# Investigating the perception of travel distance using visual and non-visual self-motion cues

Ambika Bansal

A DISSERTATION SUBMITTED TO THE FACULTY OF GRADUATE STUDIES IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

GRADUATE PROGRAM IN KINESIOLOGY AND HEALTH SCIENCE

YORK UNIVERSITY

TORONTO, ONTARIO

September, 2025

# Abstract

Having an accurate perception of travel distance is essential for navigating and moving through the world. In Chapter 2, I show that transforming visual motion into travel distance differs depending on the speed and direction of optic flow being perceived. Motion at the slower speed was associated with people feeling like they had moved further compared to motion at the faster speeds. In Chapter 3, I use a series of 4 experiments to investigate how various characteristics of a virtual environment affects your perception of travel distance through it. The specific parameters I investigated were: (1) the structure of an environment, and presence and texture of a ground surface, (2) the naturalism and scale of an environment, (3) colour, and (4) the density of a starfield. Results show no effect of the structure of an environment, and the presence of a ground surface (Experiment 1), or between the naturalism of an environment (Experiment 2), or whether the environment has colour or not (Experiment 3). However, I did find a small effect of the texture of the ground surface and the scale of an environment. In Experiment 4, I also show that there may be a ceiling effect with the starfield density needed to accurately estimate travel distance. Together these experiments will have implications for the design of real and virtual environments where perceived motion is important and enable us to further predict our perception of moving through these environments. In Chapter 4, I used a large-field edgeless display to either visually "move" participants while they were (i) physically stationary, (ii) performing a blind walking task on a treadmill, or (iii) visually "moving" while walking on a treadmill. Optic flow simulating forward self-motion was presented either full field, in the central field (central ±20°), or in the far periphery (beyond ±90°). I show that the high sensitivity to optic flow in the far periphery is a general feature of perceptual odometry even when integrating non-visual cues with visual cues.

Acknowledgments

I would first like to thank my supervisor, Dr. Laurence Harris, for all his guidance, time, and unwavering support over the past five years. Your childlike curiosity for science is truly infectious, and I know that I would not be where I am today without you.

I would also like to thank my previous supervisors, Drs. Denise Henriques, Michael Barnett-Cowan, and Ewa Niechwiej-Szwedo, for their guidance along the way. Thank you to my committee members, Drs. Taylor Cleworth and Nikolaus Troje, for all their time and valuable feedback. Thanks to all the Harris Lab members, Björn, John, Rachel, Fatemeh, Anita, and Ahmed, and extended lab members, Meaghan and Hongyi, for their help, discussion, support, and friendship over the years.

I am deeply grateful to my Mom, Dad, Akash, Vidushi, Maya, Nandini, and Harshul for always being there. Thank you also to my friends and the rest of my family for keeping me sane throughout this process. I could not have done this without you all. And finally, thanks to Sahil for everything else.

Table of Contents

## List of Tables

# List of Figures

# CHAPTER 1: General Introduction

One of the most common, and complex functions of the human brain is to perceive our own motion. Whether it is navigating towards food, or away from life-threatening situations, self-motion perception is essential for our survival. One critical feature of our sophisticated navigation system is path integration. Self-motion information is accumulated to inform the direction and distance of a goal, regardless of local landmarks. To track one's position in space, several computations are involved to integrate the rotational angles and distance travelled into a vector by which one can learn complex landscapes. Although both direction and distance are necessary for path integration, this dissertation will focus solely on the distance component.

The main objective of this dissertation is to investigate the perception of travel distance using visual and non-visual self-motion cues. Under natural conditions, we integrate information from all our sensory systems into creating one coherent perception of self-motion. Although, even with vision alone, we are still able to get the illusion of self-motion, known as vection. A common example used to describe this phenomenon is sitting in a stationary train, while visually seeing a train move past through the window. One will get this illusion that one is moving forward, even though that train is stationary. Recently, more ecologically valid technology, such as virtual reality (VR) has been used to study these complex systems. VR allows us to create naturalistic environments, while maintaining the experimental control to manipulate specific visual characteristics of that environment. All of the experiments in this dissertation will use VR to provide visually induced self-motion.

Most researchers investigating the perception of travel distance have primarily focused on forward movements and have disregarded movements in the other directions. This led to

Chapter 2 of my dissertation, which focuses on the perception of travel distance in the up, down, and backwards directions as well. The literature is also mixed on whether there is an effect of speed on our perception of self-motion. Therefore, Chapter 2 examines how both the direction and speed of self-motion affect the perception of travel distance. Although virtual reality has been widely used to investigate the perception of travel distance, the characteristics of these virtual environments vary greatly between studies. There are numerous variables that contribute to the processing of optic flow, and therefore our perception of travel distance, although these parameters are rarely taken into consideration in peoples' experimental design. Therefore, Chapter 3 of my dissertation focuses on how manipulating the visual-field characteristics of virtual environments affects perceived travel distance.

Although vision alone can produce self-motion, taking a multisensory approach is important in understanding how perceiving travel distance occurs in the real world. When multiple sensory cues (i.e. vision, vestibular, proprioception, etc.) are available and combined in self-motion perception, this information can be redundant. When estimating travel distance, the relative contribution from these different sensory systems is still unknown. In Chapter 4, I tested the perception of travel distance using both visual and non-visual self-motion cues. This was done under sensory congruent and sensory incongruent conditions. The full set of experiments in this dissertation not only improves our understanding of the multisensory perception of our movement through the world but also aid in our ability to test this complex odometric system. This research can find application wherever humans or robotic agents need to move in unusual environments.

## 1.1 Visual Cues to Self-Motion

As we navigate through our environment, the relative motion of visual elements, such as objects and landmarks, creates a distinct pattern known as optic flow (Gibson, 1950). Optic flow and retinal flow differ in how motion is represented during movement. Optic flow refers to the motion patterns generated by the environment as we move through it. On the other hand, retinal flow describes the motion of visual input across the retina, which can also result from eye movements relative to the head (such as tracking a moving object). This makes retinal flow more complex. For example, if one moves forward while fixating on a stationary object to the right, the retinal and optic flow patterns will differ. We are typically able to distinguish between the two (Cutting et al., 1992; Rushton et al., 2007) and extract optic flow from retinal flow. Notably, optic flow continues to exist even when the eyes are closed, as it reflects movement through space, not just visual input. Optic flow in the presence of adequate scale information can provide a cue for distance travelled. The characteristics of this optic flow vary depending on the type of movement. For example, linear motion evokes a different pattern of optic flow than rotational motion, and lateral motion differs from forward-backward motion. When making linear movements, optic flow can be represented as a sphere of flow centered on the observer and radiating out from the point straight ahead of the movement (the focus of expansion, FOE, Gibson, 1979). Therefore, visually moving forward and backward can also be described as optic flow expanding or contracting, respectively (Figure 1). Some have found that self-motion perception was stronger when visually moving forward compared to when moving backward (Reinhardt-Rutland, 1982). Though, others have found contradicting results where self-motion perception was stronger when visually moving backward compared to forward (Bubka et al., 2008). One study specifically investigated the perception of travel distance in the up and down directions (Clément et al., 2020). They found that travel distance moving upwards was overestimated, meaning participants felt they moved further than they had, whereas moving downwards was underestimated, meaning participants felt they moved less than they had. Optic flow can also be parsed into two components: radial and laminar (Figure 1). The pattern of flow varies from entirely radial around the FOE (e.g. during forward translation) to entirely laminar orthogonal to the direction of travel (e.g. moving side-to-side), and this alone can simulate different directions of self-motion (Warren & Hannon, 1988). Independent systems may be responsible for processing these two types of optic flow (Harris et al., 2012). Radial flow with its giveaway FOE provides a more accurate estimation of self-motion direction than laminar flow (Crowell & Banks, 1993, 1996). Much of the research investigating the perception of travel distance has studied forward translational movements, and disregarded movement in the other directions. Although we receive different optic flow patterns when moving in different directions, and there are clear differences in radial compared to laminar optic flow processing, no one has systematically assessed the perception of travel distance in the different forward, backward, upward, and downward directions. Therefore, Chapter 2 of this dissertation examines how the direction of self-motion affects perceived travel distance.

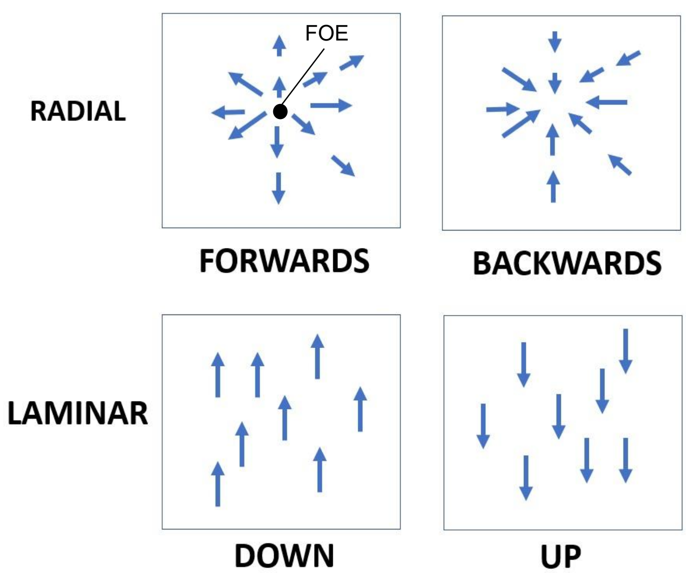


**Figure 1.1. Radial and laminar optic flow patterns.** The top left panel shows the optic flow pattern when making forward translational movements. The top left panel also shows the FOE, or the point straight ahead in which the optic flow pattern is radiating from. The top right panel shows the contracting optic flow pattern seen when making backward translational movements. The bottom row shows the laminar optic flow patterns seen when moving up and down.

The perception of travel distance using optic flow cues, known as visual odometry, requires computationally transforming visual motion to a distance estimate. This means that the motion profile can also affect visual self-motion processing. This aligns with research that has found the introduction of spatial jitter (i.e., optic flow bobbing up and down, as we get with natural walking) enhances the sensation of self-motion (Apthorp & Palmisano, 2014; Guterman et al., 2012; Kim & Palmisano, 2008; Palmisano et al., 2000, 2003, 2009) and the perception of travel distance (Bossard & Mestre, 2018; Bury et al., 2020). Some researchers have also found that simulated constant acceleration motion led to more accurate estimates of travel distance compared to when experiencing simulated self-motion of a constant velocity (Redlick et al., 2001a). They found that optic flow presented at a lower acceleration or constant velocity resulted in a greater overestimation of the motion as well, meaning participants perceived that they had traveled further. Others have also found that slower speeds resulted in overestimations of travel distance (Harris et al., 2012; McManus et al., 2017), whereas others have found no effect of speed on distance estimates (Frenz et al., 2007; Lappe et al., 2007a). Clearly, the literature is still mixed as to whether there is an effect of speed on self-motion perception. Chapter 2 addresses this question by directly testing whether the speed of self-motion affects perceived travel distance. Another study from our lab has investigated how the location of motion within the visual field can impact perceived travel distance (McManus et al., 2017a). Using a large-field edgeless display, they found that the optic flow presented only in the far periphery (eccentricities greater than +-90 degrees), resulted in overestimations, meaning participants felt like they had moved further, compared to the full field or in the central field only (Figure 2). These findings align with previous research that show that peripheral vision is more effective than central vision in evoking self-motion (Brandt et al., 1973), sway (Delorme & Martin, 1986), and perception of a faster travel speed (Pretto et al., 2009). In many of the studies investigating visual odometry, there is a sensory cue mismatch, where participants are receiving visual motion information while remaining physically stationary. In Chapter 4, I hypothesized that this effect of visual field exposure might diminish when visual and non-visual self-motion cues are congruent.

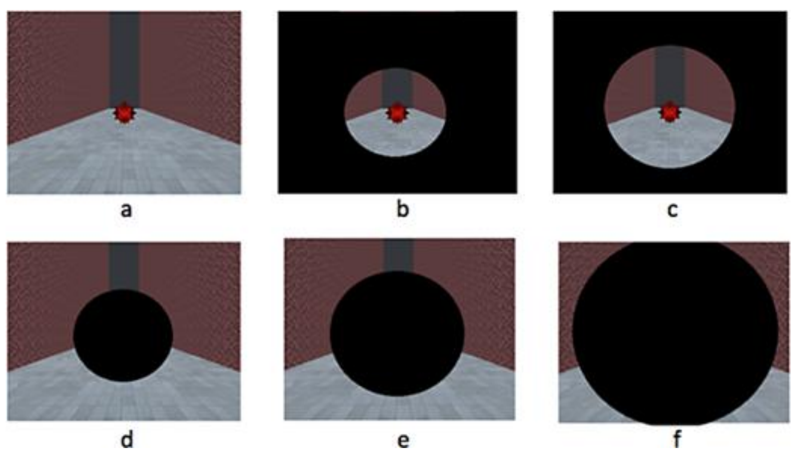



**Figure 1.2.** from McManus et al., 2017. Screenshots of the visual display. (a) full field of view, (b) central field of view ±20°, (c) central field of view ±40°, (d) peripheral field of view from ±20° out, (e) peripheral field of view from ±40° out, and (f) far peripheral field of view from ±90° out

Although visually induced self-motion has been widely used to investigate the perception of travel distance, the visual field characteristics of these virtual environments can vary greatly. There are various parameters (structure, texture, the ground surface, colour, luminance, distance to walls, etc.) that potentially contribute to the processing of optic flow (Bubka & Bonato, 2010; Seno et al., 2010; Tamada & Seno, 2015; Vaziri-Pashkam & Cavanagh, 2008). Although these variables clearly modulate self-motion perception, these factors are rarely taken into consideration when designing experiments to investigate self-motion perception. We see a great variability in travel distance estimates across studies. From our lab, we have found participants feeling like they had moved further when moving through a virtual corridor (Bansal et al., 2024) compared to less structured environments, such as a "lollipop field" (Bury et al., 2020) or a starfield (McManus & Harris, 2021). The starfield is less structured because the objects are arranged randomly with no sense of orientation or organization. The "lollipop field" was also arranged with no sense of organization, although it did provide orientation cues. These findings align with previous research that show that a stronger sensation of self-motion when moving through realistic environments compared to more abstract (B. E. Riecke et al., 2005; Trutoiu et al., 2009), and more detailed environments leading to more accurate walking trajectories compared to more sparse environments (Wood et al., 2000). Another key feature in the perception of self-motion is optic flow received from the ground surface. We have evolved moving on a stable ground surface and are therefore tuned to relevant information about self-motion from the ground (Gibson, 1979). Whether it is landing an airplane or just walking on the sidewalk, the ground surface provides important information of orientation and scale. This "ground dominance effect" has been shown in the perception of a 3-D scene (Bian et al., 2005), and in a visual search task (Mccarley & He, 2000). Others have also shown that the lower visual field demonstrated a larger effect on the perceptual upright as compared to the upper visual field (Dearing & Harris, 2011). Studying how the brain processes these various visual field characteristics is a crucial element in improving our ability to test the odometric system. In Chapter 3, I use a series of 4 experiments to examine how some of the characteristics of a virtual environment (structure, texture, the ground surface, colour, naturalism, scale, starfield density) affects how you move through it.

Another aspect of self-motion perception that has been well-studied is the perception of direction, known as heading perception. For translational self-motion heading can be inferred using the optic flow radiating from the FOE (Figure 1), regardless of where one fixates (Gibson & Gibson, 1955; Warren & Hannon, 1988). If one turns their head around while moving forward, the retinal flow pattern changes, but the FOE still aligns with the actual direction of movement (Gibson & Gibson, 1955). Humans are quite accurate when estimating heading, especially when traveling close to straight ahead, with accuracy of about just 1 degree of error (Warren & Hannon, 1988). Although I did do some collaborative research on the perception of heading throughout my PhD, assessing the precision and temporal dynamics of heading perception using continuous psychophysics (Jörges et al., 2024a) and examining heading biases when responses were made in allocentric compared to egocentric reference frames (in progress), this will not be the focus of my dissertation.

### *1.1.1 Vection*

Optic flow alone can induce an illusionary sensation of self-motion, known as vection (for review, see Dichgans & Brandt, 1978). The example mentioned in the first section of this chapter uses sitting in a stationary train while visually seeing a train move past through the window. One will get the illusion that one is moving forward even though that train is stationary. This illusion of self-motion is known as vection and has been used across many studies as a measurement of self-motion perception. Vection can be measured using its magnitude or strength of the illusion (Apthorp & Palmisano, 2014; Palmisano & Chan, 2004; B. E. Riecke et al., 2005), perceived speed (Brandt et al., 1973; Kim & Palmisano, 2008; Oman et al., 2003), onset (Bubka & Bonato, 2010; D'Amour et al., 2021), and latency (Palmisano et al., 2000). Vection can be modulated by the direction of the optic flow (Fujii & Seno, 2020), the size of the field of view (Brandt et al., 1973), gravity (Oman et al., 2003; Young & Shelhamer, 1990), and body tilt (Nakamura et al., 2010). Vection is informative enough that, even without any other cues to our motion, we can keep track of our (simulated) location (Bremmer & Lappe, 1999; Ellmore & McNaughton, 2004; Harris et al., 2012; Redlick et al., 2001). There are a few crucial points to note on how vection relates to this dissertation: (1) although the measurement of vection can inform us as to whether people feel like they are moving, it does not inform us as to the way people might use the visual motion information to perceive self-motion, (2) one can still perceive travel distance and heading without experiencing vection (i.e. without getting the illusion that they themselves are actually moving). These ideas align with previous research that show a subjective increase in vection speed in microgravity (Oman et al., 2003; Young & Shelhamer, 1990), but without corresponding differences in the perception of travel distance in microgravity (Jörges et al., 2024a). Others have also found an effect of the speed of simulated linear movement on vection speed (De Graaf et al., 1990), but there is still mixed evidence on whether there is an effect of simulated linear movement speed on perceived travel distance (Frenz et al., 2007; Harris et al., 2012; Lappe et al., 2007; McManus et al., 2017). Although one may assume that the perception of travel distance and the sensation of vection should be related, these studies highlight this idea that the sensation of vection can be altered without changes to the perception of travel distance. One can perceive simulated self-motion, without feeling like one is actually moving (e.g. playing a first-person video game). One way of interpreting optic flow information is not just experiencing that one is moving through the world, but it can also be interpreted as one staying stationary while the world is moving past them. The series of studies mentioned above that test how the components of a virtual environment can affect your perceived self-motion has focused on this experience of vection, and no one has tested how these variables may effect the perception of travel distance specifically. Chapter 3 examines whether the differences seen in vection when manipulating the virtual scene will translate to these same variables affecting our perception of travel distance.

