trials worked and in the last trial the target was presented at 200m to indicate the experiment was over.

### 2.3.7 Methods specific to Experiment 2

#### 2.3.7.1 Participants for Experiment 2

The experiment had 18 participants (mean age 25.89 ± 4.83yrs, 6 females).

2.3.7.2 Body position for Experiment 2

As in Experiment 1, there were three body postures, but here they were created by bending only the neck (see Figure 2.5). (1) An upright viewing condition where the participant stood upright. (2) A "head up" condition that mimicked the otolith placement of the Experiment 1 supine condition, referred to as the "supine-similar" posture and (3) a "head down" condition that mimicked the otolith placement of the prone condition in Experiment 1, referred to as the "prone similar" posture. In the head tilt conditions participants rested either the back of their head or the front of the Oculus on a foam pad mounted on an appropriately adjusted wooden plank. Two orthogonal spirit levels were used to ensure the plank was perfectly flat. In the supine-similar posture (Figure 2.5A) participants were asked to place the back of their head on the foam and to fixate a point directly above them so that their head was approximately a 90° to the floor and their back and shoulders were straight. Once the plank was adjusted to the correct height, participants put the oculus on and were instructed not to raise their head from the plank during the experiment (Figure 2.5B). In the prone-similar condition participants were asked to stand behind the plank and stare directly down at their toes while their back and shoulders were as straight as possible (Figure 2.5C). Participants then placed the oculus on their head and the plank was adjusted to approximately the correct height at which point the participants placed the face of the oculus on the foam to test the height to ensure it was correct. This was repeated until the height was correct.

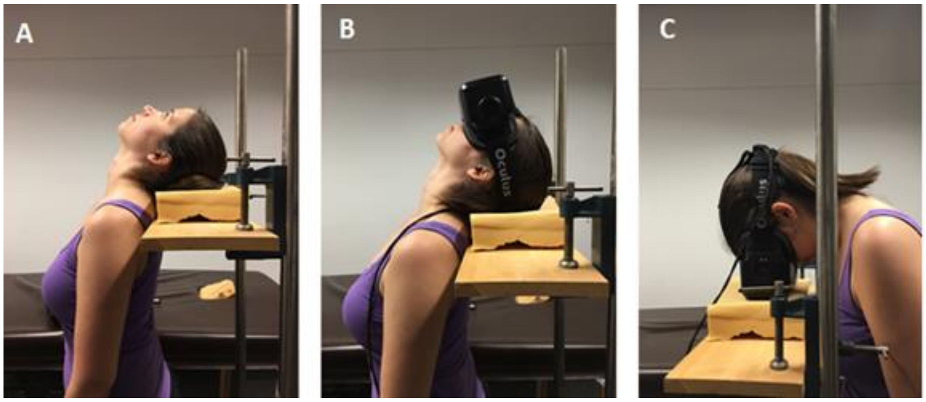



*Figure 2. 5* Depictions of how the participant was position in the supine and prone similar postures. A demonstrates how the participant's head was positioned while in the supine-similar position. B shows what this looked like with the oculus on. C shows how the head was positioned during the prone-similar position. In both cases the back was kept as straight as possible. The individual in this manuscript has given written informed consent (as outlined in PLOS consent form) to publish these images.

In all three body conditions the whole virtual environment was rotated so that the horizon, the light source and the hallway appeared exactly as in Experiment 1.

#### 2.3.7.3 Procedure for Experiment 2

The procedure and stimuli were the same as in Experiment 1. The differences were only in the body postures.

### 2.3.8 Methods specific to Experiment 3

#### 2.3.8.1 Participants for Experiment 3

The experiment consisted of 36 participants (mean age 21.17 ± 4.69yrs, 19 females). Participants were alternately assigned to either the hallway (18 participants, mean age 20.72 ± 4.11yrs, 9 females) or the starfield (18 participants, mean age 21.61 ± 5.28, 10 females) environment, ensuring as even a sex split as possible.

#### 2.3.8.2 Procedure for Experiment 3

The procedure was identical to the other two experiments.

## 2.4 Data analysis

### 2.4.1 Outlier analysis

The same initial outlier analysis was performed in all three experiments.

Firstly, for each person the data was divided into the three separate postures and organized by target distance. Each participant had 150 data points (5 target distances, 10 repetitions, 3 postures). Any mistrials were removed. For instance, a participant could mistakenly skip a trial if they hit the right mouse button twice in a row resulting in a recorded travel distance of less than 1m. Since the acceleration used was 9.8m/s/s a distance of less than one meter would correspond to the participant pressing stop around $1/10^{th}$ of a second after starting. Then, for that participant and for that target distance, the average and standard deviation (SD) of each distance measure was found. A data point was removed if it was ±2SD away from the mean. Out of the 150 data points per person, on average 7.00 ±2.89 (4.67%) were removed in Exp 1, 6.83 ±1.34 (4.56%) were removed in Exp2, 7.78 ±2.07 (5.19%) were removed in Exp3 Hallway, and 6.67 ±2.49 (4.44%) were removed from Exp 3 Starfield. Then the new averages for each distance were calculated.

In addition to data being removed according to these criteria, participants were also excluded for other reasons. The first was if they were unable to distinguish between the target distances. For example, in experiment 1 one participant was excluded because, while standing in the starfield, they were unable to distinguish between 40m, 60m, and 80m. (mean for 40m = 128.29m, SD= 37.27; 60m= 129m, SD= 22.93; 80m= 126.68m, SD= 42.90). This resulted in one participant being removed from each of these experiments: experiment 1, experiment 3 hallway, and experiment 3 starfield. In addition to this one further participant was removed in experiment 1 as they kept lifting their head while supine despite being told to keep their head on the surface. One other person was removed from Exp 3 as the screening criteria required that they did not play varsity sports, but they did.

Once these outliers were removed participants in each experiment were collected into their respective datasets.

While testing the assumptions of the ANOVAs that would form the statistical analysis both Exp 3 Hallway and Exp3 Starfield were found to still have significant outliers. This was tested using a boxplot to check for outliers where some data points fell 3 boxes away from the upper and lower hinges (the hinges for the central 50% of the data around the median) indicating the data points fell outside of 99% of the rest of the distribution. This resulted in data points being removed from two participants in experiment 3 Hallway and one person in Exp3 Starfield. Because the ANOVA requires complete datasets to function these three participants were excluded from the analysis. Applying these outlier criteria resulted in 18 participants in each of the experiments and environments.

### 2.4.2 Questionnaires

The data from the two questionnaires were analyzed the same way. For all three experiments if a participant responded with a 1 (see questionnaire descriptions above), or a description that best matched a 1, then for that actual body posture, their "perceived posture" was recorded as "felt supine". If their response was a 2 or best matched a 2, their perceived posture was marked as "felt standing", and for a response that was a 3 or best matched a 3 was recorded as "felt prone". For the 4$^{th}$ option, if participants indicated they did not feel like any of the other 3 options, or if their verbal description was a mixture of responses, for instance "I felt like I was standing, but moving downwards", this was recorded as a "felt other". The results were then tabulated, see Table 2.1. Chi-squares were run on the responses from experiment 3 to see if there was a difference in the amount of VRI reported in the starfield vs the hallway, and if the amount of VRI differed between the supine and prone postures.

Data for all experiments were the simulated travel distance necessary for participants to believe that they had reached the position of the previously seen target. Travel distance is defined as the simulated distance in meters through the virtual environment. The statistical analysis comprised repeated measures analysis of variances (ANOVAs).

Mauchly's test of sphericity was used and violations of the sphericity assumption were corrected using the Greenhouse-Geisser correction. Alpha was set at $p < .05$ and post-hoc multiple comparisons were made using least squares difference (LSD).

## 2.5 Results

### 2.5.1 VRI occurrence

The frequency of VRI reports is summarized in Table 2.1 for all three experiments. For Experiment 1 (using the hallway stimulus) all participants reported a VRI except for one person who felt "other" while supine (97%). For Experiment 2 with just head bent, a VRI was experienced 89% of the time. For Experiment 3, 50% had a VRI with the hallway stimulus which was reduced to 34% in the starfield ($X^2(1) = 5.31$, $p<0.021$). Variations in VRI rate across the different experiments are discussed further in section 5.5.4 *Measuring the VRI*. Chi squared analyses showed that in the hallway environment of Experiment 3, the VRI rate was significantly affected by posture ($X^2(1) = 7.30$, $p=0.007$), with more people reporting VRI while prone (72%) compared to while supine (28%). Posture did not affect VRI responses in the starfield ($X^2(1) = 0.966$, $p=0.326$), with 28% of people reporting a VRI while supine and 22% reporting a VRI while prone.

Overall, the hallway environment was much more likely to lead to a VRI compared to a starfield environment. Additionally, in Experiment 3, while in the hallway participants were much more likely to have a VRI while prone compared to supine. No such supine/prone difference occurred in the starfield or the other 2 experiments.

Table 2. 1 Overall VRI rates for the three experiments. Columns indicate participants' perceived orientation; rows indicate their actual posture. The numbers in brackets denotes the number of participants who reported that experience in that posture. The percentage is calculated by dividing the number in the brackets by the total number of participants in that experiment. The overall VRI rate is the mean of the supine and prone data.

| | Posture felt/ actual | Felt Standing | Felt Supine | Felt Prone | Felt Other |
|---|---|---|---|---|---|
| Experiment 1 Hallway | Standing | 100% (18) | 0 | 0 | |
| | Supine | 94% (17) | 0 | 0 | 6% (1) |
| | Prone | 100% (18) | 0 | 0 | 0 |
| | Overall VRI Rate: | 97% | | | |
| Experiment 2 Hallway | Standing | 100% (18) | 0 | 0 | 0 |
| | Supine Similar | 83% (15) | 6% (1) | 0 | 11% (2) |
| | Prone Similar | 94% (17) | 0 | 0 | 6% (1) |
| | Overall VRI Rate: | 89% | | | |
| Experiment 3 Hallway | Standing | 94% (17) | 0 | 0 | 6% (1) |
| | Supine | 28% (5) | 56% (10) | 0 | 17% (3) |
| | Prone | 72% (13) | 0 | 17% (3) | 11% (2) |
| | Overall VRI Rate: | 50% | | | |
| Experiment 3 Starfield | Standing | 83% (15) | 17% (3) | 0 | 0 |
| | Supine | 28% (5) | 44% (8) | 0 | 28% (5) |
| | Prone | 22% (4) | 0 | 78% (14) | 6% (1) |
| | Overall VRI Rate: | 34% | | | |

### 2.5.2 Variation in required travel distance

The mean distances at which participants indicated that they had arrived at the target position are shown for all conditions and target distances in Figure 2.6. Pressing the button sooner (shorter travel distances) indicates a more powerful effect of visual motion at simulating motion through the environment as less visual motion was needed for the participant to perceive that they had traveled through the target distance. Four separate 3 (body postures) x 5 (distances) repeated measures ANOVA were performed, one for each experiment.

2.5.2.1 Target Distance

Four 3 (body postures) x 5 (distances) repeated measures ANOVA were performed for each experiment. For all experiments and viewing conditions, the target distance influenced the travel distance. Experiment 1 $F(1.14, 19.45) = 147.88$, $p < 0.001$, $\eta^2_p = 0.897$, Experiment 2 $F(1.28, 21.85) = 230.56$, $p < 0.001$, $\eta^2_p = 0.931$, Experiment 3 (hallway) $F(1.61, 27.36) = 1092.51$, $p < 0.001$, $\eta^2_p = 0.985$, and Experiment 3 (starfield) $F(1.20, 20.36) = 122.58$, $p < 0.001$, $\eta^2_p = 0.878$. A post-hoc pairwise comparison with LSD correction was done for each of the experiments and found that all distances differed from each other ($p<0.001$) which means that participants were successfully able to distinguish the five target distances.

2.5.2.2 Body posture

For Experiment 1, in which whole-body posture was varied, a significant main effect of posture was found $F(1.68, 28.64) = 7.68$, $p = 0.003$, $\eta^2_p = 0.311$. A post hoc pairwise comparison with LSD correction of the main effects found that the perceived distance of travel when in the standing position differed from supine position ($p = 0.006$) and the prone position ($p = 0.009$). The supine and prone positions did not differ from each other ($p = 0.576$).

For Experiment 2, in which only head posture was varied to generate supine-similar and prone-similar conditions, a significant main effect of posture was also found $F(1.76, 30.00) = 4.91$, $p = 0.017$, $\eta^2_p = 0.224$. A post hoc pairwise comparison with LSD correction of the main effects found that the upright posture differed from the prone-similar posture ($p = 0.005$) but that the supine-similar posture did not differ from the upright posture ($p = 0.365$). The prone-similar and supine-similar postures also differed ($p = 0.031$).

For Experiment 3 (using the hallway) a significant main effect was found for posture $F(2, 34.00) = 3.85$, $p = 0.031$, $\eta^2_p = 0.185$. A post hoc pairwise comparison with LSD correction of the main effects found that the prone posture differed from standing ($p = 0.042$) but the prone and supine ($p = 0.050$) and supine and standing did not differ ($p = 0.877$).

For Experiment 3 (using the starfield) no effect was found for posture $F(2, 34) = 0.68$, $p = 0.51$, $\eta^2_p = 0.038$.

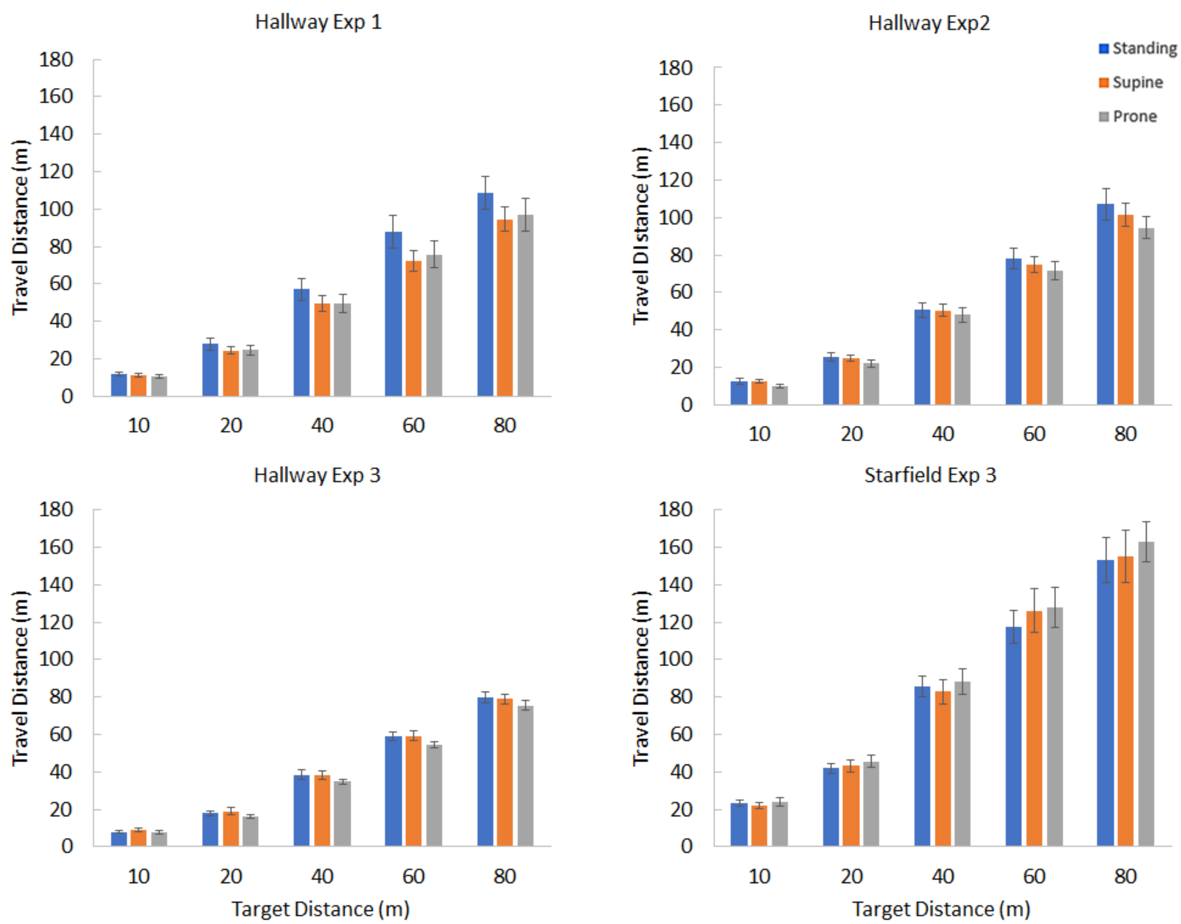



*Figure 2. 6* The average simulated travel distance needed to reach each target for each posture for each experiment. Blue bars indicate responses while standing, orange while supine, and grey while prone. Error bars are ± standard error.

2.5.2.3 Experiment 3 Environment

A mixed 2 (environment) x 3 (body postures) x 5 (distances) ANOVA was performed to explore the effect of environment on travel distance. The between subjects factor (environment) was significant $F(1, 34) = 69.36$, $p < 0.001$, $\eta^2_p = 0.67$, where the average distance traveled in the hallway was 39.7m (SE= 3.98) and the starfield was 86.6m (SE= 3.98). There was also a significant interaction between the environment and the distance traveled for each target distance $F(1.21, 41.12) = 27.78$, $p < 0.001$, $\eta^2_p = 0.45$. A post hoc analysis with LSD correction found that the distance traveled for each target distance differed based on the environment ($p < 0.001$ for all cases) with participants in the hallway condition needing to travel about half of the distance required in the starfield (Figure 2.6).

2.5.3 The Variation of Gain by Experiment and VRI Likelihood

The average gain of the travel distances for each condition were calculated and are expressed in Table 2.2 where gain is defined as perceived distance (the target distance) expressed as a fraction of the actual distance travelled. The gain represents the effectiveness of the optic flow cue in eliciting the perception of motion where a high gain represents an increased effectiveness of the optic flow compared to a lower gain.

*Table 2. 2* The mean gain for each condition. The gain was calculated by dividing the target distance (perceived distance) by the average distance traveled for each target distance (actual distance), and then computing the average across all target distances. This was done for all three postures in each of the three experiments. Note that for Experiment 2, the postures were supine-similar and prone-similar as only the head-on-trunk position was varied. Numbers less than 1 indicate that participants had to travel further than the target distance to feel they had passed through the target distance (low gains) and vice versa. The numbers in brackets are standard errors.

| | Exp 1 Body posture | Exp 2 Head only | Exp 3 Hallway | Exp 3 Starfield |
|---|---|---|---|---|
| Standing | 0.84 (0.07) | 0.86 (0.06) | 1.15 (0.06) | 0.52 (0.03) |
| Supine | 0.91 (0.06) | 0.85 (0.05) | 1.14 (0.06) | 0.53 (0.04) |
| Prone | 0.97 (0.08) | 1.00 (0.08) | 1.30 (0.10) | 0.51 (0.05) |

To assess the change in gain relative to standing for each condition, the gain while supine or prone for each participant, experiment and environment was then expressed as a fraction of the relevant standing gain.  The amount of visual motion needed to arrive at a target while standing upright in a particular environment could be thought of as the "standard" or default amount of motion needed to simulate motion through that environment for a given participant. Changes to this amount reflect changes in the effectiveness of the visual motion where numbers greater than one indicate an enhancement of the gain while tilted relative to standing, and numbers less than one indicate a reduction in the gain relative to standing. These ratios were then plotted as a function of the likelihood of experiencing a VRI in that condition (see Table 2.1) in Figure 2.7.

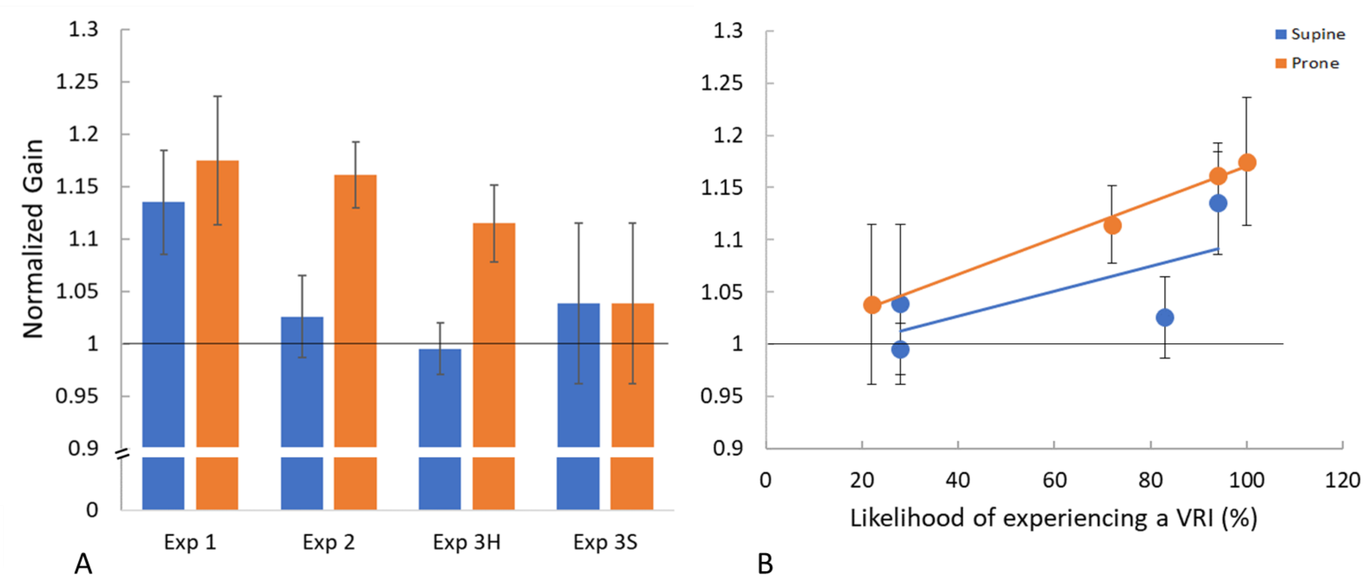



*Figure 2. 7* Both figures show the changes in gain while supine and prone relative to when standing. The solid horizontal line at 1 indicates no change with posture. In both figures blue refers to the supine data and orange refers to the prone data. Error bars are ± standard error. A shows the change in gain calculated for each participant in each experiment and environment and then averaged. B shows the same gains relative to standing in A plotted as a function of the likelihood of experiencing a VRI for all three experiments and all environments. The lines are best fit linear regressions.

In the results described above we found that in situations where the VRI rate was high the average distance traveled tended to differ from standing. When the VRI rate was low the average distance traveled did not differ from standing. In order to confirm this relationship a Pearson's correlation (2 tailed) was used to determine the relationship between the gain ratio and VRI rate (Table 2.1). The relationship between gain ratio and posture (supine relative to standing = 0 or prone relative to standing= 1) and gain ratio and environment (hallway= 0 and starfield= 1) was assessed using a point-biserial correlation (2 tailed) as they are dichotomous categorical variables.

The VRI rate was found to be significantly positively correlated with the gain ratio, though the correlation was small, $r(142)= 0.228$, $p= 0.006$. Posture was found to trend toward a significant positive correlation with the gain ratios $r_{pb}(142)= 0.162$, $p= 0.052$. We argue that any correlation here is an indirect effect. As per the chi squares above and a significant positive correlation between VRI rate and posture, $r_{pb}(142)= 0.219$, $p= 0.008$, the prone posture is more likely to lead to a VRI compared to the supine posture which would result in an apparent correlation between posture and gain ratio. We partialled out the effect of VRI in the correlation between posture and gain ratio and the result was no longer significant ($r_{pb}(141)= 0.118$, $p>0.05$).

No significant correlation was found between gain ratio and environment ($r_{pb}(142)= -0.120$, $p> 0.05$). Of course, the environment does lead to differences in a gain as per Table 2.2, just not once the variation found while standing in that environment is removed. However, environment and VRI rate were negatively correlated ($r_{pb}(142)= -0.739$, $p< 0.001$), where the starfield had a lower VRI rate (Figure 2.7); this is also supported by the chi square analysis.

## 2.6 Discussion

Overall, in all of the three hallway conditions participants required *less* visual motion (higher visual gains) to simulate passing through a given target distance while tilted in a hallway environment compared to a standing posture or a starfield environment (Figure 2.6) but only if the likelihood of experiencing a VRI was high (Figure 2.7 B). The hallway environment led to participants more often reporting a VRI compared to the starfield (50% vs 34%). The prone posture in the hallway environment in particular elicited a higher VRI rate compared to the supine posture (72% vs 28%). This difference in the prone and supine posture's VRI rate was not seen in the starfield environment (22% vs 28%). Neither the starfield environment nor the supine posture in the hallway led consistently to the experience of a VRI (Table 2.1).

### 2.6.1 When gravity is not where it should be: the additive hypothesis

Our cognitive hypothesis postulated that there would be changes associated with a VRI and our additive hypothesis postulated that there would be a detectable additive effect such that when participants had a VRI and were supine so that the normal force of gravity and visual motion pointed in the same direction they would need less visual motion (higher gain) in order to perceive that they had arrived at a given target location compared to when standing and, vice versa, when prone with a VRI they would require more visual motion (lower gain) compared to standing. In agreement with the cognitive hypothesis, we found a clear effect of a VRI on the effectiveness of the visual motion (Figure 2.7 B). However, regardless of the direction of tilt, in conditions where the likelihood of experiencing a VRI was high, participants always required less visual motion (higher gains) relative to standing to reach a given target distance compared to when the VRI rate was lower thus disproving our additive hypothesis.

Referring to Figure 2.7 B, there is a clear relationship between VRI rate and gain relative to standing. As the likelihood of reporting a VRI increased, the effectiveness of the visual motion also increased compared to the standing posture. Both tilted postures in experiment 1 and the prone posture in experiment 2 were associated with high levels of VRI and had correspondingly high gains compared to standing. On the other hand, participants in the starfield environment reported a VRI much less often than those in the hallway environment and the ratio of their gains while tilted compared to standing were close to 1, this was also true of the supine posture in experiment 3 in the hallway environment which also showed a low VRI rate (see Figure 2.7 A).

From our results, it is clear that participants' high-level interpretation of their environment is an important factor in visual self-motion processing, confirming our cognitive hypothesis. However, it appears that the alteration in perceived self-motion is not an additive process in which the acceleration of gravity is added to or subtracted from the visual motion since it did not matter in which direction the participant faced. Instead, it appears to be a weighting effect in which more weight or emphasis is put on vision when gravity is not where it should be: when it is not aligned with the long-axis of a perceptually upright body.

For the starfield displays, which were far less likely to generate a VRI, participants strongly overshot the target (low gain) compared to their performance in the hallway (Figure 2.6, Table 2.2). In an unstructured optic flow field with no orientation cues considerably more visual motion was required to simulate moving through a given distance. This is also consistent with our cognitive hypothesis as a low likelihood of experiencing a VRI is associated with less increase in gain relative to standing. But why is the self-motion gain so low in a starfield?

### 2.6.2 Oriented vs unoriented environments

The gains while standing when simulating self-motion in the starfield were substantially lower than when in the hallway (0.52 compared to 0.84 or 1.15 in the hallway, Table 2.2). That is, participants needed about twice as much visual motion in the starfield as they did in the hallway in order to perceive they had traveled through the same distance. We do not know why this is. In both instances the targets were viewed binocularly and were displayed at the same range of distances. Few studies have used perceived distance traveled, visual odometry or path integration, as their measure of simulated self-motion – a more common method of assessment being a magnitude estimate of the sensation of vection, often normalized to the display being used with instructions such as "estimate the perceived magnitude where your response to this display is 100%". During physical walking, it seems that non-visual cues dominate in path integration (Chance, Gaunet, Beall, & Loomis, 1998; Kearns, Warren, Duchon, & Tarr, 2002; Mittelstaedt & Mittelstaedt, 1980, 2001) although path integration is possible from visual cues alone (Lappe et al. 2007; McManus et al. 2017; Redlick et al. 2001) but this is first time that the effect of visual environment on gain has been systematically investigated. We postulate that the lack of oriented structure is responsible for this lesser effectiveness of the visual motion in the starfield, but clearly further study is needed. Previous studies that looked at the experience of vection found that polarized environments (Howard & Childerson, 1994), more colourful environments (Bubka & Bonatoô, 2010), and the use of a floor surface (Trutoiu, Mohler, Schulte-Pelkum, & Bülthoff, 2009) all lead to enhancements to the perception of vection, which might stem from enhancements to the optic flow cues. It is also possible that the blinking on and off of the stimuli in the environment might have caused a "loss" of some of the optic flow during the movement through our environments. In the context of this paper, an unstructured environment evokes a poorer interpretation of orientation and therefore, according to our cognitive hypothesis in which the interpretation of the environment affects the effectiveness with which visual motion is processed, will result in a reduced effectiveness in simulating self-motion.

Overall, oriented environments increased the incidence of VRIs compared to visual environments without orientation cues (Table 2.1). In the hallway environment, participants reported over 70% experience of a VRI, with the exception of the supine posture in Experiment 3 hallway, while in the starfield environment people reported a VRI rate of 34%. This finding is expected and is similar to previous findings by Howard et al. (Howard et al. 2005) using a mirror bed arranged to make an earth-vertical surface behind the viewer appear parallel to the supine viewer. Adding strong orientation cues, such as a ball resting on a shelf or a standing human, however, lead to a strong VRI rate of 60%-80% in which the surface was interpreted as an earth-vertical wall and the supine observer felt as if they were actually standing. “Other” perceptions varied between 1-10%. These values are similar to those found in our hallway environments in the three experiments (see Table 2.1), though the VRI rate found in Experiment 1 and 2 is higher than the rate reported by Howard and colleagues (Howard et al. 2005). It is possible that our immersive virtual environment lead to a stronger VRI experience, perhaps due to the novelty of virtual reality.

The VRI rate we recorded was higher than expected in the starfield condition (Table 2.1) as VRIs were not expected to occur at all during exposure to this non-oriented display. It is possible that without a clear visually defined direction of up, the participants perceived orientation was dominated by their idiotropic up (“head is up”, Mittelstaedt 1983). However, referring to Table 2.1 and the chi-squared analyses, it is clear that the starfield environment did evoke a much lower VRI rate than the hallway. We also saw that in the hallway environment, participants needed much less visual motion than they did in the starfield to simulate passing through a given target distance (Figure 2.6).

Three participants in the starfield environment reported feeling supine while upright (Table 2.1). This misperception has been reported previously, such as in Allison et al. (1999) where, when upright and viewing a room moving in roll, seven of their 35 participants felt that the they were in fact lying on the backs looking up and rotating about a vertical axis on at least one trial. This supine-while-upright perception has also been reported by Howard and Childerson (1994) .