## 1.2 Non-Visual Cues to Self-Motion

Although much of the research investigating self-motion perception, and the perception of travel distance, has used visual cues alone, our other non-visual potential cues are never "turned off". Conditions in which participants are moving only visually (e.g., in virtual reality with no head movements), introduce a sensory cue conflict, in which their visual system is sensing movement, and their non-visual cues are sensing that they are stationary. The first two projects of this dissertation focus solely on the perception of travel distance using visual self-motion cues. Chapter 4 introduces both visual and non-visual self-motion cues, examining both sensory congruent and incongruent conditions.

Although vision alone can give a sense of distance traveled, self-motion can still be tracked in the absence of vision (Clark & Stewart, 1968; Roditi & Crane, 2012). There are several non-visual cues to the perception of self-motion. Under natural self-motion conditions, the following non-visual cues can contribute to the perception of self-motion: (1) vestibular cues, (2) proprioceptive cues about the movement of the limbs and efference copy of the motor commands to move the limbs, (3) auditory cues, (4) tactile cues, (5) olfactory cues for both humans (Ache et al., 2016; Schwarz & Hamburger, 2023) and birds (Gagliardo, 2013), (6) as well as other cognitive factors. Of these various multisensory cues, the proprioceptive, vestibular, auditory, and tactile cues, as well as the cognitive factors that influence the perception of self-motion, will be reviewed below.

### *1.2.1 Vestibular Cues*

Before examining how vestibular cues contribute to self-motion perception, we must first understand the basic anatomy and physiology of this complex sensory system. The vestibular system is responsible for processing information of head rotation, translation, orientation, and the gravitational forces acting on the body (Day & Fitzpatrick, 2005). This sensory system is a crucial element in maintaining balance and spatial orientation during movement. Within the inner ear, there are five vestibular organs that make up the vestibular labyrinth, which are sensitive to different types of acceleration (Figure 3). There are two otolith sensors that detect linear acceleration, called the utricle and saccule. Then there are three semicircular canals that are responsible for sensing rotational acceleration of the head: the horizontal, anterior, and posterior canals. The directional sensitivity of the three canals is based on their anatomic orientation. The horizontal canal is sensitive to motion in the yaw plane, whereas both the anterior and posterior canals are sensitive to pitch (anterior-posterior) and roll (side-to-side) movements (Figure 3).

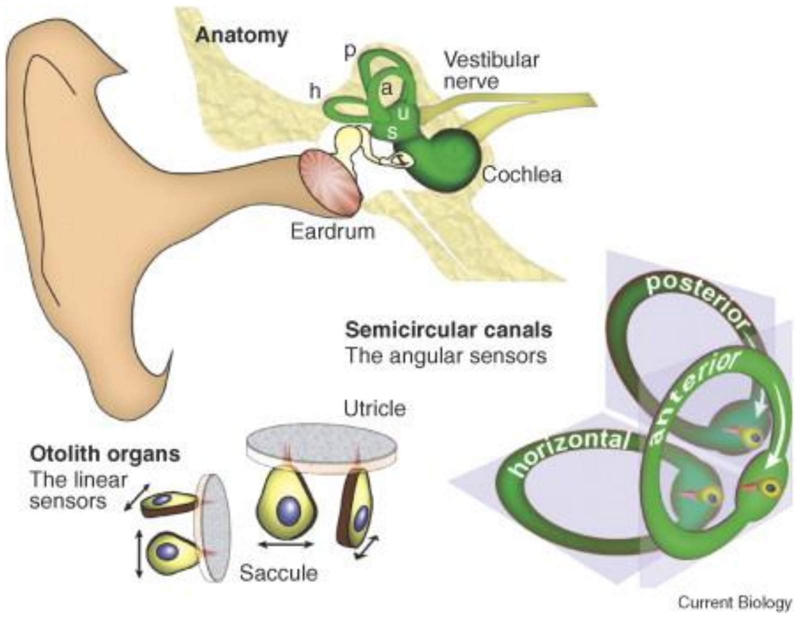



**Figure 1.3.** from Day & Fitzpatrick, 2005. Depiction of the five vestibular organs that make up the vestibular labyrinth: the two otolith organs (utricle and saccule), and the three semicircular canals that are responsible for sensing rotational acceleration of the head (the horizontal, anterior, and posterior canals).

How much the vestibular system contributes during natural walking is still unclear (for review, see Yoder & Taube, 2014). Patients with bilateral vestibular lesions can walk in a straight line to a target without vision. However, they tend to be unstable laterally, to walk more slowly and to have increased head movement compared with normal subjects (Glasauer et al., 1994). Vestibular signals can provide self-motion information about the trajectory travelled at walking speed and this is not improved by the availability of proprioceptive input from the legs (Fitzpatrick et al., 1999). In contrast to goal-directed locomotion, there is no motor pattern-specific difference in vestibular control of walking or running in place (Jahn et al., 2000). Several studies on vestibulospinal mechanisms by Orlovsky in the early seventies demonstrated that lateral vestibular nucleus neurons modify the activation of extensor antigravity muscles in the stance phase of the step cycle but do not initiate locomotion patterns (for review, see Shik &

Orlovsky, 1976). Thus, vestibular input is not necessary to initiate and maintain the locomotion pattern but rather to stabilize balance and to continue on the intended path.

When it comes to behaviourally testing the role of the vestibular system on the perception of travel distance, there are multiple techniques that can be used though the vestibular system is often coupled with somatosensory or other body-based cues. Some have tested perceived travel distance underwater, to uncouple the somatosensory and vestibular cues to self-motion (Bury et al., 2023). They found no significant differences between the estimation of travel distance in underwater neutral buoyancy and Earth-normal conditions. Harris and colleagues (2000) passively accelerated participants to uncouple these body-based cues and combined this with testing either with visual cues or in the dark to isolate the vestibular and visual contributions to the perception of travel distance. Participants experienced constant acceleration self-motion either visually (using a virtual reality display), physically (moving passively in the dark), or by a combination of both visual and passive physical motion. Perceived travel distance when receiving a combination of both visual and physical motion was more similar to experiencing only physical motion, compared to when experiencing only visual motion. These findings highlight the explicit importance of vestibular inputs in estimating travel distance when substantial or maintained accelerations are involved. The vestibular system can also be artificially stimulated using galvanic vestibular stimulation (GVS), using 0g environments (i.e. microgravity, parabolic flights), or by simply lying in a supine position to alter the relation between gravity and the body. Previous research from our lab has also shown that when participants feel they are upright but are actually in a supine posture, there is an overestimation of perceived travel distance (McManus & Harris, 2021). Other researchers have also shown differences between supine and upright position, where the latency of vection onset is reduced

(Guterman et al., 2012; Kano, 1991), and the magnitude of vection is larger (Guterman et al., 2012) when supine compared to upright. During my PhD, I was part of a larger group that investigated the perception of travel distance (and orientation, and size perception), both on Earth and on the International Space Station. Our group investigated the visual and vestibular contributions to the perception of travel distance during long-term exposure to microgravity using the Move-To-Target task (Jörges et al., 2024a). We found that there were no significant differences between the perception of travel distance on Earth compared to in space during long-term exposure to microgravity. Although, we did find small differences in perceived travel distance on Earth when completing the task in a supine position compared to a seated one. This study, along with previous literature, provides mixed evidence as to the visual and vestibular contributions to perceiving travel distance.

### *1.2.2 Proprioceptive Cues*

Proprioception is the ability to sense body position and movement in space. This system relies on sensory receptors in the muscles, tendons, and joints that send information to the brain about limb position and movement. The difference between active and passive movement lies in muscle involvement. Active movement involves using one's own muscles to initiate and control the motion of a body part, such as lifting an arm. Passive movement occurs when an external force (like a therapist or a machine) moves a body part, without actively engaging one's muscles. Proprioception and vestibular cues are hard to decouple because they work closely together to provide the brain with a comprehensive sense of body position, movement, and balance. Both systems contribute to spatial orientation and motor control, but they gather information in different yet overlapping ways. In most natural movements, these systems are activated simultaneously so their inputs are integrated in the brain to form a unified perception of movement and posture. This integration makes it difficult to isolate or study one system without the other influencing the experience. A common test used to examine proprioceptive and vestibular contributions to perceived travel distance is the blind walking task, in which participants walk either freely or on a treadmill without visual information. Though there is still an integration of vestibular and proprioceptive information during this task, proprioception specifically allows participants to monitor limb movement, step length, and body position during walking. It helps track how far they have moved, and in what direction. The brain uses proprioceptive feedback to update estimates of distance traveled and maintain a trajectory toward the remembered target. Using this blind walking task, it has been established that humans are able to accurately reproduce the distance to a previously seen target with blind walking (Fukusima et al., 1997; Loomis et al., 1992; Mittelstaedt & Mittelstaedt, 2001; Rieser et al., 1990). It has been suggested that the mechanism responsible for the accuracy in the blind walking task is "step integration" (step length x step frequency x time) (Durgin et al., 2009). The step frequency component of step integration introduces a cognitive component (see section 1.2.5.) to odometry, with the potential counting of steps. Evidence for using step integration as an odometric cue has also been seen in other animals, such as the desert ant (Thiélin-Bescond & Beugnon, 2005; Wittlinger et al., 2006, 2007). During rotational movements, proprioceptive information generates the most consistent and accurate self-motion perception, followed by vestibular and then visual cues (Bakker et al., 1999). For translational motion, one study had participants compare travel distance when visual information provided through a head-mounted display was either congruent or incongruent with proprioceptive information generated from cycling on a stationary bike (Sun, Campos, & Chan, 2004). They found that when visual and proprioceptive information was inconsistent, participants responded as if optic flow were the dominant source of information, though the presence of proprioceptive information improved the visually specified distance estimates even when the cues were incongruent. An earlier study had participants walking on a treadmill at a constant speed, while manipulating the distance indicated by optic flow (Prokop et al., 1997). Their results also showed participants changed their movements to align with the optic flow manipulations more so than with the constant speed of the treadmill, although they did not completely rely on optic flow. These studies provide evidence for a higher weighting of visual cues over non-visual cues during linear self-motion perception, in contrast to the proprioceptive dominance in rotational self-motion. More recent research integrating visual cues with either walking on a treadmill (Kopiske et al., 2023) or free walking (Campos et al., 2010; 2012) found that, as in the earlier experiments on rotational movements, non-visual cues were weighted higher than visual when estimating travel distance. Clearly the relative sensory contributions to the perception of linear travel distance are still an open question.

### *1.2.3 Auditory Cues*

In the previous section, the visually induced illusion of self-motion was introduced as vection though, the sensation of self-motion can also be induced using auditory cues as well, known as auditory vection (for review, see (Väljamäe, 2009). Unlike visual cues, auditory cues are omnidirectional, meaning one can receive signals in all directions, and can provide crucial information even when visual cues are unavailable (e.g. moving in the dark, fog, heavy rain, etc.) (Riecke, 2016). Auditory vection can be obtained in stationary blindfolded listeners who can experience the sensation of self-motion when listening to moving sound sources (Väljamäe, 2009). Previous research has shown that this illusion of auditory vection is much weaker than visual vection, though the integration of auditory and visual cues can increase the intensity and duration of linear vection compared to experiencing visual cues alone (Murovec et al., 2021). This powerful additive quality of auditory cues to visual cues is present when experiencing circular vection as well (Riecke et al., 2005, 2009). Previous researchers have also investigated the perception of travel distance using audio and physical linear self-motion cues from a passively moving cart (Kapralos et al., 2004). Although auditory vection stimuli result in less accurate estimations of travel distance, Kapralos et al.'s results provide evidence for a significant contribution of auditory cues to the estimation of travel distance. Similar to vection magnitude and duration (Murovec et al., 2021), audio cues combined with physical motion cues resulted in more accurate estimations of travel distance compared to the audio only or physical motion cues alone. Though auditory cues of self-motion can be highly ambiguous, due to the sources of auditory information (e.g. cars, tigers, people, etc.) tending to move, these studies together highlight the importance of auditory cues in self-motion perception.

### *1.2.4 Tactile Cues*

When visual cues are not available (i.e., because of blindness, lack of light, etc.), feeling one's way through an environment becomes essential. Like the auditory cues mentioned above, tactile cues alone can induce vection (Murovec et al., 2021). Most researchers investigating the role of tactile information on self-motion perception have used vibrotactile cues in combination with other sensory cues. Some studies have found that linear vection was enhanced when participants had vibrotactile cues, either via vibrotactile transducers and bass-shakers under the feet consistent with taking physical steps (Kruijff et al., 2016) or via a sawtooth waveform tactile simulation to the feet (Nordahl et al., 2012), combined with congruent visual and auditory cues. Although interestingly, another study has shown that circular vection magnitude was reduced when tactile cues were added to the visual rotating random dot pattern (Rupert & Kolev, 2008). This implies that there may be a difference in the role of tactile information when experiencing linear compared to circular vection. The location of where the vibrotactile cues are administered might also impact the sensation of vection. Tinga and colleagues (2018) had participants walking in a straight line while wearing a belt of vibrators around their waist that provided tactile stimulation encircling the waist clockwise or counterclockwise. They found that using this method, majority of people did not feel a sense of circular vection.

Although most of the literature examining the role of tactile information has used these cues in combination with others, one study has studied it in isolation (Murovec et al., 2021). This study found no significant difference in vection magnitude when experiencing auditory compared to tactile cues, though they did find a significant increase in vection intensity and duration when tactile and visual cues were combined, compared to when just receiving visual cues alone. In addition to using artificial vibrotactile cues, tactile flow can also be obtained by running your fingers along a stationary surface while walking (i.e. running your fingers along the wall while walking down a hallway), or by experiencing airflow to the face and body while moving. Previous literature has shown that air flow to the face can also be a cue for self-motion in humans (Murata et al., 2014; Seno et al., 2011) as well as other animals, such as birds (Liechti, 1995). Some have found that tactile cues can not only be additive with other cues but can surprisingly dominate other physical motion cues when perceiving self-motion speed and timing (Harris et al., 2017). They suggest that in addition to tactile cues being helpful in promoting stability, they could also potentially assist in the perception of self-motion to those who may need aid. Although the literature is still unclear on the role of tactile cues on the perception of self-motion, majority of the research does highlight the additive quality that tactile information can provide in understanding our movement.

*1.2.5 Cognitive Factors*

The majority of the research mentioned above has focused on the perception of self-motion as being a bottom-up perceptual process, without attention to the higher-level cognitive components. One aspect of a visual stimulus that was mentioned above was the naturalism of a scene. Some have found that a more natural scene led to stronger vection compared to a scrambled unnatural scene (Riecke et al., 2005, 2006). Although no one has tested how naturalism may affect the perception of travel distance. The second experiment in Chapter 3 addresses this question.

Others have investigated this cognitive component to the perception of self-motion deeper (for review, see (Riecke et al., 2009). Some researchers were able to modulate the perception of vection using the sounds of baby laughter, associated with a positive emotion, compared to experiencing the same visual stimuli with a neutral sound (Sasaki et al., 2012). Another study found an inhibition of vection when exposed to the optic flow stimulus with an audience compared to without an audience (Seno, 2013). Many others have shown that just the possibility of actual self-motion can enhance this illusion of vection. When seated on a "moveable" chair, participants report an enhancement of both visual vection (D'Amour et al., 2021; Wright et al., 2006), and auditory vection (Riecke et al., 2009). One study had children ages 7 and 11 years old seated on a stationary chair (Lepecq et al., 1995). Half of the children were told that the chair could move, and the other half were told that it could not. Even when seated on an “immoveable” chair, the cognitive condition in which there was plausibility of moving resulted in a shorter vection latency. These studies together provide evidence for the powerful influence that these cognitive factors can have on the perception of vection. Another cognitive cue of self-motion perception can be the step frequency component of step integration, referred to in the section 1.2.2. on proprioceptive cues. Of course, when walking, we can always use step count as a cue of how far we have travelled. Although there has been many researchers studying the cognitive factors that impact the perception of vection, very few have examined the impact that these factors may have on the perception of travel distance. In Chapter 3, I investigate how naturalism may affect the perception of travel distance, though more needs to be done to answer these open questions.

## 1.3 Testing the Perception of Travel Distance

When it comes to self-motion perception, the perception of heading and vection are two components that are well-studied. The perception of travel distance is much less studied, which is why I chose to focus on this for my dissertation. There are two tasks that are often used to test the perception of travel distance. The first is the Move-To-Target task, in which participants judge travel distances by stopping at the location of a previously seen target (Figure 4A). The second is the Adjust-Target task, in which participants adjust a target to indicate the extent of a previous movement (Figure 4B). In the Move-To-Target task people tend to make underestimations in which they stop before the previously seen target location, and in the Adjust-Target task people tend to make overestimations in which they adjust the target further away than the actual extent of their previous travel (Lappe et al., 2007a). Most studies investigating the perception of travel distance use either the Move-To-Target task or Adjust-Target task, few have used both. In this dissertation, I use both tasks in all experiments and compare the behaviour between the two. The majority of the research on perceived travel distance also uses virtual environments as a proxy for the real world. (Lappe & Frenz, 2009) tested the ecological validity of whether the differences in travel distance estimates that we see in a virtual environment are comparable to the behaviour we see in the real world. They found that physically walking in the real world, results in the same inaccuracies in travel distance estimates. This study supports the idea that we can test participants in a virtual environment with both ecological validity and laboratory control.