Interestingly, there was also a large decrease in the likelihood of experiencing a VRI in Experiment 3 vs Experiment 1 and 2 for the supine posture - from 80%+ down to 28%. Previous studies have shown large individual differences in the experience and duration of VRIs, with some participants reporting a VRI every trial, and others only on some trials (Howard & Hu, 2001). It is possible that differences in VRI rate reported here are result from the fluctuations in participant experience.

### 2.6.3 Head Tilt vs Body Tilt: the head-tilt hypothesis

Experiment 2 manipulated head and body tilt separately to determine the effects of the body on visual motion processing. When participants are supine or prone in the hallway environment their body- and visually-defined “uprights” are in line with each other but misaligned with the gravity upright. By having participants stand with their head tilted in a supine-similar or prone-similar orientation, their “body up” (at least below the neck) remains in line with gravity but is no longer aligned with the “visual up” (see Figure 2.3 I and J). We hypothesised that in this head-tilt-only condition we would see a reduction in the occurrence of a VRI (relative to the truly supine and prone conditions) as perceived orientation became less reliable and the activation of neck muscles might also support the perception of tilt over translation (Crane, 2014)– our head-tilt hypothesis. However, this was not the case (Table 2.1) and of the likelihood of experiencing a VRI was not significantly reduced. It is possible that in experiment 2 while supine the older questionnaire overestimated the likelihood of experiencing a VRI.

If experiencing a VRI was not causing the increased effectiveness of visual motion cues (higher gains) but instead any changes were exclusively due to body posture, we would expect to see posture-related differences while tilted in both the hallway and starfield environments. However, for both tilted postures in the starfield, the ratio between tilted and standing performance was close to 1 indicating the gains while tilted were very similar to standing (See Table 2.2 and

Figure 2.7 B). Table 2.1 shows that the prone posture is more likely to evoke a VRI experience than the supine posture in the hallway environment. This is the opposite of what was found by Howard and Hu (2001) who found that people were more likely to experience a VRI in a supine rather than a prone posture. However, their prone position involved being tied onto a bed and essentially hanging from the straps – a level of discomfort more akin to our supine-similar condition in experiment 2.

### 2.6.4 Alternative explanations for changes in self-motion gain

If participants were using other strategies to arrive at the target distances (such as estimating the time needed to reach the targets), we would expect to see no differences between the standing and the tilted body postures in either environment. Neither of these is the case. Instead it appears that the participants' high-level interpretation of their environment is an important factor for visual self-motion processing. Similarly, the time to contact (tau) might be used by participants to estimate when they might theoretically impact the target. Tau is the ratio of the optical size of the target to its instantaneous rate of expansion as it is approached (Lee 1976; Keshavarz, Campos, DeLucia, & Oberfeld, 2017). An important feature of using tau is that the object's absolute size does not matter. Tau may not be relevant in the MTT as no target object is present during the visual motion. If participants were attempting to collide with an invisible target they would have to rely on an internal representation of the object and update it based on their perception of the optic flow. In the end, regardless of if participants were using the optic flow to keep track of their distance traveled or using it to update an internal representation of the target as they moved, the important factor is their use of the optic flow cues which I have shown varies based on their VRI rate.

Another possibility is that lying down could result in a rescaling of the environment such that distances appear closer when supine or prone. Harris and Mander (2014) found that supine participants, or participants who felt that they were supine, perceived a rod to be closer than when they were upright suggesting a rescaling of the perceived size of the environment. However, any such rescaling could not explain our results. If environmental cues were compressed, both the travelled motion and the target distance would be compressed, resulting in the same distance estimations as in a room that was perceived as larger. Additionally, undershooting was not found when our participants were tilted in the starfield environment, or when they were less likely to be experiencing a VRI.

### 2.6.5 Misinterpreting the vestibular signal: the reweighting hypothesis

So, if we cannot explain our changes in visual gain in terms of timing, the additive hypothesis or rescaling of the room, then we are left with the cognitive hypothesis which predicted a change in the visual gain without specifying which direction it would go in while experiencing a VRI. Here, we show that the gain is increased during a VRI: why might this be?

The presence of a VRI suggests a conflict between the visual up and the gravity up (Garzorz & MacNeilage, 2019) where the participants have resolved the conflict by giving dominance to the visual cues. A conflict does not have a polarity, which might explain why we did not see undershooting while supine and overshooting while prone as hypothesized in the additive hypothesis. We therefore introduce a reweighting hypothesis which states that when a conflict is experienced, visual cues dominate, the vestibular cue is ignored, and therefore visual motion becomes more effective in simulating motion through an environment, resulting in higher visual motion gains than when no conflict is experienced.

During a VRI, participants who are tilted report the feeling of being upright, however the vestibular cue is still present. If participants were not interpreting the vestibular cue as tilt and allowing the visual cues telling them they are upright to dominate, then they might interpret the vestibular cue as motion, suggesting a sort of reverse somatogravic (oculogravic) illusion (Gillingham & Wolf, 1985; Graybiel, 1952). With an increased perception of motion we would then expect the higher gains that we observed. While tilted, the vestibular system indicates the direction of gravity's acceleration, as do the body's other acceleration sensors, such as the kidneys (Mittelstaedt, 1996; Oman, 2007). The presence of acceleration information from both the head and body, along with the addition of visual motion and visual cues indicating they are upright, might more causally lend itself to the interpretation of translation instead of tilt: this hypothesis has been referred to as the otolith-tilt-translation reinterpretation (OTTR) hypothesis (Parker, Reschke, Arrott, Lichtenberg, & Homick, 1985) and would be the basis for our additive hypothesis. While the study by Crane (2014) provides support for this hypothesis -- since participants who were tilted backwards perceived some forward motion and participants who were tilted forwards perceived some backward motion -- other studies have failed to find supporting evidence (Merfeld, 2003), including the experiments reported here.

Another scenario is that participants who were tilted and experiencing a visual-vestibular conflict resolved this conflict by ignoring the gravity vector in favour of vision (Howard & Hu, 2001): our reweighting hypothesis. An increased reliance on visual cues would then lead to an unsigned effect in which the gain was increased (more undershooting) in both orientations (supine and prone) relative to standing. Our reweighting hypothesis is that conflict detection may have introduced a weighting effect in which more weight or emphasis was put on vision when gravity is not where it should be: when it is not aligned with the long-axis of a perceptually upright body.

2.6.5 Reweighting?

Tracking how far one has moved during a physical motion with eyes open involves combining potentially redundant information from multiple sources – in particular visual and vestibular signals. In many instances of multisensory integration this is done by averaging the various signals' estimates after weighting them according to their reliabilities (Ernst & Banks, 2002; Ter Horst, Koppen, Selen, & Medendorp, 2015).

Fetsch, Turner, DeAngelis and Angelaki (2009) found that when the visual vection cue and the vestibular cue were mismatched, people (and monkeys) dynamically reweighted the emphasis put on each cue. It is possible then that instead of interpreting the vestibular cue as motion, participants in the present experiment viewed the visual information as more reliable and therefore weighted it more heavily. When cues to upright are misaligned we see other examples of higher sensory weighting being given to vision in determining upright (Harris, Herpers, Hofhammer, & Jenkin, 2014). For instance, Ward et al. (2017) found that as the head and body are rolled, vision becomes more important for determining the direction of gravity. They argue that as the effect of gravity is applied to different parts of the otolith system the reliability of their signal decreases and vision is weighted more. This has also been suggested to occur in microgravity environments where in the absence of a gravity cue, astronauts become more sensitive to visual cues, such as cues to visual motion (Harris, Jenkin, Jenkin, Zacher, & Dyde, 2017; Oman et al. 2003).

In the present experiment participants could either rely on physical cues to tell them they were tilted, or on visual cues to tell them they were standing. A participant who correctly perceived themselves as tilted and experienced visual motion consistent with up or down movement through a tilted visual environment should have no change in their visual weighting compared to the default weight (the visual weight assigned when the person correctly perceives themselves as upright in an upright environment). However, the presence of a VRI would suggest that the person has determined the visual cues are the more reliable than the gravity cue for determining upright and therefore reweights the cues by favouring vision, leading to a relative increase in the visual weight and a relative decrease in the weight given to the gravity vector. If this is a generalized visual weighting, then we would expect it to occur in other tasks as well. A higher visual weight in one task might lead to changes in the effectiveness of visual cues in other tasks. A higher visual weight could then lead to changes in the effectiveness of the visual motion cues in simulating movement through the environment and could explain the undershooting (higher gain) found in this experiment in the hallway environments during a VRI. A model for this is presented in Figure 2.8. If all cues to upright are aligned, as indicated by the left stream in Figure 2.8, and the participant correctly feels upright, their visual weighting should be their “default” visual weight (w). The gain of the visual motion would then be processed as the visual information multiplied by w. We postulate that when a visual-vestibular conflict is detected the visual weighting would be increased to w’ relative to the other cues.  In the absence of a detected conflict the gain would be w resulting in performance for no-VRI participants, the participants who did not report VRIs, being the same as standing, and the VRI participants having a higher visual weighting (w’) where they need less visual motion in order to simulate passing through a given distance.

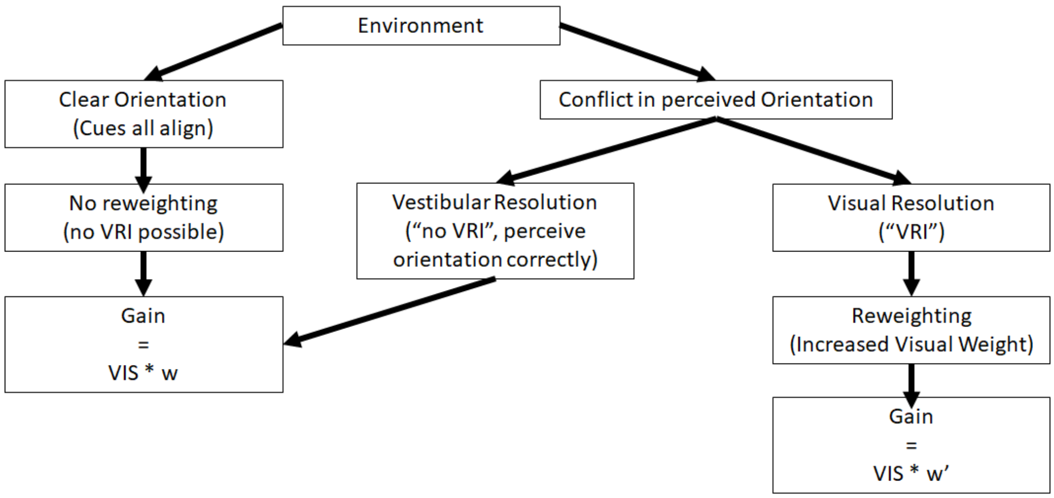



Figure 2. 8 A model of how the perceived orientation, influenced by visual cues present in an environment, might affect perceived motion. VIS refers the optic flow information. The left side indicates the situation when all cues are aligned. The right side indicates how the detection of conflict may alter perceived travel distance. w represents the baseline weighting assigned to vision relative to the other cues. w' is the increased visual weight relative to the other cues.

## 2.7 Conclusion

We have shown that the structure of the environment affects the gain of the response to visual motion. Overall, gains were much higher in a structured environment and depended on whether the observer experienced a VRI (the cognitive hypothesis). As the chances of experiencing a VRI increased so did the effectiveness of the visual motion cue in simulating motion through the environment. Visual effectiveness did not vary with the direction of tilt relative to gravity (the additive hypothesis) but instead was increased when visual-vestibular conflict was resolved by visual domination over vestibular signals that resulted in a visual reorientation illusion (the reweighting hypothesis). Head-tilt did not affect VRI likelihood (the head-tilt hypothesis) presumably because the conflicts it evoked were similar to posture changes of the whole body. These findings suggest that participant's high-level interpretation of their posture and their environment may lead to changes in visual weighting and a consequent change in the effectiveness of the use of optic flow.

# CHAPTER 3: The weighting of cues for orientation perception does not predict the effectiveness of visual cues in evoking self-motion

*This chapter has been written with intention of being submitted to the Royal Society Open Science journal.*

*My contributions are the same as the Chapter 2 and include designing the experiment, programing the tasks, writing up the ethics forms, running pilot tests, testing participants, analysing and interpreting the data, and writing up the paper.*

*Dr. Harris' contributions are the same as Chapter 2 and include helping with the design of the experiments (such as discussing the background literature and discussing the rational of the tasks), providing feedback on the experimental tasks, providing feedback on the interpretations of the results, editing and providing feedback on all written work, and updating the ethics forms. Dr. Harris also designed Figure 3.1.*

*John Kim, a PhD student in the lab, provided an earlier version of the C# PEST code he wrote for a previous experiment, which I modified for the OChaRT task in this chapter. Matthew Inglis-Whalen, a PhD student in a different lab helped with modifying the C# PEST code.*

## 3.1 Abstract

Perceiving our orientation and motion requires sensory information provided by vision, our body and gravity, which we combine to create our percepts of orientation and motion. Normally, these sensory cues are redundant, but in some situations the information provided can be in conflict such as in virtual reality – either intentionally or unintentionally. We created such a conflict by simulating a constantly body-upright world and assessed the perception of “forward” distance travelled induced by visual motion alone while upright, supine and prone. Some participants felt they were standing throughout indicating a visual reorientation illusion (VRI). VRI-sensitive participants needed less visual motion to feel that they had passed through a given target distance than VRI-resistant participants, suggesting that visual information was weighted more heavily in VRI-sensitive individuals. We then assessed the relative weightings given to the visual and non-visual cues in both groups using the Oriented Character Recognition Test while upright and rolled left-side-down. VRI-sensitive individuals placed less emphasis on visual cues (lower weight) and more on gravity (higher weight) compared to VRI-resistant individuals. We suggest that the higher gravity weighting may increase the likelihood that VRI-sensitive individuals detect a visual-vestibular conflict leading to a reweighting of the cues.

## 3.2 Introduction

In our day-to-day life we use a variety of cues to determine which way is up, such as gravity, pressure from the support surface (Horak, Nashner, & Diener, 1990) and visual cues (see Howard 1982 for a review), as well as an internal prior that assumes our body is always upright: Mittelstaedt's "idiothetic vector" (Mittelstaedt, 1996). These cues may be integrated to provide a single overall estimate of the direction of up according to Bayesian principles (Fetsch et al. 2009; Dyde et al. 2006) in which they are assigned weightings according to their reliabilities (Ernst & Banks, 2002; ter Horst, Koppen, Selen & Medendorp, 2015) or by inferring which cues might have a causal role in the perception of up and integrating the cues based on that likelihood (Körding, Beierholm, Ma, Quartz, Tenenbaum, & Shams, 2007; Shams, & Beierholm, 2010; Fetsch, Turner, DeAngelis, & Angelaki, 2009).

Although normally the various cues to self-orientation agree and are redundant, in some environments they may not indicate the same direction. For example, when underwater without the somatosensory reference provided by a support surface the local horizon suggested by the structure of the ocean floor may not be orthogonal to gravity. In the even more extreme environment of space both vestibular and somatosensory cues to self-orientation are absent leading to an arbitrary personal definition of up that is subject to sudden change. In virtual reality environments the orientation of the simulated visual world is also arbitrary and so any amount of disagreement between visual and non-visual cues can be created. This is most noticeable, and usually unavoidable, when self-motion is simulated but can also be deliberately done, for instance by tilting the visual environment such that the visual up does not agree with the gravitational defined up.  Here we have used virtual reality to deliberately separate visual and non-visual cues to self-orientation and find inter-individual differences in how much perceived self-orientation is dominated by the orientation of the visual cue. We then assessed the relative weightings given to the visual and non-visual cues in determining orientation to see if one predicted the other.

There are multiple ways of assessing the perception of up, including the subjective haptic vertical (SHV; Schuler, Bockisch, Straumann, & Tarnutzer, 2010), the subjective visual vertical

(SVV; Asch & Witkin, 1948; Barnett-Cowan, Dyde, Thompson, & Harris, 2010), or the perceptual upright (PU; Dyde et al. 2006).

One measure of upright makes use of people's implicit or prior assumptions that light tends to come from above (Ramachandran 1988). When people view flat disks with a shaded gradient between light and dark in which the top is lighter than the bottom, people tend to view it as concave. When the top is darker, the disk appears convex. By varying the direction of the gradient and asking people to judge whether the shape is concave or convex the most effective orientation can be found, and the direction taken as "above" deduced. Using this method, the contributions of the visual background, the orientation of the head, and gravity for determining upright can be determined (Oman et al. 2003; Howard, Bergström, & Ohmi, 1990). When the shaded disk is viewed against a plain grey background and the orientation of the disk and participant are varied it appears that "up" indicated by this method – corresponding to the assumption of where the illumination is coming from - is from the top of the head and that the gravity vector only plays an inconsistent role (Howard et al. 1990).

Curiously, the different methods of assessing perceived orientation do not always agree (Fraser, Makooie, & Harris. 2015) suggesting that contributions of the various cues may differ depending on the task at hand. For instance, the SVV is based on imagining the direction in which a ball would fall and therefore cannot provide an estimate of "up" in microgravity (Dyde, Jenkin, Jenkin, Zacher, & Harris, 2009). In contrast, the PU, the orientation in which things look most upright and are most recognizable (Hock & Tromley, 1978; Dyde et al. 2006), is still present as an "up" even without gravity (Dyde et al. 2009).

The PU can be measured using the oriented character recognition test (OChaRT) (Dyde, Jenkin, & Harris, 2006). Participants view an ambiguous symbol " ᑫ " in various orientations and indicate whether it looks more like a p or more like a d. The OChaRT finds the two most ambiguous orientations, where participants are equally likely to see a p or a d, the bisector of which is taken as the PU. By varying the relative orientations of the main component cues (visual, gravity and the body), for example by having participants stand and lie on their side, and varying the orientation of the visual background, the relative contributions of vision, the body, and gravity can be determined by simple geometry (see Figure 3.1). Typically, vision accounts for about 25% - 36% of the cue contribution to the PU, the body about 52 - 54% and gravity about 10 - 20% (Dyde et al. 2009; Dyde et al. 2006), however large individual differences are seen (Dyde et al. 2009; Dyde et al. 2006). Additionally, the weighting of the contributions can vary based on the environment. For instance, in Jenkin, Zacher, Dyde, Harris, & Jenkin, (2011) the contribution of vision to determining the PU was compared on Earth and during parabolic flight. During both the 1g and 0g phases of the flight a dynamic environment (a video of people walking around) led to a significant enhancement of the visual contribution to the PU, relative to the body contribution, compared to the effectiveness of a static background (a still frame from the dynamic scene) (Jenkin et al. 2011).

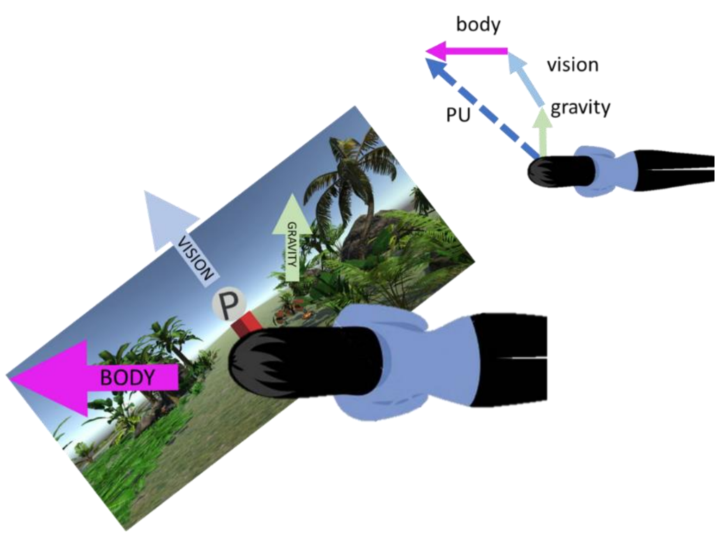



*Figure 3. 1* How the cues that signal "up" can be separated into different directions. In this case a person is lying on their left side while viewing a visual environment tilted at 45 degrees. By measuring the PU as these orientations are varied, the strengths of their various contributions can be calculated by simple geometry- see inset.

However, at times there might not be clear cues to upright such as when underwater with an uneven seabed, or perhaps even conflicting cues to upright such as when reading while lying on your side in bed. In extreme ambiguous cases, such as in space or in virtual environments, people can experience an illusion where the identity of surfaces such as 'floor' can vary based on attention (Oman, 2007). For instance, if you hang over the side of your sofa and view the world upside down while imagining that that ceiling is the floor or, in a more controlled laboratory setting, if you lie on your back in a fully furnished room that can be rotated through 90 degrees such that visual up is aligned with your longitudinal body axis. Using such a room, Howard and Hu (2001) found that 84% of individuals felt that they were actually standing upright when supine but with the room aligned with their body axis. This perceived reorientation based on visual cues is referred to as a Visual Reorientation Illusion (VRI) (Howard & Hu, 2001, Mast & Oman, 2004; see also Asch & Witkin, 1948; Koffka 1935) and has been frequently anecdotally reported in microgravity (Oman, 2007). The VRI concept is shown diagrammatically in Figure 3.2. On Earth, in a strange visual environment with palm trees growing horizontally out of the wall, there is a conflict between gravity and the direction of "up" indicated by visual information. It appears that most people resolve this conflict within the complete immersion provided by a full-field room, visually and ignore or put much less weight on the gravity vector (Howard & Hu, 2001), leading to a VRI.

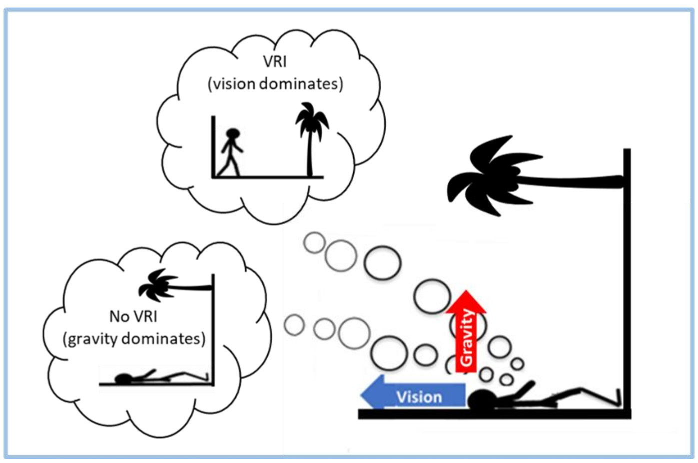



*Figure 3. 2* Visual reorientation illusion (VRI). A person is lying on their back in a room that has been tilted such that the visually signalled direction of up aligns with their body orientation. The visual cues in the environment (blue arrow) indicate that the person is upright, while the up denoted by gravity (red arrow), signals that the person is lying down. If the person cannot detect the conflict between the cues, they should feel as if they were lying down and looking at a tree growing out of the wall (lower thought bubble). If the person detects a conflict between the two uprights they might then rely on the visual cues and experience a VRI in which they would feel they were standing upright and were aligned with a tree growing out of the floor (top thought bubble).

While studies that investigate or incorporate VRIs on Earth are rare, Preuss et al. (Preuss, Brynjarsdóttir and Ehrsson, 2018) induced a whole-body illusion where participants gained ownership over a rotating virtual body through synchronous visual-tactile stimulation. When the participants had ownership of the virtual body, they perceived the orientation of a shaded disk in line with the rotated virtual body and not with their own physical body, indicating a VRI. Interestingly, when participants had ownership over the virtual body, they also experienced an increase in the sensation of self-motion during the virtual rotation. Preuss et al. (2018) argued that ownership over the body increased the emphasis on the visual cue compared to the vestibular cue making it more effective at producing the perceived motion and affecting perceived orientation.

Such an increase in the effectiveness of the visual cue during a VRI has also been found in our lab (Chapter 2). We have shown that in situations where people are more likely to report a VRI, they require less visual motion (optic flow) to create the illusory sensation of moving through a given distance in virtual reality. In a series of experiments, participants were placed in either a polarized virtual environment (a hallway) or one with few cues to upright (a starfield). Participants were more likely to report a VRI in the virtual hallway environment while tilted prone or supine, and also to require less visual motion to visually travel through a given distance compared to when tilted in the starfield environment. Requiring less visual motion to evoke the sensation of travelling a given distance suggests an increased relative sensitivity to the optic flow information. We argued that the findings reflected an enhancement of the visual cue and was not directly due to posture as participants in both the VRI and non-VRI group were in the same postures in the hallway and starfield. During a VRI, there is a conflict between the visual up and the up indicated by gravity. The presence of a VRI suggests a visual resolution in which the PU is mainly determined by vision. This would imply a greater visual weighting and a relatively lower weighing assigned to the gravity and/or body contributions in those experiencing a VRI (Howard & Hu, 2001; Preuss et al. 2018) compared to individuals who do not report a VRI.

The otoliths constantly register an ambiguous acceleration that could theoretically be interpreted as arising from either gravity or translation or both. During a VRI, with a visual environment indicating that the participant is upright, participants might be more inclined to interpret the ambiguous vestibular cue as indicating translation in the direction of the red arrow in Figure 3.1. If so, we would not expect differences in the weighting of the visual cue between those who report a VRI and those who do not. Instead, we would expect that while supine, participants would show an enhancement of their self-motion perception as the gravity vector would now support the visual motion, but while prone self-motion perception should be hindered as the visual motion would now be opposed to the gravity vector. However, in Chapter 2 we found enhancement of self-motion in both postures, suggesting a general increase in the weighting of visual cues irrespective of agreement in direction between the acceleration of gravity and the direction of simulated visual motion.

In order to obtain a measure of the relative weighting for visual, body and gravity cues in people who were or were not susceptible to VRIs and consequently would be expected to show different modulation of the effectiveness of visual cues to self-motion, we performed two experiments: 1) a move-to-target task (MTT) as used in Chapter 2 to quantify the perceived motion relative to the environment induced by the optic flow - referred to as the "effectiveness" of the optic flow, and 2) OChaRT to assess the relative weightings of the cues determining the PU (after Dyde et al. 2006). Participants were divided into two groups according to their vulnerability to a VRI. We hypothesized that individuals who reported a VRI would require less visual motion to travel through a given distance in virtual reality compared to those who did not report a VRI (based on Chapter 2). We further hypothesized that individuals who reported a VRI would rely more on vision when determining the PU than those who did not report a VRI as indicated by an increased relative visual weighting

## 3.3 Methods

### 3.3.1 Participants

The experiment consisted of 41 participants (mean age 21.05 ± 4.33, 25 females). The experiment was conducted in agreement with the Declaration of Helsinki and followed guidelines approved by the ethics committee of York University. All observers signed informed consent forms before taking part in the experiment and were naïve as to the purpose of the study at the time of testing. They reported normal or corrected-to-normal vision and no vestibular, balance, or depth problems.

### 3.3.2 Apparatus

Stimuli were presented in an Oculus Rift CV1 virtual headset. The CV1 has a field of view that extends approximately ±110° diagonally. The screen has a 1,080 x 1,200-pixel resolution per eye and a 90Hz refresh rate. Stimuli were created in Unity (Version 5.5.2f1, Unity Technologies SF, US) on an Alienware Area-51 R2 with an intel i7 core, and a Nvidia GeForce GTX 980 graphics card. The projection was stereoscopic and was actively linked to the position of the participant's head. Therefore, distance cues were available from stereoscopic cues and motion parallax.

### 3.3.3 Visual Stimuli

#### 3.3.3.1 Move-to-Target Task Stimuli

The virtual hallway was the same as used in Chapter 2 and consisted of a multicolored stained-glass floor with a simulated width of 9m. There were walls on either side of the floor that had vertical black and white stripes (each stripe was approximately 1m wide) and were 1000m high so that the viewer could not see over the top (see Figure 3.3 B). The walls and the floor extended 10,000m in front of the viewer. There was no ceiling, so the simulated blue sky and sun provided the light source. In additional there were no shadows in the environment. The horizon was at eye level so that participants could see down the hallway and was also present when the walls were not visible (Figure 3.3 A).

The target distance was indicated with a red 3D rectangular box 5m x 1m x 1m in size (see Figure 3.3 A) drawn with one edge towards the viewer. The hallway's walls were not visible at the same time as the target was presented. The distance to the target was defined as being from the center of the participant (the location of the camera) to the center of the target.  Participants' eye height was set to the top of the pillar so that the viewing angle of the scene was the same for all participants.

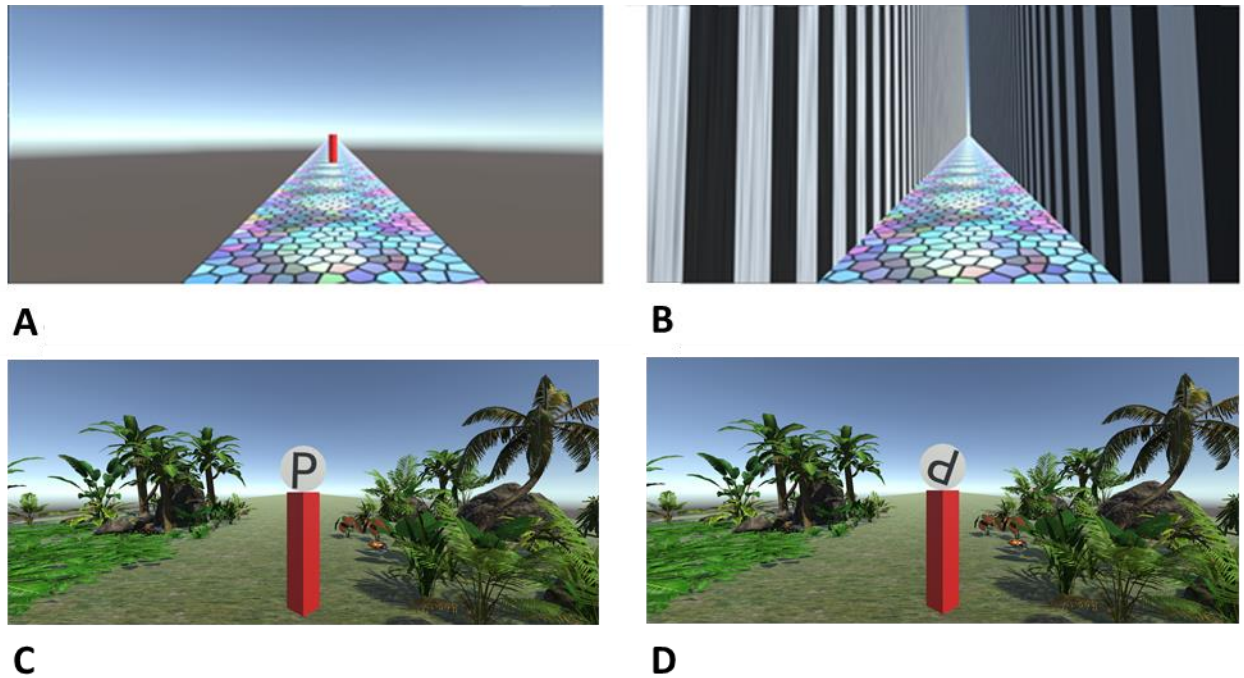



*Figure 3. 3* Screen captures of the different environments. (A) is the hallway while the target is visible, and the walls are invisible and (B) is the hallway once the participant has clicked the left mouse button and they are beginning to move. (C) is an example of the upright (0 degree) visual scene in the OChaRT environment. (D) Is the same visual scene from C but with the ambiguous shape at a different orientation.