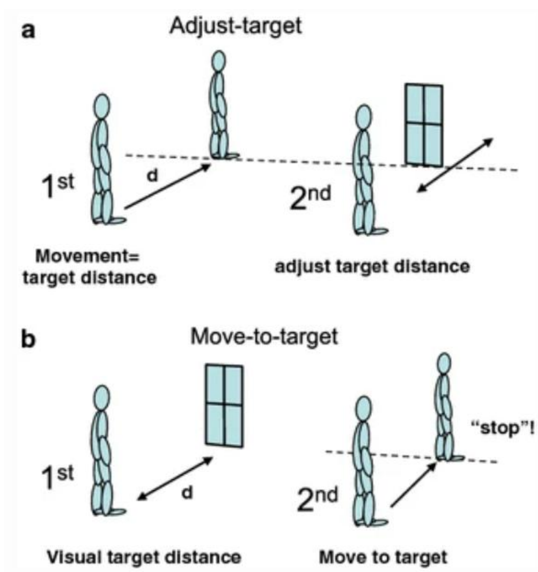



**Figure 1.4.** from Lappe et al., 2007. A) depiction of the Adjust-Target task B) depiction of Move-To-Target task

1.4 The Leaky Spatial Integrator Model

With both the Move-To-Target and Adjust-Target tasks, there seems to be a non-linearity to the perception of travel distance (Lappe et al., 2007). The further you move, the worse you are at being able to gauge that distance travelled. One model used to explain the perception of travel distance is the leaky spatial integrator model, which accumulates perceived travel distance by integrating over space (Lappe et al., 2007a). The leaky spatial integrator model accounts for these seemingly inconsistent mis-estimations of travel distance as resulting from (1) the integration "leaking" as a function of distance moved, and (2) a gain factor involved in transforming visual motion to travel distance (Lappe et al., 2007a). This model can describe the non-linear behaviour in both the Move-To-Target and Adjust-Target tasks (Figure 5). The model assumes that this decay happens over distance, though I hypothesized that it might be a decay over time as well. It might not just be the further you move the worse you are being able to gauge that distance travelled, it might also be the longer you move the worse you are at being able to gauge distance travelled.

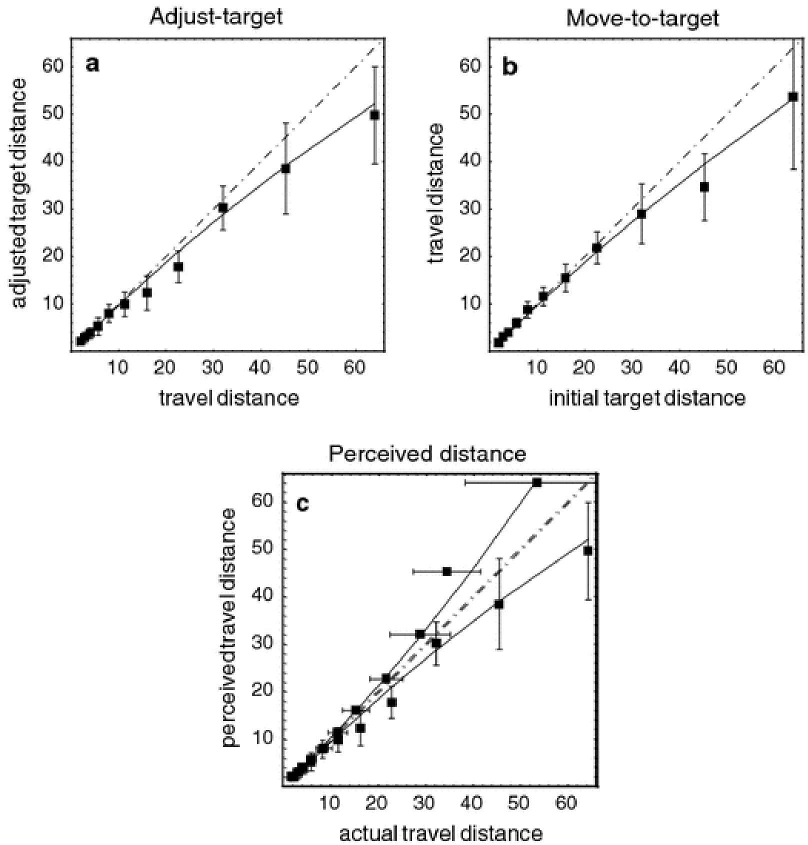



**Figure 1.5.** from Lappe et al., 2007. Fits of the leaky spatial integrator model. The top left is the individual leaky spatial integrator model fit to the Adjust-Target task and the top right is the individual model fit to the Move-To-Target task. The bottom panel shows the leaky spatial integrator model fit to both the Move-To-Target and Adjust-Target tasks together. In all panels, the dotted line represents perfect performance for both tasks.

In this dissertation, I highlight the strengths and weaknesses of the Lappe model. In Chapter 2, I examine this idea that when perceiving travel distance, there may be an integration over time as well as space. Most of the research investigating visual odometry, and the leaky spatial integrator model, has focused on forward translational movement. In Chapter 2, I also investigate how this model fits data to non-forward directions of self-motion. Although a previous study (Lappe & Frenz, 2009) used the leaky spatial integrator model to explain the perception of travel distance when walking and receiving optic flow information, this study did not compare the model to a simple linear fit. In Chapter 4, I examine how the leaky spatial integrator model compares to a linear fit when visual and non-visual cues are congruent and incongruent.

## 1.5 Overview of Projects

In Chapter 2, I tested whether the speed and direction of self-motion would affect the perception of travel distance. I hypothesized that the slower speeds and non-forward self-motion directions would lead to higher gains.

In Chapter 3, I performed a series of experiments that investigated how the characteristics of a virtual environment can affect the perception of travel distance through it. The specific parameters investigated in this series of experiments were: (1) the structure of an environment, and presence and texture of a ground floor, (2) the naturalism and scale of an environment, (3) the density of a starfield, (4) colour. I hypothesized that since such variables may contribute to the processing of optic flow, they would also affect the perception of travel distance.

In Chapter 4, I examine the differences in perceived travel distance from central versus peripheral optic flow when standing and treadmill walking. I predicted that, similar to McManus and colleagues (2017), participants would feel that they had moved further when receiving only peripheral optic flow, compared to when receiving optic flow in the full field or in the central field only. I also hypothesized that if non-visual cues were weighted higher than visual cues when estimating travel distance, the peripheral enhancement would diminish when visual and non-visual cues were combined.

# CHAPTER 2: Perceived travel distance depends on the speed and direction of self-motion

*This chapter has been published in PLoS ONE:* Bansal, A., McManus, M., Jörges, B., & Harris, L. R. (2024). Perceived travel distance depends on the speed and direction of self-motion. *PLOS ONE*, *19*(9), e0305661. https://doi.org/10.1371/journal.pone.0305661. *I am the first author, Dr. Meaghan McManus is the second author, Dr. Björn Jörges is the third author, and Dr. Laurence Harris is the last author.*

## 2.1. Abstract

Although estimating travel distance is essential to our ability to move through the world, our distance estimates can be inaccurate. These odometric errors occur because people tend to perceive that they have moved further than they had. Many of the studies investigating the perception of travel distance have primarily used forward translational movements, and postulate that perceived travel distance results from integration over distance and is independent of travel speed. Speed effects would imply integration over time as well as space. To examine travel distance perception with different directions and speeds, we used virtual reality (VR) to elicit visually induced self-motion. Participants (n=15) were physically stationary while being visually "moved" through a virtual corridor, either judging distances by stopping at a previously seen target (Move-To-Target Task) or adjusting a target to the previous movement made (Adjust-Target Task). We measured participants' perceived travel distance over a range of speeds (1-5 m/s) and distances in four directions (up, down, forward, backward). We show that the simulated speed and direction of motion differentially affect the gain (perceived travel distance / actual travel distance). For the Adjust-Target task, forwards motion was associated with smaller gains than either backward, up, or down motion. For the Move-To-Target task, backward motion was associated with smaller gains than either forward, up or down motion. For both tasks, motion at the slower speed was associated with higher gains than the faster speeds. These results show that transforming visual motion into travel distance differs depending on the speed and direction of optic flow being perceived. We also found that a common model used to study the perception of travel distance was a better fit for the forward direction compared to the others. This implies that the model should be modified for these different non-forward motion directions.

## 2.2. Introduction

As we move through the world, we generate relative movement between our environment and ourselves; this creates visual optic flow. Optic flow alone can generate the sensation of self-motion (Brandt et al., 1973) and, in the presence of adequate scale information, can provide a cue for travel distance (Redlick et al., 2001). Although odometry is essential to our ability to move and navigate through the world, distance estimates can be imprecise and inaccurate (Harris et al., 2012; Lappe et al., 2007; McManus et al., 2017; Redlick et al., 2001).

Odometry errors are dependent on the task. When moving to the location of a previously seen target, the further the intended target distance, the more people tend to undershoot its location (Lappe et al., 2007; Redlick et al., 2001). However, when instead participants are asked to judge the distance of a previously made movement, they tend to overshoot (Frenz & Lappe, 2005; Lappe et al., 2007).

Perceived travel distance has been modelled as a leaky spatial integrator (LSI), in which these mis-estimations are both modeled as occurring because (1) the integration "leaks" with increasing distance and (2) there is a gain factor (perceived distance/target distance) involved in transforming visual motion to travel distance (Lappe et al., 2007). The LSI model postulates that perceived travel distance results from integration over distance and is independent of time and travel speed. The literature is still mixed as to whether there might be an effect of speed on the accuracy of the perception of distance travelled. Some researchers have found that slower speeds result in higher gains (Harris et al., 2012; Lappe et al., 2007; McManus et al., 2017; Redlick et al., 2001), whereas others have found no effect of speed on distance estimates (Frenz et al., 2007; Lappe et al., 2007). The effects of speed imply integration over time as well as space. Therefore, one focus of this paper is measuring perceived linear travel distance over a range of speeds and distances.

The literature examining the effects of optic flow direction on the sensation of self-motion is also mixed. Reinhardt-Rutland (1982) found that when using a rotating spiral stimulus, the sensation of self-motion was stronger when visually moving forward compared to when moving backward. However, later research has provided evidence to the contrary. Some have found that the onset of self-motion perception was faster and the magnitude of self-motion was stronger when visually moving backward rather than forward (Bubka et al., 2008). These authors suggest that this could be because we are more sensitive to large-field optic flow patterns compatible with moving backward than forward (Edwards & Ibbotson, 2007). These studies only looked at self-motion magnitude and latency: variations in perceived travel distance with optic flow direction have not previously been reported. The vast majority of the research investigating visual odometry (and the leaky spatial integrator model) has focused on forward translational movement (Allison et al., 2014; Harris et al., 2012; McManus et al., 2017), however, one recent study examined the perception of travel distance in the vertical direction (Clément et al., 2020). They found that travel distance moving upwards was overestimated (undershooting the target distance), meaning participants felt they moved further than they actually had, whereas moving downwards was underestimated (overshooting the target distance), meaning participants felt they moved less than they actually had. This was true when asked to report verbally and when participants pulled themselves up or down using a rope while blindfolded. Here we compare perceived travel distance when making forward, backward, up, and down translational movements.

The main objective of this study was to investigate the effects of speed and direction of self-motion on visual odometry. As a secondary objective, we also wanted to assess whether the LSI can be used to model data in the other non-forward direction as well. Since we most often move in the forward direction, we hypothesized that (1) the gains will be higher (i.e., participants would undershoot) for vertical and backward motion compared to forward motion because movements in these directions may be associated with a greater sense of danger (Bremmer, Duhamel, et al., 2002; Clément et al., 2020), and (2) the gains will be higher for the slower speeds, as seen in previous studies, because the perception of travel distance may involve an integration over time as well as space (Harris et al., 2012; McManus et al., 2017; Redlick et al., 2001).

## 2.3. Methods

*Participants*

Sixteen participants (4 female; mean age 24 yrs, SD ±6.2) participated in this study. The recruitment period was between February 21st, 2022 and March 30th, 2022. Due to the COVID-19 pandemic the data were all collected remotely. All participants used their own personal virtual reality head mounted displays (HMD): two used the Oculus Quest 1, six used the Oculus Quest 2, and eight used the Oculus Rift CV1. While this mode of data collection is unlikely to yield a sample representative of the larger population, to our knowledge, no variables connected to VR equipment ownership (e.g., socio-economic status) have been shown to impact perceived traveled distance. One participant was removed during the outlier removal process (see below), so the subsequent analysis was completed on the remaining 15 participants. The protocols used in this study were approved by the York Human Participants Review Sub-committee (#e2021-407), and conducted in accordance with the Declaration of Helsinki. All participants gave prior informed written consent and were naive to the purpose of the study.

*Stimuli*

The experiment was performed in virtual reality (VR) using visually induced self-motion, while remaining physically stationary. Since the data were collected remotely, we set the participants' view in the headset to be head-fixed, such that the visual stimuli did not move with head movement. This ensured that all participants received the same visual stimuli. The participants began both tasks in a simulated horizontal corridor (1.86m x 1.86m, with the simulated eye height in the center of the corridor at 0.93m above the textured ground plane) with a reference ball (radius 0.25m) 1.5m in front of them and 0.25m below their simulated eye height (Fig 2.1A). Since these tasks simulated participants' movements in different directions, we could not have them use their body as a reference for when they had travelled a particular distance because they would have had to report when different parts of their body reached the targets. To make the tasks consistent, we used a reference ball that was fixed relative to their body. For each direction of motion, participants indicated when the appropriate surface touched the remembered location of the target (Fig 2.1B). When they moved forward, they used the far side of the ball as their reference. When they moved backward, they used the near side. When moving upward they used the top, and when moving downward they used the bottom. This small variation in stopping point was taken into account when analyzing the data. This experiment was programmed in Unity version 2021.2.

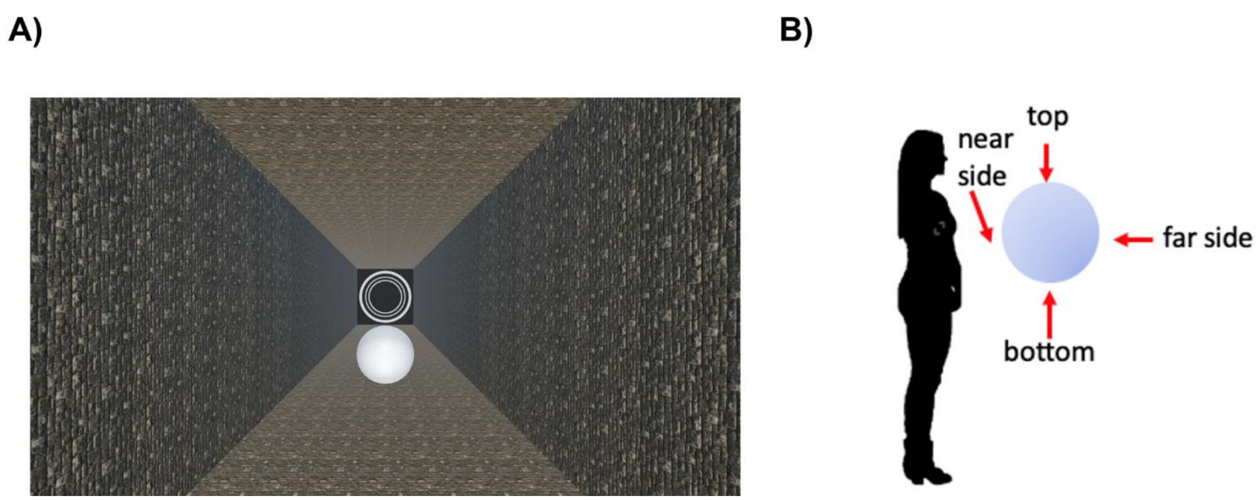



**Fig 2.1. Stimuli.** A) The corridor and target that the participants saw in the virtual reality headset. The reference ball was a white sphere 1.5m in front of the participant; the target is the black square with the circles drawn on it. B) Diagram showing which part of the reference ball participants used to indicate when they had reached the location of the previously seen target in each direction: top for upwards movement, bottom for downwards movement, far side for forward movement and near side for backward movement.

*Move-To-Target Task*

Each trial started with a simulated target presented in a horizontal corridor in front of them (Fig 2.1A). They then pressed a button which triggered a visual rotation of the environment around them. For the upward and downward conditions, the corridor was rotated upwards (pitched), such that the participant was facing towards "the floor" (for the upward condition) or ceiling (for the downward condition) of the corridor. For the backward condition the environment was rotated 180° around an Earth-vertical axis, and for the forward condition, it was rotated 360°around an Earth-vertical axis to ensure there was a rotation component in every condition. The rotation took 1.1 seconds for each condition. The target then disappeared and motion towards the target's position was simulated with optic flow. Participants indicated when they felt that the appropriate surface of the reference ball had touched the now invisible target by pressing the button once more.

*Adjust Target Task*

Participants sat in the same corridor as for the move-to-target task and began by pressing a button to rotate themselves (as in the Move-To-Target task). They then experienced simulated movement either upward, downward, backward, or forward through a pre-specified distance. Once they had traveled through this distance, they were moved back to their original position and orientation in the corridor (upright and looking forward) and a target appeared in front of them. Participants then used the arrow keys to slide the target back and forth along the corridor until it was as far away as the distance through which they felt that they had just been moved. They pressed the space bar to end the trial.

*Procedure*

Participants were sent the experimental programs, along with the instructions for each task (see Appendix S1 for more details). They were first asked to sit in a chair, and read the instructions. Once they felt they had fully understood the task, they were asked to start the practice. To get familiar with the button presses, they were given first a practice session which included 8 trials (2 trials in each direction) at randomized distances between 5-40m. Once the practice was completed, participants ran the full version of each task, and sent the data back to the experimenter.

This study was a within-subjects design, such that every participant completed both the move-to-target and adjust target tasks. The order in which the tasks were completed was counterbalanced, such that half completed the Move-To-Target first and the other half completed the Adjust Target task first. Each task consisted of the same twelve target distances (5, 8, 11, 14, 17, 20, 23, 26, 29, 32, 35, 40 m), three speeds (1, 3, 5 m/s), and four directions of self-motion: (upward, downward, forward, and backward). Each condition was presented only once. All distance and speed conditions were randomized to remove any order effects. The tasks were blocked by direction and the order in which these blocks were presented was also randomized. The instructions were presented in the HMD again at the beginning of each block and at those times the participants were able to take a break if needed. Both tasks began with a practice of 8 trials (2 trials in each direction). The whole experiment took about 1 hour (30 minutes for each of the two tasks).

*Data Analysis*

Each participant completed 288 trials (4 directions x 3 speeds x 12 distances x 2 tasks x 1 repetition). First, an outlier removal was completed. The outlier removal was performed at the group level for each distance in every condition (3 speeds x 4 directions x 2 tasks). Any data less than the 'Lower Quartile - 1.5 x Interquartile Range' or above the 'Upper Quartile + 1.5 x Interquartile Range' were removed. Participants with more than ¼ of the trials removed from a task were removed from the subsequent analysis. Therefore, one participant (participant 7) was removed.