3.3.3.2 OChaRT Environment Stimuli

The virtual environment consisted of a grass floor surface with several types of virtual plants, rocks, and motionless virtual frogs. In the center of the environment was the same red target pillar from the MTT environment. It was presented at a simulated distance of 10m from the participant and had the same size and orientation as the pillar in the MTT environment. Resting on top of the red target was a flat white disk with a diameter of 2m. In the center of the dish was an ambiguous symbol “ ᗡ ” (Figure 3.3). Illumination was from the same location and direction as the hallway environment and the horizon was presented at eye height.

### 3.3.4 Tasks

#### 3.3.4.1 Move-to-Target Task (MTT)

At the beginning of every trial, participants saw the target (Figure 3.3A) projected at a pseudo-randomly determined distance of either 10, 20, 40, 60, or 80m. Participants were instructed to pay attention to how far the target was from them and, when ready, to click the left mouse button. Immediately upon the click, the target disappeared, the hallway walls appeared, and the participant began to virtually accelerate at $9.8 m/s^2$ down the hallway. When the participant felt that they had reached the location of the previously visible target (when their head was inside the target) they clicked the right mouse button to stop the motion. Immediately afterwards the next trial started with the participant repositioned at their original position in the hallway, with the target at a new distance from them, and the walls rendered invisible. Each target distance was presented to each participant 10 times resulting in 50 trials per participant. Two additional trials, one at the beginning of the experiment at 5m and one at the end presented at 200m were also included but were not used in the analysis. The first was used to familiarize the participant with the environment and how the trials worked and in the last trial the far target indicated the experiment was over.

Participants completed the task three times, standing upright, lying supine on a bed with their feet against a wall, and lying prone on a bed with their head off the edge of the bed. In the prone posture a box was placed beneath the person's feet to simulate the wall. The order of body orientations was determined using a Latin square method.

#### 3.3.4.2 OChaRT

The participant's task was to decide if an ambiguous symbol  (Figure 3.3 C and D), presented in various orientations, looked more like a "p" or more like a "d". The response was forced choice and were made with mouse clicks- a left clicked was used to indicate a "p" and a right click was used to indicate a "d". The stimuli were presented for 500 milliseconds at which point the screen went black if no response was made and stayed black until a response was made.

The angle of the symbol was varied in the subsequent trial based on the participant's response following a Parameter Estimation by Sequential Testing (PEST) function (Taylor & Creelman 1967). The PEST finds the point of subjective equality (PSE) where the  is equally likely to be identified as a "p" or a "d".

Participants completed the task once lying on their left side and once standing, with the order varying by participant. In the left-side-down posture, layers of foam were placed under the participant's head so that it would be level. For each of the two body postures there were five visual angles of the visual environment. For each of the five visual background angles there were two ranges of orientations of the character, one that started with the character at 0° (an upright 'p') relative to the visual environment, and one that started at 180° (a 'd') relative to the visual environment. For the starting points, a random angle between +45° and -45° (where positive indicates tilted left relative to upright in the visual environment) was added. There were thus 10 staircases per body posture, which were interleaved such that on each trial one of the 10 staircases and its corresponding background would be randomly selected but could not be selected again until all ten had had a trial. Each body posture took approximately 10-15mins to complete.

### 3.3.5 VRI Measures

VRI experience was measured in three different ways over the course of the experiment.

#### 3.3.5.1 Method 1. Questionnaire following the move-to-target task

At the end of each body posture during the move-to-target task (MTT), after the participant was instructed to remove the HMD, participants verbally answered a questionnaire to assess how their posture was perceived during the task. The instructions were read in full after the first posture but for the 2$^{nd}$ and 3$^{rd}$ body posture the first paragraph was omitted so that it would be less repetitive for the participant.

> “I am going to describe 3 different ways you could have felt while you were in the virtual environment. It’s important that you think about how you felt while you were in the virtual environment, while you were stationary and while you were moving.
> Due to the nature of virtual reality people can have different experiences, all of these are normal, and I am interested in how *you* felt while you were in the virtual environment. While you were in the virtual environment you might have felt one of 3 things, or possibly a combination of them. So, did you feel like you were:
>
> 1. looking up, and when moving, moving upwards. You might think of this lying down while flying upwards towards the sky
> 2. looking forwards, and when moving, moving forwards. You might think of this as moving similar to how you regularly move when not in VR, such as standing upright and moving forwards
> 3. looking down and when moving, moving downwards. You might think of this as lying down and looking over an edge down a cliff or maybe like falling
> 4. Some combination or other experience”

Participants reported which of the four options best described how they felt while they were wearing the HMD. The order of options 1-3 was randomized each time they were asked. Option 4 always came last. The participant’s response was recorded by writing it down and they were then asked to elaborate on how their body’s orientation felt during the experiment, which was also recorded. While this did mean that when answering the questions, the participants had to reflect back on their experience, it allowed for the experimenter to use props to demonstrate the perceived postures, for instance the experimenter oriented their hand in different ways to help clarify the orientation and motion being described. If option 2 was selected participants were grouped as having a VRI and given a score of 1. If option 1 or 3 was selected participants were grouped as “No VRI” and given a score of -1. If option 4 was selected participants were grouped as “Other” and given a score of 0.

#### 3.3.5.2 Method 2. VRI Over Time

After completing all three postures of the MTT task the participants completed an additional ten trials of the MTT while supine. All participants completed the same set of five distances twice, with the final target distance being the target presented at 10m. After this, participants were asked if their perceived orientation more closely matched the perception of "Standing upright, with your feet on a floor surface, looking forward" or "Lying down with your feet on a wall surface looking up". They were then told that their perceived orientation would be measured for approximately 1 ½ minutes to get an idea of how it persists over time. They were told that if they felt closer to "Standing upright, with their feet on a floor surface, looking forward" they should click the left mouse button and hold it. If they felt their experience was closer to "Lying down with their feet on a wall surface looking up" they should click and hold the right mouse button. They were told to hold the button for as long as the feeling persisted and if at any point their perception should change, they should change which button they were holding. They were also instructed that it was possible their perception might not change and that was fine as well, so long as they were holding one of the two buttons at all times. The computer counted how many frames out of 5,000 frames at 90 frames a second (approximately 1.5minutes) the left mouse button was pressed. An "upright" response for a total of 2,500 frames (half the time) or more was classified as "VRI" and the participant was given a score of +1. Zero frames was scored as "No VRI", score -1. If the VRI button was pushed for between 1 and 2,400 frames they were grouped as "Other", score 0.

#### 3.3.5.3 Method 3. VRI Verbal Report

After completing the left-side-down posture for the OChaRT, participants were asked to describe how they felt generally during the task, with regards to their orientation. If their verbal report more closely matched an upright experience they were grouped as "VRI", score +1. If it more closely matched lying down, they were grouped as "No VRI", score -1. A response closer to "unsure", "sometimes", or "confused" were grouped as "Other", score 0.

#### 3.3.5.4 VRI Group Decision

During the OChaRT, the visual background changed every trial so a VRI could not be determined at the end of each body posture as accurately as the MTT. As well, the VRI likelihood while left-side-down might not be the same as the likelihood of experiencing a VRI while supine or prone. Therefore, in order to determine the VRI groups the scores for each of the different VRI measures was summed. If the sum was positive then the participant was grouped as being "VRI likely" and was considered a "VRI" person, if the sum was negative the participant was grouped as "VRI unlikely" and was considered a "no-VRI" person, and if the sum was "0" the person was grouped as "Other".

### 3.3.6 General Procedure

After reading and signing the consent form, participants were shown a letter p and a letter d and had to verbally indicate what they saw. Order was counter balanced. All participants could correctly identify the letters. Participants were reminded they could stop at any time during the experiment without penalty.

Participants were then shown how to put on the HMD and how to adjust it using the straps on the side and top of the headset so that the visual environment was clear. They then adopted the appropriate first MTT posture and ran through the MTT task (see above). Afterwards they removed the HMD and completed the VRI MTT measure (see above). Their responses were recorded by the experimenter. The MTT task was then repeated in the 2$^{nd}$ and 3$^{rd}$ body postures and the VRI MTT measured after each posture. In all, the three postures, explanations, and VRI measures took approximately 30 minutes.

Once the MTT task was complete, the concept of a VRI was explained to participants in detail with examples. Participants were told that some people experience the illusion often, some people experience some of the time, and some people never do, and that each type of person was valuable to the experiment. Participants were told their data would be analyzed based on which VRI group they were in, so it was important they answer honestly. This was done to try to reduce any "good participant" bias where the participant might claim to experience a VRI when they did not. Once we felt participants understood the concept, participants put the HMD back on and completed the VRI Over Time measure (method 2 above). In all, including explanation this task took approximately 10 minutes.

After the VRI Over Time measure was completed, participants removed the HMD. They were then placed in either a standing posture or the left side down posture and the instructions were explained. Once the headset was back on the OChaRT task was started for that posture. Upon completion participants removed the HMD, were put into the next posture and completed OChaRT in that posture. In all, with explanation, the OChaRT task took 20 minutes in total. After the left-side-down OChaRT posture, the VRI verbal report was completed and recorded by the experimenter. Overall, the entire experiment took about 65minutes.

## 3.4 Data analysis

### 3.4.1 Moving to target

Once the MTT data were collected, the average distance traveled was found for each target distance in each posture for each participant, resulting in 15 means for each participant.

Two participants were removed from the MTT analysis as they either could not perform the task or were not able to discriminate between the different distances. The first participant went to a distance of 38.99m for the 10m condition, 10.27m for the 20m condition, and 29.91m for the 40m condition. The other participant went to a distance of 64.80m for the 10m condition, 136.01m for the 20m condition, and 23.64m for the 40m condition.

An outlier analysis was then run on the remaining participants where, for each target distance in each posture, data were removed if they fell outside ±2 standard deviations from the mean. Then, the residuals were plotted in QQ plots and boxplots to check for any remaining outliers. It was revealed that some additional data points were still significant outliers. For example, with the boxplots there were still data that fell 3 boxes or more away from the upper and lower hinges (the hinges for the central 50% of the data around the median) indicating they fell outside of 99% of the rest of the distribution (the distribution of data following the ±2 standard deviation removal). These data points were removed. Due to the outlier removal all the data from one participant (15 errant data points) were completely removed resulting in a total of 35 out of 585 data points being removed (5.98%). See Figure 3.4 for the distribution of the data.

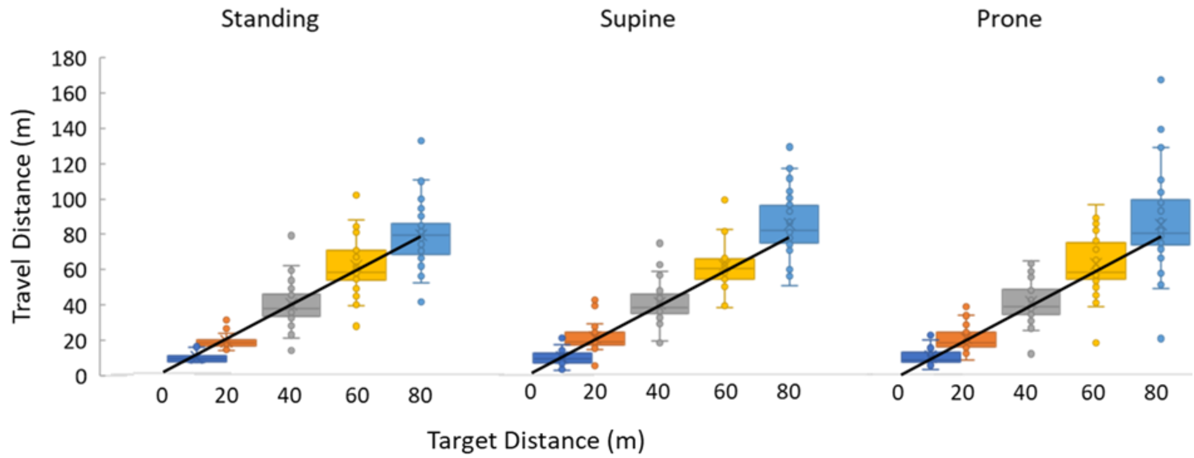



*Figure 3. 4* The distribution of the data for each target distance for each posture are plotted in boxplots. A boxplot divides the data into quantiles where the box represents a range of one quartile and the line represents the median. The "whiskers" on either end define 1.5 quartiles from the edge of the box. Mild outliers fall outside of that range with extreme outliers falling 3 quartiles from the edge of the box. Overall participants appear to have been able to distinguish the different target distances in each posture. The black line represents perfect performance.

Participants were then divided into the VRI groups using the results of the VRI measures described above. Four participants were in the "Other" group and their data were not used in the rest of the analysis. Of the two participants who were removed for not being able to discriminate distances, one was from the no-VRI group, and one was from the Other group. The participant whose data were completely removed during the outlier analysis was from the VRI group.

Then, for each person, the gains of the travel distances for each target distance were calculated for each posture. The gain is defined as perceived distance (the target distance) expressed as a fraction of the actual distance travelled and was used as a measure of the effectiveness of the optic flow cue in eliciting the perception of motion. Gains less than 1 indicate that participants had to travel further than the target distance to feel they had passed through the target distance (less effective use of visual cues to motion, low gain) and vice versa.

3.4.2 Modeling the contribution of vision, the body, and gravity on the PU

For the OChaRT, the midpoint between the two PSEs was found. This resulted in 10 estimates of the PU for each participant (2 postures and 5 background orientations). Reported angles are in body coordinates, with 0° being above the head, and negative numbers counterclockwise.

Before fitting the OChaRT data to the model, outliers were removed. For each of visual angles the average angle and standard deviation was found. Any value that fell outside of 2 standard deviations from the mean was removed. This resulted in 22 out of 410 (5.37%) OCHaRT data points being removed. For any participant who had missing data, when their weightings were fit to the model that visual angle for that posture was simply excluded from the fit. However, after the outlier analysis one participant had only 3 data points left, with no data from their lying posture. Because of this no reliable estimate of the PU could be obtained and they were removed from the analysis resulting in a total of 26 out of 410 (6.34%) data points being removed.

For each participant, we modeled the relative contributions of the visual, body, and gravity cues (see Figure 3.1) in determining the PU using a weighted vector sum model (see Dyde et al. 2006), where the length of each vector corresponds to its relative weight, by fitting the following formulae to each person's data set.

$$\overrightarrow{PU} = \overrightarrow{vis} \cdot w_v + \overrightarrow{gravity} \cdot w_g + \overrightarrow{body} \cdot w_b \qquad \text{Equation (1)}$$

$$w_v + w_g + w_b = 1 \qquad \text{Equation (2)}$$

Where $w_v$, $w_g$, and $w_b$ correspond to the weights assigned to the visual, gravity and body vectors respectively. The model was fit to each person's data using the Marquardt-Levenberg technique (Marquardt, 1963). The model was constrained such that a negative weight was set to 0.

## 3.5 Results

### 3.5.1 VRI group

Based on the VRI measure (see methods) 51% of participants were classified as VRI, 39% were found not to have a VRI. and 10% were classified as “Other”. See Table 3.1 for a break down of the VRI results based on each of the VRI measures.

*Table 3. 1* The table contains the percent of participants who were grouped as having a VRI, no VRI, or “Other” on the three VRI measures described in the methods, as well as the results of the overall VRI group classification. The “MTT Supine” and “MTT Prone” rows show the results of the questionnaire following the MTT task while supine or prone. The “Time” row shows the results of the “Over Time” method, and the “OChaRT LD” refers to the response given during the “VRI Verbal Report” following the left side down posture of the OChaRT. The “VRI Group” row shows the result of the overall “VRI Group Decision” summation based on the results of the other VRI measures. The numbers in the brackets are the number of participants in each group.

| VRI Measure | VRI % | No VRI % | Other % |
|---|---|---|---|
| MTT Supine | 46.34 (19) | 31.71 (13) | 21.95 (9) |
| MTT Prone | 36.59 (15) | 26.83 (11) | 36.59 (15) |
| Time | 51.22 (21) | 31.71 (13) | 14.63 (6) |
| OChaRT LD | 24.39 (10) | 63.41 (26) | 12.20 (5) |
| VRI Group | 51.22 (21) | 39.02 (16) | 9.76 (4) |

#### 3.5.1.1 Post-hoc comparison between the MTT and the OChaRT LD VRI distributions

Two chi-square tests were run that examined the relationship between VRI rate (VRI, no-VRI, and Other) and VRI measurement type between the MTT task and the OChaRT task. The MTT Supine measure was significantly different from the OChaRT LD measure $X^2(1) = 8.27$, $p= 0.016$. The MTT Prone measure was significantly different from the OChaRT LD $X^2(1) = 12.08$, $p= 0.002$. The differences remained significant if only the VRI and no-VRI rates were compared for each of the measures. Overall, the OChaRT LD task lead to a significantly lower VRI rate than the MTT while tilted.

Referring to Table 3.1, during the MTT 46% participants experienced a VRI while supine and 37% while prone with many other participants experiencing “Other” changes to their perceived orientation (for a total of 68% while supine and 74% while prone). However, during the OChaRT task significantly fewer participants reported a VRI (24%); and even when the “Other” category was included (total of 37%) the difference was close to a 50% reduction in the number of people reporting a VRI.

### 3.5.2 Move-to-target

#### 3.5.2.1 Gain by VRI group

A linear mixed model was chosen to analyse the gain data. This method was chosen as after the outlier analyses some participants had missing data so using a repeated measure ANVOA would have resulted in losing those participants.

The linear mixed model compared the effects of VRI group (2), target distance (10), and posture (3) on travel distance in the virtual reality environment.

Posture and target distance were set as fixed repeated effects, VRI was set as a fixed effect, and the participant ID was set as a random effect (random intercept) to help take into account the variability in performance between participants. Degrees of freedom were approximated using the Satterthwaite method (Satterthwaite, 1946). Before running the linear mixed model, the assumptions of a LMM was tested.

The presence of additional outliers was determined by plotting the residuals in QQ Plots. If the data fell past 3 quantiles it was considered an extreme outlier and removed. This resulted in the removal of an additional 16 data points, or 3.07% of the remaining data. All other assumptions were met.

A main effect of VRI group on gain was found $F(1, 304.543) = 4.888$, $p < 0.028$. The average gains for each VRI group and the gains for each participant at each VRI group are displayed in Figure 3.5.

A main effect of distance on gain was found $F(4, 152.07) = 4.859$, $p < 0.001$. A post hoc analysis with Sidak correction revealed that the 10m (mean= 1.25, SE= 0.52) distance differed from 60m condition (mean= 1.04, SE= 0.034, $p = 0.010$) and the 80m distance (mean= 1.00, SE= 0.25, $p < 0.001$). The effect of distance on gain will be discussed further in section 5.3 *Visual self-motion perception and gain*.

No other effects were found.

#### 3.5.2.2 The Presence of a VRI

A simplified model was then run where the standing posture was removed. This was done in order to between compare how the experience of a VRI would affect gain. All other factors were the same.

A main effect of VRI group on gain was found $F(1, 201.669) = 4.028$, $p < 0.046$.

A main effect of distance on gain was found $F(4, 128.792) = 3.896$, $p < 0.005$. A post hoc analysis with Sidak correction revealed that the 10m (mean= 1.27, SE= 0.71) distance different from the 80m distance (mean= 0.979, SE= 0.30, $p = 0.003$). The effect of distance on gain will be discussed further in section 5.3 *Visual self-motion perception and gain*.

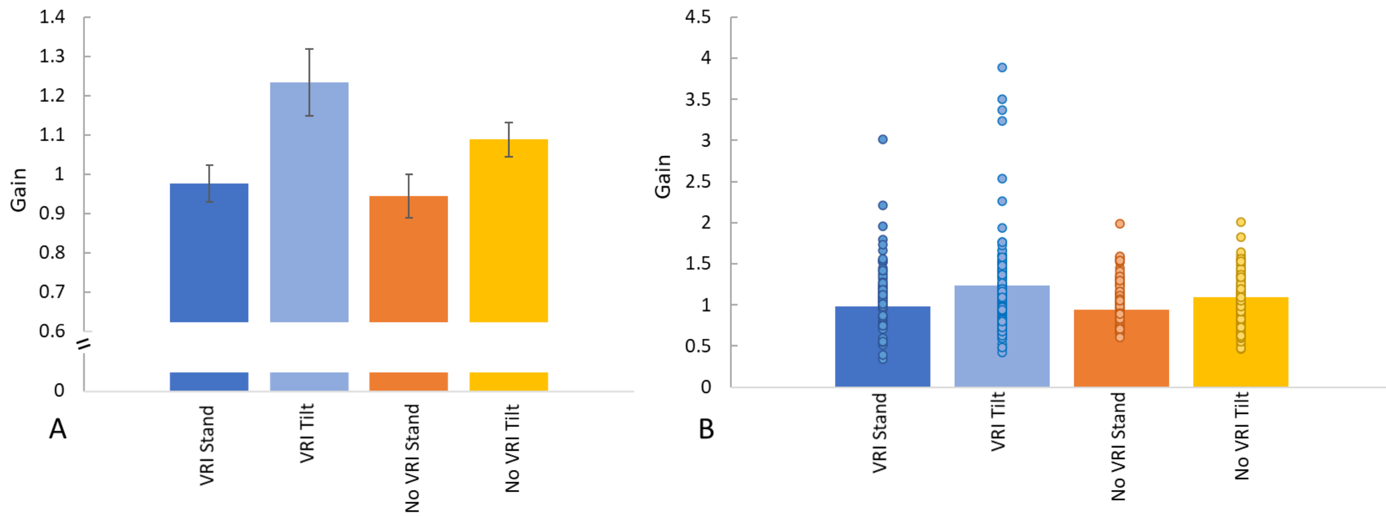



*Figure 3. 5* The bars in each plot display the average vection gains (target distance divided by actual distance) for the standing and the average of supine and prone body postures. The plot A shows the supine/prone data divided according to the original VRI categorization (see methods). The circles in plot B are the individual data points for that VRI group and posture. Blue, VRI group, orange no-VRI group. Note the different Y-axis.  Error bars in A and B are ± standard error of the mean.

3.5.3 OChaRT Results

Data were fitted with the three-vector model as described in the methods to calculate the relative weights of vision, the body and gravity for each participant. Three 2 tailed t-tests with heterogenous variance (Welch's t-test) were run on these weightings, with alpha set at 0.05. Each t-test looked to see if one of the weightings, such as the gravity weightings, differed between the VRI group and the no-VRI group. The results are shown in Table 3.2 and the data for each participant are plotted as a ternary plot in Figure 3.6 for both the VRI and no-VRI group. Data from the "other" group are not included in this analysis. Gravity was given a significantly higher weighting and vision a significantly lower weighting in the VRI group compared to the no-VRI group.

*Table 3. 2* The results of the three t-tests comparing sensory weight between the VRI and no-VRI groups. The average relative contribution, in percent, of each of the three cues when determining the PU. The numbers in brackets are the standard deviation. The columns are the three cues, the rows are the VRI group. The alpha denotes the significance value from the t-test, with the bolded alphas indicating a result with a p less than 0.05.

| **Mean Weight (SD)** | **Gravity %** | **Body %** | **Vision %** |
|---|---|---|---|
| **VRI group** | 12.66 (±10.59%) | 54.01 (±15.93%) | 32.93 (±11.41%) |
| **No-VRI group** | 5.95 (±7.76%) | 53.22 (±13.22%) | 40.82 (±10.16%) |
| **T- test (alpha)** | ***t*(35.55)= 2.49, *p*= 0.035, *d*= 0.81** | *t*(31.49)= 0.18, *p*= 0.723 | ***t*(31.19)= -2.32, *p*= 0.027, *d*= -0.77** |

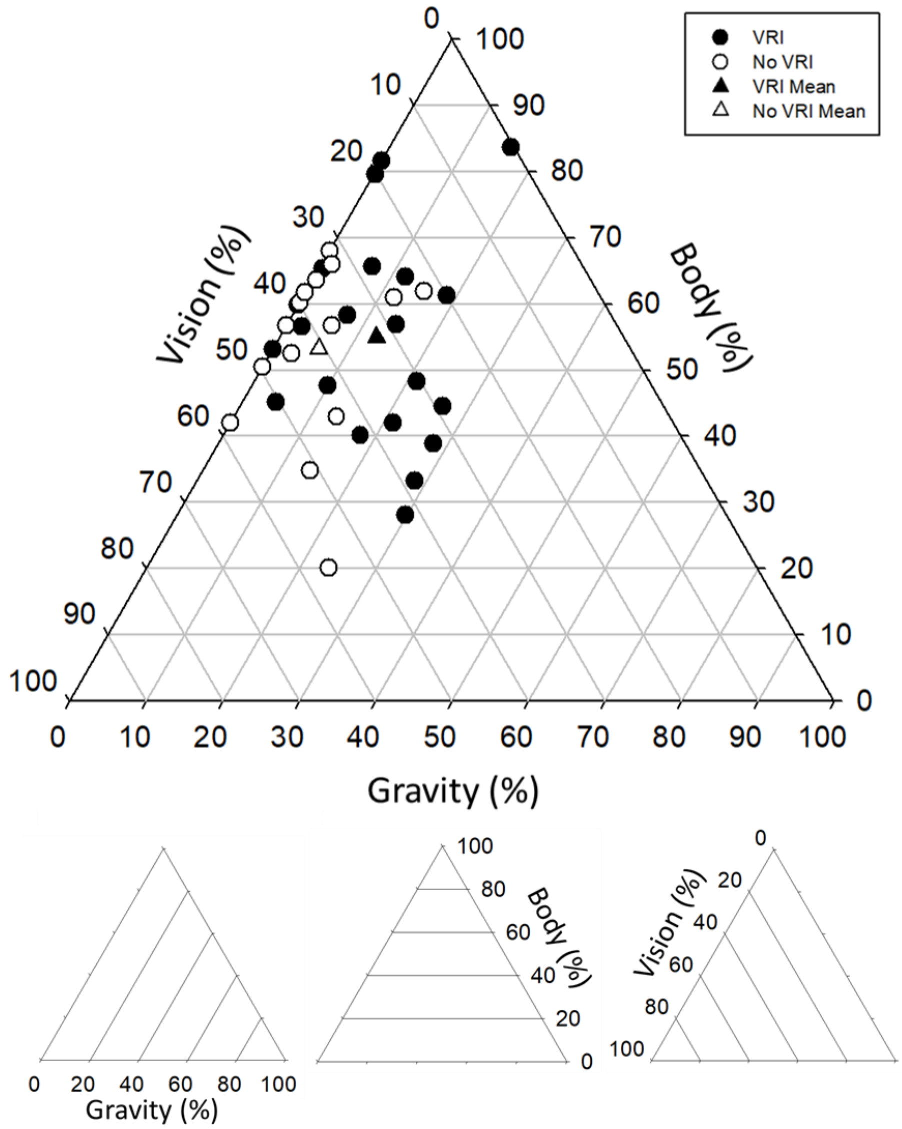



*Figure 3. 6* The relative weighting of vision, the body and gravity for participants in the VRI (filled circles) and no-VRI (open circles) groups sum to 100% and are plotted as a ternary plot. Means are shown as filled (VRI) and open triangles (non-VRI). The inset is a key indicating how to read a ternary plot. The gravity weightings are read along the diagonal lines starting at the bottom left of the triangle where 0% gravity weighting corresponds to the left-most diagonal line. The body weights are read along the horizontal lines with 0% body weighting corresponding to the bottom-most horizontal line. The visual weights are read along the diagonal lines starting at the apex of the triangle where 0% visual weight corresponds to the right-most diagonal line.

## 3.6 Discussion

When people experience multiple alternative frames of reference indicating lying and standing at the same time, some are dominated by the visual cue and are said to be experiencing a visual reorientation illusion (VRI). Others are more aware that they are lying down and do not experience a VRI. Here, we confirm our earlier work (Chapter 2) showing that a person who is experiencing a VRI needs less visual motion to feel that they have travelled through a given distance than a person who is less likely to experience a VRI. These results are also in line with Preuss et al. (2018). In the present experiment our VRI group, who were likely to have experienced a VRI while tilted, needed to travel approximately 13% less far through a virtual environment to perceive that they had passed through a particular distance than individuals without a VRI, the no-VRI group (Figure 3.5). This suggests an enhancement in the processing of visual information during a VRI which we hypothesised might correspond to such individuals placing a higher weighting on vision in the multisensory process of determining their motion and orientation (Chapter 2; Preuss et al. 2018; Howard & Hu 2001). We found that indeed there were significant differences in the relative weightings given to the visual, body, and gravity cues for determining perceived orientation in individuals who were more likely to experience a VRI compared to those who were less likely to experience a VRI. Interestingly however, and contrary to our hypothesis, members of the VRI group relied more heavily on the gravity cue, and actually less on vision when determining the perceptual upright (Figure 3.6 and Table 3.2). This seems counterintuitive, why might it be?

### 3.6.1 OChaRT

Our no-VRI group had lower vection gains while tilted compared to individuals who were tilted and experiencing a VRI (Figure 3.5). The no-VRI individuals also placed a higher weighting on vision and less on gravity when determining the perceptual upright (Figure 3.6 and Table 3.2) compared to our VRI group. Indeed, referring to Figure 3.6, many (n=12) of our participants actually had a 0% gravity weighting when determining their perceptual upright, which was especially true for the no-VRI group where 47% of this group had a 0% gravity weight compared to the VRI group where only 24% of the group had a 0% gravity weight. Interestingly, the visual weight decreases in astronauts (relative to the weighting of the remaining body cue) initially in space (Harris, Jenkin, Jenkin, Zacher, & Dyde, 2017) despite them also, like our VRI group, showing enhanced visually induced self-motion (Oman et al. 2003; Young et al. 1986).

The findings here might reflect the weightings of each sense depending on the task (Fraser, Makooie, & Harris, 2015) with a different weightings being applied during orientation and self-motion tasks. The reliability of the cues for each task may be different (Ward, Bockisch, Caramia, Bertolini, & Tarnutzer, 2017). Determining the subjective upright depends on the reliability of up signaled by each different sense. During visual motion perceived location depends on how reliable each sense is in determining location during the motion. For instance, during the OChaRT task the pressure on the person's side as they were lying left-side-down might have enhanced the vestibular upright. On the other hand, during the MTT the constant pressure on the back or stomach might have led to the proprioceptive cue being seen as less reliable, particularly if the visual upright were favoured.

However, it is possible that the relative weights we measured during the OChaRT task could explain the different gains we found in the MTT in the two groups. The presence of visual-vestibular conflict between the orientation cues that was present during the MTT task could have affected the reliability of the cues indicating the change in location (Fetsch et al. 2009). We might expect that individuals who rely more on gravity for orienting on Earth would be more impacted if gravity suddenly becomes less reliable and is ignored. Similarly, individuals who rely less on gravity should be less impacted by its removal.

### 3.6.2 Conflict detection and cue weighting

#### 3.6.2.1 Orientation

On Earth, in situations where a conflict between gravity and the visual upright occurs, individuals who rely more on gravity cues might be more likely to detect that the visual and gravity vectors are not aligned – they might be more sensitive to the conflict. Correspondingly, individuals who place less emphasis on gravity or vestibular cues on the other hand might be less likely to register a conflict.

It has been proposed that intersensory conflicts, when two senses provide contradictory information, can lead to motion sickness (Reason & Brand, 1975). The perceived conflict might arise from the difference between the expected sensory cues and the experienced sensory cues. As the difference or error increases, the likelihood and severity of motion sickness increases (Oman 1990; see review by Gallagher & Ferrè, 2018). Building upon this theory, Bles et al. (1998) propose that all motion sickness might arise from a conflict between the sensed and expected vertical.

Reports from astronauts, particularly in the first few days in orbit, suggest a relationship between the occurrence of a VRI and motion/space sickness (Oman 2007; Young et al. 1986). If an astronaut experiences a conflict in their perceived orientation, where they might feel the area below their feet is the "floor" but then they see a co-worker at a different orientation, a VRI might provide a resolution to this conflict since one cannot maintain two "ups".

A lower level of VRIs then would then indicate a lower level of conflict between the potential ups in an environment. This suggests that the OChaRT environment may have had less conflict present than the MTT environment - potentially due to the visual up varying with each trial during the OChaRT procedure. This could explain the approximately 50% reduction in VRI rate found in the OChaRT environment (see Table 3.1). In the MTT environment, there was more conflicting information as both orientation and motion information generated conflicting visual and non-visual cues, compared to the OChaRT environment where only orientation cues were in conflict. Additionally, during the MTT there was only one visual scene that was always visible, and it was presented at only one orientation (relative to the observer). For the OChaRT task, multiple different visual scenes were presented for just 500msec each. The addition of visual motion during the MTT may have also enhanced the perceived orientation. In a study by Howard and Childerson (1994) when participants were seated in a static fully furnished room that was placed at different orientations between 0° (upright with respect to the person) and 120° participants only felt partially tilted (less than 20° in all cases). However, when the room was visually rolled around the participants, up to 60% of the participants felt that they were rolling through the full 360° degrees suggesting that concurrent motion might enhance or support visual orientation.

A study on Earth by Dichgans, Held, Young, and Brandt (1972) had people view a rotating scene while they were stationary. The visual and vestibular cues in this case were in conflict, with the visual cues indicating rotation and the vestibular cues indicating that the person was stationary. The participants resolved the conflict by combining the two perceived ups into a single percept and experienced a partial tilt. Cerebellar damaged patients however perceived a greater tilt (Dakin, Peters, Giunti & Day, 2018), despite still having access to somatosensory information telling them they were not tilted (MacNeilage & Glasauer, 2018) pointing to the cerebellum as the locus of conflict detection.

Similarly, in a study by Weech, Calderon, and Barnett-Cowan (2020a) they had people play a nauseating virtual reality game and report how nauseous they felt. The nausea experienced in the virtual environment likely resulted from conflicting visual and vestibular sensory cues. When vestibular noise was induced via galvanic vestibular stimulation (GVS) participants experienced less nausea while in the virtual environment. The authors argued that when noisy GVS was applied the vestibular cue was seen as less reliable and down weighted which reduced the experience of nausea.

The cerebellum uses sensory information, including vestibular information, to create internal models which can predict the consequences of new sensory information as well as planned actions (see Cullen 2019 and Therrien, & Bastian, 2015, for review). The error between the predicted and the actual experience can then be used to recalibrate perception and behaviour (Cullen, 2019; Laurens, & Angelaki, 2017; Merfeld, Zupan, & Peterka, 1999). Dakin et al. (2018) argue that for the patients with cerebellar degeneration their vestibular cue would be less reliable because of the cerebellum being so intimately involved in processing vestibular information (Dakin et al. 2018; Laurens, Meng, & Angelaki, 2013; Bronstein, Grunfeld, Faldon, & Okada, 2008) and so the vestibular (gravity) cue would be down weighted in such patients following maximum likelihood estimation principles (Ernst & Banks, 2002). The relatively increased visual weight would then result in them experiencing more perceived tilt.

Our participants had normally functioning vestibular systems, so like the control participants in Dakin et al. (2018), they would experience conflict between visual and vestibular cues. This is relevant here because participants who weighted the gravity cue more should experience a more intense visual-vestibular conflict than participants who weighted gravity less.

### 3.6.3 Robustness

According to Bayesian integration, during multisensory integration information from each sense is weighted depending on its reliability. That is, the less noisy a cue is, the higher it is weighted (Ernst & Banks, 2002). Since VRI-likely individuals weighted gravity more, this would imply that the gravity cue had a higher internal precision leading to the higher weight found in the OChaRT task.

Integrating cues works well to improve the reliability of the overall estimate when the difference between the information provided by each cue is small. But sometimes cues can give very different estimates, such as the different uprights of the ambiguous hallway environment used in the current experiment. If the difference between the two estimates is large, a person might exhibit robust integration where the cue that is more discrepant is discounted, or "vetoed" (Ernst & Banks, 2002; Young, Landy, & Maloney, 1993; Rosas, Wagemans, Ernst, & Wichmann, 2005; Landy, Maloney, Johnston, & Young, 1995).

Robust integration can lead to changes in behaviour (Ernst & Banks, 2002). In their review on Causal Inference, Shams and Beierholm (2010) discuss reports that animals that navigate using both path integration and landmarks give a larger weight to landmark cues if the two cues provide similar estimates. However, if there were a large discrepancy between the information provided by path integration and landmarks, then the landmark cue is ignored and the animal relies on path integration. But how is the discrepant cue determined?

When integrating cues, a cue with a more precise estimate, and thus a lower variance, will be more sensitive to small changes compared to less precise cues. So, when integrating cues with very different estimates, the more precise cue might appear to be the more discrepant cue. Thus, the less precise visual estimate should be favoured. Additionally, vision and gravity are not the only cues being used. During the MTT the body up is inline with the visual up. The agreement between the body and vision should help in the determination of which cue is the discrepant cue, again leading to the gravity cue being discounted.

Overall, the results on the OCHaRT appear to support the findings on the MTT task. When placed lying down in the MTT environment, the estimates provided by the visual and gravity up become discrepant. Participants who rely more on gravity cues will be more likely to notice the conflict and the more precise gravity cue should be the cue to ignore. Ignoring the gravity cue will then lead to an increased reliance on visual cues, reflected as a higher gain and an increased likelihood of experiencing a VRI.

### 3.6.3 Conflict Model

In Chapter 2, I proposed a “reweighting model” to explain the findings of the higher gain during a VRI. When all of the orientation cues in the environment (visual and non-visual) provide the same estimate of upright, the participant should correctly feel upright and their visual weighting will be their “default” visual weight (w). In the absence of a detected conflict (no-VRI individuals), the visual weight would be unaffected. However, if a visual-vestibular conflict were detected the visual weighting under this model would be increased to w’. The gain of the visual motion would then be processed as the visual information multiplied by the weighting: VRI participants having a higher visual weighting (w’) would therefore need to travel less far to perceive themselves as having gone through a given distance. Based on the findings here, we have now extended our model to include the idea that individuals who are more likely to detect the conflict and then reweight -- leading to a VRI and a higher visual gain -- are those with initially higher gravity weightings that suggest the gravity estimate is more precise in such people leading to robust integration in which the gravity cue is rejected as discrepant. This model is drawn out in Figure 3.7.

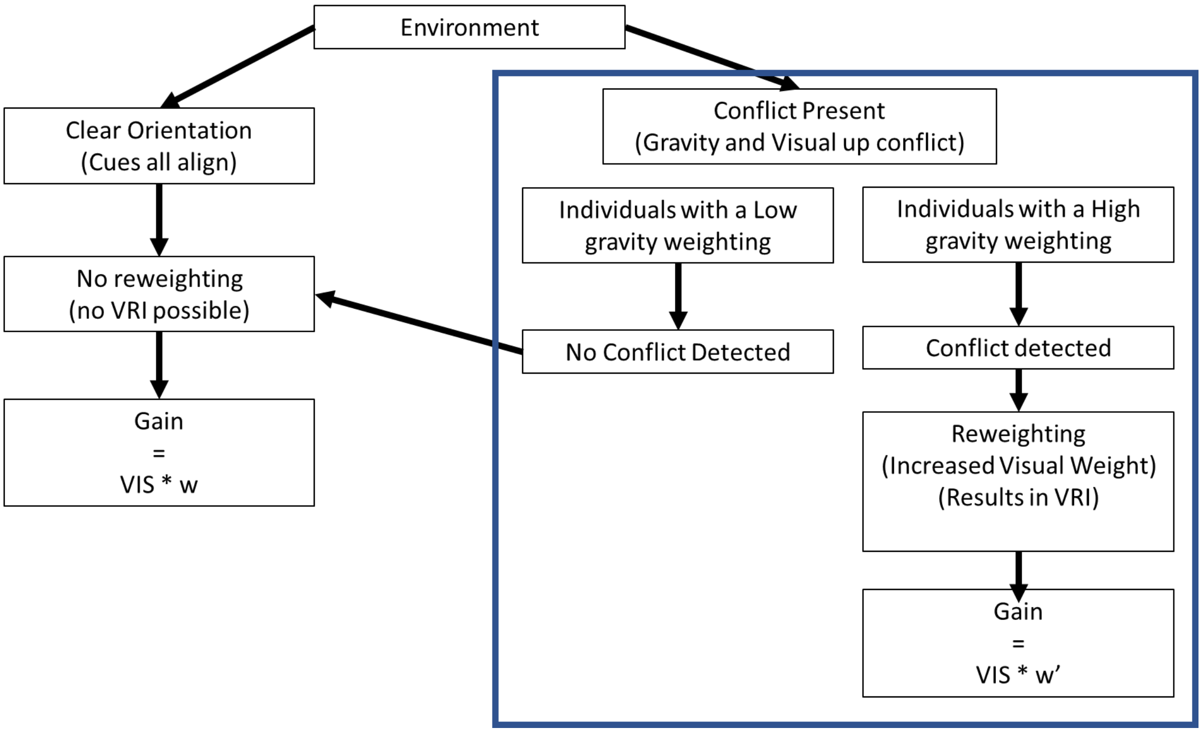



*Figure 3. 7* A model of how conflict between visual and vestibular cues to orientation might affect perceived motion. VIS refers the optic flow information and w refers to the weight given to the cues. Within the blue box are two groups of participants, those with relativity high gravity weights (left), and those with relatively low gravity weights (right). The model indicates how the relative weights might alter perceived travel distance.  The left side of the diagram indicates the situation when all cues are aligned.

## 3.7 Conclusion

People's vulnerability to experiencing a visual reorientation illusion affects their vection gain: VRI-vulnerable people generally have higher vection gains. Here, we measured the relative weighting of the visual and non-visual cues to orientation and found that VRI vulnerable people, in addition to having higher vection gains also tended to put greater weight on the gravity cue to orientation. These findings can be reconciled by considering the response to conflict in VRI vulnerable and VRI resistant people.

# CHAPTER 4: The effects of long-term microgravity exposure on perceived distance traveled

*The data used in this chapter are part of a larger project called VECTION sponsored by the Canadian Space Agency with my supervisor, Dr. Harris, as the PI. VECTION looks at orientation, self-motion, and distance perception on Earth and in 0g and consists of three tasks, with the task in the current paper being the 2nd of the three. The results presented here are preliminary with approximately half of the planned data currently collected. I joined the VECTION project after the proposal had been submitted and accepted but have working on it throughout the development and data collection phase.*

*Along with the other members of the VECTION team I took part in the discussions about the design of the three tasks. I ran pilot tests on the prototypes to determine if the experiment looked and functioned as intended, as well as calibrating the environment to ensure the distances used matched the intended real-world distances. I also took part in two parabolic campaigns where we ensured the equipment would work in a 0g environment.*

*I helped with the documentation and paperwork, such has helping to write or edit the standard operating procedures (SOPs), Experiment Requirements Document, midterm review, participant instructions, etc.*

*I helped to acquire the equipment (such as headsets, laptops, neck braces, earplugs, suitcases, pens, USB keys, etc.) needed to run the experiment at York and at the Johnson Space Centre (JSC) in Houston, and ensured that the equipment, such as the laptops, matched the equipment on the International Space Station (ISS) (both hardware and software).*

*Lastly, I helped with the data collection in Houston, and occasionally with the control data collection at York University, along with the organization and analysis of the data.*

## 4.1 Abstract

Previous studies (Allison, Zacher, Kirollos, Guterman, & Palmisano, 2012; Oman, Howard, Smith, Beall, Natapoff, Zacher, & Jenkin, 2003; Young & Shelhamer, 1990) have found that while free floating in 0g people may be more sensitive to visual information, particularly visual self-motion information. Complementary to this observation, my previous chapters have shown that when participants are placed in an ambiguous environment in which visual and gravity "ups" are not aligned, some participants reported their orientation as being aligned with the visual environment suggesting that they tended to ignore gravity in favour of vision, resulting in a visual reorientation illusion (VRI). Such VRI-vulnerable participants also show an increased sensitivity to visual self-motion (a higher gain). However, in Chapter 3 I reported that VRI sensitive individuals weighted gravity information as more important, and visual information as less important, for determining their perceived upright compared to individuals who were less vulnerable to VRIs. I proposed a reweighting hypothesis in which this increased sensitivity to gravity made VRI individuals more sensitive to visual-vestibular conflict. I hypothesised that the inter-sensory conflict then led to reweighting the sensory cues such that vision was favoured. If ignoring gravity led to an increased visual weight, I hypothesized that removing gravity should as well. However, after testing astronauts in microgravity, I found that after a few days in 0g there was actually no significant change in vection gain. After adapting to 0g by being in space for several months, however, I found that the gain decreased, which suggested a decrease in the visual weight. This reduced gain continued upon re-entry to 1g. A reduction in gain on the MTT could be related to a decrease in the weight given to visual cues and potentially an increase in the weight given to body cues which has been found previously for perceived orientation in 0g and upon return to Earth (Harris et al. 2017). Overall, this suggests that the reweighting hypothesis may be insufficient to explain the results found in this dissertation.

## 4.2 Introduction

### 4.2.1 Self-motion and Gravity

Moving around on the International Space Station is done very differently from moving around on Earth. The lack of gravity means that astronauts glide around smoothly and that their otoliths are stimulated only by their own acceleration. In Chapters 2 and 3 of this dissertation, I demonstrated that altering the relationship between gravity and the body affects the amount of optic flow needed to create the perception of having travelled through a given distance. Here, I investigate the effect of taking gravity away altogether on visually simulated self-motion.

Visual cues seem to become more important when gravity is removed. Oman, Howard, Smith, Beall, Natapoff, Zacher and Jenkin (2003) speculated that in microgravity people might increase the weight given to vision which may cause changes in the experience of the visually induced sensation of self-motion (vection). They had three participants view visual motion through a hallway environment and indicate when they started to feel vection as well as how fast the motion felt subjectively. Vection onset time was reduced and participants felt significantly faster motion while in 0g compared to their pre-flight baseline. While free floating, two of the three participants also experienced significantly faster motion compared to when they were restrained with a force spring pulling them “down” to the deck surface. There was also a significant difference in their perceived speed pre-flight versus early post-flight while sitting, particularly for faster visual motion speeds (2 out of the 3 participants showed the effect for faster speeds). While the direction of the effect unfortunately is not stated, based on the verbal report it seems to be the case that vection experience was impaired soon after returning to Earth.

In this same series of experiments, they also looked how entrance into 0g affects the perception of rotational motion. Participants looked at one of two rotating hallways, or a rotating dot display, which rolled about the line of sight, and indicated the magnitude of vection on a 5-point scale. Overall, vection magnitude was higher in 0g than pre-flight, and was stronger while free floating than when they were restrained. Pre-flight they found no difference between supine and sitting conditions. The findings here are similar to another study by Young and Shelhamer (1990) which also looked at the intensity of vection induced by the same rotating dot display. Participants were tested sitting and supine on Earth, and free floating in space. There was also a tactile condition in 0g where bungee cords secured the astronaut's feet to a surface. Participants indicated vection magnitude through deflections of a joystick. Vection intensity was found to be higher in 0g compared to the on-earth conditions. However only 3 of the 7 participants showed a reliable effect of the tactile condition, where the tactile cues lowered vection intensity relative to the free-floating condition.

The anecdotal reports from the Young and Shelhamer (1990) paper support their quantitative findings that rotational vection was stronger in 0g and that there were fewer dropouts (periods of loss of vection sensation). One participant summed it up nicely by saying "Vection was stronger (in flight). It came on sooner. It was easier to maintain. I had fewer dropouts in the free-floating rotating dome." Additionally, the results of Young and Shelhamer (1990) show an increase in vection intensity from the first day in 0g until about the $3^{rd}$ day in orbit (out of the 4 test days and 7 days in orbit in total). Overall, they concluded that their results indicated an increased reliance on visual cues in 0g compared to on Earth.

However, these observations are not supported by a study by Allison, Zacher, Kirollos, Guterman, and Palmisano (2012) who had people view smooth and jittering visual motion (see Chapter 1.4 *Reweighting or Reinterpreting*) on Earth and during brief periods of microgravity created by parabolic flight. While on Earth (and during the 1g phase of the flights), they found that jitter enhanced vection relative to the smooth motion, as had been reported previously (Palmisano, Gillam, & Blackburn, 2000; Palmisano, Allison, & Pekin, 2008). In 0g, jitter was also found to enhance vection compared to smooth motion, but to less of an extent. Importantly, they found no enhancement of the strength of smooth vection during the 0g phase. However, consistent with previous studies, they found that that there was a decrease in vection strength post flight.

Overall, these few studies suggest that while free floating in 0g people may be more sensitive to visual information, at least for perceived self-motion. This increased effectiveness of visual self-motion might result from an increased visual weight due to a loss of the gravity vector, which in turn might be reduced when increasing the emphasis of the body vector using bungy cables (Oman et al. 2003; Young & Shelhamer, 1990). Additionally, based on the findings of Allison et al. (2012) and Oman et al. (2003), the speed and strength of vection appears to be impaired upon return to Earth suggesting that people might be less sensitive to visual motion upon return to 1g compared to their baseline performance.

### 4.2.2 Orientation and Gravity

Further evidence for an increased reliance of visual cues in microgravity comes from orientation perception in 0g. The loss of gravity results in an unstable perception of "down" and visual cues in particular appear to influence a person's perceived orientation where polarized cues such as other people and the visual "up" of a room can induce spontaneous reorientations in a person's perceived upright (for a review see Oman, 2007). Specifically, visual reorientation illusions (VRI) occur when the identity of surfaces such as "floor" change due to visually attending to an object or location. VRIs can be induced intentionally in space by attending to the area below the feet or another surface, or unintentionally such as when suddenly seeing a person who is in a different orientation (Oman, 2007). VRIs indicate the importance of visual environment cues to self-orientation in microgravity. The decreased perception of a stable down in 0g might also hold over post flight based on the findings from an astronaut in a study by Harm and Parker (1993). Prior to microgravity flight the astronaut found it difficult to reinterpret the walls as a floor when navigating a virtual/simulated environment. However, one day post flight he found this task easy. After a week post flight, he reported difficulty in mentally rotating the environment again.

On Earth, VRIs can occur in certain environments where the visual "up" indicated by the environment and the gravity "up" are put into conflict. A VRI indicates a visual resolution to this conflict and suggest a reliance on visual cues over gravity cues (see Chapter 3; Howard & Hu, 2001).

While the studies described above suggest a higher visual emphasis upon entry to 0g, the idea that the loss of gravity results in an increase in the weighting given to visual information was not supported by findings by Harris, Jenkin, Jenkin, Zacher, and Dyde (2017). The authors measured the relative contributions of vision, the body, and gravity for determining upright while on Earth and the contributions of vision and the body in microgravity. They found no changes in the visual weight in microgravity compared to on Earth, which they interpreted as an increase in relative weighting of the body. Upon return to Earth this increased reliance on the body compared to vision was still found.

These results are interesting in the context of the findings reported in Chapters 2 and 3 of this dissertation. Chapter 2 described how when participants were exposed to a virtual environment that had conflicting visual and gravity ups, some participants experienced a VRI. The VRI indicated a visual resolution to this conflict, in which participants showed a higher perceptual gain when using vision to determine their motion. This is consistent with the anecdotal reports of what happens to vection in space when gravity is also unreliable. We labelled this apparently increased emphasis our "reweighting hypothesis". However, Chapter 3 describes how, despite having a perceived up that was verbally reported as being mainly influenced by vision and having a higher perceptual gain during a move-to-target task, participants with a VRI actually relied less on visual cues (lower visual weight) and more on gravity cues when determining the perceived "up", compared to individuals who were less likely to have a VRI. Although counterintuitive at first sight, both of these observations are compatible with what seems to happen to vection and cue weighting in space.

In the previous Chapters it was still unclear if ignoring the gravity vector, suggested by the VRI, led to an increased emphasis or weight given to visual cues as seemed to be indicated by the increased gain for VRI individuals during the MTT. The ultimate test to see if vision is impacted by changes in the use of gravity is to remove gravity. The previous experiments, discussed above, relied on measures of the sensation of vection produced by optic flow. Here we use the move-to-target task (MTT) to quantify the perceived motion relative to the environment induced by the optic flow. Participants were moved through a hallway at 0.8m/s/s and had to stop when they felt they had arrived at the position of a previously seen target. The distance they traveled allows us to determine the effectiveness of the optic flow, where shorter travel distances indicate more effective optic flow. The low acceleration was used in order to reduce the blurring of the screen during faster motion.

### 4.2.3 Hypotheses

In the current experiment, I investigate how changes in the level of gravity might affect the amount of visual motion necessary to reach different distances in a virtual reality environment.

Prior to microgravity exposure participants completed the MTT sitting and supine. When the VECTION project was proposed it was argued that the supine condition would simulate the effects of 0g on Earth, similar to how bedrest studies are used to simulate the effects of microgravity on the body (See reviews by Hargens & Vico, 2016 and Taibbi, Cromwell, Kapoor, Godley, & Vizzeri, 2013). Before carrying out the experiments reported in chapters 2 and 3 I would have hypothesized that the supine posture would be associated with a higher self-motion gain than the sitting posture as there should be an increased sensitivity to visual cues when supine similar to in those instances mentioned above. However, based on my findings in Chapter 2 and 3, I now predict that any such affect would be based on the presence of a VRI. In the current experiment we unfortunately did not collect VRI data. It is difficult to predict if the environment might lead to a high likelihood of experiencing a VRI in the participants as we have seen previously that hallway environments can lead to high levels of VRI in some people but also low levels in others, particularly while supine. If participants travel less far while supine compared to sitting this might indicate that the majority of the participants experienced a VRI while supine, working backwards from the findings in Chapter 2.

I hypothesize, based on the findings reported in Chapter 2 and Chapter 3, as well as the findings of Oman et al. (2003) and Young and Shelhamer (1990), that (1) when the MTT is performed in 0g there will be an enhancement to visual cues early in flight resulting in an increased undershooting (a greater perceived distance of travel for a given amount of visual movement) in 0g compared to baseline measurements taken on Earth while sitting. Further, based on the findings of Harris et al. (2017), Allison et al. (2012), Oman et al. (2003), and Young and Shelhamer (1990), I hypothesise that, (2) upon return to Earth, there will be an overall decrease in vection gain, perhaps reflecting a decrease in visual weighting, potentially due to an increased emphasis placed on body cues. In addition, I hypothesise (3) that this decrease in gain after return will be greater for the sitting posture than the lying posture as when sitting the participants may feel more of the force of gravity pushing them down along their long body axis compared to while lying supine. Additionally, when sitting upright participants have to continuously make adjustments to their posture to stay upright. Sitting off center or tilted might result in problems remaining upright and might result in increased attention given to body cues, particularly following exposure to 0g where this would not be a concern and given that after long term exposure to 0g some of the participants might have lost some muscle and balance capacity.

Lastly, I hypothesise (4) if any tilt-translation-reinterpretation (see section 1.5 *Gravity and visual self-motion perception* for a summary of the tilt-translation interpretation hypothesis) occurs, there will also be an increased gain while supine, relative to sitting after return.

An Earth-based control group was tested in parallel to the astronaut participants in order to determine if any effects seen might be due to practise effects. The control participants were of similar age and sex as the astronaut participants.

## 4.3 Methods

### 4.3.1 Participants

#### 4.3.1.1 Astronaut participants

The experiment consisted of 11 participants (mean age 45.44 ± 4.39yrs, 5 females). The participants were all astronauts from NASA, the CSA, and the ESA. All participants were or are scheduled to be in space at least 100 days. At the time of writing this chapter not all of the participants had completed all of the experiment. See Table 1.1 for a breakdown of how much each subject had completed. My analysis will therefore be based on just the data collected so far.

| Astronauts | Pre Lying | Pre Sitting | Space Early | Space Late | Return Lying | Return Sitting |
|---|---|---|---|---|---|---|
| 1 | ■ | ■ | ■ | ■ | ■ | ■ |
| 2 | ■ | ■ | ■ | ■ | ■ | ■ |
| 3 | ■ | ■ | ■ | ■ | ■ | ■ |
| 4 | ■ | ■ | ■ | ■ | ■ | ■ |
| 5 | ■ | ■ | ■ | ■ | ■ | ■ |
| 6 | ■ | ■ | ■ | | | |
| 7 | ■ | ■ | | | | |
| 8 | ■ | ■ | | | | |
| 9 | ■ | ■ | | | | |
| 10 | ■ | ■ | | | | |
| 11 | ■ | ■ | | | | |

*Table 4. 1* This table displays how much of the experiment each of the eleven astronaut participants have completed. A filled in green square represents a completed experimental session for that participant.

4.3.1.2 Control Participants

The control group consisted of 20 participants (mean age 42.6 ± 1.61yrs, 10 females). The participants were recruited from York University and via personal correspondence. All the control participants completed all of the experiment.

The experiment was conducted in agreement with the Declaration of Helsinki and followed guidelines approved by the ethics committee of York University, the Canadian Space Agency, and NASA (Human Research International Multilateral Review Board). All participants signed informed consent forms before taking part in the experiment and were aware of background information regarding the experiment but not to the possible outcomes. Participants reported normal or corrected-to-normal vision and no vestibular, balance, or depth problems.

### 4.3.2 Hardware

Stimuli were presented in an Oculus Rift CV1 virtual headset. The CV1 has a field of view that extends approximately ±110° diagonally. The screen has a 1,080 x 1,200-pixel resolution per eye and a 90Hz refresh rate. The projection in the HMD was presented as head fixed. This was done as there are no motion sensors for the CV1 onboard the ISS and without the gravity cue the accelerometers are affected. The experiment was programmed in Unity.

The computer used in orbit was the HP ZBook15 Gen2 with an Intel Core i7-4810MQ Quad Core, and it had an NVIDIA Quadro K610M graphics card, to which access was kindly granted by the ESA. The computer used on Earth was the closest commercially available hardware to the ESA computer in orbit, the HP IDS DSC 4D Z15 Base NB PC with an Intel Core i7-4810MQ Quad Core and it also had an NVIDIA Quadro K610M graphics card. The computer used on Earth was also reimaged so that its software matched the computer in orbit. All responses were made using the *3G* Green *Globe Co Ltd* (FDM-G62 P) finger mouse.

### 4.3.3 Stimuli

The virtual hallway consisted of a dark floor surface and a lighter ceiling. The simulated hallway was 3.3m wide and 3.3m high. The walls were black with glowing white circles presented on the wall. The circles were used to provide optic flow cues during simulated motion through the environment. The circles appeared and disappeared at random time intervals such that they could not be used as landmarks to solve the task without relying on optic flow.

The target distance was indicated with a blue window frame box that occupied the entire hallway (see Figure 4.1A).

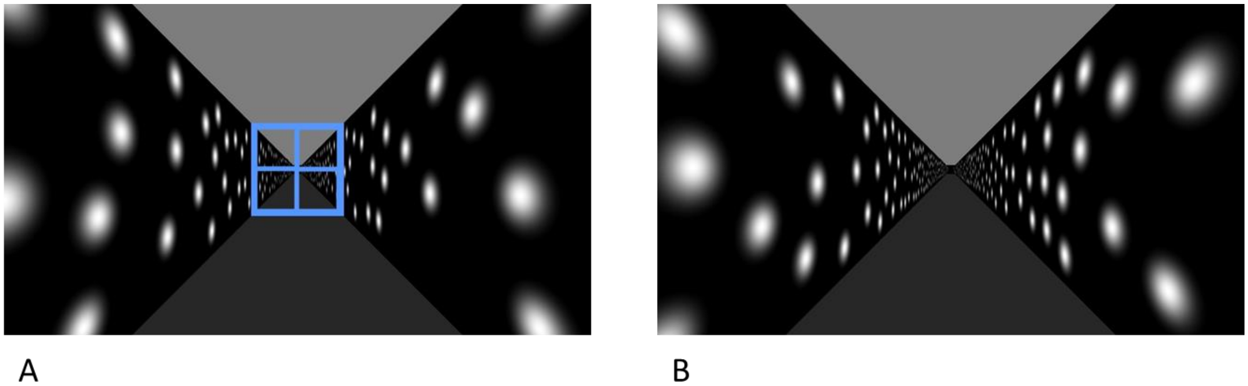



*Figure 4.1* A depiction of the virtual environment that participants saw. A) shows the blue target that indicates the distance through which the participants had to travel. B) Shows the view that participants saw once the blue target was extinguished and they were accelerating down the hallway.