The gains were then calculated for each trial for both tasks. In both tasks, gains were calculated by dividing perceived travel distance over actual travel distance. In the Move-To-Target task, this translates to the target distance / the distance travelled before pressing the button to stop:

| | |
|---|---|
| $Gain_{Move\text{-}To\text{-}Target}$ = Target Distance / Self-Motion Distance | (1) |

For the Adjust-Target task, this translates to where participants adjusted the target to / the distance that participants were moved to:

| | |
|---|---|
| $Gain_{Adjust\text{-}Target}$ = Adjusted Target Distance / Self-Motion Distance | (2) |

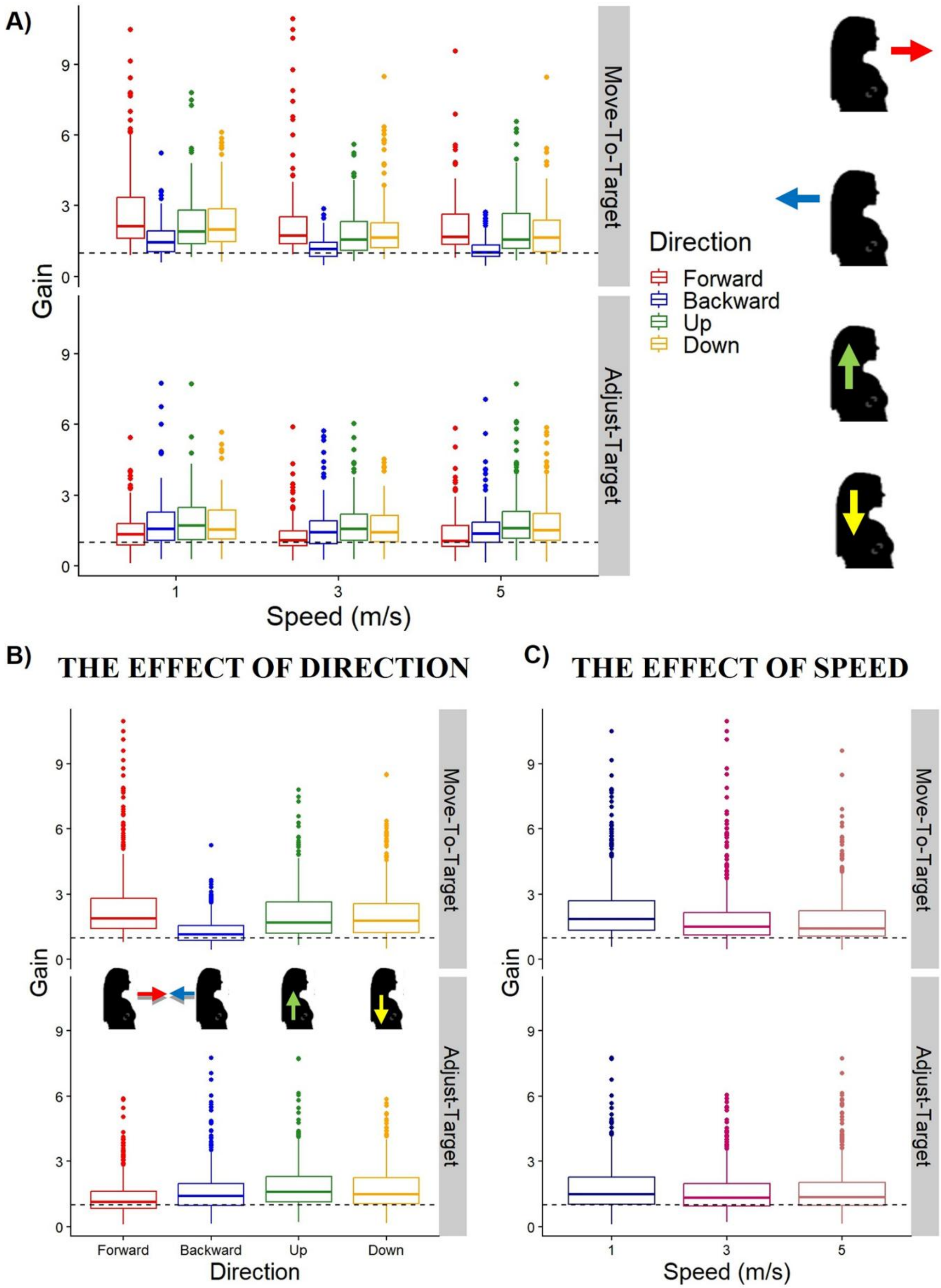
In both cases, a gain greater than 1 would imply that participants felt like they had moved further than they had, and vice versa. Perfect performance in both cases would be a gain of 1. Before testing any differences between conditions, we tested for whether any effects between condition would differ between tasks. Since we did find differences between tasks, we decided to analyze the tasks separately. A Linear Mixed Model was performed independently for both tasks using the lme4 package (13) for R (version 4.3.0.) on the gains. To determine the most appropriate model structure, we decided to "keep it maximal" as per Barr et al[14], i.e., we started with a maximal model including all relevant experimental variables (speed, direction, distance) as slopes per participant and compared to simpler models until no significant differences were found between models. We first removed the random slopes for distance per participant since keeping them would have led the model to exceed the recommended ratio of data points per fitted parameter. Using Barr et al.'s [14] model comparison approach, random slopes for direction and speed per participant were kept for both models (see Appendix S2). The fixed effect structure was chosen as a function of our hypothesis, where we were interested in the main effects of direction and speed. We further also included distance as a fixed effect in order to capture as much variability in the data as possible. We did not include an interaction between direction and speed because we had no specific hypotheses about the interaction term. The final model structure for the gains LMMs reads as follows:

| | |
|---|---|
| Gain ~ Direction + Speed + Distance + (Direction + Speed \| Participant) | (3) |

We then computed bootstrapped confidence intervals at an alpha level of 0.05 to test for statistical significance using the confint() function from the base R with the "boot" argument and default settings otherwise. All data and data analysis can be found at

(https://github.com/ambikabansal/Speed_Direction).

## 2.4. Results



A)
Move-To-Target
Adjust-Target
Gain
Speed (m/s)
Direction
Forward
Backward
Up
Down
B)
THE EFFECT OF DIRECTION
Move-To-Target
Adjust-Target
Gain
Forward
Backward
Up
Down
Direction
C)
THE EFFECT OF SPEED
Move-To-Target
Adjust-Target
Gain
Speed (m/s)

**Fig 2.2. Raw Gains.** (A-C) Box plots of the group gains for both the Move-To-Target (top row) and Adjust-Target (bottom row) tasks for each direction (B) and speed (C). (A-B) The forward direction is represented in red (left most), backward direction in blue (second from left), upward direction in green (second from right), and downward direction in orange (right most). The black dashed line represents perfect performance (gain of 1).

***Effect of Direction***

| | Forward | Backward | Upward | Downward |
|---|---|---|---|---|
| Move-To-Target Task | 2.43 ± 1.61 | 1.31 ± 0.61 | 2.07 ± 1.18 | 2.08 ± 1.22 |
| Adjust-Target Task | 1.35 ± 0.85 | 1.65 ± 1.02 | 1.87 ± 1.07 | 1.75 ± 0.97 |

Table 2.1: Means and standard deviations of the raw gains for the different directions.

Results from the linear mixed model for the effect of direction on the gains of the Move-To-Target task are shown in Table 2. The backward condition (mean = 1.31, SD ± 0.851) resulted in significantly lower gains than the forward (mean = 2.43, SD ± 1.61), upward (mean = 2.07, SD ± 1.18), or downward (mean = 2.08, SD ± 1.22) conditions (see Table 1). However, we found no significant differences between the forward and up, forward and down, and up and down conditions. The gains are shown in Fig 2.2, top row.

*Move-To-Target Task*

| | Regression Coefficient | Standard Error | 95% CI (lower) | 95% CI (upper) | Significant |
|---|---|---|---|---|---|
| Forward vs. Backward | 1.18 | 0.30 | 0.59 | 1.82 | * |

| | | | | | |
|---|---|---|---|---|---|
| Forward vs. Up | 0.41 | 0.31 | -0.11 | 1.04 | n.s. |
| Forward vs. Down | 0.45 | 0.32 | -0.19 | 1.09 | n.s. |
| Backward vs. Up | 0.76 | 0.15 | -1.04 | -0.45 | * |
| Backward vs. Down | 0.72 | 0.18 | -1.09 | -0.37 | * |
| Up vs. Down | 0.03 | 0.09 | -0.15 | 0.21 | n.s. |

Table 2.2: Results from the Linear Mixed Model run with the gain set as the dependent variable, with both direction and speed set as fixed effects, and direction set as a random effect. This table reports differences in the direction. This table reports unstandardized regression coefficients.

Results for the linear mixed model for the effect of direction on the gains of the Adjust-Target task are shown in Table 3. We found significantly smaller gains in the forward condition (mean = 1.35, SD ± 0.851) compared to the backward (mean = 1.65, SD ± 1.02), upward (mean = 1.87, SD ± 1.07), or downward (mean = 1.75, SD ± 0.974) conditions, and significantly smaller gains in the backward condition compared to the upward condition (see Table 1). However, there were no significant differences between the backward and down conditions, or the up and down conditions. The gains are shown in Fig 2.2, bottom row.

*Adjust-Target Task*

| | Regression Coefficient | Standard Error | 95% CI (lower) | 95% CI (upper) | Significant |
|---|---|---|---|---|---|
| Forward vs. Backward | -0.30 | 0.06 | -0.44 | -0.15 | * |
| Forward vs. Up | -0.04 | 0.10 | -0.71 | -0.31 | * |
| Forward vs. Down | -0.40 | 0.09 | -0.59 | -0.20 | * |
| Backward vs. Up | -0.19 | 0.08 | -0.03 | -0.04 | * |
| Backward vs. Down | 0.01 | 0.07 | -0.24 | 0.04 | n.s. |
| Up vs. Down | 0.08 | 0.04 | -0.009 | 0.18 | n.s. |

Table 2.3: Results from the Linear Mixed Model run on data from the Adjust-Target task with the gains set as the dependent variable, both direction and speed set as fixed effects, and direction set as a random effect. This table reports differences in the direction. This table reports unstandardized regression coefficients.

***Effect of Speed***

| | 1 m/s | 3 m/s | 5 m/s |
|---|---|---|---|
| Move-To-Target Task | 2.25 ± 1.36 | 1.86 ± 1.27 | 1.81 ± 1.13 |
| Adjust-Target Task | 1.75 ± 1.02 | 1.57 ± 0.92 | 1.65 ± 1.05 |

Table 2.4: Means and standard deviations of the raw gains for the different speeds.

Results from the linear mixed model on the effect of speed on the gains for the Move-To-Target and Adjust-Target tasks are shown in Table 5 and Table 6, respectively. For the Move-To-Target task, we found significantly higher gains for the 1 m/s (mean = 2.25, SD ± 1.36) compared to the 3 m/s (mean = 1.86, SD ± 1.27) and 5 m/s (mean = 1.81, SD ± 1.13) conditions (see Table 4). However, we found no significant differences between the gains for the 3 m/s and

5 m/s conditions. For the Adjust-Target task, we found significantly higher gains for the 1 m/s (mean = 1.75, SD ± 1.02) and 3 m/s (mean = 1.57, SD ± 0.924), however no differences between the 1 m/s and 5 m/s (mean = 1.65, SD ± 1.05) and the 3 m/s and 5 m/s (see Table 4).

*Move-To-Target Task*

| | Regression Coefficient | Standard Error | 95% CI (lower) | 95% CI (upper) | Significant |
|---|---|---|---|---|---|
| 1 m/s vs. 3 m/s | -0.18 | 0.05 | -0.55 | -0.14 | * |
| 1 m/s vs. 5 m/s | -0.06 | 0.08 | -0.66 | -0.12 | * |
| 3 m/s vs. 5 m/s | 0.005 | 0.005 | -0.06 | 0.17 | n.s. |

Table 2.5: Results from the Linear Mixed Model run on data from the Move-To-Target task with the gain set as the dependent variable, both direction and speed set as fixed effects, and direction set as a random effect. This table reports differences in speeds. This table reports unstandardized regression coefficients.

*Adjust-Target Task*

| | Regression Coefficient | Standard Error | 95% CI (lower) | 95% CI (upper) | Significant |
|---|---|---|---|---|---|
| 1 m/s vs. 3 m/s | -0.18 | 0.05 | -0.27 | -0.07 | * |
| 1 m/s vs. 5 m/s | -0.06 | 0.08 | -0.22 | 0.08 | n.s. |
| 3 m/s vs. 5 m/s | -0.11 | 0.06 | -0.02 | 0.005 | n.s. |

Table 2.6: Results from the Linear Mixed Model run on data from the Adjust-Target task with the gains set as the dependent variable, both direction and speed set as fixed effects, and direction set

as a random effect. This table reports differences in speeds. This table reports unstandardized regression coefficients.

## 2.5. Modeling

*Leaky Spatial Integrator Model*

The mis-estimations that occur when estimating travel distance can be modeled as a leaky spatial integrator (Lappe et al., 2007). With this model, both the underestimations typically seen with the adjust-target task, and the overestimations typically seen with the move-to-target task can be accounted for in a single equation. The model assumes that there is a state variable (the current distance from the start), that is incremented as the movement progresses by a constant gain factor. Leakage also occurs as the movement progresses, and this state variable is reduced in proportion to a leak factor (alpha). The leakage reduces the current estimate of travel distance in the adjust-target task and reduces the current estimate of the target distance in the move-to-target task. This is why the model predicts that the further we travel, the larger these errors in distance estimates will be. Perfect performance corresponds to a gain of 1, and an alpha of 0 (no leakage). A prerequisite of the model is that alpha cannot be lower than 0. Overestimations of travel distance correspond to a gain larger than 1, and an underestimation correspond to a gain lower than 1. The larger errors in the further distances are represented by a larger alpha.

Equation 1 is used to fit the data from the adjust-target task.

| | |
|---|---|
| p(d0) = (gain/alpha) * ( 1 - exp(-d0*alpha)) | (4) |

Equation 2 is used to fit the data from the move-to-target task.

| | |
|---|---|
| p(d0) = (log(d0+gain/alpha)-log(gain/alpha))/alpha | (5) |

Where p(x) is the perceived distance travelled, "gain" is the gain factor, "alpha" is the leak factor, and $d_0$ is the target distance. These two equations were fitted to the data obtained from both the Adjust-Target task (eq 1) and the Move-To-Target task (eq 2) simultaneously by minimizing the combined sum-of-square errors (see Fig 2.3). Previously, the model has mainly been used to explain the perception of travel distance in the forward direction. Here, we test Lappe's leaky spatial integrator model in the backward, upward, and downward directions as well.

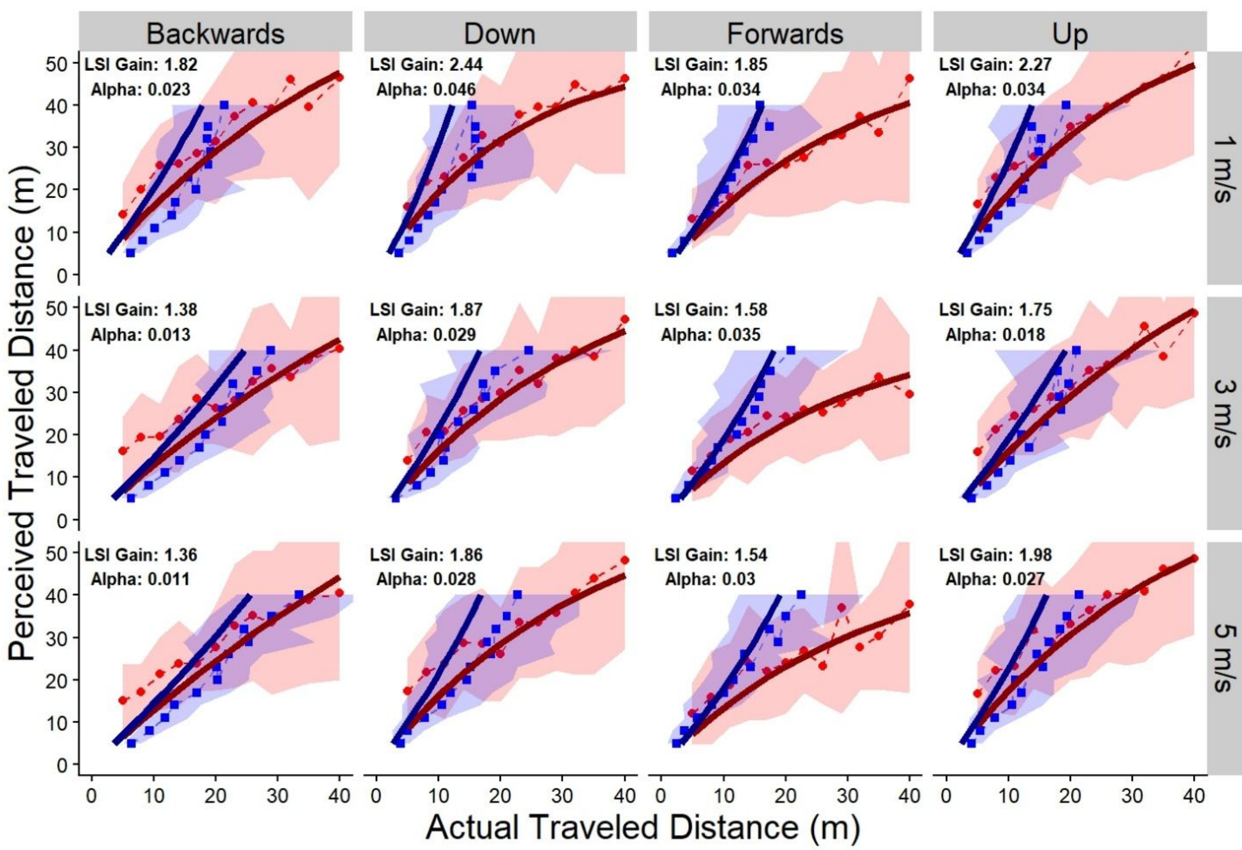



**Fig 2.3. Leaky spatial integrator model fits.** Leaky spatial integrator model fitted to through the mean of all data across all participants. Each column of panels corresponds to a different

direction (forward, backward, up, down) and each row of panels corresponds to a different speed (1, 3, 5 m/s). The red symbols represent data from the Adjust-Target task, and the blue symbols represent data from the Move-To-Target task. The dashed lines represent the raw data averaged across participants for both tasks, whereas the solid lines represent the model fits (dark red for Adjust Target, eq 1, and dark blue for Move-To-Target, eq 2). The confidence bands represent one standard deviation above and below the mean of the raw data.