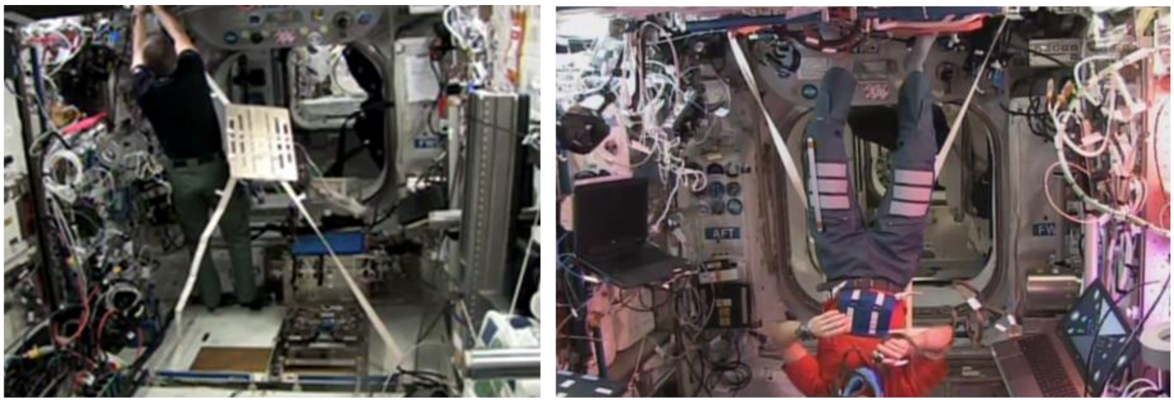
### 4.3.4 Test session

#### 4.3.4.1 Astronaut group

The experiment spanned five test sessions: One pre-flight session that had to be conducted between 60 and 180 days before launch (baseline data collection, BDC 1); two sessions in space, the first of which (Space Early) had to be completed as soon as possible after arrival on the space station (between three and six days after launch); the second in-space testing (Space Late) was conducted between 80 and 100 days after arrival in orbit. Astronauts were also tested twice on Earth after re-entry: once as soon as possible after re-entry (BDC 2; between three and six days after re-entry) and once 50 to 70 days after re-entry (BDC 3). This final testing was done to confirm whether participants had returned to baseline performance. Since the hypothesis addressed with this final testing session is not within the scope of the present dissertation, it has been excluded from the analysis.

For each on earth-based testing session (BDC 1 and BDC 2), participants completed the task twice: once supine and once sitting. BDC 1 Lying is referred to as “Pre Lying” and BDC 1 Sitting is referred to as “Pre Sitting”. The BDC 2 postures are referred to as “Post Lying” and

“Post Sitting”. The order of the postures was counterbalanced across subjects and test session. In orbit, the task was completed once, semi free floating where the participant was attached to a back plate that was tethered to the deck to ensure the participant didn’t float into the walls of the ISS and that the participants’ legs did not touch the deck. See Figure 4.2 for an image of the backplate.



A B

*Figure 4.2* This figure depicts the backplate. Figure 4.2A shows the backplate being set up. Figure 4.2B shows an astronaut secured to the backplate. Their head is positioned out of the picture in order to help maintain anonymity, during testing their head and feet are visible to the researchers to check that no movement or contact with surfaces takes place.

4.3.4.2 Control Group

For the control group each session followed the same timeline as the astronaut group however for Space Early and Space Late were of course still performed on Earth. In these sessions the participants completed the VECTION experiment once during each session in the supine posture. Space Early for the control group will be referred to as “Control Early” and Space Late will be referred to as “Control Late”. BDC 1, BDC 2, and BDC 3 were performed the same as the astronauts - participants completed the experiment in both a sitting and supine posture. The BDC’s for the control group will be referred to as “Control BDC” followed by the number. The order of the postures was counterbalanced across subjects and test session.

As for the astronauts’ data described here, the final testing of the control participants (BDC 3) was excluded from the analyses presented here.

### 4.3.5 Procedure

#### 4.3.5.1 On Earth Procedure

If the testing was being done on Earth, the experimenters arrived in the testing room prior to the participant and set up the experimental laptop and organized the equipment that would be used. Once the equipment was set up and the participant was ready, they put on a neck brace (Proglide Cervical Collar) to help limit any head movement during the experiment. They also put in ear plugs to reduce background noise. With the help of the experimenter, they then got into either the sitting or lying posture and were handed the Oculus which they put on and adjusted so that it was clear and comfortable. They were shown how to adjust the headset at BDC 1. They were then handed the finger mouse and could start the experiment when ready.

With the headset on, participants perceived themselves to be in a virtual reality hallway in which they completed a Move-To-Target task (MTT). During the MTT, participants viewed the target presented at a simulated distance and were asked to note the distance to the target (Figure 4.1A). Once ready, they pressed either top button on the finger mouse and the target disappeared (Figure 4.1B). At this point, the participant began to visually accelerate forwards at 0.8m/s/s. Once they felt they had passed reach the previously seen target's position, they clicked either top button on the finger mouse to stop the motion. Then, their location was reset in the hallway, and a new target was shown at one of the simulated target distances. There were 10 possible target distances (6-24m, in steps of 2m) and each distance was presented three times during the experiment corresponding to 30 trials in total.

During the BDCs, once the first posture was completed, participants removed the headset but left on the neck brace and earplugs. They also answered questions regarding any nausea or dizziness. If none was present, they were then directed to the next posture, replaced the headset, and began the experiment again. Upon completing the second posture, and questions, the participant was thanked, and they left.

#### 4.3.5.2 On-Orbit Procedure

Prior to the start of the experiment the participant arrived at the testing location, usually in the Columbus module of the ISS, and set up the backplate. This was done by securing straps to beams on two surfaces opposite each other in the ISS module as shown in Figure 4.2A. The participant also set up two cameras at positions such that their body and head could be seen and recorded. This was done in order to determine if any additional movement occurred which could affect the results of some of the VECTION tasks. The participant then set up the experimental laptop.

Once the experiment was ready, the participant put on the neck brace following the directions given to them in BDC1 and put in their ear plugs. Afterwards the participant got into the harness (see Figure 4.2B) and secured themselves with the straps. They then put on the headset that was floating nearby and took hold of the finger mouse. The experiment then progressed identically to the On-Earth Procedure (section 4.3.5.1 *On Earth Procedure*) except that there was only the one posture and no questions were asked regarding dizziness or nausea.

Once the VECTION experiment was completed, the participant removed the headset and removed themselves from the harness. They then collected the data from the laptop using a USB device and placed it in another computer from which it could be transmitted down to Earth. They then stowed the equipment. The participant was thanked, and they left the area.

## 4.4 Data analysis

### 4.4.1 Astronauts

The data reported here are the visual travel distances in meters at which the participant stopped indicating that they felt they had moved to the position of the target presented on that trial. Before averaging, values were labelled as a “mistrial” and removed if the participant did not stop the visual motion before 100m.

In the subsequent analysis of each participant's data, data points were removed if they fell outside of ±3 SD of all participants' data for that target distance and test session. This resulted in the removal of 70 data points out of 1590 (4.41%). Once outliers were removed, the average distance traveled was found for each target distance for each participant in each posture and test session, resulting in a total of 60 means for each participant. The mean data are plotted in Figure 4.3.

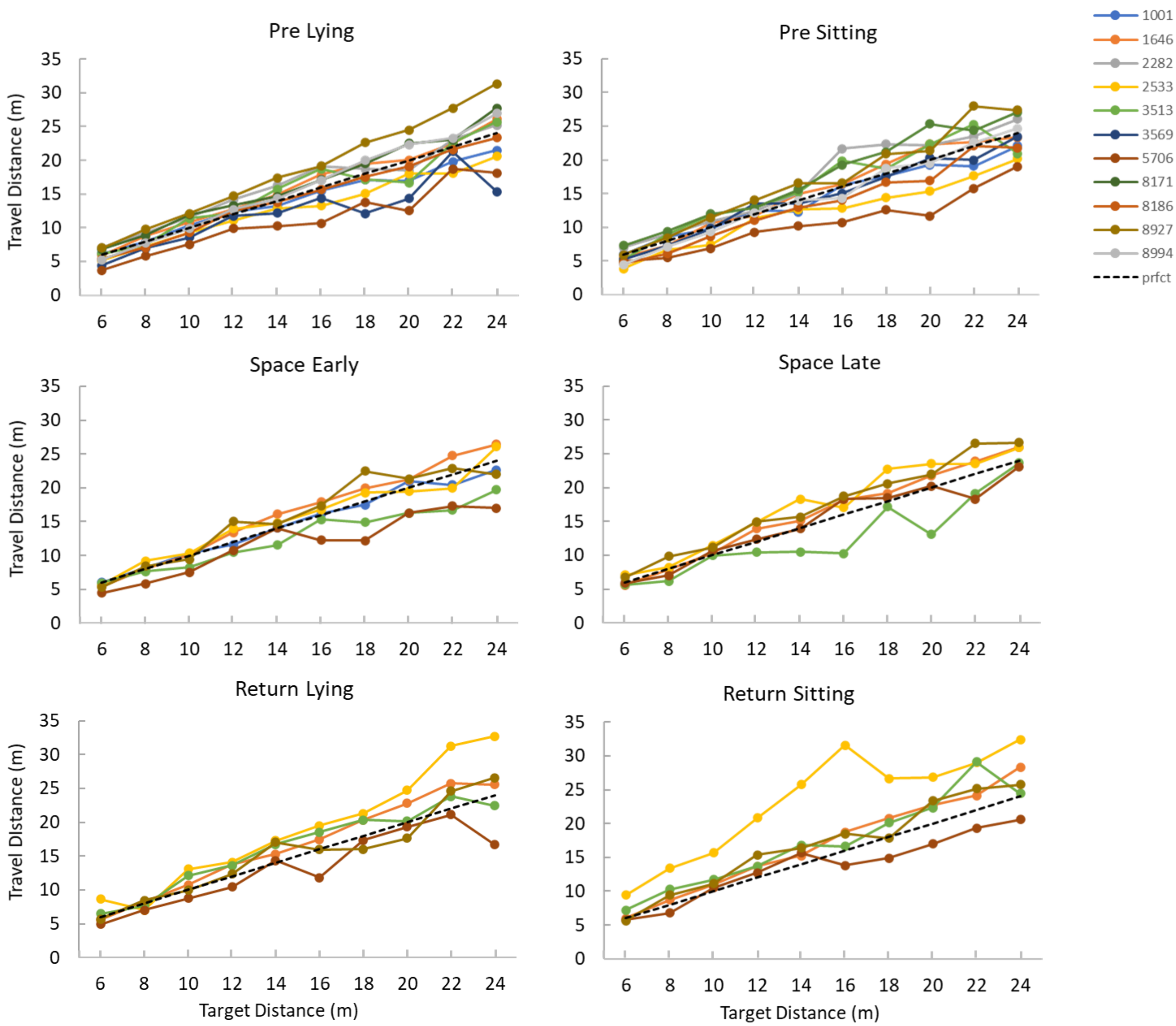



*Figure 4. 3* Each panel displays the distance each astronaut traveled for a given target distance for each of the six data collection sessions. The black hashed line indicates perfect performance. Astronauts are identified by code numbers as shown.

### 4.4.2 Controls

Before averaging, values were labelled as a "mistrial" and removed if the participant did not stop the visual motion before 100m.

In the subsequent analysis of each participant's data, data points were removed if they fell outside of ±3 SD of all participants data for that target distance and test session. This resulted in the removal of 10 data points out of 3600 (0.278%). Once outliers were removed, the average distance traveled was found for each target distance for each participant in each posture and test session, resulting in a total of 60 means for each participant. The mean data are plotted in Figure 4.4.

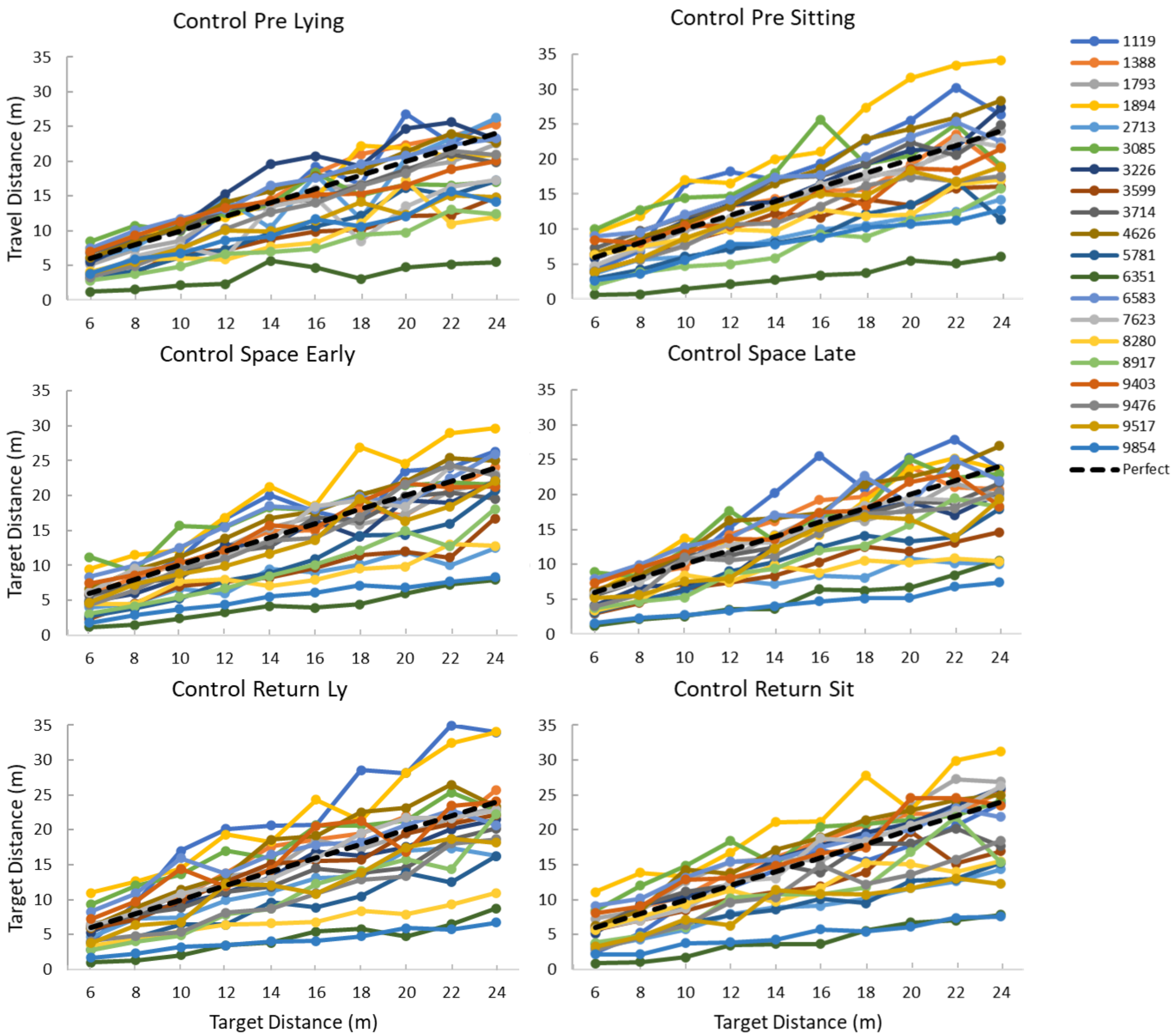



*Figure 4. 4* Each panel displays the distance each control participant traveled for a given target distance for each of the six data collection sessions. The black hashed line indicates perfect performance. Participants are identified by code numbers as shown.

### 4.4.1 Gains

The mean gain was calculated for each test session. The gain was calculated by dividing the target distance (perceived distance) by the average distance traveled for each target distance (actual distance), and then computing the average across all target distances. The gain represents the effectiveness of the optic flow cue in eliciting the perception of motion where a high gain represents a higher effectiveness of optic flow compared to a lower gain. This was done separately for both the astronaut and control data sets.

### 4.4.2 Linear Mixed Model

Two linear mixed models were chosen to analyse the gain data, one for the astronaut data and an identical one of the control data. This method was chosen due to the number of incomplete data sets in the astronaut group, since the experiment is on-going. In the case of the astronaut group participants were included even if they were missing data.

The linear mixed models compared the effects of test session (6 test sessions) and target distance (10 target distances) on travel distance in the virtual reality environment.

Test session and target distance were set as fixed repeated effects, and the participant ID was set as a random effect (random intercept) to help take into account the variability in performance between participants. Degrees of freedom were approximated using the Satterthwaite method (Satterthwaite, 1946).

### 4.4.3 Assumptions of the linear mixed model

Before running the linear mixed model, the assumptions of the model were tested. For the assumption of normality there were still a few outliers present after the initial outlier analysis.

Similar to the additional outlier analysis in Chapters 2 and 3, the presence of additional outliers was determined by plotting the residuals in boxplots and in QQ Plots. For the boxplots, if a value fell three boxes away from the upper and lower hinges (the edges of the central 50% of the data, with the middle being the median) this indicated that it was outside of 99% of the rest of the distribution and was an extreme outlier. For the QQ Plots, any point that did not fall close to the line was removed.

#### 4.4.3.1 Astronaut Group

Overall, this additional outlier analysis resulted in the removal of 16 data points out of 430, or 3.72% of the data. The data were still found to be mildly positively skewed based on the Shapiro-Wilk tests of normality, but not the Kolmogorov-Smirnov. To be sure the skew was not affecting the results the response data were log transformed and the analysis was rerun. The data were then found to no longer be skewed but the results were not affected. Because of this I decided to continue the analysis with the untransformed data for simpler interpretation. The residuals were also found to be homoscedastic and the residuals of the dependant variable were linearly related to Target Distance. Since Test Session is categorical, no assumption of a linear relationship with the dependant variable is possible.

#### 4.4.3.1 Control Group

The data for the control group were found to be positively skewed so the data were log transformed. However, the data did still show some skew (see Figure 4.5). Because of this I left the data as transformed for the analysis though whether or not the data were transformed did not affect the overall results described below. The additional outlier analysis was run on the transformed data. Two participants' datasets were removed completely. For one participant all of their data were outliers and for the second participant over half of their data points were outliers. Removing these two participants did not change the overall results of the analysis, however it did help to reduce the positive skew. From the remaining 18 participants, 12 additional data points were removed out of 1080, or 1.11% of the data. All other assumptions were met.

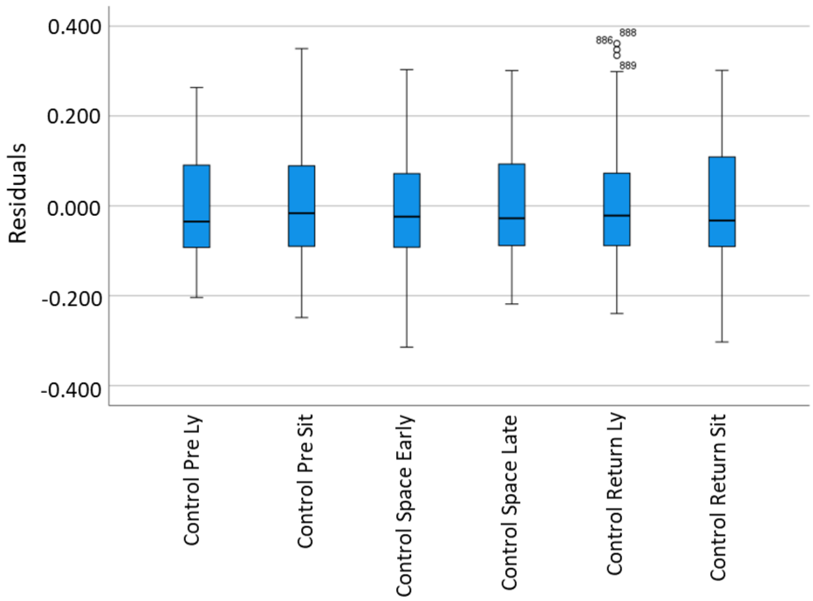



*Figure 4.5* The distributions of the residuals for each test session for the control participants are plotted above in Figure 4.4. Most of the data show a positive skew.

## 4.5 Results

### 4.5.1 Astronauts

A main effect of test session on gain was found $F(5, 56.84)= 8.655$, $p< 0.001$. The average gains for each test session and the gains for each participant at each test session are displayed in Figure 4.6. Post hoc pairwise t-tests were run to determine which of the test sessions differed from each other. No adjustments were made for multiple comparisons. The results of the post hoc tests are displayed in Table 4.1.

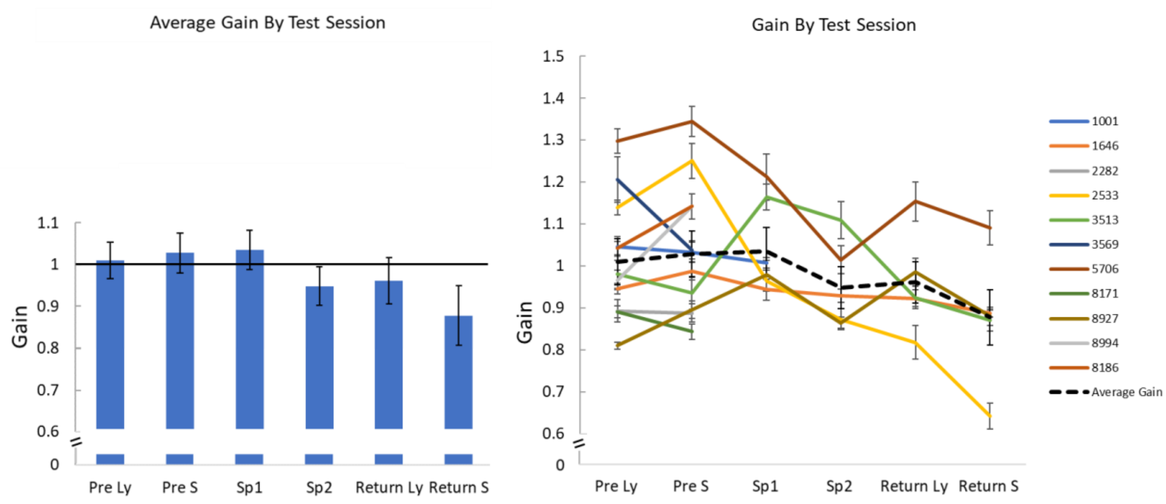



*Figure 4.6* The figure plots how the gain changes over the course of test session for the astronauts. A higher gain indicates less visual motion is needed to arrive at a target distance. The panel on the left shows the average gain for each test session, while the panel on the right shows the average gain for a test session for each participant. The black hashed line is the average gain for that test session determined from the panel on the left. Error bars are ± standard error.

*Table 4.2* The results of the post-hoc pairwise t-tests between test sessions. Mean Difference: the difference between the average gain for a row test session minus the average gain for a column test session. Positive values indicate a higher gain in the row and a negative value indicates a higher gain in the column. DOF: Degrees of Freedom. Number of Participants: the number of participants in the row condition X the number of participants in a column condition. Bolded red values indicate that the values test one of my hypotheses proposed in Section 4.2.3 *Hypotheses*.

| | | Pre Lying | Pre Sitting | Space Early | Space Late | Return Lying |
|---|---|---|---|---|---|---|
| Pre Sitting | Mean Difference | **0.018** | | | | |
| | DOF | **175.034** | | | | |
| | Number of Participants | **11 x 11** | | | | |
| | Alpha | **0.429** | | | | |
| Space Early | Mean Difference | 0.025 | **0.007** | | | |
| | DOF | 88.841 | **95.146** | | | |
| | Number of Participants | 6 x 11 | **6 x 11** | | | |
| | Alpha | 0.286 | **0.770** | | | |
| Space Late | Mean Difference | -0.062 | **-0.080** | **-0.087** | | |
| | DOF | 71.742 | **77.757** | **57.543** | | |
| | Number of Participants | 5 x 11 | **5 x 11** | **5 x 6** | | |
| | Alpha | 0.006 | **0.001** | **<0.001** | | |
| Return Lying | Mean Difference | -0.050 | -0.067 | -0.074 | 0.013 | |
| | DOF | 50.908 | 54.573 | 50.538 | 44.802 | |
| | Number of Participants | 5 x 11 | 5 x 11 | 5 x 6 | 5 x 5 | |
| | Alpha | 0.073 | 0.018 | 0.011 | 0.642 | |
| Return Sitting | Mean Difference | -0.132 | **-0.150** | -0.157 | **-0.070** | **-0.083** |
| | DOF | 62.513 | **66.350** | 61.575 | **55.405** | **59.867** |
| | Number of Participants | 5 x 11 | **5 x 11** | 5 x 6 | **5 x 5** | **5 x 5** |
| | Alpha | <0.001 | **<0.001** | <0.001 | **0.021** | **0.016** |

No main effect of target distance on gain was found *F*(9, 36.979)= 1.793, *p*=0.103. There was no interaction between test session and target distance on gain *F*(45, 16.365)= 0.660, *p*= 0.865.

### 4.5.2 Controls

There was no main effect of test session on gain *F*(5, 298.887)= 2.012, *p*> 0.05. No main effect of target distance on gain was found *F*(9, 175.407)= 1.475, *p*> 0.05. There was no interaction between test session and target distance on gain *F*(45, 66.105)= 0.169, *p*> 0.05. See Figure 4.7.

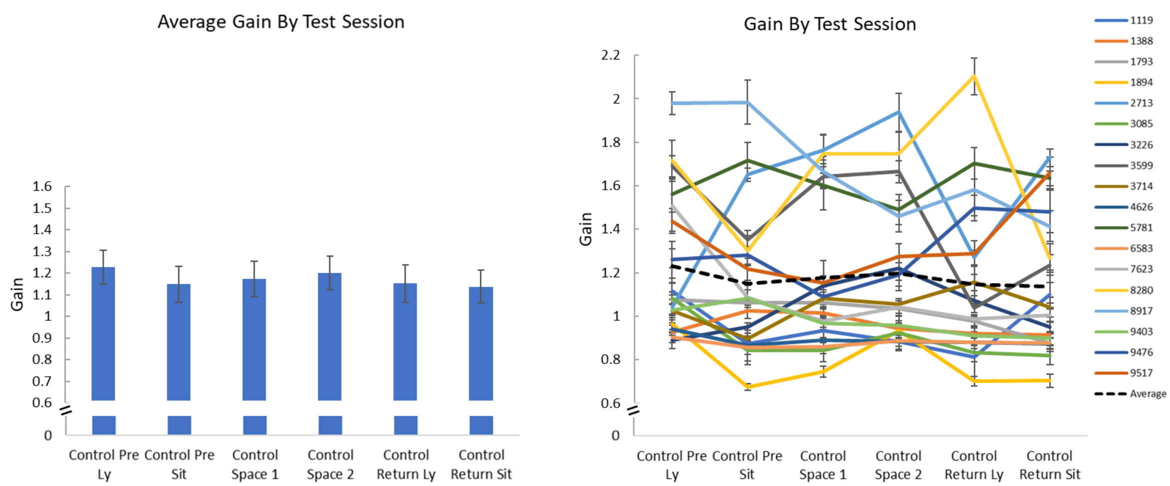



*Figure 4.7* The figure plots how the gain changes over the course of test session for the control participants. A higher gain indicates less visual motion is needed to arrive at a target distance. The panel on the left shows the average gain for each test session, while the panel on the right shows the average gain for a test session for each participant. The black hashed line is the average gain for the controls for that test session determined from the panel on the left. Error bars are ± standard error of the mean.

## 4.6 Discussion

Much of the research on self-motion perception in 0g has found increased sensitivity to the experience of visual self-motion, such as an increase in the perceived speed or onset of vection after a few hours or days (Allison et al. 2012; Oman et al. 2003; Young & Shelhamer, 1990). The methods used here looked at how exposure to and adaption to microgravity affected the effectiveness of optic flow cues in determining distance traveled as an estimate of vection.

Overall, we found that gain was affected by changes in gravity state. However, my hypothesis that there would be a significant increase in gain within the first few days (between 3 and 6 days) in microgravity was not supported. Adaption to microgravity, however, lead to a significant decrease in gain relative to early on in orbit as well as to the baseline conditions. The gain decrease remained upon re-entry to 1g, particularly while sitting, which is in agreement with my hypotheses, as the gain was different from the pre-flight conditions (see Figure 4.6 and table 4.2). These findings suggest that adaption to microgravity leads to a decrease in the effectiveness of optic flow for determining distance traveled after somewhere between 5 and 100 days in space.

We found no significant difference pre-flight between the supine and sitting conditions, however there was a significant difference post flight with higher gains while supine compared to the sitting posture (Figure 4.6). In the previous two chapters, we found a larger visual gain when participants were tilted supine or prone during a MTT task compared to upright, but only if a VRI was likely to be being experienced. A high gain during a VRI was taken as support for the reweighting hypothesis (refer to section 2.6.5 *Misinterpreting the vestibular signal: the reweighting hypothesis*) where we argued that a conflict between the visual upright and the gravity upright would lead to a higher visual weight. Based on the findings in Chapter 2 and Chapter 3, we might then expect to find a higher gain while supine compared to sitting if participants were experiencing a VRI. Since no VRI measure was taken, we cannot reliably know if they were or not feeling upright while lying. However, given that the supine posture does not always reliably lead to a VRI (See Chapter 2 Table 2.1) it could be the case that the difference in results between the pre and return sessions is due to differences in the amount of perceived conflict between the visual and gravity uprights while tilted before and after exposure to 0g where participants experienced more conflict (and more VRI) upon return.

### 4.6.1 Control Data

The lack of significant main effect of test session on gain for the control participants indicates that we have supported the null hypothesis that gain will not change over time. It is likely that no practise effect exists (Figure 4.7).

### 4.6.2 Gain Changes in Space

We observed no significant change in gain on first going into space (Figure 4.6 and Table 4.2). The results here are in conflict with previous research which suggested that visual cues would be enhanced when gravity was removed (Oman et al, 2003; Mueller, Kornilova, Wiest, & Deecke, 1994; Young & Shelhamer, 1990), or ignored (Chapter 2 and Chapter 3, and Preuss, Brynjarsdóttir & Ehrsson, 2018). These studies predicted an increase in gain on first going into space. It is possible that the lack of such an effect in the current experiment reflects adaption that may have already occurred to the microgravity environment as I was not able to test astronauts until after 3-6 days in orbit. However, the study by Young and Shelhamer (1990) showed that the intensity of the sensation of vection builds up upon entry to 0g until the $3^{rd}$ day, which is the earliest time at which I could start testing. We would expect that an increase in vection intensity would be related to a higher visual gain.

### 4.6.3 Adaptation to Space

Interestingly, after ~90 days of exposure to microgravity the visual self-motion gain was found to be significantly lower than early in flight and compared to baseline performance (Figure 4.6, Table 4.2) with more visual motion being needed to reach the target distances.

This decrease in gain is interesting as without gravity people are forced to use vision to navigate, as they would have to see where they wanted to go and then push off of a surface in order to get there. While the otolith cue would still indicate a brief, initial acceleration as they pushed off, their flying motion after that would be extremely smooth without acceleration or deceleration—if the person in orbit realizes the are moving too fast or slow towards a target, assuming there is nothing between them and the target to hold on to, they cannot change their motion like they can while walking on Earth.

It is possible this decrease in gain reflects an optimal strategy for navigating in 0g. In 0g should you find yourself not near anything to push off of it would be very difficult to move. This decrease in gain, meaning needing to travel further to reach a target and resulting in overshooting it, might represent a safety mechanism, by means of which participants are ensuring they reach a location. Though with the lack of friction while moving it is unlikely the person would not make it to their target location eventually.

It is possible that some of the visual motion while moving in 0g could have been misinterpreted as tilt, in a type of visually induced somatogravic illusion (see introduction section 1.3 *Visual-vestibular integration* for information on the somatogravic illusion). Surprisingly, in 0g centrifugation is perceived as tilt instead of translation (see introduction section 1.5 *Gravity and visual self-motion perception*; Clément, Moore, Raphan, & Cohen, 2001), so it is possible that visual motion might lead to similar interpretations in microgravity as the restraining otolith cue is absent.  While unlikely, this interpretation of translation as tilt should lead to a decrease in gain.

Alternatively, the decrease in gain could reflect changes in the perceived depth of the environment, with a lower gain suggesting an expansion of perceived depth. A low gain would indicate that for a given target distance a participant had to travel further to feel they had passed through the distance. If the distance the participant travels is taken as an accurate perception of the target distance this would mean that when they see a target placed at, for example, 10m, they perceive it as actually being further than 10m. Some evidence suggests that depth perception might be compressed in microgravity (Clément, Lathan, & Lockerd, 2008), however changes in depth are unlikely to explain changes in gain as, if the visual environment is compressed (or expanded) the visual motion should also be similarly affected since it results from the optic flow induced from stimuli in the environment.

Lastly, the lower gain could reflect a compensation for the faster perceived vection speed reported in Oman et al. (2003). Anecdotal reports of astronauts, reported in Oman et al. (2003), and Young and Shelhamer (1990), indicate that they are aware that they are perceiving the motion faster or of greater intensity in 0g. If they are aware, they might try to compensate for this increased perceived speed by traveling further, to try to mitigate a potential undershoot caused by misperceiving the motion as faster than it really is. As stated above, if this change is only in the perception of the motion then if a participant were to compensate for such a change in perceived speed – knowing their perception was faulty - such as by waiting, they would end up traveling further to reach the target which appears here as a lower gain.

### 4.6.4 Changes on Return to Earth

The reduction in gain found after adaptation to microgravity continued upon re-entry to 1g where astronauts continued to require more visual motion to arrive at a target distance while sitting compared to the early exposure to 0g, after adaptation to 0g, and to the baseline measures. The Return Lying condition also showed some reduction in gain as it differed from the Pre-Sitting and Space Early condition. This continued reduction is unlikely to be due to a practise effect as the controls showed no such effect (Figure 4.7).

The reduction in gain found after returning to Earth is in line with previous studies (Allison et al. 2012; Oman et al. 2003; and Young & Shelhamer, 1990) that found a decreased perceived speed or strength of visual motion compared to baseline upon re-entry to Earth. The results are also in line with findings from Clément and Wood (2014) who found an increased gain for physical motion (in the dark) following return from 1g. We might expect that following a decrease in visual sensitivity there might be a corresponding increase in physical sensitivity.

Reintroduction to the long-lost gravity cue has been argued to lead to changes in the activation of the otolith cue, which would now respond once again to the constant acceleration of gravity. It is possible that the participants in Clément and Wood (2014) could have misinterpreted some of the now-present gravity cue stimulating the otoliths as translation. This would lead to an increased gain during physical motion. Alternatively, an increase in vestibular activity could have driven down the visual cue, leading to a decrease in gain.

The reduction in gain found upon return to Earth appears to be particularly strong when participants were sitting where the gain differs from all of the other conditions, while the Return Lying condition only differs from the Pre-Sitting and Space Early conditions, (Figure 4.6). As discussed in section 1.5 *Gravity and visual self-motion perception*, when in 0g the otoliths are no longer stimulated by head tilt, and only by physical acceleration. After returning to Earth a tilt of the head might be incorrectly partially interpreted as translation (Merfeld, 2003). This theory is referred to as the Otolith Tilt Translation Reinterpretation hypothesis (OTTR).

The OTTR theory argues that because the otoliths only signal translation in 0g, upon return to Earth misestimations of the direction of gravity will lead to additional translation being perceived (Merfeld, 2003). Additional translation during head tilt should result in changes in gain, where if participants were to misperceive their tilt angle, the OTTR would predict that that the vestibular tilt cue would be misinterpreted as translation and would be perceived as an acceleration in the direction opposite to tilt (forwards for supine, backwards for prone), so a tilt backwards under these models should result in some forwards perceived motion. This might then enhance the visual motion indicating motion in the same direction. We would therefore expect that, under these models while lying down immediately after returning from space, there should be a higher gain when supine relative to sitting as the perceived motion would be "gravity assisted". The difference in gain found while supine compared to sitting after returning to Earth could potentially be due to a misinterpretation of some of the tilt as motion, leading to a higher gain. Based on the preliminary dataset here, the results might support the OTTR where there is a trend toward the supine posture having a higher gain. However, in order to be sure participants have misinterpreted their degree of tilt, in the future participants' perceived orientation should be recorded.

The higher gain while supine compared to sitting in the Return condition might also support the Reweighting Hypothesis proposed in Chapters 2 and 3. After adapting to a 0g environment where up is determined based on visual and body cues, it is possible that returning to 1g and reintroducing the gravity cue resulted in an increase in the perceived conflict between the visual and gravity uprights while titled during the MTT compared to the pre-flight conditions. This would result in the difference in gain found for the two post flight conditions compared to the pre-flight conditions.  However, because no measure of VRI was taken we cannot be sure that the higher gain is due to changes in perceived conflict.

Overall, it appears that upon returning to Earth the decrease in gain noted in space was retained, suggesting a decrease in the use of the visual cue for signalling perceived distance traveled.

## 4.7 Conclusion

In chapter 2, I demonstrated that when participants are experiencing a VRI, due to ignoring the gravity vector and favouring visual cues during a visual-vestibular conflict, they required less visual motion to feel they had passed through a target distance (increased visual gain). If ignoring the gravity vector led to a higher gain, I hypothesized that the removal of gravity altogether should also lead to a higher gain, at least during short-term exposure to microgravity.

The results described in this chapter however showed no such difference in gain during early exposure to 0g and in fact a decrease in gain during late flight which persisted upon return. It is possible that participants may have already adapted to a 0g environment by day 3-6 when they were tested where they would have had an initially high gain but by the time of the Space Early testing it was already starting to decline. I believe that my findings demonstrate that in 0g there is an eventual reduction in the weight given to visual cues with this reduction continuing after return to 1g.

The evidence from these space-based experiments does not support the reweighting hypothesis as the gain was not increased with the removal of the gravity cue as would be predicted from the hypothesis. However, the increase in gain while supine compared to the sitting posture after returning to Earth does support the reweighting hypothesis and suggests the model as a whole might not be incorrect but that it is not able to accommodate some of the effects present.

# CHAPTER 5: General Discussion

The purpose of this dissertation was to examine the contributions of visual and vestibular cues to our perception of our orientation and self-motion, and the interactions between them. In previous studies (e.g., Nakamura & Shimojo, 1998; Guterman, Allison, Palmisano, & Zacher, 2012; Kano, 2010) when a participant was tilted and viewing visual motion it seemed to be assumed that they were perceiving themselves as tilted and viewed the motion as intended. Even in starfield environments participants could have differences in perceived orientation and direction of motion, as found in Chapter 2. Little research has looked at how participants' perceived body orientation affects self-motion perception (Preuss, Brynjarsdóttir, & Ehrsson, 2018; Guterman & Allison, 2019), despite finding that differences in a person's perceived orientation does impact the interpretation of visual stimuli, such as vection experience (Preuss, Brynjarsdóttir, & Ehrsson, 2018; Guterman & Allison, 2019), and shape from shading (Oman, Howard, Smith, Beall, Natapoff, Zacher, & Jenkin, 2003). In the studies undertaken for this dissertation, I looked at how visual self-motion perception varied based on a participant's perceived orientation in order to explore how the relative use of visual and gravity cues affected self-motion perception. See section 1.9 *Aims of this dissertation* for a brief overview of the goal of each experimental chapter as well as a list of all of the main hypotheses in this dissertation.

## 5.1 The reweighting hypothesis and conflict

On Earth, when people are placed in an environment with an ambiguous up direction in which visual and vestibular cues are in conflict, many participants will report a visual reorientation illusion (VRI) where their perceived up appears to depend only on the visual cues (Howard & Hu, 2001). In Chapter 2 I hypothesized that this VRI should lead to a partial reinterpretation of tilt as translation where there is an enhancement in the effectiveness of optic flow in simulated motion through a virtual environment while supine (hypothesis 1) and a reduction while prone (hypothesis 2). In the first experiment I instead found a general increase in optic flow effectiveness while participants were tilted and there was a high likelihood of experiencing a

VRI. While this technically supported hypothesis 1, it is unlikely to be due to reinterpreting the tilt as translation as hypothesis 2 was not supported. In the second experiment I hypothesized that tilting the head should decrease the VRI rate and thus weaken the effectiveness in optic flow found in experiment 1. Instead, the decrease in gain was only seen in the supine posture and there was no change in the VRI rate, so hypothesis 3 was only partially supported. In the third experiment I compared the effectiveness of optic flow in two different environments, a polarized hallway which should lead to a high VRI rate and thus an increased effectiveness of the optic flow cues (hypothesis 4) and a less polarized starfield environment which should lead to a low level of VRI and thus no increased effectiveness of the optic flow cues (hypothesis 5). I found that the hallway environment led to a generally higher level of VRI compared to the starfield. Then in cases where the VRI rate was high (while prone in the hallway) there was also an increased effectiveness of the optic flow cues (supporting hypotheses 4 and 5). Overall, in Chapter 2 I found in situations where the VRI rate was high there also tend to be a higher gain during a move-to-target visually-induced self-motion task regardless of body tilt or visual environment suggesting an increased emphasis on visual cues (higher visual weight), although the two different environments did also lead to overall differences in the effectiveness of the optic flow cues.

Based on the findings in Chapter 2, I rejected the idea that the VRI was leading to a reinterpretation of the motion as translation. Instead, I proposed a "reweighting" theory where, when in a visual-vestibular conflict situation, some participants will prioritize the visual information over vestibular information leading to a higher visual weight and lower gravity weight (hypothesis 7). The higher visual weight would result in the experience of a VRI and also the higher gain on the move-to-target-task (hypothesis 6). In Chapter 3 I found that the participants who reported a VRI appeared also had a lower visual weight and higher gravity weight when determining upright compared to the no-VRI people, people who did not experience VRIs, leading me to reject hypothesis 7. However, I did find that while tilted the individuals who were more likely to report VRIs had a higher gain compared to the no-VRI individuals which supported hypothesis (6). These findings led to updating the model proposed in Chapter 2 where I argued that individuals with a higher gravity weight would be more likely to detect when the visual and gravity uprights are in conflict. Because of the higher weight given to the gravity cue, indicating a more precise internal estimate, when the two ups provided by gravity and vision were in conflict, such as during the MTT while lying down, robust integration of the cues should lead to the gravity cue being the more likely cue to be discounted, leading to a higher relative visual weight. No-VRI people, who place less emphasis on gravity, would be less likely under this theory to detect when the uprights are in conflict and so would either not reweight the cues, or would reweight them less.

The main argument of the Reweighting model is that during a visual-vestibular conflict, when the gravity cue is ignored or downweighed the visual cue is upweighted. Extending this model, we would expect similar changes in 0g, where when the gravity cue is effectively removed, the visual cue should also be upweighted, at least for short duration exposure to 0g, leading to a higher gain on the MTT compared to on Earth (hypothesis 8). This would also be consistent with previous studies that found that the experience of vection, such as the perceived speed (Oman et al. 2007; Young & Shelhamer, 1990) was increased in 0g. However, we instead found that the gain did not change after a short duration exposure to microgravity and that it decreased following adaption to 0g, leading me to reject hypothesis 8.

In Chapters 2 and 3 a higher gain in the MTT was associated with the experience of a VRI, which is a change in perceived orientation where vision is favoured. This would suggest a generalized increase in the relative weight given to the visual cue, that would show during the performance on both orientation and self-motion tasks. In Chapter 4 there was no change in the emphasis on vision upon entry into 0g.

Following prolonged microgravity exposure there was a decrease in vection gain relative to early microgravity exposure and the baseline conditions, implying a decreased effectiveness of visual cues (lower gain, Figure 4.6). This is similar to findings in Oman et al. (2003) where, when in 0g their participants were restrained with springs that put pressure along their long body axis and participants' perception of the vection speed was decreased. These springs may have increased attention to the body and strengthen the assumption that they were not moving, leading to a weakening of the experience of self-motion. The decrease in gain found in Chapter 4 after adaptation to 0g continued upon returning to Earth, particularly while sitting upright, (Figure 4.6 and Table 4.1). After adapting to weightlessness, the experience of the force of gravity on their body might also cause an increase in the expectation that they were stationary, similar to the springs in Oman et al. (2003), leading to a continued decrease in gain. The findings upon return to Earth are also in-line with Oman et al. (2003) who found a decrease in the perceived speed of vection upon return.

Interestingly, prior to microgravity exposure gains in the MTT for the sitting and supine postures did not differ, suggesting participants did not experience a strong conflict between the visual up and the gravity vector. This is not completely unexpected as the findings in Chapter 2 showed that a supine posture did not reliably lead to changes in gain. However, after reintroduction to gravity, there was a difference in the gain between the two postures. A higher gain while supine compared to sitting in the Return conditions is in line with predictions made by the Reweighting Hypothesis proposed in Chapters 2 and 3, where a conflict between the visual and vestibular upright appears to lead to an increase in the weight given to visual cues, reflected as a higher gain while tilted and the experience of a VRI. Prior to microgravity exposure, it appears that the conflict in the ups signaled by the visual cues and by gravity was not significant enough to lead to reweighting. However, upon return to Earth, when gravity is reintroduced, the supine and sitting posture now differ in their effects on the MTT gain. In a 0g environment the otoliths are only stimulated by acceleration induced by moving through the environment, so upon return to 1g the newly reintroduced gravity vector might be perceived as less reliable, leading to a downweighing of the vestibular cue and an upweighting of the visual cue. This would explain why the supine posture had a higher gain compared to the sitting posture in the Return conditions in Chapter 4 while the Pre-flight conditions showed no difference. However, without a measure of VRI I cannot be sure the results are due to changes in the experienced conflict.

The lack of increase in the gain when gravity was removed contradicts the main idea of my reweighting hypothesis, which posits that when the gravity cue is ignored this leads to an increased visual weight. When the gravity cue was removed there was no substantial change after early exposure to 0g – at least not by day 5 of the flight when these experiments were carried out. However, the increase in gain following reintroduction to 1g does potentially support the reweighting hypothesis, though a stronger argument could be made if I had taken a measure of their perceived orientation. Overall though, the findings in Chapter 4 suggest that the visual cue is not prioritized in 0g as I hypothesized based on the Reweighting model. Based on the findings in my previous Chapters I cannot currently support my Reweighting Hypothesis in full as an explanation for the increase in gain during the MTT in Chapters 2 and 3.

Overall, the results presented suggest that while the higher gain found for VRI individuals might indeed be associated with a higher visual weight, ignoring or removing the gravity cue does not always lead to a higher visual weight. The reweighting model appears to be insufficient to explain the results found in the previous chapters.

It is possible that the changes in the reliance on the visual cue found in Chapters 2-4 reflect differences in how the cues are most optimally combined. When lying in a virtual environment with conflicting visual and gravity uprights on Earth it might be more optimal to rely on the visual up. In 0g, when the gravity cue is effectively removed the most optimal reweighting might not be one that prioritizes vision.

## 5.2 The Optimality of Cue Reweighting

As we move through our environment, we take in potentially redundant information provided by our senses about our motion and orientation. This sensory information is combined into one coherent perception, a process referred to as multisensory integration (Laurienti, Burdette, Maldjian, & Wallace, 2006). One method of modeling sensory integration states that the cues taken in by the senses are combined based on how reliable they are, where more noisy cues are weighted less, resulting in an optimal combination of cues (Ernst, & Banks, 2002; see Fetsch, DeAngelis, & Angelaki (2010) for a review on optimal visual and vestibular cue combination). Refer to Chapter 1.3 *Visual-vestibular integration*, for a more in-depth explanation.

It is possible that the differences in the reliance on the visual cue found in the previous chapters reflect differences in how the cues are most optimally combined based on the task and environment. In Chapter 3.6.2.1 *Orientation*, two papers on nausea and cue reweighting were discussed. The first paper by Weech, Wall, and Barnett-Cowan (2020b) demonstrated that when people were exposed to galvanic vestibular stimulation, creating a noisy vestibular signal, they experienced less nausea while playing a nauseating VR game compared to when no vestibular noise was present. The video was likely causing nausea due to the conflicting visual and vestibular cues present while engaging with the virtual environment. When noise was applied to the vestibular organ via the galvanic vestibular stimulation, the vestibular cue would likely have been perceived as less reliable and consequently down weighted, which would have reduced the conflict and the experience of nausea. In another study by Weech, Calderon, and Barnett-Cowan (2020a) participants were asked to stand with one leg in front of the other, rendering them less stable. They were then exposed to oscillating visual motion causing body sway. In this experiment the visual and vestibular cues were in conflict but prioritizing the visual cue would lead to increased instability.

Weech et al. (2020a) argued that as the speed of the visual motion increased the changes in sway length would reflect the weight given to the visual cue. A shorter sway length at higher oscillations would result from participants down weighting their reliance on the visual cue, presumably in order to be more stable. More sway at the higher oscillation magnitudes would reflect a failure to down weight the visual cue despite leading to postural instability. They found that participants who did not down weight the visual cue during the sway task also experienced more nausea on a subsequent virtual reality task suggesting again a poorer ability to reweight conflicting cues.

The results of the two studies demonstrate reweighting of the visual and vestibular cues where the visual cue is prioritised in one case but down weighted in another. The results also show that some participants are less able to reweight the sensory cues during a conflict. It is possible that these participants were not able to detect the conflict or that they might have reweighted the cues more slowly.

The presence of a VRI on Earth while tilted supine or prone suggests that the visual cue has dominated, which would explain the higher visual gain. During the OChaRT task, where participants were asked to orient an ambiguous shape, since the visual up changed every trial it might be more optimal to prioritize gravity information over visual information as the gravity up was more stable. This higher gravity weight might also help to explain the significantly lower VRI rate during the OChaRT task compared to during the MTT.

In 0g, it is possible that the optimal strategy would not be to prioritize the visual cue. Based on the findings by Mader et al. (2011) a decrease in visual acuity in 0g might lead to a decrease in the weight given to visual cues. This is discussed further in section 5.5.2 *Changes in Visual Acuity with Changes in Gravity*. However, given that I was only able to test participants after 3-6 days exposure to 0g, it is possible that in the first few days they show an increased gain on the MTT that I was not able to capture.

Overall, the results of the studies here most likely show that when the gravity cue was down weighted the remaining cues were reweighted in the most optimal way where in some cases the visual cues dominated and a VRI was experienced along with a higher visual gain. In other cases, the body cues were weighted higher (and the visual cues were likely also down weighted) and the gain decreased. The no-VRI group might also constitute a similar group of participants as in Weech et al. (2020b) who have a deficit or delay in their ability to reweight their senses, potentially stemming from not being able to detect conflicting visual and vestibular cues. An interesting follow up study would be to replicate the findings of Weech et al. (2020b) and try to correlate VRI susceptibility with body sway. I predict that no-VRI individuals would show more sway as the magnitude of visual oscillation increased.

In this dissertation the main measure of the contribution of visual cues was the effectiveness of the optic flow cue in simulating visual self-motion perception, expressed as a gain (target distance/ actual distance traveled). The following section discusses my use of this gain term and whether the gain accurately reflects participants' performance.

## 5.3 Visual self-motion perception and gain

In Chapters 2-4 I determined the effectiveness of the optic flow cues by measuring the distance traveled during the MTT, and then expressed the data as a gain. The use of a gain which was defined as target distance/distance moved and then averaged, assumes a linear trend where the error for near targets is similar to the error for far targets and that the simulated distance traveled is linearly related to their perception of how far they have gone. While this might seem like a reasonable assumption, previous studies have not always found linear travel distances with increasing distance (Harris et al. 2012; Lappe, Jenkin, & Harris, 2007). Instead, it appears, in some cases, that there is a decay in people's memory depending on the distance they must travel, where their perceived motion can be modeled as a leaky spatial integrator (Lappe et al., 2007). For a MTT, the leaky spatial integrator model predicts that the distance traveled for a given target distance is based on a gain along with a distance-dependent decay factor where, for each "step" the person makes there is a decrease in the remembered distance that they still have to travel. This decay results in non-linear data where the further the distance of the target the more the participant undershoots the distance indicated by the target with significant deviations from linearity at longer travel distances (Lappe et al. 2007).

In the experiments reported in this dissertation, evidence of a non-linearity in the travel distance would be apparent in a change in gain across target distance, where the gains for the further distances should differ significantly from the near gains. The presence of a decay, similar to the one found in Lappe et al. (2007) would appear as a higher gain at further distances compared to nearer distances.

Using the results of the MTT tasks from Chapters 2 and 3, I took the average distance traveled for each target distance, for each posture for each experiment, and calculated a gain and standard error as a function of distance. The results are plotted in Figure 5.1 below. Inspection of Figure 5.1 suggests that there may be a change in gain from the 10m target distance to the 20m target distance, particularly for Chapter 2 Experiment 3 Hallway while prone. Generally, however, there appears to be minimal change in gain across the target distances, particular for the further target distances, where we would expect to see more decay. This suggests that the data, at least over most of the range, is indeed well modeled by a single value of gain without reference to a decay term.  I also plotted the data from Chapter 4 in the same way but used Test Session instead of posture in Figure 5.2.

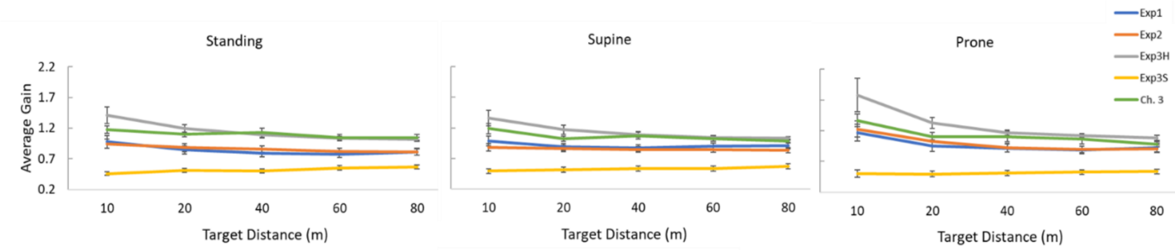



*Figure 5. 1* The average gain (target distance/actual (simulated) distance travelled) for each experiment and each posture from Chapters 2 and 3 plotted as a function of target distance. Exp1 – Exp 3 stands for the Chapter 2 Experiments 1, 2, and 3. Exp3H stands for Experiment 3 Hallway. Exp3S stands for Experiment 3 Starfield. Ch.3 stands for the Chapter 3 data. Error bars are ± standard error of the mean.

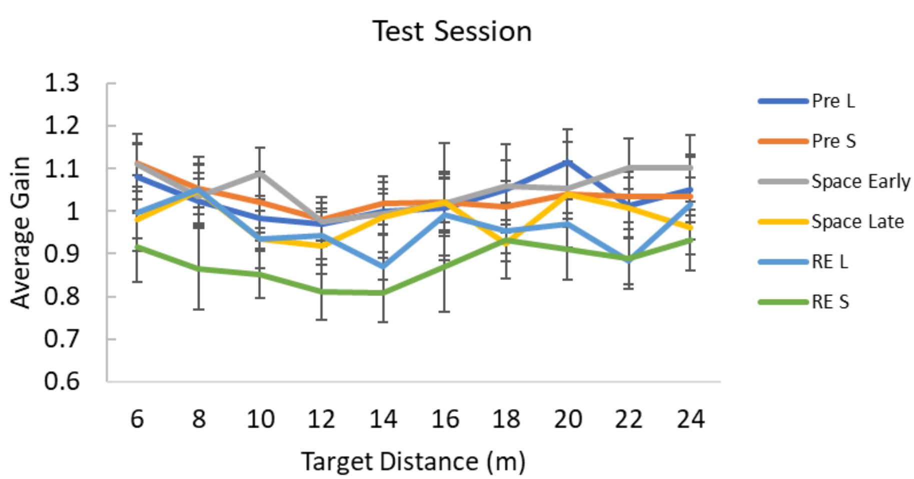



*Figure 5. 2* The average gain (target distance/actual distance traveled) for each test session from Chapter 3 plotted as a function of target distance. Pre L and Pre S stand for the Pre Lying and Pre Sitting conditions. Re L and Re S stand for the Return Lying and Return Sitting conditions. Error bars are ± standard error of the mean

Given that in Chapter 4, no effect of target distance on gain was found during the MTT, and based on the data plotted in Figure 5.2, I feel that that the data in Chapter 4 is well modeled by the single gain term. However, any decay present would become more apparent with further distances. In Chapter 3 I reported that the gain to reach the 10m target distance did differ from the gain when traveling through the 60 and 80m distances. In order to determine if any non-linearity was present across the travel distances used in Chapters 2, four linear mixed models were run in the same way as in Chapter 4, in order to allow for me to better compare the results. Gain was set as the dependant variable, posture and target distance were repeated variables and were set as fixed factors, the participant ID was set as a random effect (random intercept).

There was no effect of target distance on gain in Chapter 2 Experiments 1, 2 and 3 Starfield ($p$>0.05 in all cases) as is also evident in Figure 5. 2. It seems in these cases, as in Chapter 4, the travel distances were effectively linearly related to target distance. The target distance did have a significant effect on the gain in Chapter 2 Experiment 3 Hallway $F(4, 73.668) = 8.276$, $p < 0.001$. A post hoc analysis using Sidak correction was run and the significant results are presented in Table 5.1. All other comparisons were not significant (adjusted p> 0.05).

*Table 5. 1* The significant post hoc comparisons from the linear mixed models for Chapter 2 Experiment 3 Hallway and Chapter 3. The Gain Mean Difference column is the average gain for the target distance given in the Distance m (i) column – the average gain the in the Distance m (j) column. The Adjusted Alpha column is alpha value adjusted for multiple comparisons such that p<0.05 is significant.

| Experiment | Distance m (i) | Distance m (j) | Gain Mean difference (i-j) | Adjusted Alpha |
|---|---|---|---|---|
| Chapter 2 Experiment 3 Hallway | 10 | 40 | 0.401 | 0.010 |
| | | 60 | 0.452 | 0.002 |
| | | 80 | 0.473 | 0.001 |
| | 20 | 60 | 0.163 | 0.013 |
| | | 80 | 0.184 | 0.003 |
| Chapter 3 | 10 | 60 | 0.209 | 0.010 |
| | | 80 | 0.243 | <0.001 |

In the cases reflected in Table 5.1, the gain for the 10m distance (and in 2 cases for 20m) is higher than the gains for the other distances. This result is not in line with the findings of the Lappe et al. (2007) for the move-to-target condition which would predict that it should be lower, and instead suggests the presence of a decay related to distance traveled instead of the remaining distance to the target. However, I argue that effect seen in these two experiments suggests that the participants may have reacted to the 10m target distance differently than the other distances (Figure 5.1). This could have occurred due to rate of acceleration used in the experiments. With a target at 10m and an acceleration of 9.8ms/s participants would arrive at the target within approximately 1.43 seconds. In this case the reaction time of the participant might matter. In Chapter 2 Experiment 3 Hallway the 10m target distance had a gain of 1.5, which would correspond to a stopping time of approximately 1.17 seconds. It is possible that for this target distance some participants were simply stopping the motion as fast as possible in order to not overshoot the target, leading to a higher gain. For the further target distances the participant would have more time to prepare and be accurate. This would also explain why the effect in Table 5.1 is only seen in 2 out of 6 experiments as well as why the effect doesn't appear to be very consistent in magnitude. The difference in gain between the 10m and 60 and 80m conditions in Chapter 2 Experiment 3 Hallway to the is more than twice as large as the difference in Chapter 3 (Table 5.1). Overall, I believe that the use of an average gain in the previous chapters is justified as any decay present is minimal.

The experiments reported in this dissertation differ in a few ways from other experiments that have found a significant decay (Harris et al. 2012; Lappe et al. 2007), specifically the use of immersive and dynamic headsets. A virtual reality MTT experiment was done by Redlick, Jenkin, and Harris (2001), using a virtual reality headset that updated with head movements (though it was not stereoscopic). Referring to their Figure 2 and 3, which plots the distance traveled by target distance and fitted linear regression lines to the data, the distances traveled by the participant appears to be relatively linear. While simply looking at a figure isn't the most precise measurement method, it is possible that the lack of, or reduction in, decay found in Redlick et al. (2007) and in the previous chapters the use of an immersive headset could be a contributing factor. This would also explain why some minor decay is found in the data reported in Chapter 4 as it may have been less immersive given that the view was head fixed. While participants were asked not to move their heads in Chapters 2 and 3 they may still have made small movements during the task which would lead to the screen updating and an increase in the immersiveness of the environment.

The next section discusses the variations in gain found across the different chapters and compares it to other experiments that have been done in order to determine what factors might cause systematic variations in gain.

## 5.4 Visual environment and self-motion perception

Traditionally, research on visual self-motion perception has focused more on the experience or sensation of the vection, such as the perceived speed of vection (Palmisano, Allison, & Pekin, 2008; Oman et al. 2003), the magnitude of vection (Guterman, Allison, Palmisano, & Zacher, 2012; Palmisano, & Chan, 2004), and the onset of the sensation of vection (Allison, Zacher, Kirollos, Guterman, & Palmisano, 2012; Brandt, Dichgans, & Koenig, 1973). While the measurement of the experience of vection can inform us as to how people perceive the visual motion it does not inform us as to how people might use the motion information. Instead, the MTT allows us to measure how effective visual cues are at causing the perception of moving through the environment. Self-motion perception during the MTT differs from the experience of vection in that participants do not have to have a feeling of self-motion, their perception of distance traveled can come simply from their interpretation of the optic flow. This might explain why where Oman et al. (2003) and Young and Shelhamer (1990) found that 3-4 days exposure to microgravity led to an increase in the perceived speed or intensity of visual self-motion but I found that there was no difference in participants' distance traveled.

This isn't to say that the different factors that affect the sensation of vection might not impact the results of the MTT task. For instance, since the MTT can be done without the experience of vection, we might expect that regardless of how compelling vection might be, it should not impact the perceived distance moved during the MTT. On the other hand, uncompelling vection might suggest a poverty of the visual stimulus, such as poorly registered optic flow cues, which might impact performance on the MTT task. More research is needed in order to determine which factors might affect the gain of the MTT task

In Chapters 2 and 3 we found that a person's perceived orientation while tilted had an effect on gain during a MTT. However, the gain for the standing posture was also found to vary between the different experiments. It is possible that variations in equipment, participant demographics, motion profile, and environment all affected the overall gain in each experiment with the VRI then modifying the resulting gain.