To test the leaky spatial integrator model in the different directions, we compared the fits to a "no alpha model", where alpha was set to just greater than 0 (alpha = 0.000001). In all directions, Lappe's leaky spatial integrator model was a better fit than the one parameter model (likelihood ratio < 0.0001 for all 4 comparisons). The measure of "goodness of fit" is the mean squared error between the model and the data. We also found that the leaky spatial integrator model was a significantly better fit to the forward direction compared to the backward (likelihood ratio < 0.001), upward (likelihood ratio < 0.001), downward (likelihood ratio < 0.001) directions (Fig 2.4). This implies that the leaky spatial integrator model might need to be expanded to more accurately fit the data in these non-forward directions of self-motion as well.

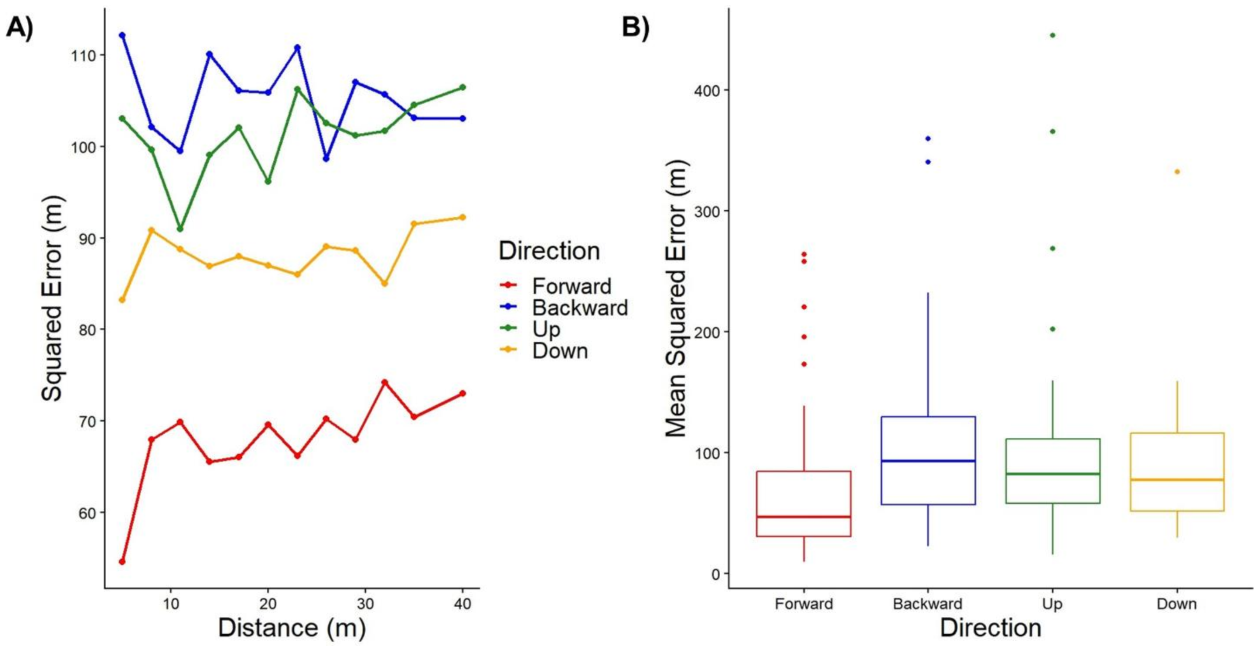



**Fig 2.4. "Goodness of fit" measure of the leaky spatial integrator model for each direction.** The forward direction is represented in red, backward direction in blue, upward direction in green, and downward direction in orange. (A) Squared errors for each distance and direction averaged across participants. (B) Mean square error for each fit collapsed across direction and speed.

## 2.6. Discussion

Here, we have shown that both the simulated speed and direction of self-motion affect the perception of travel distance. The perception of travel distance also differed between the Move-To-Target and Adjust-Target tasks. In the Move-To-Target task, the backward motion was associated with lower gains than either forward, up, or down motion, and for the Adjust-Target task, the forward direction was associated with lower gains than either backward, up, or down motion. Motion at the slower speed (1m/s) was associated with higher gains than either of the faster speeds (3m/s and 5 m/s) for the Move-To-Target task, and higher than the 3 m/s for the Adjust-Target task.

### *High gains*

For all conditions, participants felt like they had travelled further than they actually had in both the Adjust-Target and Move-To-Target tasks - our participants indicated that they had reached the target considerably before they actually had for the Move-To-Target task but also felt the distances they had moved in the Adjust-Target task were much longer than they really were. One possible explanation for these high gains could be the nature of the visual scene presented in the HMD (see Fig 2.1). The gains found while moving in our virtual corridor were larger (people pushed the button earlier) than has previously been reported in studies using less structured environments (e.g., Bury et al., 2020; McManus & Harris, 2021). This aligns with research from other labs showing that environments with more structure and complexity induce a stronger sense of self-motion (Bonato & Bubka, 2006; Riecke et al., 2005; Trutoiu et al., 2009). Experiencing a stronger sense of self-motion with more structured environments would lead to needing less optic flow (higher gains) to feel one had visually moved to that same location in a less structured environment. There are numerous parameters (texture, luminance, distance to walls, etc.) that contribute to the processing of optic flow, and therefore to the perception of travel distance (Bubka & Bonato, 2010; Seno et al., 2010; Tamada & Seno, 2015; Vaziri-Pashkam & Cavanagh, 2008). Therefore, we should not concentrate on the absolute values of the gains but rather their variation with direction and speed.

### *Effect of Speed*

We found an effect of speed in which slower speeds were associated with higher gains than faster speeds. This aligns with previous research that found an effect of speed, with slower speeds evoking higher gains (Harris et al., 2012; McManus et al., 2017; Redlick et al., 2001). Most research addressing this question, including the present study, used speeds in the range of 1-5 m/s, and find differences mostly with the slowest speeds. Future research might want to use speeds slower than 1 m/s to fully understand the effect of speed when making distance estimates. Our findings of an effect of speed suggest that when making distance estimates, there is likely an integration across time as well as across space, whereas the Lappe model assumes no effect of speed. This implies that Lappe's leaky spatial integrator model should be expanded to include a speed term as well.

### *Effect of Direction*

As we hypothesized, forward motion was associated with smaller gains than either the backward, up, or down motion in the Adjust-Target task. Although for the Move-To-Target task, backward motion was associated with smaller gains than either forward, up, or down motion.. To the best of our knowledge, this study is the first to report differences in gains dependent on these four directions of movement. This is the first to compare the model fits of Lappe's leaky spatial integrator model in these different directions as well. We found that the model fits were significantly better in the forward direction compared to the backward, upward, or downward directions. This suggests that Lappe's leaky spatial integrator model should be modified to more accurately model the perception of travel distance in these different directions.

An interesting finding that emerged from the raw gains of the Move-To-Target task was that backward motion resulted in lower gains than motion in other directions bringing the gains closer to unity or accurate performance. Though, again considering that our interpretation of optic flow is dependent on so many factors (Bansal et al., 2023) it is likely that these gains are not approaching unity so much as they are simply lower than they are for other directions. This aligns with research from Reinhardt-Rutland (1982) who showed that the sensation of self-motion was stronger when visually moving forward as opposed to backward. Neurophysiological evidence also shows that more cells in the monkey posterior parietal cortex are tuned to forward compared to backward motion (Bremmer, Schlack, Shah, et al., 2001; Bremmer, Duhamel, et al., 2002). If this were the case here, then the overestimations in perceived travel distance should be greater when moving forward as well, as we indeed report in the Move-To-Target task. From an evolutionary standpoint, any mis-estimations when moving backward are much riskier than when moving forward. Moving backward makes it more difficult to spot any potential threats compared to when moving in the direction in which you are looking and would therefore expect a more cautious odometric system. In addition, because backward movement is much less common, optic flow processing in this direction may be less effective and therefore lead to lower gains. The higher gains when experiencing visual upward motion during the Adjust-Target task also align with previous research from Clément and colleagues (2020) who show that people had higher gains (tended to undershoot more) in the upward direction, both when verbally reporting and during a physical blind pulling task. Clearly, more research needs to be done to fully understand the mechanisms involved in estimating travel distances in the different directions.

### *Conclusions*

We have shown that both speed and direction of self-motion can affect participants' estimates of travel distance. These differences in direction may be due to the pattern of optic flow that they are receiving, although further research is needed to fully parse out the inaccuracies that we are seeing in the odometric system. Our data show that Lappe's leaky spatial integrator model well describes the response to forward linear movement, but that it should be expanded to include a speed term and modified when modelling the perception of movement in other directions as well. Overall, this study aids our understanding of the processes involved in making travel distance estimates and helps us more accurately model this complex odometric system.

# CHAPTER 3: How the characteristics of a virtual environment affects the perception of travel distance through it

*This chapter is under review at PLoS ONE. I am the first author, Dr. Meaghan McManus is the second author, and Dr. Laurence Harris is the last author.*

## 3.1. Abstract

Although simulated self-motion through virtual environments has been widely used to investigate perceptual odometry, the characteristics of the virtual environments used and the reported results have varied greatly. Here, we systematically vary the characteristics of the environment through which observers are moved in order to explore the effect of (1) the structure of an environment including the presence and texture of a ground surface, (2) the naturalism and scale of an environment, (3) colour, and (4) the density of a starfield and how it might affect perceived travel distance. In all four experiments, participants were visually moved forwards through a virtual environment and perceived travel distance was estimated by either (1) stopping at the location of a previously seen target (the Move-To-Target Task) or (2) adjusting the position of a target to indicate a previously travelled distance (the Adjust-Target Task). Data were analyzed in terms of gain (perceived travel distance/actual travel distance). Results show no significant differences that depended on the structure of an environment or on the presence or absence of a ground surface (Experiment 1), or on the naturalism of the environment (Experiment 2), or on whether the environment was in colour or in black and white (Experiment 3). However, there was a small effect of the texture of the ground surface and of the scale of the environment. In Experiment 4, we show that there may be a very low ceiling effect in the density of a starfield needed to accurately estimate travel distance. Together these experiments have implications for the design of real and virtual environments where perceived motion is important and will enable us to further predict our perception of moving through an environment.

## 3.2. Introduction

Understanding how we interpret our environment is crucial to fully appreciate how we perceive our movement through it. Although visually induced self-motion has been widely used to investigate the perception of travel distance (how far a person perceives themselves to have traveled through an environment), the visual characteristics of the virtual environments used vary greatly between studies. There are various parameters of a virtual environment (structure, texture, ground surface, colour, luminance, distance to walls, etc.) that have been shown to contribute to the processing of optic flow (Bubka & Bonato, 2010; Seno et al., 2010; Tamada & Seno, 2015; Vaziri-Pashkam & Cavanagh, 2008). Although these variables have been shown to clearly modulate self-motion perception and therefore the perception of travel distance, these parameters are rarely taken into consideration when designing self-motion experiments or virtual gaming environments. Understanding how these various visual field characteristics might affect the perception of travel distance is a crucial element in improving our understanding of this system.

Optic flow alone can induce an illusionary sensation of self-motion (Fischer & Kornmiller, 1930; Brandt et al., 1973). A real-world scenario in which it is common to experience vection is when sitting in a stationary train while visually watching another train move past you through the window. You will get the illusion that you are moving in the opposite direction of the passing train even though your train is stationary. This illusion of self-motion is known as vection and has been used in many studies as a correlate of self-motion perception. However, one can still experience self-motion and perceive one's travel distance without experiencing vection (i.e., without the sensation that one is actually moving). Using a similar environment to our virtual corridor in Experiment 1, McManus and Fiehler (2025) have shown that when participants feel vection, the felt speed of self-motion and perceived travel distance are correlated, and if no vection is experienced then the two are not found to be correlated. Although it should be noted that in majority of their trials, participants did not actually experience any vection at all. Many studies investigating how the characteristics of an environment affect self-motion perception have used the self-reported magnitude of the sensation of vection as a measurement, but here we are specifically concerned with the effect of the environment on perceived travel distance.

Humans have evolved to move around on a stable ground surface and are tuned to pick up relevant information about their self-motion largely from the ground (Gibson, 1979). Understanding how we process the movement information provided by the ground surface is crucial not only to understand our naturalistic movements, but also when considering the processing involved when experiencing modern forms of motion such as in driving or aviation and the safety issues involved in these unnatural forms of self-motion. Whether it is taking off or landing an aircraft, driving or walking, optic flow received from the ground surface is an important feature in the perception of self-motion. Bian and colleagues (2005) introduced the idea of a "ground dominance effect" in the perception of a 3-D scene. When comparing information across all four environmental surfaces (ground, ceiling and the sidewalls), participants are consistently dominated by visual information from the ground surface. Previous research has found that projecting optic flow patterns onto a ground surface results in body sway corresponding to the flow direction (Flückiger & Baumberger, 1988). This is true for both children and adults (Baumberger et al., 2004). A previous study has manipulated the size, position, and speed of the components of a random dot stimulus on a floor projection to investigate the effects of these properties on linear vection and body sway (Tamada & Seno, 2015). Results show that some of the stimulus properties of the ground surface had an effect on both vection and body sway. Trutoiu and colleagues (2009) tested the effects of a floor projection on the perception of vection for linear forward, linear backward, circular left, and circular right directions. They found that adding a floor projection of a starfield significantly increased the sensation of linear vection, but not circular vection. This ground dominance effect has also been replicated using visual search tasks (McCarley & He, 2000). These observations provide further evidence that visual-field characteristics can modulate optic flow processing. Surface texture has also been shown to influence vection. More specifically, surface textures containing high spatial frequencies with realistic lighting (e.g., bark, wood) enhance vection, whereas smooth or reflective surfaces (e.g., glass, metal) provide less motion-relevant visual information, and therefore tend to reduce vection strength (Morimoto et al., 2019). Although the ground surface and its texture seem to be critical features in visual perception, little has been done to examine its effects on perceived travel distance. In Experiment 1, we test this question directly. Previous research from our lab has found variations in perceived travel distance in which participants felt they had moved further when emersed in a virtual corridor (Bansal et al., 2024) compared to studies using less structured environments (e.g., Bury et al., 2020; McManus & Harris, 2021). These "less structured environments" included a starfield stimulus and a "lollipop field". Although it is difficult to fully quantify environmental structure, the star field and lollipop environments are considered to be less structured because in the starfield there were no polarized cues to orientation, and in both environments, the objects were arranged with no systematic structure and can thus be considered more abstract and less naturalistic than, for example, a realistic virtual simulation of a corridor. More detailed environments have also been shown to lead to more accurate walking trajectories than less detailed environments (Wood et al., 2000).

Though differences in travel distance estimates have been observed across studies, no one has yet systemically tested the effects of environmental structure on perceived travel distance.

Extracting the optic flow created by moving in natural environments is complex because of the continuously changing distance to all the objects in the environment producing continuously changing angular velocities of the images of all the objects in the field. One possible confounding variable for studies investigating environmental structure and the ground surface on vection is simply the ability of participants to extract an appropriate amount of optic flow information. In more complex environments, it could be that denser optic flow information could lead to a stronger sensation of vection, and a longer perceived distance of travel. In Experiment 4, we directly investigate the starfield density needed to accurately estimate travel distance.

More naturalistic environments have been shown to lead to a stronger magnitude of vection. Visually moving through a photo-realistic three-dimensional simulation of a town presented in a large-screen virtual environment induces a stronger sensation of vection compared to moving through a star field (Trutoiu et al., 2009) or through abstract stimuli (Riecke et al., 2005; 2006). These researchers describe how the "believability" of a visual scene or environment may contribute to one's sense of presence, and therefore the strength of vection. Some researchers have also tested how the semantic meaning of a scene may affect vection (Ogawa & Seno, 2014; Seno & Fukuda, 2012). One such study used the train illusion described above to induce vection, where participants viewed animated scenes of a train passing (Seno & Fukuda, 2012). The train-context triggered faster onset and longer vection duration compared to abstract stimuli moving past at the same speed. Another study found that when perceiving a pattern of optic flow in the downward direction there was a reduction in vection when the falling objects were recognizable compared to meaningless, abstract dots, despite identical visual motion patterns (Ogawa & Seno, 2014). In a second experiment from the same study, vection was also reduced when participants were holding an umbrella (feeling sheltered – while viewing these falling objects) compared to when they were holding a sword (with no contextual meaning), again, despite identical motion. These studies provide evidence that vection is not solely driven by bottom-up visual motion. It is clearly also modulated by top-down factors like semantic context and scene interpretation. Here, we use variations in “naturalism” to manipulate semantic meaning. However, it is difficult to quantify “naturalism”. In this study, we describe a scene as natural if it obeys the rules of the natural world (i.e., do the scale and orientation of the scene’s objects align with the real world?). While the relationship between vection and self-motion is not well researched, it is possible that the enhancement to vection by more naturalistic environments (as described above) might also lead to changes in perceived distance traveled during a self-motion task. No one has yet investigated how the naturalism of a scene may affect the perception of travel distance. In Experiment 2, we test this question directly.

Colour has also played an increasingly recognized role in self-motion perception. Similar to the work on naturalism and vection perception, past research has found that more “complex” environments lead to improved sensation vection where complexity was increased by increasing the visual-field characteristics of the drum lining of an optokinetic drum, for example, by changing a stripe pattern to a checkerboard pattern or by adding different colours to the stripes (Bonato & Bubka, 2006). One study tested how chromatic colour, specifically red versus green, affected vection over a series of seven experiments (Seno et al., 2010). They found that: (1) a red background consistently produced weaker vection compared to a green background, (2) red moving dots on black also yielded reduced vection compared to green dots on black, (3) a moving red grating induced weaker vection than a green grating, (4) combining red dots on red background led to even weaker vection, while green-on-green produced stronger vection, and (5) these effects were not due to luminance artifacts. Together, this series of experiments suggest that red visual stimuli suppress vection, and that colour does have an effect on self-motion perception. In a carefully luminance-controlled environment, chromatic dots (i.e., dots with colour) produce stronger vection compared to achromatic dots (i.e., gray and white dots), (Seya et al., 2015). Another study showed that coherent colour modulation, irrespective of colour type, results in significantly reduced vection strength, meaning longer onset latencies, shorter durations, and lower magnitude scores (Nakamura et al., 2010). These studies clearly support the idea that the colour of an environment can affect self-motion perception. Therefore, in Experiment 3 we examine how the colour of an environment may affect the perception of travel distance.

Many studies on the perception of travel distance have used either the Move-To-Target (where participants estimate travel distance by stopping at the location of a previously seen target) or the Adjust-Target task (where participants adjust a target to indicate the distance of a previous movement). Few have used both to measure travel distance estimates. Since we have previously found differences in travel distance estimates between these two tasks (Bansal et al., 2024), we used both tasks here to measure travel distance estimates in the present study.