In Chapter 2, two different virtual reality headsets were used, the Oculus DK2 and the CV1, which had differences in field of view, refresh rate, and number of pixels. In Chapters 2 and 3 the view in the headset was dynamic where it updated with head movement. While participants were asked not to move their heads, even minor movements would lead to small changes in the view in the headset possibly leading to a more immersive experience and could also reinforce the vestibular cue. The headsets also provided stereoscopic information. In Chapter 4, the Space experiments, however it was necessary for technical reasons for the view in the HMD to be head fixed such that it did not update as the head moved and was not stereoscopic. Finally, while the motion profile used was the same in Chapters 2, 3, and 4, in which all experiments used a constant acceleration motion profile, the rate of acceleration differed substantially (9.8m/s/s vs 0.8m/s/s respectively).

By comparing the gains measured in the experiments reported in Chapters 2-4 to the gains reported in the literature we can determine what factors might have affected the gain other than the VRI rate and posture. In Table 5.2, I provide the average gain while sitting measured in my experiments along with the gain found in four other papers, Redlick, et al. (2001), Lappe et al. (2007), Bossard, Goulon and Mestre (2016), and McManus, D'Amour and Harris (2017). All of the experiments presented in Table 5.2 were move-to-target tasks done in an upright (sitting or standing) posture. If exact gains were not explicitly stated in the paper, they were determined from the figures or the text itself. In papers with more than one type of gain-- e.g., where there is both a simple gain (target distance/travel distance) and a modeled gain with a decay value a la Lappe et al. 2007-- only the simple gain was used.

The experiments were compared on the types of display used, as different types of displays would have had different refresh rates and different amounts of pixels per inch leading to potential changes in the perceived motion. The motion profile is also included along with the acceleration as Chapters 2 and 3 differed in their acceleration compared to Chapter 4 and different gains were found. The field of view (FOV) of the display was included as a factor as different gains were found between Chapter 2 Experiment 1 and 2 and Experiment 3 and the headsets used in these experiments differed based on FOV. Additionally, a study by Ott, Pohl, Halfmann, Hardiess and Mallot (2016) found that in order to maintain a consistent speed through a hallway, participants had to slow their speed when it was viewed through a narrowing tube and increase their speed when it was viewed through a widening tube, relative to when viewed through a tube of constant width, suggesting that the field of view might impact our perception of motion. However, a study by Knapp and Loomis, 2004 found that limiting the field of view through the use of a simulated HMD (a box attached to a pair of goggles), did not impact movement to a target or estimations of its distance from the observer.

*Table 5. 2* This table compares the gains found in Chapters 2-4 while standing to the gains found in other studies. In the “Chapter or Paper” column “Bossard” refers to Bossard, et al. (2016). The gain was determined based on their Figure 3 block 8. “Redlick” refers to the Redlick, et al. (2001) paper. The gains were determined based on their Figure 4 and is divided up based on the motion profile. “Lappe” refers to the Lappe et al. (2007) paper. For the Lappe et al. (2007) paper the gain was determined based on the example described in the text on their page 40 “For example, for an initial distance of 45.26m the median travel distance was 34.6m.”. While the gain varied across the different distances due to the decay factor, the distance of 45 is close to the average distance used in the MTT in Chapters 2 and 3 (42m). “EGG” refers to McManus et al. (2017). The gains presented are from the full field condition collapsed across the 3 different speeds that were used. The “Display” column indicates the type of display used. The motion profile column indicates if the motion was an acceleration (“Accel”) or constant velocity

("Constant velo") along with the rate in either m/s/s or m/s respectively. The "FOV" column indicates the size of the field of view. The "Stereo" column indicates whether the display was stereoscopic, with "y" being yes and "n" being no. The "Dynamic" column indicates whether the view on the screen or headset updated with head or body movement ("y" or "n"). The final column displays the approximated gain.

| **Chapter or Paper** | **Display** | **Motion profile** | **FOV** | **Stereo** | **Dynamic** | **Approx. Gain** |
|---|---|---|---|---|---|---|
| Chapter 2, Exp 1-2 | Oculus DK2 | Accel 9.8 | 95° x 106° | y | y | 0.84-0.86 |
| Chapter 2, Exp 3 Hallway | Oculus DK2 | Accel 9.8 | ±110° diagonally | y | y | 1.15 |
| Chapter 3 | Oculus CV1 | Accel 9.8 | ±110° diagonally | y | y | 0.96 |
| Chapter 2, Starfield | Oculus CV1 | Accel 9.8 | ±110° diagonally | y | y | 0.51-0.53 |
| Chapter 4 | Oculus CV1 | Accel 0.8 | ±110° diagonally | n | n | 1.03 |
| Bossard | Cave | Constant velo | Full (±90°) | y | y | 1.09 |
| Redlick | Liquid Image MRG | Accel <= 0.2 | 84°×65° | n | y | 1.75-1.25 |
| Redlick | Liquid Image MRG | Accel > 0.2 | 84°×65° | n | y | 1 – 1.1 |
| Redlick | Liquid Image MRG | Constant velo | 84°×65° | n | y | 1.75 |
| Lappe | Cave | Constant velo | Full | n | y | 1.31 |
| EGG | Cave | Constant velo | Full | n | n | 0.53 |

The use of stereoscopic cues and whether or not the display was dynamic were also included as both factors might lead to better depth perception for near (stereopsis) and far (motion parallax) target distances, which might lead to variations in gain.

It is evident from Table 5.2 that the variations in gain are not consistently due to the display used. Nor does it seem that the other factors led systematically to changes in gain. The presence of these factors undoubtedly modulates the gain in some way, but it does not seem that the presence of, for example, stereoscopic cues, consistently leads to a high gain while its absence leads to a low gain, at least across the experiments presented here.

In Chapter 2, I found that the hallway environment had a higher gain while standing compared to the starfield environment. Both environments were displayed on the same headset, so the display, motion profile, FOV, presence of stereoscopic cues, and the dynamic information cannot explain the differences in gain. Instead, it is likely that differences in the visual environments impacted the gain.

The environments in each experiment in Table 5.2 differed based on the amount of orientation information present, such as directional lighting, a horizon, and the use of intrinsically and extrinsically polarizing cues. Intrinsic cues are objects that have an inherent up or down (Howard & Hu, 2001), such as a tree. Extrinsic cues would be objects that do not have a specific up or down but that denote orientation information by their relation to other objects, for instance a target or other object resting on a surface (Howard & Hu, 2001).

A study by Howard and Childerson (1994) found that environments with more polarzied information led to a more compelling sensation of roll vection compared to unpolerizered environments. Rotating polarized environments also led to more body sway during walking tasks compared to nonpolarized environments, as well as a more intense vection experience (Richards, Mulavara, & Bloomberg, 2004). This would suggest that environments with more polarized cues might lead to a more compelling sensation of motion. The presense of a floor surface has been found to enhance the intensity and compellingness of linear vection (Trutoiu, Mohler, Schulte-Pelkum, Bülthoff, 2009; Mohler, Thompson, Riecke, & Bülthoff, 2005). If polarized environments and environments with distinct floor surfaces lead to more a complelling sensation of self-motion, this could explain some of the variations in gain seen in Table 5.3 – especially the differences between the gains found during self-motion through a starfield compared to along a hallway.

In the experiments presented in Table 5.2 the variety of colour present in the environments also varied. Colour has been found to enhance vection experience (Bubka & Bonatoô, 2010) and could potentially lead to changes in gain.

In Table 5.3, I compare the variations in the gains from Table 5.2 based on differences in their visual environments. Since no variation in gain was found in Table 5.2 based on motion profile, the data from Redlick et al. (2007) paper were collapsed into one row. I also collapsed Chapter 2 Experiments 3 hallway and Chapter 3 together as they used same headset and the same virtual environment. Lastly, since Chapter 2 Experiments 1 and 2 used a different headset than Experiment 3 it is possible that how the colours appeared in the two headsets varied, such as how vibrant they looked, so the findings are left in separate rows.

In order to better compare how the environmental factors influenced the gain, if one of the factors was present in the environment (indicated with a "y") it received a score of 1. If the factor was absent (indicated with an "n") it received a score of 0. If the cue was present but limited/impoverished, it received a score of 0.5. An example of this would be the starfield environment in Chapter 2, which was in black and white but had a red target. The scores were then summed and are shown in the "sum" column in Table 5.2. The presence or absence of the factors was determined from the figures of the visual environments and the methods section in each paper.

It is apparent that at least some of the variation in gain while upright appears to be related to the availability of orientation information and colour in the different environments. This relationship is plotted in Figure 4.

*Table 5. 3* This table displays some of the variation in gain that might be due to differences in the visual environments. The "Colour" column indicates whether or not a variety of colours were used in the visual environment. If only one distinct source of colour (outside of black, white, and shades of grey) was used the paper was indicated as having "limited" colour. The "Directional Lighting Column" indicates if any light sources could be identified, as a light source could provide orientation information as light is typically viewed as coming from above (Jenkin, Dyde, Jenkin, Howard, & Harris, 2003; Ramachandran, 1988). This column could only be coded as yes ("y") or no ("n"). The "Floor Surface" column indicates if a floor was present in the environment and can only be coded as yes or no. The "Horizon" column indicates if a horizon was visible in the environment and simulated to at least 5km. If a horizon was visual but was not simulated into the far distance (for instance, if it was simulated at 50m away) this was indicated as "limited". The "Polarized Cues" column indicates if things like walls, targets that could be aligned to the self, or objects resting on other objects were present in the environment. The presence of only one polarizing cue was considered "limited". CV1 Hallway referes to the Chapter 2 Experiment 3 and Chapter 3 MTT where the Oculus CV1 was used.

| Chapters or Paper | Colour | Directional Lighting | Floor Surface | Horizon | Polarized Cues | **Sum** | Approx. Gain |
|---|---|---|---|---|---|---|---|
| Chapter 2 Exp 1-2 | y | y | y | y | y | **5** | 0.84-0.86 |
| CV1 Hallway | y | y | y | y | y | **5** | 0.96 - 1.15 |
| Chapter 2 Starfield | limited | n | n | n | limited | **1** | 0.51 |
| Chapter 4 | limited | y | y | limited | y | **3.5** | 1.03 |
| Bossard | limited | n | y | y | y | **3.5** | 1.09 |
| Redlick | y | y | y | n | y | **4** | 1.0-1.75 |
| Lappe | y | n | y | limited | y | **3.5** | 1.31 |
| EGG | limited | n | y | limited | limited | **2.5** | 0.53 |

In both cases where the summation of the available cues is 2.5 out of 5, indicating an environment that has poor orientation and colour information, the gain is low at approximately 0.5. When the cues sum to more than 2.5, the gain is always close to 1 or over, except for the Hallway Experiment 1-2 where the gain is 0.84-0.86. The use of colour in particular appears to be associated with a higher gain, again with the exception of the Hallway Experiment 1-2. Once there is a sufficient amount of orientation and colour in the environment there is an enhancement to self-motion perception.

The increased presence of orientation cues and colour could reflect a more realistic or more enriched environment leading to more compelling self-motion. A study by Riecke, Schulte-Pelkum, Avraamides, Heyde, and Bülthoff (2006) found that a natural scene (a plaza) produces more compelling vection than the same scene inverted or scrambled, possibly by increasing the feeling of presence.

Overall, while the comparison to previous studies here is brief, it is likely that some of the variation in gain seen in the previous chapters, particularly in Chapter 2 between the Hallway and Starfield environment, stemmed from differences in available orientation and colour information present in the environments. Of course, the variation in gain as VRI likelihood increased cannot be explained by these different factors as the variations in gain were found within the same environment. However, the presence of these factors, particularly the polarizing objects, most likely affected how likely a person was to experience a VRI (Howard, Hu, Saxe, & Zacher, 2005).

## 5.5 Neural Basis

As we move through our environment, place cells in the hippocampus fire when an individual is in a particular place (O'Keefe & Dostrovsky, 1971) and provide an allocentric representation of space so that we can keep track of our location within our environment as we move (O'Keefe & Nadel, 1978). Place cells respond to stimuli that define an area, such as visual or olfactory cues (Zhang, & Manahan-Vaughan, 2015; Save, Nerad, & Poucet, 2000; Quirk, Muller, & Kubie, 1990; O'Keefe, & Conway, 1978) and also respond to far stimuli such as landmarks (Knierim, 2002). They may require that the animal is facing in a particular direction (Muller, Bostock, Taube, & Kubie, 1994), though directionality is mainly encoded by head direction cells which fire when the animal faces a particular direction (Taube, Muller, & Ranck, 1990). Head direction cells rely on both visual and vestibular information (Blair, & Sharp, 1996) and at least in rodents only respond to horizontal head position (Taube, Muller, & Ranck, 1990). As the person or animal moves through their environment, different place cells fire in their respective "place fields" and together represent a cognitive map of the environment (Muir, & Taube, 2002; Wilson, & McNaughton, 1993; O'Keefe, & Nadel, 1978. See Moser, Kropff, & Moser, 2008 for a review).

If a place cell only fires in a specific location in the environment we might expect that as a person navigates a 3D environment the presence of a VRI might impact place cell firing. In a study by Knierim, Poe, and McNaughton (2003) in 0g, place cells were recorded as three rats navigated the corners of a cage. If the rats maintained a correct 3D representation of their environment, they should only show place cell activation in a given location on one of the surfaces. If the rats experienced a VRI in which different surfaces became identified as "the floor" then we might then expect activation on two or more of the surfaces. The rats were tested on their $4^{th}$ day in 0g. One rat showed activation on only one surface, one rat showed activation on each surface, and the other showed disordered activation suggesting it was disoriented. By the $9^{th}$ day all 3 rats showed activation in only one location suggesting they had learned the 3D environment and were no longer experiencing VRIs.

If the same place cells were always activated as a person, or rat, changed their orientation we might expect difficulty then in forming a 3D map as the VRI would result in a failure to encode an allocentric location (Oman, 2007). But such a failure to lock into a particular location might also result from the inability or difficulty in forming a 3D cognitive map of the environment. If people experience difficulty in forming 3D maps, they might reorient in order to attempt to explain their new perception, that is they may experience a visual reorientation illusion.

At a cortical level activity in the medial superior temporal area (MST) is related to heading perception in humans during visual self-motion perception (Schmitt, Baltaretu, Crawford, &

Bremmer, 2020) and this area also shows both visual and vestibular responses (Their and Erickson, 1992; Cardin and Smith 2010; Smith et al, 2017).

In summary, it seems likely that the changes in gain that I found in the MTT result from cue reweighting when participants experienced conflicting visual and vestibular uprights. The neural location of this multisensory integration may include both cortical and hippocampal areas.

## 5.6 Limitations and further suggestions

The research described in this dissertation examined the contributions of visual and vestibular cues to our perception of our orientation and self-motion**.** My conclusions are supported by the results provided. However, the research is not without its limitations. In addition to the issues raised throughout the dissertation, the next section will discuss two major limitations present in my experiments. Addressing these limitations would be of benefit to any future experiments and would help us to arrive at the more comprehensive model to explain the variations found in gain as the likelihood of experiencing a VRI increases.

### 5.6.1 Differences in Eye Movements

During the MTT participants were asked to look down the hallway as they would if they were walking down a regular hallway and to try and not fixate on any one thing for too long. When they were not moving, participants could look around freely. However, because no eye tracking was done it remains possible that the eye movements differed between participants and between experiments.

Any participants who fixated on parts of the environment during the visual motion might have experienced eye movements consistent with an optokinetic reflex, where the observer's eyes track a moving object until it moves out of view and then the eye makes a fast movement back to the starting point (like when watching telephone poles go by through the side window of a car). The participants who stared straight ahead would have suppressed this reflex as they would have still seen the movement of the floor in their periphery. A study by Becker, Raab, and Jürgen

(2002) had participants view circular motion in an optokinetic drum. They found that when participants were asked to track the motion with their eyes, inducing an optokinetic reflex, they reported a lower perceived speed of the visual motion compared to when trying to suppress the reflex. An interesting follow up to the studies in Chapters 2 and 3 would be to compare eye movements on the MTT between individuals who report a VRI and individuals who do not. Differences in whether or not a participant who fixated on parts of the environment during the visual motion could explain some of the variations in gain.

Some eye movements are also found to differ depending on head orientation. For instance, the vestibular ocular reflex (VOR) in which the eyes move in the opposite direction of head movement, is known to depend on head orientation (Peterka, Gianna-Poulin, Zupan, & Merfeld, 2004; Coats & Smith, 1967). For instance, while supine a caloric-induced horizontal VOR (horizontal relative to the head) is larger than while prone (Coats & Smith, 1967; Peterka, Gianna-Poulin, Zupan, & Merfeld, 2004).

An interesting follow up study could look at the differences in the magnitude of horizontal VOR induced by caloric stimulation and compared between tilted participants who are either experiencing a VRI or not. Because the VRI results from attending to orientation information, and is likely a higher-order process, we would expect no differences in VOR amplitude between VRI individuals and no-VRI individuals while tilted, as the occurrence of the VRI should happen in higher brain areas than those brainstem systems responsible for the VOR (Angelaki, 2004).

Recording eye movements during the MTT could also allow us to determine if VRI individuals attend to different features in the environment compared to no-VRI individuals. It is possible that the people who report VRI might attend more to polarizing cues in their environment, such as where the target and the floor surface meet, compared to no-VRI individuals.

### 5.6.2 Changes in Visual Acuity with Changes in Gravity

I concluded section 5.2 *The Optimality of Cue Reweighting* by arguing that changes in the gain on the MTT reflect changes in the visual weight in line with optimal cue reweighting dependant on the task. A higher gain on the MTT during the visual and vestibular conflict suggests the visual cue was seen as more reliable and the gravity cues were down weighted, resulting in the VRI and higher gain. The results from Chapter 4, where the gain on the MTT was decreased following long-term exposure to 0g suggests that the visual cue might have been seen as less reliable in 0g leading to it being down weighted or to the body cues being upweighted relative to the visual cues (Harris et al 2017). The decrease in visual gain after early exposure to 0g is counter to hypothesis 8 proposed in section 1.9 *Aims of this dissertation*, that effectively removing the gravity vector should result in an increase in gain similar to the findings on the MTT during a VRI on Earth, due to an increase in the visual weight. What could have caused the lower gain?

A study by Mader et al. (2011) that collected survey data from 300 astronauts after short- and long-duration missions found that 23% and 48%, respectively, had trouble with near vision after returning, with 11% and 34% showing changes in refraction post flight. Mader et al. (2011) state that these changes have been reported to last for months or years post flight, with permanent or long-term changes more likely to occur the longer the time spent in 0g. The study did not specify what they meant by short- and long-duration space flight but previous studies have defined short duration as ~4-17 days (Fritsch-Yelle, South, Wood & Bungo 2000; Ball & Evans 2001) and long as ~120 days or more (Fritsch-Yelle et al. 2000). Changes in visual acuity are thought to occur due to increased intracranial pressure (though the authors point out some issues with this argument; Mader et al. 2011). More recently, these changes have been suggested to occur due to an increase in cerebral spinal fluid levels leading to a flattening of the back of the eye (Alperin & Bagci, 2018). Changes to vision, particularly a decrease in near vision, could lead to a decrease in the reliance on, or the reliability of, visual cues, leading indirectly to a lower visual weight, a lower gain, and a proportionate increase in the weight given to body cues.

However, a study by Harris and Jenkin (2014) which measured participants perceptual upright via the OChaRT and participants' subjective visual vertical using a tilted line task, found that blurring the visual environment did not change the weight given to visual cues until the blur was equivalent to a visual acuity of 20/240 (which would make it difficult to perceive the large E on the first line of a vision Chart). For vection, a study by Fujii, Allison, Guterman, and Wilcox, (2016) found that motion blurring did not affect vection intensity. While motion blur does differ from a more general blur related to a decrease in visual acuity, it would suggest that at least some blurring during optic flow perception does not impact perceived self-motion.

While it remains possible that the decrease in gain on the MTT could stem from changes in visual acuity in 0g, the Harris and Jenkin (2014) paper and the Fujii et al (2016) paper do suggest that a decrease in visual acuity might not account for the decreased gain seen in 0g. However, more work is needed to investigate how scene blur or decreases in visual acuity, particularly prolonged decreases, affect perceived self-motion. In the future it might be advisable that when doing visual tasks in microgravity that participants visual acuity is tested before, during, and after microgravity exposure. This will allow any changes in visual performance to be correlated with potential changes in acuity.

### 5.6.3 Linearity of Travel Distance by Target Distance

In section 5.4 *Visual Self motion perception and gai*n I concluded that the data appears to be relatively linear with no obvious decay present. However, I did find that for Chapter 2 Experiment 3 Hallway and Chapter 3 the 10m target distance differed from the further target distances. I argued that this indicated that the participants may have responded to the 10m target distance differently than the other target distances, possibly due to the high rate of acceleration used in this experiment. As mentioned in section 2.2 *Introduction* the acceleration of 9.8m/s/s was used as I hoped that it might make it easier for participants to potentially confuse the visual motion with the gravitational cue. Had a slower rate of acceleration been used participants might have had more time to prepare and to react accurately to the 10m distance. This could explain why there was no non-linearity found for the Chapter 4 data, as a much slower acceleration was used (0.8m/s/s). The closest target distance in Chapter 4 was at 6m, accelerating at a rate of 0.8m/s/s means the participant had roughly 3.87 seconds to respond if they were to responded accurately.

It might be wise in the future to use distances and velocities or accelerations that give participants a few seconds to prepare before having to respond. An interesting follow up could compare a variety of near and far distances along with different rates of acceleration, as well as different constant velocities, similar to the Redlick et al, (2007) paper, in order to better compare the impact on linearity.

### 5.6.4 Measuring the VRI

Previous studies have attempted to measure the VRI through a variety of different methods, such as the use the of questionnaires (Mast & Oman, 2004), verbal report (Howard, Hu, Saxe & Zacher, 2005), orienting a rod (Howard & Hu, 2001) and the use of shape-from-shading (Preuss et al. 2018; Jenkin, Dyde, Jenkin, Howard & Harris, 2003; Oman et al. 2003). In Chapters 2 and 3, I measured VRI mainly through the use of a questionnaire and verbal report, but also the timing method as described in Chapter 3.

Throughout Chapters 2 and 3, the amount of VRI reported in the Hallway and Starfield environments varied from 100% to 22%. Why the distribution of participants experiencing (or not) a VRI varied so much between the different experiments is unknown. Throughout the experiments the method of testing the VRI, the demographics of the participants, and the HMD quality varied. Each one of these factors could have affected the VRI rate. For instance, the average age of participants in Chapter 2 Experiment 1 was 27.50 ± 7.68 while Chapter 3 it was 21.05 ± 4.33. The likelihood of experiencing a VRI has been found to increase with age (Howard, Jenkin & Hu, 2000). However, given the only slight differences in the average age in my experiments it is unlikely that this accounts for much of the difference.

Additionally, the VRI experience was not tested during every trial of the MTT, just at the end of each posture, thus it is possible that even when 100% of participants reported experiencing a VRI (such as in Chapter 2, Experiment 1) they might not have experienced a VRI on every trial (Howard & Hu, 2001). Averaging across trials could thus have led to some variations in reported VRI rate. However, I argue that it is likely that if a participant reported a VRI for a given posture, they most likely experienced a VRI during the majority of trials. In Chapter 3, I measured the persistence of the VRI over time, where for 5,000 frames participants indicated if they had a VRI or not. A report of 0 frames was taken as a no-VRI experience, and a report of 2,500 or more frames was taken as having had a consistent VRI. Out of the 40 participants only 6 experienced a VRI between 1-2499 frames. Referring to Table 5.5 below we can see that in the cases where a participant experienced a VRI for more than half of the frames (2500) they were likely to experience the VRI for 4170 frames on average. This suggests that the experience of a VRI is more dichotomous, where the participant either experiences it or not, at least over a short time frame. This would suggest that the participants who reported experiencing a VRI during the

MTT likely experienced one for the majority of the task. However, it is possible that when a new trial started on the MTT that this could “interrupt” their experience of a VRI. This could potentially lead to differences in the consistency of the VRI over several trials for 2 minutes compared to one trial over 2 minutes.

*Table 5. 4* The table shows the average number of frames participants indicated they felt they were experiencing a VRI on the VRI timing task from Chapter 3. The number in the brackets is the standard deviation.

| VRI experience | Average number of frames |
|---|---|
| No VRI (0 frames) | 0 (0) |
| Other (1-2499 frames) | 1004 (671.40) |
| VRI (2,500-5,000 frames) | 4170 (837. 34) |

Several small, unsuccessful, pilot studies were run throughout my PhD in an attempt to develop a more quantitative measure of VRI. The first attempt was the use of nine images that depicted a person at different orientations (standing, supine, or prone) with their head aligned with their body, or supine or prone similar. This method was found not to be useful as many of the participants found the task confusing despite repeated instruction and many of the participants’ verbal reports did not agree with the image they selected.

The second task that was designed was a “ball drop” task. It was performed in the same virtual hallway environment as the MTT. However, instead of a red target pillar there was a blue ball on a rope hanging in the air. Participants were asked to simply rotate the ball such that if they let go of the rope the ball would fall. This task, while simpler, resulted in a strong semantic bias in many of the participants, where they would explain that they oriented the ball such that it would fall on the floor, because “balls fall onto floors”. In this case if a participant reported a VRI the task appeared to work, but for many of the no-VRI individuals the task failed.

Lastly, a pilot study was run using an “NZ” task where participants standing upright in a hallway would perceive an “N”, which was displayed on the side of the screen as the letter “N” but when lying down with no VRI the “N” would be seen as a “Z” (see Figure 5.4). If the participant had a VRI the “N” should look still like the letter “N”. This task was found to also result in a strong bias where the first letter seen was always what participants reported. Participants were unable to change the frame of reference used to interpret the letter. For instance, when one participant was supine and viewed the “N” they reported seeing the letter “Z” and they also verbally reported no VRI. This was viewed as a success. Then the participant was moved to a standing posture and viewed the “N” while standing in an upright hallway environment. They still reported the “N” object as the letter “Z”. On the last trial they were asked if it could be an “N”, after a few seconds the participant agreed that now they could see it as the letter “N”. In the end, I felt that the verbal report and questionnaire used in Chapters 2 and 3 were the most reliable method.

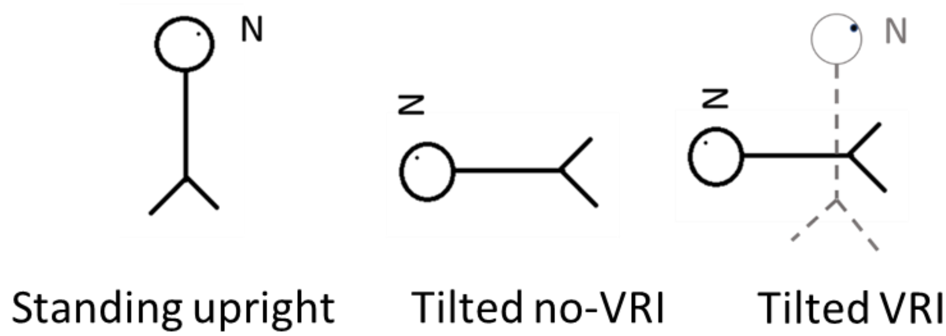



*Figure 5. 3* This figure depicts how a person might perceive the ambiguous shape “N” that is presented beside their head. While standing upright both the person and the letter are aligned with gravity so the person should interpret the “N” as the letter “N”. When both the person and the shape are tilted back by 90 degrees, while not experiencing a VRI the person should interpret the shape as a “Z” due to the gravity vector. If while tilted the person experiences a VRI such that they perceive themselves and the figure as upright (as indicated by the checkered grey stick figure) they should view the shape as an “N” just like in the standing posture despite the gravity vector being no longer in line with their body or the shape.

Since it is apparent that participants’ perception of their perceived orientation has an impact on visual weight and on visual self-motion tasks, a consistent, quantifiable way to measure the VRI should be developed. While self-report does appear to work reliably as a measure and is time efficient and convenient in any environment or task, some participants struggle with accurately and consistently describing how they perceive their orientation. One potential method could be inferring the time from the hands of a blank analog clock where the response would indicate where participant perceived “up” to be, and the amount and consistency of the deviation from a gravitational upright could indicate the magnitude of the VRI.

Overall, the current method of measuring a VRI, by verbal report, appears to work well but it is not without its drawbacks. It relies on participants to accurately and honestly report their perceived orientation in a potentially confusing situation. It also relies on the experimenter to accurately record this information and to not influence the participant’s response, which can be tricky if the participant is giving conflicting responses. If more studies will be done investigating VRI, or even simply perceived orientation in an environment, more quantified methods should be developed.

## 5.7 General Conclusion

Humans expect visual and non-visual cues to orientation and self-motion to match. We expect the direction of gravity to correspond to the orientation of trees and the accelerations we see to match those we feel. When they do not, there are perceptual consequences. Here we use virtual reality to create a conflict between the visual upright and the upright signaled by gravity. This results in some participants reporting a visual reorientation illusion, usually reported only in space, that causes some participants to feel upright while actually tilted. My results contribute to a growing body of research that looks at higher order perception and self-motion (e.g., Guterman & Allison, 2019). Here I show, for the first time, that different participants in the same physical orientation use optic flow cues differently based on their perceived orientation. Participants who report VRIs were more likely to have a higher visual gain compared to individuals who do not report VRIs, resulting in more undershooting of a target distance in the former group. The VRI-vulnerable participants were also more likely to rely more on gravity and less on vision when determining upright compared to no-VRI individuals.

It is likely that the differences in gain found on the MTT task on Earth and in 0g, and on the weights on the OChaRT task reflect differences in the optimal combination of cues when the gravity and visual cues to up are in conflict, or when the gravity cue is effectively removed. Additionally, the no-VRI group might reflect a population of individuals who experience difficulty either with reweighting or identifying cue conflicts. The presence or absence of a VRI while tilted in a compelling virtual environment may provide an efficient way for us to predict participants' responses on other tasks. For instance, individuals who are better able to reweight cues during a conflict might experience less nausea on other tasks (Weech et al. 2020b). The development of a more quantified assessment of VRI on Earth could help to provide more consistent results.

It is clear from the research presented in this dissertation that how participants interpret their orientation within their visual environment affects how effectively they use other visual cues to move through their environment or to orient ambiguous objects in their environment. This could have important consequences for future self-motion experiments. Other experimenters should take care to monitor how participants interpret the environment shown to them. Additionally, the results found here could be beneficial in designing training programs to help people navigate environments with conflicting uprights or in 0g, or when controlling vehicles in low gravity environments as the individuals can gain experience navigating environments with an unstable up. Lastly the results found here could be beneficial to virtual reality game designers, where environments can be designed to induce VRIs leading to fun experiences for the players, or the environment can be designed in a way to limit VRIs, by providing strong allocentric cues to orientation, in order to help ensure different players all have a consistent experience while moving through a particular environment.

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# Appendix A

## Ethics Approval for Chapter 2

YORK U
UNIVERSITÉ
UNIVERSITY

| | |
|---|---|
| **Certificate #:** | **e2015 - 033** |
| **Initial Approval:** | **02/03/15-02/03/16** |
| **Amendments:** | |
| **Renewals:** | **02/17/16-02/17/17**<br>**02/10/17-02/10/18**<br>**02/12/18-02/12/19** |
| **Current Approval Period:** | **02/12/18-02/12/19** |

**OFFICE OF RESEARCH ETHICS (ORE)**

[redacted]

# ETHICS RENEWAL

**To:** **Professor Laurence Harris**
Department of Psychology
Faculty of Health
[redacted]

**From:** Alison M. Collins-Mrakas, Sr. Manager and Policy Advisor, Research Ethics
*(on behalf of Veronica Jamnik, Chair, Human Participants Review Committee)*

**Date:** Friday, February 23, 2018

**Title:** **The perception of tilt**

**Risk Level:** ☒ Minimal Risk ☐ More than Minimal Risk

**Level of Review:** ☒ Delegated Review ☐ Full Committee Review

---

I am writing to inform you that this research project, **"The perception of tilt"** has received ethics review and renewal by the Human Participants Review Sub-Committee, York University's Ethics Review Board and conforms to the standards of the Canadian Tri-Council Research Ethics guidelines.

Note that renewal is granted for one year. Ongoing research – research that extends beyond one year – must be renewed prior to the expiry date.

Any changes to the approved protocol must be reviewed and approved through the amendment process by submission of an amendment application to the HPRC prior to its implementation.

Any adverse or unanticipated events in the research should be reported to the Office of Research ethics [redacted] as soon as possible.

For further information on researcher responsibilities as it pertains to this approved research ethics protocol, please refer to the attached document, **"RESEARCH ETHICS: PROCEDURES to ENSURE ONGOING COMPLIANCE".**

Should you have any questions, please feel free to contact me at: [redacted] or via email at: [redacted]

Yours sincerely,

Alison M. Collins-Mrakas M.Sc., LLM
Sr. Manager and Policy Advisor,
Office of Research Ethics

# Appendix B

## Ethics Approval for Chapter 3

YORK UNIVERSITÉ UNIVERSITY

| | |
|---|---|
| **Certificate #:** | **e2017 - 111** |
| **Initial Approval:** | **03/28/17-03/28/18** |
| **Amendments:** | **Amendment approved: 09/14/18**<br>**2nd Amendment approved: 11/09/18** |
| **Renewals:** | **03/28/18-03/28/19**<br>**02/13/19-02/13/20** |
| **Current Approval Period:** | **02/13/19-02/13/20** |

**OFFICE OF RESEARCH ETHICS (ORE)**
[redacted]

# ETHICS RENEWAL

**To:** **Professor Laurence Harris**
Centre for Vision Research
[redacted]

**From:** Alison M. Collins-Mrakas, Sr. Manager and Policy Advisor, Research Ethics
*(on behalf of Veronica Jamnik, Chair, Human Participants Review Committee)*

**Date:** Wednesday February 13, 2019

**Title:** **The effect of gravity on perception and navigation**

**Risk Level:** ☒ Minimal Risk ☐ More than Minimal Risk

**Level of Review:** ☒ Delegated Review ☐ Full Committee Review

---

I am writing to inform you that this research project, **"The effect of gravity on perception and navigation"** has received ethics review and renewal by the Human Participants Review Sub-Committee, York University's Ethics Review Board and conforms to the standards of the Canadian Tri-Council Research Ethics guidelines.

Note that renewal is granted for one year. Ongoing research – research that extends beyond one year – must be renewed prior to the expiry date.

Any changes to the approved protocol must be reviewed and approved through the amendment process by submission of an amendment application to the HPRC prior to its implementation.

Any adverse or unanticipated events in the research should be reported to the Office of Research ethics [redacted] as soon as possible.

For further information on researcher responsibilities as it pertains to this approved research ethics protocol, please refer to the attached document, **"RESEARCH ETHICS: PROCEDURES to ENSURE ONGOING COMPLIANCE".**

Should you have any questions, please feel free to contact me at: [redacted] or via email at: [redacted]

Yours sincerely,

Alison M. Collins-Mrakas M.Sc., LLM
Sr. Manager and Policy Advisor,
Office of Research Ethics

# Appendix C

## Ethics Approval for Chapter 4

HRMRB NOTIFICATION OF APPROVAL

July 22, 2020

Laurence Harris, Ph.D.
[redacted]

SUBJECT: Human Research Multilateral Review Board (HRMRB) Approval for the Amendment to the Protocol, "The Effect of Long Duration Hypogravity on the Perception of Self-Motion (VECTION)"

| | |
|---|---|
| Protocol Number: | Pro2472 (MOD000000834) – Amd-8 |
| Method of Review: | Full Board |
| Type of Review: | Amendment |
| HRMRB Disposition: | Approve |
| Approval Validity: | July 24, 2019, to July 23, 2021 |
| Risk Level: | Greater Than Minimal |
| Medical Monitor: | Level 4 |
| NASA MPA Number: | NASA7116301606HR |
| FWA Number: | 00019876 |

The amendment to this protocol consists of:

- Increase the number of enrolled subjects from 10 (5 males and 5 females) to 12 (5 male subjects + 1 male contingency subject and 5 female subjects + 1 contingency female subject).

- Amended the VECTION Protocol Form and the HRMRM Multinational Consent Form to reflect the changes made to the number of subjects from 10 to 12.

- Uploaded an updated version of the CITIs Certificates related to the following study team members: Laurence Harris, Michael Jenkin, Rob Allison, Nils Bury and Meaghan McManus.

- Uploaded a renewed version of York Ethics Approval.

HRMRB approval is valid for a period of two (2) years from the time of the initial review and/or protocol renewal. Changes, including action item responses or modifications, do not extend the initial review and/or protocol renewal date. There is no grace period beyond two (2) years from the last approval date. In order to avoid lapses in approval of your research and the possible suspension of subject enrollment, please submit your continuation request at least six (6) weeks before the protocol's expiration date. It is your responsibility to submit your research protocol for continuing review.

The Investigator must report any adverse reactions or unexpected problems resulting from this study to the HRMRB Chair.

The proposal was reviewed and approved by the HRMRB in accordance with Article 11.5 of the Memorandum of Understanding (MOU) between the National Aeronautics and Space Administration (NASA) and the Canadian Space Agency (CSA), NASA and the European Space Agency (ESA), NASA and the Government of Japan (GOJ), and NASA and the Federal Space Agency (FSA), formerly the Russian Space Agency.

[redacted]

Marisa Covington, Ph.D., CIP
Chair, Human Research Multilateral Review Board

# Appendix D

## Example Informed Consent Form for Chapters 2 and 3

**Informed Consent Form**

**Date**: March 2017

**Study Name**: The effect of gravity on perception and navigation

**Researchers**: *Laurence Harris* [redacted], *Meaghan McManus* [redacted]

**Purpose of the Research: To investigate the effect of gravity in perception and navigation**

**What You Will Be Asked to Do in the Research**: You will be asked to either wear a virtual reality helmet or view a computer screen in which you will be able to see a virtual environment. You will carry out the experiments while standing, lying on your side, or while lying supine or prone on a bed. You may be asked to tilt your head forwards or backwards. For some experiments you will be strapped in a chair in the Tumbling Room or Sphere Room. (These rooms are designed to position participants at any orientation). Orientations beyond ±90° will be maintained for a maximum of 5 minutes. Once positioned you will view a virtual environment and make judgments about orientation, and/or the direction and amount of illusory movement simulated on the display. You may be asked to judge the orientation of yourself, the environment, or cues in the environment. While movement through the virtual environment is simulated you may be asked to keep track of the distances or directions you moved. Following each orientation you will be asked to fill in a questionnaire about your experience. The experiment will take approximately 1 hour in total with no longer than 15 mins in any one body orientation.

**Risks and Discomforts**: We do not foresee any risks or discomfort from your participation. Some conditions may make you feel nauseous. If this becomes uncomfortable let the experimenter know and the experiment will be stopped immediately.

**Benefits of the Research and Benefits to You**: You will receive course credits at the rate of 1 credit/hr.

**Voluntary Participation**: Your participation in the study is completely voluntary and you may choose to stop participating at any time. Your decision not to volunteer will not influence the nature of the ongoing relationship you may have with the researchers or study staff or the nature of your relationship with York University either now, or in the future.

**Withdrawal from the Study**: You can stop participating in the study at any time, for any reason, if you so decide. If you decide to stop participating, you will still be eligible to receive the promised course credit for agreeing to be in the project. Your decision to stop participating, or to refuse to answer particular questions, will not affect your relationship with the researchers, York University, or any other group associated with this project. In the event you withdraw from the study, all associated data collected will be immediately destroyed wherever possible.

**Confidentiality**: All information you supply during the research will be held in confidence and your name will not appear in any report or publication of the research. Data will be collected through the experimental computer program and by the researcher. Your personal information will be safely stored in a locked facility only research staff will have access to this information. Your data will be held until the study is complete. At this time your data will be destroyed. Confidentiality will be provided to the fullest extent possible by the law.

**Questions About the Research?** If you have questions about the research in general or about your role in the study, please feel free to contact Dr. Harris either by telephone at [redacted] or by e-mail [redacted]. This research has been reviewed and approved by the Human Participants Review Sub-Committee, York University's Ethics Review Board and conforms to the standards of the Canadian Tri-Council Research Ethics guidelines. If you have any questions about this process, or about your rights as a participant in the study, please contact the Sr. Manager & Policy Advisor for the Office of Research Ethics, 5th Floor, York Research Tower, York University (telephone [redacted] r e-mail [redacted].

**Legal Rights and Signatures**:

I *(fill in your name here)*, consent to participate in *Perception of tilt study* conducted by Laurence Harris, Michael Jenkin and Meaghan McManus. I have understood the nature of this project and wish to participate. I am not waiving any of my legal rights by signing this form. My signature below indicates my consent.

**Signature** ______________________ **Date** ______________
Participant

**Signature** ______________________ **Date** ______________
Principal Investigator

# Appendix E

## Example Informed Consent Form for Chapter 4

**MULTINATIONAL CONSENT FORM FOR**

**SPACEFLIGHT-RELATED PARTICIPATION IN HUMAN RESEARCH**

**ABOUT THIS RESEARCHCONSENT FORM**

You may be eligible to take part in a research study as part of your space mission(s).

A research study is carefully planned and designed to increase scientific knowledge.

This consent form describes important information related to participation in a research study including the purpose, planned procedures, and potential risks. Both the study and this form have been reviewed and approved by the Human Research Multilateral Review Board (HRMRB).

Please take time to review this information carefully. Talk to the researchers about the study and ask any questions you have. **Make sure you fully understand what will be expected of you and the risks associated with participating in this study.** You may also wish to talk to others (for example, your friends, family, or doctors) about your participation in this study. If and when you decide to be a participant, you will be asked to sign this form and you will be given a copy.

Taking part in this study is completely **voluntary**. The decision to participate is yours. You may also leave the study at any time. If you leave the study before it is finished, there will be no penalty to you.

**Note: Failure to disclose pre-existing medical conditions may place you at greater risk for injury or other adverse events resulting from your participation in this study.**

**d1. GENERAL INFORMATION**

1.1 Your study title is VECTION: The Effect of Long-Duration Hypogravity on the Perception of Self-Motion.

1.2 Your study team includes a Principal Investigator, Co-Investigator, Key-Personnel (names, degrees, affiliations):

| | | |
|---|---|---|
| Principal Investigator | Laurence Harris, PhD | York University, Dept. of Psychology, Toronto, Canada |
| Co-Investigator | Robert Allison, PhD | York University, Dept. of Electrical Engineering and Computer Science, Toronto, Canada |
| Co-Investigator | Michael Jenkin, PhD | York University, Dept. of Electrical Engineering and Computer Science, Toronto, Canada |

| | | |
|---|---|---|
| PhD Student | Meaghan McManus, MA | York University, Dept. of Psychology, Toronto, Canada |
| Post-Doctoral Fellow | Nils-Alexander Bury, PhD | York University, Centre for Vision Research, Toronto, Canada |
| Post-Doctoral Fellow | Bjoern Joerges, PhD | York University, Centre for Vision Research, Toronto, Canada |
| Test Operator - Remote BDC (Primary) | Gilles Clement, PhD | KBR Houston, TX, USA |
| Test Operator – Remote BDC (Backup) | Scott Wood, PhD | NASA Johnson Space Center (JSC), Houston, TX, USA |

1.3 This study is sponsored or funded by: **Canadian Space Agency (CSA).**

1.4 a) Key Information:

The VECTION project assesses how the sensation of self-motion evoked by vision alone, and the perception of depth and orientation are affected by extended exposure to hypogravity.

b) Risk Characterization: reasonable according to section 6.1 of this document; “More than minimal” according to section 2.1 d) NASA eIRB.

c) What we will do in this study: You will be shown visual motion by means of a virtual reality head mounted display and asked to judge how far you feel yourself to have travelled. You will also be asked to judge your orientation and the size of displayed objects.

d) Participation timeframe: You will be tested pre-flight, early in flight, late in flight, when you first return to earth and again several weeks later. The pre- and in-flight tests will take 60 mins and the post-flight tests will take 50 mins each.

e) Study participants: Twelve (12) astronauts (5 male subjects + 1 male contingency subject and 5 female subjects +1 female contingency subject) are required to complete this study.

## 2. PURPOSE OF THIS STUDY (History and Background)

2.1 You are being asked to join this study because:

In a normal 1-g environment the perception of self-motion is a multi-sensory task, with the vestibular and visual systems predominating. The vestibular system must transduce both external forces and gravity. In a micro-gravity environment, the vestibular system is no longer affected by gravity, which may disrupt the astronauts’ perception of distance, self-motion and interpretation of tilt and translation. Astronauts are routinely required to estimate their motion in order to complete mission requirements. Understanding how self-motion is estimated, and in particular how self-motion is estimated under unusual gravity conditions, is key to continuing mission safety.

NASA's Human Research Roadmap identifies a range of risks due to vestibular/sensorimotor alterations associated with spaceflight. One knowledge gap was identified as: "What are the effects of long-duration spaceflight on sensorimotor function over a crewmember's lifetime? What are the changes over the course of a mission?" The VECTION project will develop a model of how human visual self-motion perception is altered under long-duration microgravity conditions. The model will help us understand visual-vestibular interactions in space and on earth and will significantly improve safety wherever movement under microgravity conditions is required. Since some previous studies suggest differences between males and females in vestibular-visual perception, we will furthermore evaluate sex differences. Experimental outcomes may lead to suggestions about controlling vehicles in low-gravity environments, either as drivers or pilots or under teleoperation. This study will also make important contributions to the perception of self-motion on earth – especially in clinical conditions in which navigation and gait control are perturbed, such as in Parkinsonism.

The VECTION experiments will be conducted in-flight and pre-and post-flight in order to develop a model of the time course of adaptation to, and re-adaptation from, the perceptual effects of microgravity.

## 3. STUDY PARTICIPANTS

3.1 In order to be eligible to participate, you may be asked to undergo the following screening tests or procedures:

- You must experience the illusion of self-motion during the presentation of the stimuli and respond with estimates that are within inter-subject variation derived from our baseline control trials. Screening will occur during the pre-flight BDC session.
- Your glasses must fit within the head mounted display unit. To be screened during the first pre-flight BDC session.
- You must be assigned to an ISS mission of 100 days or longer.
- You must have normal visual acuity (with prescribed correction if required) and normal vestibular function.
- Medications that may affect vision, vestibular function or may affect your performance during testing must be identified prior to any data collection session (e.g. antihistamines (e.g. Dimenhydrinate), anticholinergics (e.g. Scopolamine), antiemetics (e.g. Promethazine), antibiotics, tetracyclines, diuretics, anti-inflammatory, anti-depressants, anti-hypertensive, Cholesterol-lowering).

3.2 You are one of _ Twelve (12) subjects. More precisely, 5 male subjects + 1 male contingency subject and 5 female subjects + 1 female contingency subject will be tested to reflect the sex differences as indicated in the previous section.

## 4. STUDY DESCRIPTION

4.1 In this section you are provided a study description in layman's terms that you should easily understand and that provides you the following as applicable: a detailed explanation of each test, including what data will be collected and what equipment will be used; the amount of time each test will take; the frequency of testing, and whether testing is continuous or intermittent; a chart or calendar as a possible addition to the explanation of the tests; the study's duration and when it will be completed; any need for follow-up examinations or tests; the location of the testing; the amount of blood, urine, saliva, other biological samples and/or tissue that will be taken and how often; whether joining this study limits your chance to join other studies; whether "standard" medical procedures are included in the study; how your other activities may be affected by the study (exercise, diet, medications, physical activities, etc.); and a detailed list of any data that have been collected by other means that will be used by or shared with this study.

Each BDC and in-flight session will consist of three (3) Experiments: 1) Ambiguity between translation and tilt will be explored by measuring perceived orientation following a simulated linear translation. 2) The ability of astronaut subjects to perform spatial updating based on visual motion cues will be assessed by measuring how far a participant needs to "travel" in a simulated visual environment to reach a previously viewed target. 3) The perception of distance in virtual reality (VR) and the influence of microgravity on the perception of distance will be evaluated through the comparison of the length of a virtual object to a real-world reference object. All experiments will be performed using a head mounted display (HMD) to elicit a sense of self-motion or in which to view objects. Since some previous studies suggest differences between male and females in vestibular-visual perception, experiments based on sex differences will be performed furthermore as stated in section 2.

Details of the experiments are as follows:

*Experiment 1*) You will virtually "travel" down a corridor after which you will indicate your orientation with respect to your initial orientation.

*Experiment 2*) You will be presented with a target presented at some simulated distance. You will be asked to view the target and build a mental estimate of the distance to the target. Once complete, the target will be extinguished and you will experience simulated visual motion towards the now extinguished target and will indicate when you have reached the position at which the target was previously presented.

*Experiment 3*) You will indicate whether the length of a viewed square is longer or shorter than a reference object that is in the real world. Errors in matching the length of the projected line to the reference length will reveal errors in perceived distance.

For on-ground BDCs, the above experiments will be performed seated and also lying supine. For in-flight sessions, you will be held in place using a tether. For all experiments, a neck brace will be worn to restrict motion of the head relative to the body.

For in-flight sessions, video will be used to monitor the experimental setup.

<u>Experiment windows are as follows</u>:

| | **Pre-flight** | **In-flight** | | **Post-flight** | |
|---|---|---|---|---|---|
| **Time point (days)** | L -180/-60d | L + 3/6d | L + 80/100d | R + 4/6d | R + 50/70d |
| **Session** | HMD session (seated & supine) | HMD session | HMD session | HMD session (seated & supine) | HMD session (seated & supine) |
| **Time (min)** | 60 mins | 60 mins | 60 mins | 50 mins | 50 mins |
| **Location** | JSC or EAC | ISS | ISS | JSC or EAC | JSC or EAC |

Note: JSC: Johnson Space Center; EAC: European Astronaut Centre

Data will be collected from the following experiments to support VECTION:

*Preflight*
MedB 1.1 (Pre-and Post-flight Physical Exam for Long-Duration Crews, eye and neurologic tests)
MedB 1.10 (Ophthalmology Examination)

*Inflight*
MedB 1.10 (Ophthalmology Examination)
MedB 1.3 (Medication log for private medical conference – information about motion sickness medication and any others that may affect vestibular function or vision)

*Postflight*
MedB 1.1 (Pre-and Post-flight Physical Exam for Long-Duration Crews, eye and neurologic tests)
MedB 1.10 (Ophthalmology Examination)

4.2 You are being told if the study you are joining includes one of the following categories:

- ☐ *"Randomized"* means that you are put into a study group by chance (e.g., like flipping a coin). Neither you nor the principal investigator will choose what study group you will be in. You will have a chance of being placed in any study group.
- ☐ *"Blinded"* means you will not know what study group you are in.
- ☐ *"Double-Blinded"* means that neither you nor the Principal Investigator (double-blinded) will know what study group you are in.
- ☐ *"Placebo"* means a pill with no medicine. In a placebo-controlled study, you may be given a study medication and it will contain either (name of drug) or placebo (pills with no medicine).
- ☐ *"Not Applicable"*

## 5. DRUGS, BIOLOGICS or NEW MEDICAL DEVICES or PRODUCTS

In this section you are being told whether the study uses any drugs, blood or blood components, allergenic substances, vaccines, investigational new medical devices or other similar products used to investigate human anatomy or physiology or to prevent or treat disease or injury.

__X___No study drug, biologic, or investigational new medical device or product will be used.

_____Yes, the study drug, biologic, and/or investigational new medical device or product is:

________________________________________________________________________.

If “Yes” is checked above, then the investigator(s) will also provide you with a description of the drug or other substance and/or investigational new device. For investigational new drugs or devices, the investigator will also provide you with any relevant investigational regulatory approval number(s). In all cases the investigator(s) will also provide you with any other materials you require to best assist you with making an appropriately informed decision regarding your participation.

## 6. INFORMATION ABOUT RISKS AND HAZARDS

6.1 You are joining a study that is:

- ☐ “Minimal risk” means that the probability and magnitude of harm or discomfort anticipated in the research are not greater in and of themselves than those ordinarily encountered in daily life or during the performance of routine physical or psychological examinations or tests.
- ☐ “Reasonable risk” means that the probability and magnitude of harm or discomfort anticipated in the research are greater in and of themselves than those ordinarily encountered in daily life or during the performance of routine physical or psychological examinations or tests, but that the risks of harm or discomfort are considered to be acceptable when weighed against the anticipated benefits and the importance of the knowledge to be gained from the research.

6.2 Hazards represent conditions that have the potential to cause harm. Risks, in turn, originate from hazards. For example “A wet deck on a boat” is a hazard, whereas potential risks associated with that hazard might include slipping and falling down or overboard.

6.3 The risks of joining the study and the steps taken to protect against harm include:

Risk and Harm

- Injury from falling due to loss of balance during ground BDCs when wearing the head mounted display during seated or injury from collisions with the surroundings when aboard the ISS.

Risk Mitigation

- A team member will be near the subject at all times in the unlikely event that the subject loses their balance when wearing the head mounted display (HMD) during the seated portion of testing.
- Aboard the ISS when the subject is wearing the HMD the subject will be tethered to prevent drifting into objects during testing.

Risk and Harm

- Nausea due to visual stimuli viewed using the HMD.

Risk Mitigation

- At any time if the subject feels discomfort or dizziness the simulation will be stopped immediately.

6.4 The hazards and the steps used to minimize the hazards include:

Hazards include:

- Exposure to visual stimuli when using the head mounted display.
- Impaired vision while using the head mounted display.

Hazards shall be minimized by:

- Reducing time required using the HMD to the minimum required for experimental objectives.

## 7. TREATMENT, INJURY AND COMPENSATION INFORMATION

Even though the investigators have taken steps to minimize the risks, you may experience problems or side effects. Therefore, the following statement applies for you the participant: “In the event of injury resulting from this study, I understand that I will receive medical attention and available treatment. I also understand that I will be compensated for any injuries to the extent permitted under the laws and regulations applicable to me and the provisions of the contract between me and (space agency of crewmember subject). My agreement to participate shall not be construed as a release of liability which may arise from or in connection with the above procedures for **Canadian Space Agency (CSA)** or any third party.

## 8. BENEFITS INFORMATION

8.1 Potential benefits to You: Participation in York University studies generally result in no direct benefit to you as an individual. It is hoped that the information learned from this research study will help the international science partners learn more about human physiological changes for future space flight missions.

8.2 Potential benefits to the Researchers: The research team will utilize this section to inform you whether any member of the research team might potentially receive additional financial or other benefits through the conduct of this research, for example through his/her business affiliations, holdings of stocks or other securities, patents or patent applications, trademarks or trademark applications, etc.

_X___The researchers declare that they have no otherwise undisclosed potential financial benefits.

____Potential additional financial benefits to the researchers are (include researcher name(s) and nature of benefit(s)):_______________________________________________________________________
_______________________________________________________________________________.

## 9. NEW FINDINGS

9.1 If new information is obtained during the study after you have joined, you will be informed. You may change your mind about continuing in the study. You may be asked to sign a new consent form that includes the new information.

## 10. STUDY WITHDRAWAL and/or TERMINATION

10.1 You may withdraw from the study at any time. If you decide to leave before the study is finished, please tell the investigator or study staff. Your withdrawal could have undesired consequences for your health and/or the health of other subjects. A responsible physician will tell you if there could be any harm to you if you decide to leave before the study is finished. If you tell the researchers your reasons for leaving the study, that information will be part of the study record.

10.2 Your withdrawal or refusal to participate in the study will not result in any penalty or loss of benefits to which you are otherwise entitled.

10.3 If you decide not to join the study, or to withdraw from it you may nevertheless be eligible to participate in other studies.

10.4 Researchers may need to stop your participation in the study even if you want to continue participation. The research may also be stopped at any time by: the Human Research Multilateral Review Board (HRMRB), the Crew Surgeon or other assigned medical monitor, the Flight Director, or the ISS Commander, as appropriate, if the research would endanger any ISS Crew Member, including you, otherwise threaten the mission success, or for any other reason. Some examples of possible reasons include:

- The researcher believes that it is not in your best interest to stay in the study;
- Any problem with following study related instructions;
- Any problem with following clinic or laboratory policies and procedures;
- Any serious complication during the study;
- Inappropriate behavior;
- The study is suspended or canceled;
- The subject's information is or becomes unusable for any reason;
- Events beyond the participating agencies' control occur, for example: fire, explosion, disease, weather, floods, terrorism, wars, insurrection, civil strife, riots, government action, or failure of utilities;
- Existing data reveal answers earlier than expected.

## 11. COST and FINANCIAL INFORMATION

11.1 There are no costs or bills to you for participation in this study.

## 12. SUBJECT RECORD CONFIDENTIALITY AND AUTHORIZATION TO RELEASE PROTECTED HEALTH INFORMATION (PHI)

12.1 Your privacy and the confidentiality of data collected or used as a part of this research study will be protected from unauthorized disclosure according to applicable law.

12.2 Your protected health information (such as name, geographic identifier, dates, phone number) may be used or shared by York University offices of research oversight or quality assurance, medical monitors, and researchers for the reasons below:

- To conduct and oversee the research;
- To make sure the research meets York University requirements;

- To conduct monitoring activities (including situations where you or others may be at risk of harm or reporting of adverse events);
- To become part of your medical record if necessary for your medical care;
- To review the safety of the research;
- To support operational clinical activities where clinical experts evaluate relevant medical and research data to recommend clinical practice guidelines or medical requirements specifically for space flight. These data will not include names although other information may implicitly link the information to you.

12.3 For the purposes of ensuring the safety of the study and yourself, and of verifying compliance with applicable laws and regulations, information about you, including protected health information, may be used or seen by the researchers or others, on a need-to-know basis, during or after this study. Examples include:

- The researchers may need the information to make sure you can take part in the study;
- The participating agencies and other government officials may need the information to make sure that the study is performed in a safe and proper manner;
- Other officials may need to review the information if the study involves the use of an experimental drug or device;
- Safety monitors, medical personnel, or safety committees may review your research data and/or medical records for the purposes of medical safety, for verification of research procedures, or if any injuries or other adverse events occur;
- A data and safety monitoring board (DSMB) may oversee the research, if applicable.

12.4 In addition to the cases mentioned in 12.2 and 12.3 above, your protected health information obtained through this research may be used or shared with others through separate Data Sharing Agreements to which you yourself have also concurred beforehand by providing a separate signature. The results may be used by the research team and possibly be presented/published in journals or at scientific conferences, but in such cases will not include information that could identify you, directly or by inference, without your consent.

12.5 You have the right to withdraw your consent for the researchers to use or share your protected health information. The researchers will not be able to withdraw all the information that already has been used or shared with others to carry out related activities such as oversight, or to ensure quality of the study. To withdraw your consent, you must submit a written request to do so to the researcher and, if relevant, the Data Sharing Agreement administrator.

12.6 You have the right to request access to your study records after the study is completed. To request this information, you must do so in writing by contacting the researcher. Should your personal data in those study records be incorrect, you have the right to request that this be corrected.

12.7 Any data (including but not limited to standard measures, laboratory data, psychological, or physiological measurements) obtained from you for this research study may become part of the participating agencies' data archives, conditioned on each specific agency's arrangements with their investigators. These data may be used in this research, may be used in other research, and may be shared with other organizations. All applicable laws and regulations concerning the privacy and confidentiality of these data will be followed. Records stored in these archives will not be released or used in a way that identifies you by name – a code will be assigned. However, records may be implicitly linked to you through fields such as mission duration, gender, age, etc.

## 13. CONTACT INFORMATION

13.1 You may contact the Principal Investigator to:

- Obtain more information about the study;
- Ask a question about the study procedures;
- Report an illness, injury, or other problem;
- Leave the study before it is finished;
- Express a concern about the study.

Principal Investigator: Dr. Laurence Harris

[redacted]

Study Coordinator: Dr. André Gerges

[redacted]

You may express a concern about this study by contacting the Bioethical committee of your Space Agency or the Human Research Multilateral Review Board (HRMRB) listed below:

Office of Research Assurance: Research Integrity & Protection of Human Subjects
Attention: Human Research Multilateral Review Board Administrator
[redacted]

[redacted]

## 14. RECORD of INFORMATION PROVIDED

14.1 Your signature in the next section means that you have received copies of all of the following documents:

- This Multinational Space Station "Consent to be Part of a Research Study" document;
- Video, Audio, and Photo Consent, as applicable;

  Other (specify): ________________________________

## 15. SIGNATURES

**Research Subject:**

I understand the information printed on this form. I have discussed this study, its risks and potential benefits, and my other choices with Dr. Laurence Harris and I hereby give my consent to participate in this study as a research subject. My questions so far have been answered. I understand that if I have more questions or concerns about the study or my participation as a research subject, I may contact the study team. I understand that I will receive a copy of this form at the time I sign it and later upon request.

Signature of Subject: ___________________________________ Date: ________________

Name (Print legal name): ____________________________________________________________

**Video, Audio, and Photo:**

I understand that this study will utilize video, audio and/or still photography to analyze study results and I consent to the use of these materials.

☐ I accept

☐ I do not accept

☐ Not applicable (study will not utilize video, audio or still photography)

Signature: ______________________________

**Principal Investigator (or Designee):**

I have given this subject information about this study. I believe this to be accurate and complete. The subject has indicated that he or she understands the nature of the risks and benefits of participating in this study.

Name: ____________________________________ Title: ___________________________

Signature: _________________________________ Date: ___________________________

**Note:**

Principal investigators are required to retain the signed, dated copy of this form with any attachments for at least three (3) years beyond the date of the completion of the study.