The overarching objective of the present study was to investigate how different characteristics of a virtual environment may affect the perception of travel distance through it. In Experiment 1, the objective was to test the effects of structure, the presence of a ground surface, and its texture on perceived travel distance in virtual reality. In Experiment 2, the objective was to test whether there was an effect of naturalism on perceived travel distance. In Experiment 3, the objective was to test how colour affects the perception of travel distance. In Experiment 4, the objective was to test how the density of a starfield can affect perceived travel distance.

We hypothesize that since the variables of the first three experiments have already been shown to affect vection and self-motion perception (as reviewed above), the presence and texture of the ground surface, the addition of more structure and more naturalism, and the presence of colour would lead to larger estimates of travel distance, meaning participants will feel like they have moved further in these conditions. We also hypothesize that there may be a ceiling effect with the starfield density needed to make accurate travel distance estimates. This study will give us a deeper understanding of how the specific components of visual motion contribute to our perception of self-motion.

## 3.3. Experiment 1: Environmental Structure, Texture, and the Ground Surface

### 3.3.1. Methods

*Participants*

Eighteen subjects (9F, 9M, mean age 19.4 yrs, SD ±2.1) participated in this study. The recruitment period was between January 21st, 2023 and April 3rd, 2023. All participants were recruited using the Kinesiology Undergraduate Participant Pool at York University. The protocols used in this study were approved by the York Human Participants Review Sub-committee (#e2021-407) and conducted in accordance with the Declaration of Helsinki. All participants gave prior informed written consent and were naive to the purpose of the study.

*Apparatus*

The equipment used in this experiment was a virtual reality (VR) head mounted display (HMD) and Alienware computer (Intel Core i7-8700K CPU, 3.70 GHz). The virtual stimuli were presented via an Oculus Rift CV1 (Oculus VR; 90 Hz refresh rate, 1080 × 1200 resolution per eye).

*Stimuli*

The experiment was performed in virtual reality using visually induced self-motion, while the participants remained physically stationary. There were two virtual environments in which this experiment was performed. The first, more structured environment was a virtual corridor that was 1.86m x 1.86m, with the simulated eye height set to the center of the corridor at

0.93m above the ground (Fig 3.1, top row). The second was a less structured "starfield" environment, with a starfield density of 3,000 stars and a ground surface (Fig 1, bottom row). Each star in the starfield environment was 3.5m in diameter and had an infinite lifetime. In both environments, there were three ground surface conditions. The first had a ground surface with a virtual grass texture, the second had a vertical striped pattern on the ground surface with no texture which therefore did not provide any optic flow information, and the last condition had no ground surface at all. In the no-ground-surface condition, the block started by having the ground "drop" before participants began the first trial to stress how there was no visible ground surface while they were experiencing the simulated movement.

There were six different conditions (2 environments x 3 ground surface options). In the starfield environment (bottom row of Fig 3.1.), the stars were only present above the horizon in the visual display, and had the same texture as the virtual corridor, to more closely match the visual display characteristics of the virtual corridor. The starfield environment was arranged such that the stars could not hit the participant. As to not create a "box" of stars around the participant, the stars were placed at a random location to the left, right, or above them. On the left, the stars were placed anywhere between -25m and less than a random number between -4 or -6m, on the right, the stars were placed between +25m and greater than a random number between +4 and 6m, and on top, the stars were places between +25m and greater than a random number between +9 and +11m. The stoney texture on the walls of the corridor was arranged such that the stones were randomly placed in a non-repeating pattern. Participants were visually moved at a constant velocity of 5 m/s, which was the velocity used in our previous study (Bansal et al., 2024). The visual stimuli were always presented stereoscopically and world-fixed, such that the visual environment updated with the participant's head movement, though participants were asked to keep their head straight.

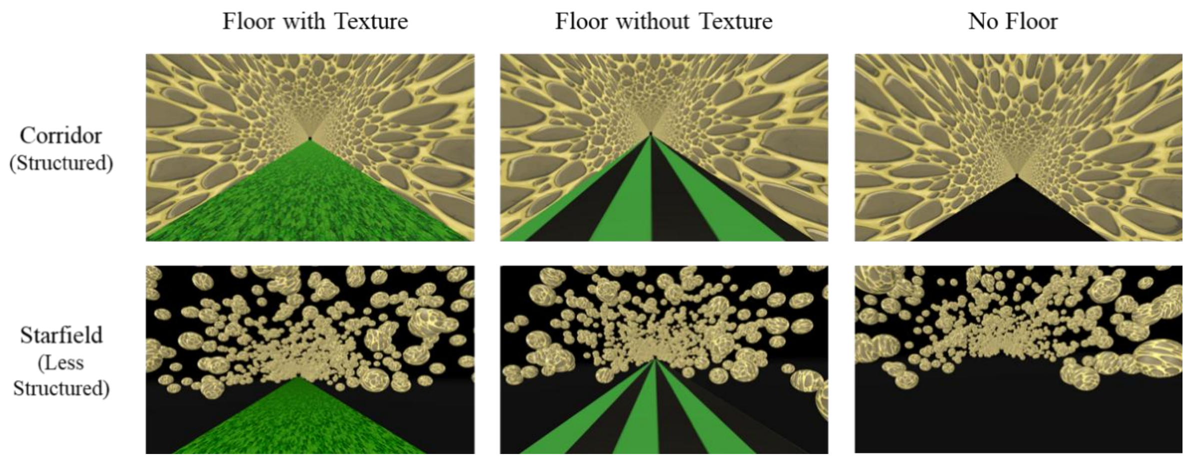



**Fig 3.1. Visual scenes seen inside the virtual reality headset.** The top row displays the virtual corridor (more structured) environment. The bottom row displays the starfield (less structured) environment. The first column shows both virtual environments containing the ground surface with a "grass" texture. The second column shows both environments containing the ground surface without a texture (plain green). The last column shows both environments without the ground surface.

*Move-To-Target Task*

Each trial started with a simulated target (a black-and-white checkered pillar measuring 1m x 5m) presented straight in front of them (Fig 3.2). The target was presented in a separate sparse black environment with a black and white striped ground surface, so participants did not have any landmarks to use as the target's location during the "movement phase". They then pressed a button on a mouse which triggered the target to disappear and motion in the virtual corridor or starfield to be simulated with optic flow. Participants indicated when they felt they reached the now invisible target by pressing the button once more.

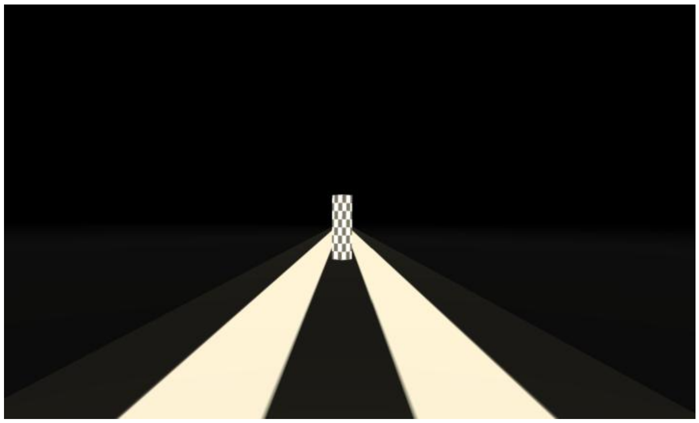


**Fig 3.2. Visual display of the target environment.** For the Move-To-Target task, this was the target presented in front of the participants at the beginning of each trial. For the Adjust-Target task, this was the target that participants had to adjust to the distance they felt they had been moved.

*Adjust-Target Task*

Participants sat in the same virtual environments as for the Move-To-Target task and began by pressing a button. They then experienced simulated movement through a pre-specified distance. Once they had traveled this distance, they were teleported back to their original position and the same target appeared in front of them as for the Move-To-Target task. Participants then used the up and down arrow keys of a keyboard to slide the target back and forth along the corridor until it was as far away as the distance through which they felt that they had just been moved. They pressed the space bar to end the trial.

*Procedure*

Participants were first asked to sit in a chair, while the instructions were explained to them by the experimenter. At the beginning of each task, participants were first given a practice session which included 6 trials (2 trials in each of the three ground surface conditions) at randomized distances between 5-40m. Once the practice was completed, the full version of each task was run.

This study was a within-subjects design, such that every participant completed both the Move-To-Target and Adjust-Target tasks. The order in which the tasks were completed was counterbalanced such that half completed the Move-To-Target first and the other half completed the Adjust-Target task first. For each task the participants experienced two structured environments: corridor or starfield, which each had three ground surfaces (grass textured, plain green, or no ground surface). Within each of these conditions the environments moved at 5 m/s through one of twelve target distances (5, 8, 11, 14, 17, 20, 23, 26, 29, 32, 35, 40 m). Each condition was presented only once. All conditions were randomized to cancel out any order effects. The tasks were blocked by surface and environment conditions and the order in which these blocks were presented was also randomized. The instructions were presented in the HMD again at the beginning of each block and at those times the participants were able to take a break if needed. The whole experiment took about 30 minutes (15 minutes for each of the two tasks).

*Data Analysis*

Each participant completed 144 trials (2 structured environments x 3 ground surface conditions x 12 distances x 2 tasks). First, an outlier removal was completed. The outlier removal was performed at the group level for each distance in every condition (2 environments x 3 ground surface conditions x 2 tasks). Any data less than the 'Lower Quartile - 1.5 x Interquartile Range' or above the 'Upper Quartile + 1.5 x Interquartile Range' were removed. Out of 2,592 data points, 59 data points were removed.

The ratio of travel distance to target distance (gain: output/input) was then calculated for each trial for both tasks. In the Move-To-Target task, this translates to the target distance (how far they thought they had moved) divided by the distance travelled (the amount they were simulated to move) before pressing the button to stop:

| | |
|---|---|
| $Gain_{Move\text{-}To\text{-}Target}$ = Target Distance / Self-Motion Distance | (1) |

For the Adjust-Target task, this translates to where participants adjusted the target to (how far they thought they had moved) divided by the distance that participants were moved through (the amount they were simulated to move):

| | |
|---|---|
| $Gain_{Adjust\text{-}Target}$ = Adjusted Target Distance / Self-Motion Distance | (2) |

Perfect performance in both cases would be a gain of 1. In both cases, a gain greater than 1 would imply that participants felt like they had moved further than they had, and vice versa. Before testing any differences between conditions, we tested whether any effects for a condition differed between MTT and AT tasks. Since we did find differences between tasks, we analyzed the tasks separately. A Linear Mixed Model was performed independently for both tasks using the lme4 package (Bates et al., 2015) for R (version 4.3.0.) on the gains. To determine the most appropriate model structure, we used Barr et al.'s (2013) model comparison approach. We started with a maximal model including all relevant experimental variables (environment structure, and ground surface condition) as slopes per participant and compared to simpler models until no significant differences were found between models. Random slopes for environment structure and ground surface condition per participant were kept for both models. The fixed effect structure was chosen as a function of our hypotheses, where we were interested in the main effects of environment and ground surface. We did not include an interaction between environment and ground surface because we had no specific hypotheses about the interaction term. The final model structure for the gains LMMs reads as follows:

| | |
|---|---|
| Gain ~ Environment + Ground Surface + (Environment + Ground Surface \| Participant) | (3) |

We then computed bootstrapped confidence intervals at an alpha level of 0.05 to test for statistical significance using the confint() function from the base R with the "boot" argument and default settings otherwise. All data and data analysis can be found at https://github.com/ambikabansal/Virtual-Environments.

### 3.3.2. Results

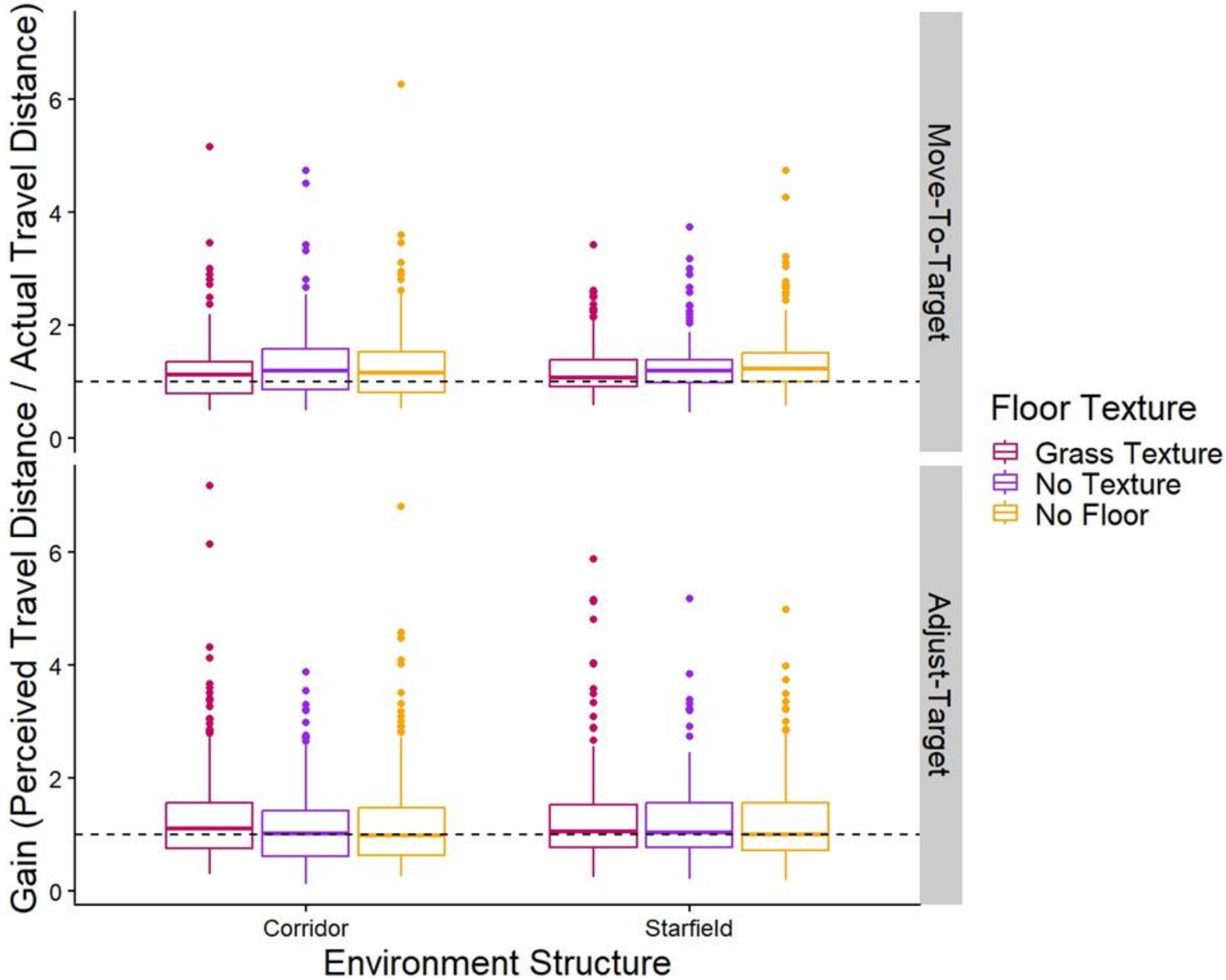



**Fig 3.3. Gains.** Box plots of the group gains for both the Move-To-Target (top row) and Adjust-Target (bottom row) tasks for each Environment Structure and Ground Surface Condition. The middle line represents the median, the boxes extend from the first quartile to the third quartile, the whiskers extend up to 1.5 times the interquartile range, and the outliers are shown as individual points beyond the whiskers. The grass texture is represented in maroon (left most), no texture in purple (second from left), and no ground surface in yellow (right most). The black dashed line represents perfect performance (gain of 1).

***Effect of Environment Structure***

*Move-To-Target Task*

The top row of Table 1 shows the means and standard deviations of the gains for the Move-To-Target task. Table 2 shows the results from the linear mixed model for the effect of Environment Structure on the gains of the Move-To-Target task. We found no significant differences between the corridor and starfield environment conditions. The gains are shown in Fig 3.3.

*Adjust-Target Task*

The bottom row of Table 1 shows the means and standard deviations of the gains for the Adjust-Target task. Table 2 shows the results from the linear mixed model for the effect of Environment Structure on the gains of the Adjust-Target task. There were no significant differences between the corridor and starfield environment conditions. The gains are shown in Fig 3.3.

| | Corridor | Starfield |
|---|---|---|
| Move-To-Target Task | 1.24 ± 0.61 | 1.28 ± 0.51 |
| Adjust-Target Task | 1.25 ± 0.88 | 1.26 ± 0.77 |

Table 3.1: Means and standard deviations of the gains for the different Environmental Structure conditions.

| | Regression Coefficient | Standard Error | 95% CI (lower) | 95% CI (upper) | Significance |
|---|---|---|---|---|---|
| Corridor vs. Starfield (Move-To-Target Task) | 0.02 | 0.07 | -0.10 | 0.14 | n.s. |

| | | | | | |
|---|---|---|---|---|---|
| Corridor vs. Starfield (Adjust-Target Task) | 0.01 | 0.07 | -0.11 | 0.15 | n.s. |

Table 3.2: Results from the Linear Mixed Models run on data from the Adjust-Target and Move-To-Target tasks with the gain set as the dependent variable, with both Environment Structure and Ground Surface Condition set as fixed effects. This table reports differences in Environment Structure. This table reports unstandardized regression coefficients.

***Effect of the Ground Surface***

*Move-To-Target Task*

The top row of Table 3 shows the means and standard deviations of the gains for the Move-To-Target task. Table 4 shows the results from the linear mixed model for the effect of the ground surface condition on the gains of the Move-To-Target task. We found that the grass texture led to significantly lower gains than the no texture or no ground surface conditions, these effects were small. We also found no significant differences between the no-texture and no-ground surface conditions. The gains are shown in Fig 3.3.

*Adjust-Target Task*

The bottom row of Table 3 shows the means and standard deviations of the gains for the Adjust-Target task. Table 4 shows the results from the linear mixed model for the effect of ground surface condition on the gains of the Adjust-Target task. Contrary to the results from the Move-To-Target task, we found that in the Adjust-Target task, the grass texture led to significantly higher gains than the no texture or no ground surface conditions, although again, these effects were small. There were also no significant differences between no texture and no ground surface conditions. The gains are shown in Fig 3.3.

| | Grass Texture | No Texture | No Ground Surface |
|---|---|---|---|
| Move-To-Target Task | 1.19 ± 0.51 | 1.28 ± 0.55 | 1.31 ± 0.62 |
| Adjust-Target Task | 1.32 ± 0.89 | 1.20 ± 0.72 | 1.25 ± 0.85 |

Table 3.3: Means and standard deviations of the gains for the different ground surface conditions.

| | Regression Coefficient | Standard Error | 95% CI (lower) | 95% CI (upper) | Significance |
|---|---|---|---|---|---|
| Grass Texture vs. No Texture (Move-To-Target Task) | 0.07 | 0.03 | 0.008 | 0.13 | * |
| Grass Texture vs. No Ground Surface (Move-To-Target Task) | 0.12 | 0.04 | 0.05 | 0.18 | * |
| No Texture vs. No Ground Surface (Move-To-Target Task) | -0.04 | 0.03 | -0.11 | 0.02 | n.s. |
| Grass Texture vs. No Texture (Adjust-Target Task) | -0.12 | 0.07 | 0.001 | 0.13 | * |
| Grass Texture vs. No Ground Surface (Adjust-Target Task) | -0.07 | 0.09 | 0.03 | 0.18 | * |

| | | | | | |
|---|---|---|---|---|---|
| No Texture vs. No Ground Surface (Adjust-Target Task) | -0.05 | 0.06 | -0.18 | 0.08 | n.s. |

Table 3.4: Results from the Linear Mixed Models run on data from the Move-To-Target and Adjust-Target tasks with the gain set as the dependent variable, with both Environment Structure and Ground Surface Condition set as fixed effects. This table reports differences in Environment Structure. This table reports unstandardized regression coefficients.

## 3.4. Experiment 2: Naturalism

### 3.4.1. Methods

*Participants*

Eighteen subjects (9F, 9M, mean age 20.2 yrs, SD ±2.8) participated in this study. The recruitment period was between January 23rd, 2024 and March 20th, 2024. All participants were recruited using the Kinesiology Undergraduate Participant Pool at York University. The protocols used in this study were approved by the York Human Participants Review Sub-committee (#e2021-407) and conducted in accordance with the Declaration of Helsinki. All participants gave prior informed written consent and were naive to the purpose of the study.

*Apparatus*

Same as Experiment 1.

*Stimuli*

There were three virtual street environments in which this experiment was performed (see Fig 3.4). The first condition was moving through a natural street scene where all the objects in the environment (people, trees, streetlights, houses) were scaled and oriented normally and remained stationary as the viewer moved past. The second "scaled up" condition, was a version of the virtual street where all the objects in the environment were twice as large as in the "natural" condition – if they therefore felt at half the distance, perceived speed might be expected to increase. The last condition was an unnatural condition in which all the objects in the environment were rotated and scaled randomly. In this last “unnatural” condition, each object was changed such that its original size was multiplied by a random number between 0.5 and 2.0, and rotated on each of its x, y, and z axes by +/- 180 degrees randomly, although in the y-axis the object was then set to the closest 0, 90, or 270 degree. The road and paving stones remained the same size and orientation in all conditions. The target (black and white checked pillar, measuring 1 x 5m) was presented in the same sparse black environment as Experiment 1 (see Fig 3.2).


**Fig 3.4. Visual scenes rendered inside the virtual reality headset.** The top panel shows the natural condition, where objects in the environment were scaled normally. The central panel shows the scaled-up condition, where objects in the environment were 2x larger than the natural condition. The lower panel shows the unnatural condition, where objects in the environment were rotated and scaled randomly.

*Procedure*

Same as Experiment 1. Participants completed both the Move-To-Target and Adjust-Target tasks. Visual self-motion was simulated at 5 m/s down the street. Each task consisted of the same twelve target distances (5, 8, 11, 14, 17, 20, 23, 26, 29, 32, 35, 40 m), with no repetitions.

*Data Analysis*

Same as Experiment 1. Out of 1283 data points, 66 data points were removed using the same outlier analysis as Experiment 1. Using the same Barr et al.'s (2013) model comparison approach to determine the LMMs, random slopes for Environment per Participant were kept for both the Move-To-Target and Adjust-Target models. Therefore, the final model structure for the gains LMMs reads as follows:

| | |
|---|---|
| Gain ~ Environment + (1 + Environment \| Participant) | (4) |

## 3.4.2. Results

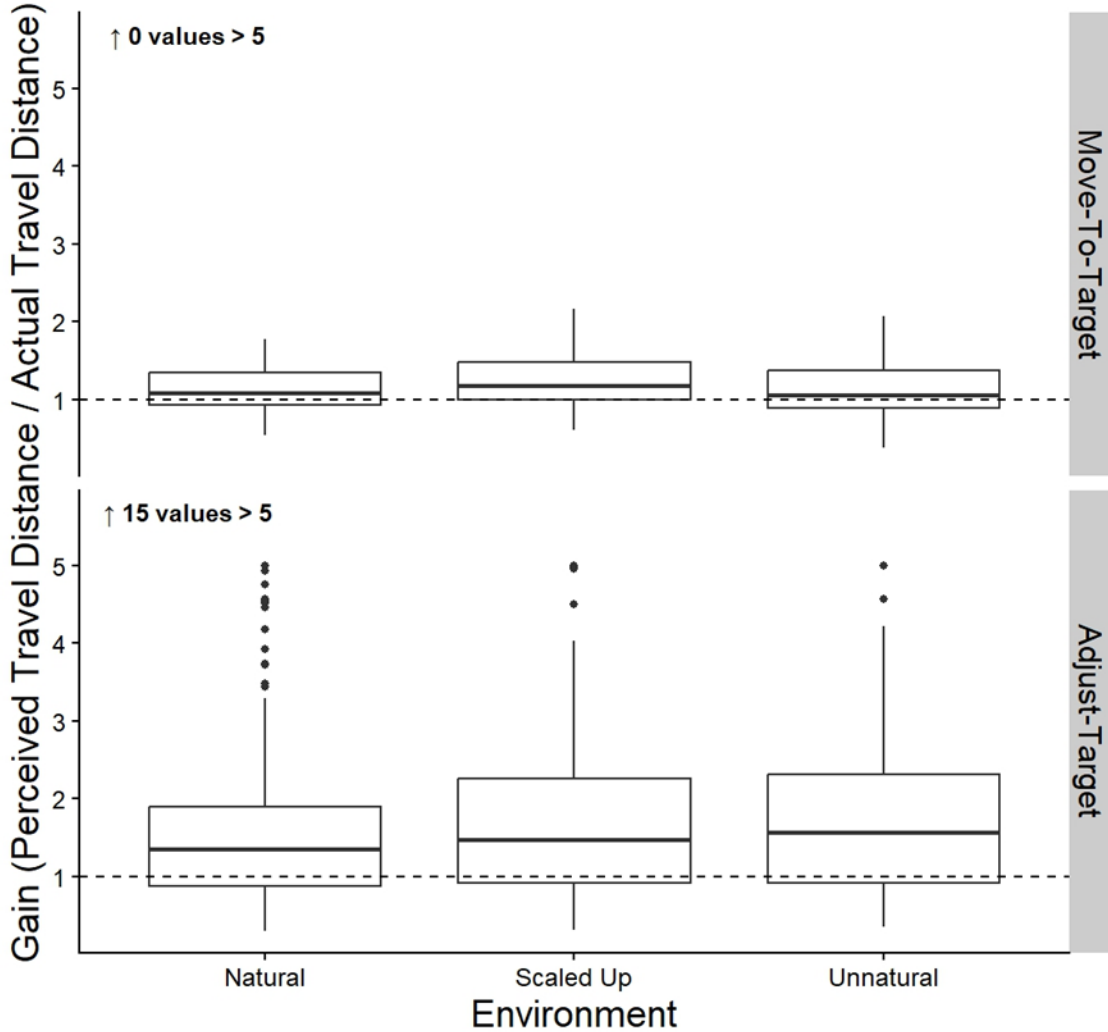



**Fig 3.5. Gains.** Box plots of the group gains for both the Move-To-Target (top row) and Adjust-Target (bottom row) tasks for each Environment. The middle line represents the median, the boxes extend from the first quartile to the third quartile, the whiskers extend up to 1.5 times the interquartile range, and the outliers are shown as individual points beyond the whiskers. The black dashed line represents perfect performance (gain of 1).

***Effect of Naturalism and Scale***

*Move-To-Target Task*

The top row of Table 5 shows the means and standard deviations of the gains for the Move-To-Target task. Table 6 shows the results from the linear mixed model for the effect of Environment on the gains of the Move-To-Target task. We found that the scaled-up condition led to higher gains than the natural or unnatural conditions. However, we found no significant differences between the natural and unnatural conditions. The gains are shown in the top half of Fig 3.5.

*Adjust-Target Task*

The bottom row of Table 5 shows the means and standard deviations of the gains for the Adjust-Target task. Table 6 shows the results from the linear mixed model for the effect of Environment on the gains of the Adjust-Target task. There were no significant differences between the natural, scaled up, or unnatural conditions. The gains are shown in the bottom half of Fig 3.5.

| | Natural | Scaled Up | Unnatural |
|---|---|---|---|
| Move-To-Target Task | 1.12 ± 0.27 | 1.24 ± 0.33 | 1.12 ± 0.35 |
| Adjust-Target Task | 1.60 ± 1.02 | 1.82 ± 1.41 | 1.76 ± 1.12 |

Table 3.5: Means and standard deviations of the gains for the different Environment conditions.

| | Regression Coefficient | Standard Error | 95% CI (lower) | 95% CI (upper) | Significance |
|---|---|---|---|---|---|
| Natural vs. Scaled Up (Move-To-Target Task) | 0.12 | 0.04 | 0.04 | 0.18 | * |

| | | | | | |
|---|---|---|---|---|---|
| Natural vs. Unnatural (Move-To-Target Task) | 0.008 | 0.05 | -0.08 | 0.11 | n.s. |
| Scaled Up vs. Unnatural (Move-To-Target Task) | -0.11 | 0.03 | -0.18 | -0.05 | * |
| Natural vs. Scaled Up (Adjust-Target Task) | -0.25 | 0.16 | -0.54 | 0.06 | n.s. |
| Natural vs. Unnatural (Adjust-Target Task) | 0.18 | 0.08 | -0.08 | 0.11 | n.s. |
| Scaled Up vs. Unnatural (Adjust-Target Task) | -0.08 | 0.16 | -0.37 | 0.23 | n.s. |

Table 3.6: Results from the Linear Mixed Models run on data from the Move-To-Target and Adjust-Target tasks with the gain set as the dependent variable, with Environment Condition set as a fixed effect. This table reports differences in the Environment Condition. This table reports unstandardized regression coefficients.

## 3.5. Experiment 3: Colour

### 3.5.1. Methods

*Participants*

Eighteen subjects (11F, 7M, mean age 19.9 yrs, SD ±2.8) participated in this study. The recruitment period was between September 28th, 2024 and November 3rd, 2024. All participants were recruited using the Kinesiology Undergraduate Participant Pool at York University. The protocols used in this study were approved by the York Human Participants Review Sub-committee (#e2021-407) and conducted in accordance with the Declaration of Helsinki. All participants gave prior informed written consent and were naive to the purpose of the study.

*Apparatus*

Due to experimental setup changes, a different virtual reality HMD and computer were used for this experiment. For Experiment 3, A VIVE Pro EYE HMD (field of view of 110°, resolution 1440 × 1600 per eye, 90 Hz refresh rate) was used to present the stimuli. The program was run on an Alienware laptop (16 GB RAM, Intel Core i7-9750H CPU, 2.60 GHz, NVIDIA GeForce RTX 2060).

*Stimuli*

There were two virtual environments in which this experiment was performed. Both environments were a starfield environment with a density of 3,000 stars. The size of the various “stars” in both starfield environments were the same as Experiment 1. The stars were randomly placed similar to Experiment 1, except in the y-axis, the stars were also placed below the horizon. The stars were placed anywhere between -25m and less than a random number between -2 or -5m, or between +25m and greater than a random number between +8 and 10m. The first environment was in colour, and the second was in greyscale (Fig 3.6). Both scenes had “stars” with various textures. Since luminance has been shown to influence vection (Guo et al., 2021), both scenes were matched in terms of luminance. The mean luminance of the two scenes was measured using a Colorimeter (Radiant I29). The colorimeter was positioned against the right lens of the headset. To keep the luminance levels the same (approximately 0.30), the global illumination of the grey scale environment within the Unity environment had to be reduced from 1.0 to 0.8. This value was calculated as the average from five different views in the headset (i.e., the program was restarted and measured five times, as the position of the spheres change on each trial). The target (black and white checked pillar, measuring 1 x 5m) was presented in the same sparse black environment as Experiments 1 and 2 (see Fig 3.2).

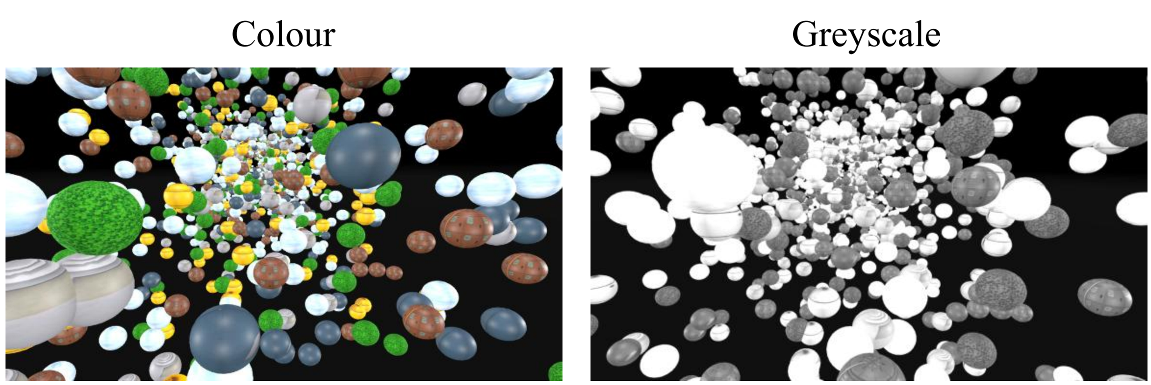



**Fig 3.6. Visual scenes seen inside the virtual reality headset.** The left panel shows the starfield of 3,000 stars in colour. The right panel shows the same starfield in greyscale.

*Procedure*

Same as Experiments 1 and 2.

*Data Analysis*

Out of 2,447 data points, 115 data points were removed using the same outlier analysis as Experiment 1. Like Experiment 2, random slopes for Environment per Participant were kept for both the Move-To-Target and Adjust-Target LMM models, therefore we used the same model structure for both LMMs:

| | |
|---|---|
| Gain ~ Environment + (1 + Environment \| Participant) | (5) |

### 3.5.2. Results

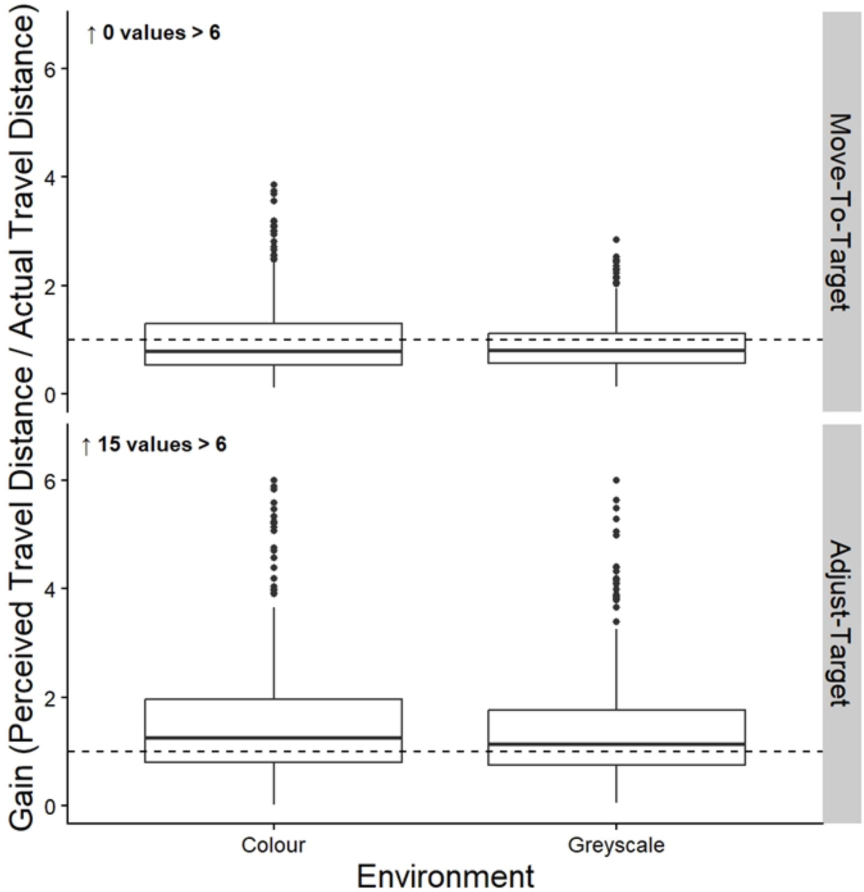



**Fig 3.7. Gains.** Box plots of the group gains for both the Move-To-Target (top row) and Adjust-Target (bottom row) tasks for the Colour and Greyscale conditions. The middle line represents the median, the boxes extend from the first quartile to the third quartile, the whiskers extend up to 1.5 times the interquartile range, and the outliers are shown as individual points beyond the whiskers.

***Effect of Colour***

*Move-To-Target Task*

The top row of Table 7 shows the means and standard deviations of the gains for the Move-To-Target task. Table 8 shows the results from the linear mixed model for the effect of

Colour on the gains of the Move-To-Target task. We found no significant differences between the colour and greyscale conditions. The gains are shown in the top half of Fig 3.7.

*Adjust-Target Task*

The bottom row of Table 7 shows the means and standard deviations of the gains for the Adjust-Target task. Table 8 shows the results from the linear mixed model for the effect of Colour on the gains of the Adjust-Target task. There were no significant differences between the colour and greyscale conditions. The gains are shown in the bottom half of Fig 3.7.

| | Colour | Greyscale |
|---|---|---|
| Move-To-Target Task | 0.78 ± 0.67 | 0.81 ± 0.46 |
| Adjust-Target Task | 1.25 ± 1.14 | 1.13 ± 1.13 |

Table 3.7: Means and standard deviations of the gains for the coloured and greyscale conditions.

| | Regression Coefficient | Standard Error | 95% CI (lower) | 95% CI (upper) | Significance |
|---|---|---|---|---|---|
| Colour vs. Greyscale (Move-To-Target Task) | -0.12 | 0.09 | -0.29 | 0.05 | n.s. |
| Colour vs. Greyscale (Adjust-Target Task) | 0.09 | 0.31 | -0.29 | 0.03 | n.s. |

Table 3.8: Results from the Linear Mixed Models run on data from the Move-To-Target and Adjust-Target tasks with the gain set as the dependent variable, with Colour Condition set as the fixed effect. This table reports differences in the Colour. This table reports unstandardized regression coefficients.

## 3.6. Experiment 4: Starfield Density

### 3.6.1. Methods

*Participants*

Eighteen subjects (11F, 7M, mean age 19.5 yrs, SD ±2.1) participated in this study. The recruitment period was between February 15th, 2025 and Apil 11th, 2025. All participants were recruited using the Kinesiology Undergraduate Participant Pool at York University. The protocols used in this study were approved by the York Human Participants Review Sub-committee (#e2021-407) and conducted in accordance with the Declaration of Helsinki. All participants gave prior informed written consent and were naive to the purpose of the study.

*Apparatus*

Same as Experiment 3.

*Stimuli*

In this experiment, we were interested in the starfield density needed to accurately estimate travel distance. To do this, we manipulated the density of stars in the starfield environment to either 10 stars, 100 stars, or 1,000 stars in the environment at a time (Fig 3.8), as well as moving participants at three different travel speeds (1, 5, 10 m/s). The stars' locations were set to the same parameters as Experiment 3 and had a white and faint blue texture. The target (black and white checked pillar, measuring 1 x 5m) was presented in the same sparse black environment as Experiments 1-3 (see Fig 3.2).

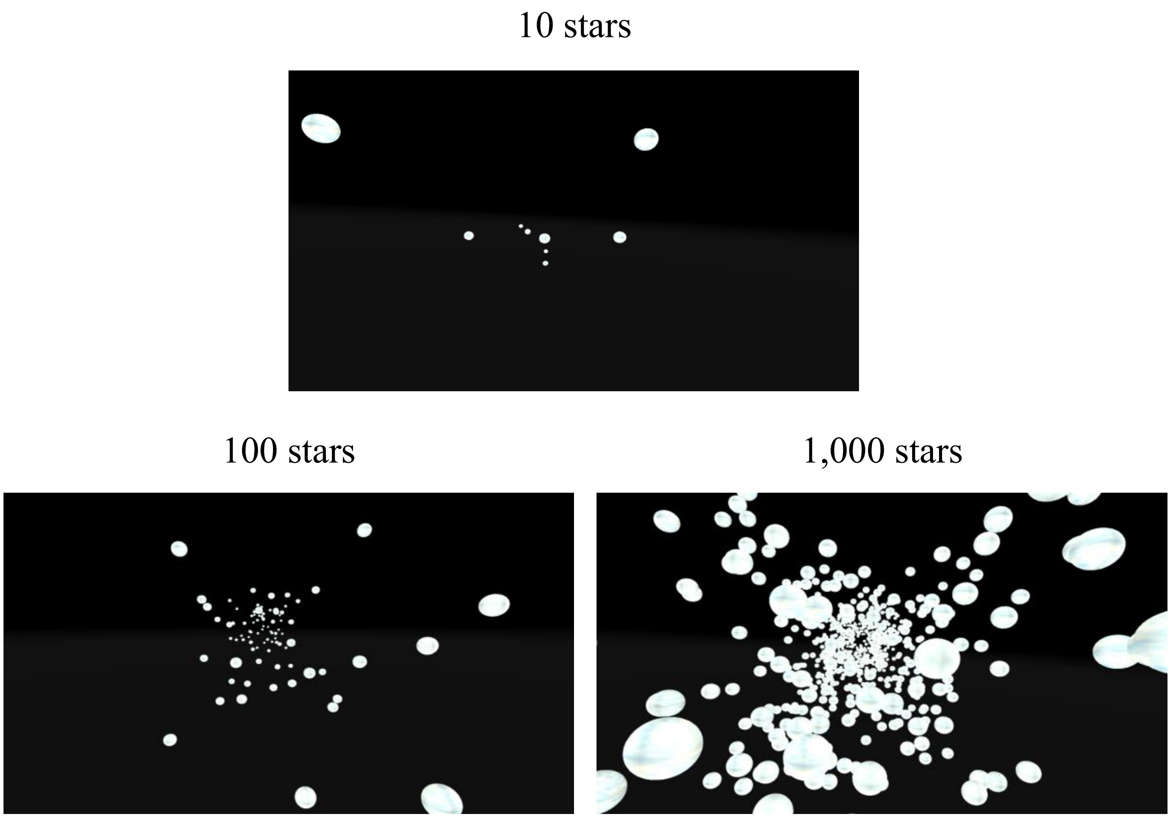



**Fig 3.8. Visual scenes seen inside the virtual reality headset.** The top panel shows the low-density condition, which contained 10 stars. The bottom left panel shows the medium-density condition, which contained 100 stars. The bottom right panel shows the high-density condition, which contained 1,000 stars.

*Procedure*

The procedure was the same as Experiments 1-3, with minor changes. Self-motion was simulated at three different speeds (1, 5, 10 m/s), the order of which was randomized in each block. Each block consisted of six target distances (10, 15, 20, 25, 30, 40 m). As in Experiments 1-3, these two tasks were counterbalanced such that half of the participants completed the Move-To-Target first and half completed the Adjust-Target task first.

*Data Analysis*

Data analysis used the same methods as used in Experiment 1. Out of 1,152 data points, 95 data points were removed using the same outlier analysis mentioned above. For the Linear Mixed Model, the most appropriate model structure was determined using Barr et al.'s (2013) model comparison approach. We started with a maximal model including all relevant experimental variables (Starfield Density and Speed) as slopes per participant and compared to simpler models until no significant differences were found between models. Only random slopes for Speed per Participant were kept for both the Move-To-Target and Adjust-Target models. We did not include an interaction between Starfield Density and Speed because we had no specific hypotheses about the interaction term. The final model structure for the LMM on the gains reads as follows:

| | |
|---|---|
| Gain ~ Density + Speed + (Speed \| Participant) | (6) |

### 3.6.2. Results

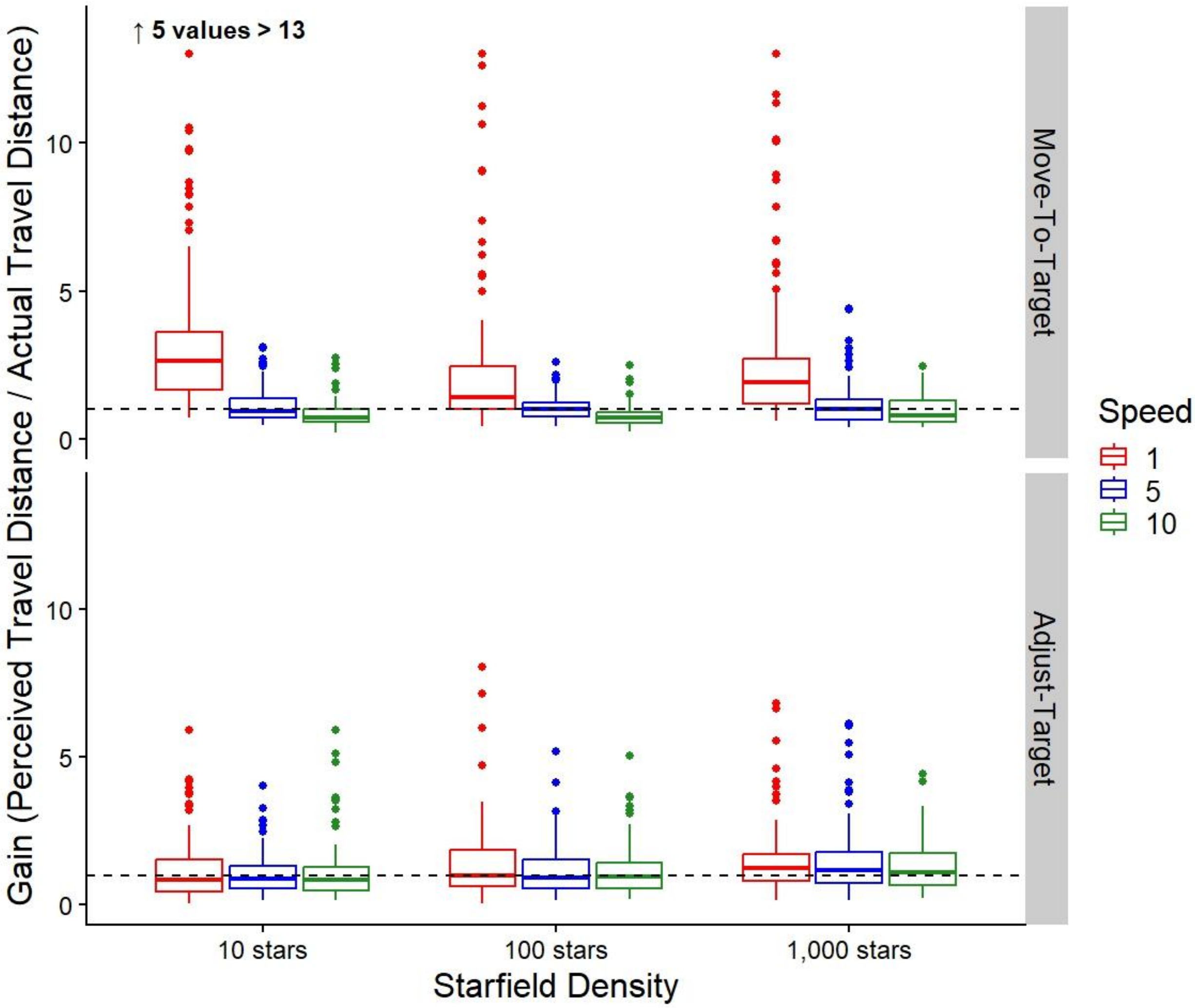



**Fig 3.9. Gains.** Box plots of the group gains for both the Move-To-Target (top row) and Adjust-Target (bottom row) tasks for each Starfield Density and Speed Condition. The middle line represents the median, the boxes extend from the first quartile to the third quartile, the whiskers extend up to 1.5 times the interquartile range, and the outliers are shown as individual points beyond the whiskers. The 1 m/s is represented in red (left most), 5 m/s in blue (second from left), and 10 m/s in green (right most). The black dashed line represents perfect performance (gain of 1).

***Effect of Starfield Density***

*Move-To-Target Task*

The top row of Table 9 shows the means and standard deviations of the gains for the Move-To-Target task. Table 10 shows the results from the linear mixed model for the effect of Starfield Density on the gains of the Move-To-Target task. We found a significant difference between the 10- and 100-star conditions, although there were no significant differences between the 10- and 1,000-starfield-density conditions or the 100- and 1,000-starfield-density conditions. The gains are shown at the top of Fig 3.9.

*Adjust-Target Task*

The bottom row of Table 9 shows the means and standard deviations of the gains for the Adjust-Target task. Table 10 shows the results from the linear mixed model for the effect of Starfield Density on the gains of the Adjust-Target task. We found no significant differences between the 10, 100, and 1,000 starfield density conditions. The gains are shown at the bottom of Fig 3.9.

| | 10 stars | 100 stars | 1,000 stars |
|---|---|---|---|
| Move-To-Target Task | 2.15 ± 2.92 | 1.68 ± 2.57 | 2.24 ± 2.84 |
| Adjust-Target Task | 1.27 ± 1.07 | 1.40 ± 1.25 | 1.67 ± 1.29 |

Table 3.9: Means and standard deviations of the gains for the Starfield Density conditions.

| | Regression Coefficient | Standard Error | 95% CI (lower) | 95% CI (upper) | Significance |
|---|---|---|---|---|---|
| 10 stars vs. 100 stars | 0.84 | 0.39 | 0.16 | 1.61 | * |

| | | | | | |
|---|---|---|---|---|---|
| (Move-To-Target Task) | | | | | |
| 10 stars vs. 1,000 stars (Move-To-Target Task) | 0.19 | 0.39 | -0.54 | 1.02 | n.s. |
| 100 stars vs. 1,000 stars (Move-To-Target Task) | -0.65 | 0.39 | -1.39 | 0.17 | n.s. |
| 10 stars vs. 100 stars (Adjust-Target Task) | 0.11 | 0.15 | -0.22 | 0.44 | n.s. |
| 10 stars vs. 1,000 stars (Adjust-Target Task) | -0.42 | 0.15 | -0.60 | 0.92 | n.s. |
| 100 stars vs. 1,000 stars (Adjust-Target Task) | -0.30 | 0.15 | -1.53 | 0.19 | n.s. |

Table 3.10: Results from the Linear Mixed Models run on data from the Move-To-Target and Adjust-Target tasks with the gain set as the dependent variable, with both Starfield Density and Speed set as fixed effects. This table reports differences in Starfield Density. This table reports unstandardized regression coefficients.

***Effect of Speed***

*Move-To-Target Task*

The top row of Table 11 shows the means and standard deviations of the gains for the Move-To-Target task. Table 12 shows the results from the linear mixed model for the effect of Speed on the gains of the Move-To-Target task. We found that moving at 1 m/s led to significantly higher gains than the 5 m/s or 10 m/s. However, we found no significant differences between the 5 m/s and 10 m/s speed conditions. The gains are shown in Fig 3.9.

*Adjust-Target Task*

The bottom row of Table 11 shows the means and standard deviations of the gains for the Adjust-Target task. Table 12 shows the results from the linear mixed model for the effect of Speed on the gains of the Adjust-Target task. Similar to the Move-To-Target task, we found that the 1 m/s condition led to significantly higher gains than the 5 m/s and 10 m/s conditions. However, there were no significant differences between the 5 and 10 m/s speed conditions. The gains are shown in Fig 3.9.

| | 1 m/s | 5 m/s | 10 m/s |
|---|---|---|---|
| Move-To-Target Task | 5.58 ± 6.14 | 1.40 ± 1.05 | 0.88 ± 0.54 |
| Adjust-Target Task | 2.17 ± 2.09 | 1.33 ± 1.03 | 1.27 ± 1.00 |

Table 3.11: Means and standard deviations of the gains for the different speed conditions averaged across the 10-, 100-, and 1,000-star conditions.

| | Regression Coefficient | Standard Error | 95% CI (lower) | 95% CI (upper) | Significance |
|---|---|---|---|---|---|
| 1 m/s vs 5 m/s (Move-To-Target Task) | -4.20 | 1.15 | -6.26 | -2.19 | * |
| 1 m/s vs. 10 m/s (Move-To-Target Task) | -4.70 | 1.23 | -7.08 | -2.43 | * |
| 5 m/s vs. 10 m/s (Move-To-Target Task) | 0.50 | 0.35 | -0.28 | 1.22 | n.s. |
| 1 m/s vs 5 m/s (Adjust-Target Task) | -0.89 | 0.25 | -6.43 | -1.83 | * |
| 1 m/s vs. 10 m/s | -0.94 | 0.26 | -7.15 | -2.33 | * |

| | | | | | |
|---|---|---|---|---|---|
| (Adjust-Target Task) | | | | | |
| 5 m/s vs. 10 m/s (Adjust-Target Task) | 0.05 | 0.14 | -0.22 | 0.35 | n.s. |

Table 3.12: Results from the Linear Mixed Models run on data from the Move-To-Target and Adjust-Target tasks with the gain set as the dependent variable, with both Starfield Density and Speed set as fixed effects. This table reports differences in Starfield Density. This table reports unstandardized regression coefficients.

## 3.7. Discussion

This study comprised a series of four experiments investigating how the characteristics of a virtual environment might affect the perception of travel distance. Aligning with our original hypotheses, we found that the texture of the ground surface (Experiment 1) and the scale of the environment (Experiment 2) had an effect on the perception of travel distance, although, these effects were small and should not be overemphasized. Contrary to our hypotheses, however, we found that manipulating the structure, the presence or absence of a ground surface (Experiment 1), the naturalism (Experiment 2), and the presence of colour (Experiment 3) in the visible scene had no effect on the ability of the observer to extract their movement information correctly and generate a consistent perception of distance moved. Experiment 4 confirmed the presence of a ceiling effect in the amount of stars needed to provide adequate optic flow to accurately estimate travel distance.

***Experiments 1-3: The Effect of Structure, Ground Surface, Naturalism, Scale, Colour***

Much of the research on self-motion perception has used vection as a measurement. Although the different measures of the experience of vection can inform us as to whether people feel like they are moving, one can still perceive travel distance without experiencing vection. This divergence aligns with previous research that shows an increase in vection speed in microgravity (Oman et al., 2003; Young & Shelhamer, 1990) but no differences in perceived travel distance in microgravity when it is actually measured (Jörges et al., 2024a). Others have also found an effect of the speed of optic flow on vection speed (De Graaf et al., 1990) but there is still mixed evidence as to whether there is an effect of speed on perceived travel distance

(Bansal et al., 2024; Frenz et al., 2007; Harris et al., 2012a; Lappe et al., 2007a; McManus et al., 2017a). Although McManus and Fiehler (2025) have shown that the perception of travel distance and the sensation of vection should be related, the studies quoted above highlight the idea that the sensation of vection is independent of the perception of travel distance. There are two ways in which you can perceive self-motion without experiencing the sensation of vection: (1) you can experience that you are moving through a virtual environment without feeling like you are actually moving (e.g., when playing a first-person video game), (2) optic flow information can be interpreted not just as the sensation that you are moving through the world (i.e., vection) but also as you staying stationary while the world is moving past you. Many studies that have tested how the components of a virtual environment can affect your perceived self-motion have focused on the experience of vection (Bubka & Bonato, 2010; Seno et al., 2010; Tamada & Seno, 2015; Vaziri-Pashkam & Cavanagh, 2008), but no one has previously tested how the components of a virtual environment affect the perception of travel distance specifically. Our findings from Experiments 1-3 show no significant differences in travel distance estimates when manipulating the structure, naturalism, or colour of a virtual environment. In Experiment 2, we did find minor differences in scale, where the scaled-up condition led to higher gains in the Move-To-Target task than the natural or unnatural conditions. Although no significant differences were found in the Adjust-Target task. One limitation to Experiment 2 on naturalism, is that in all conditions, the roads, sidewalks, and participant eye height to the ground remained the same. In the unnatural condition, the road and sidewalk could have given natural cues. In the scaled-up condition, the participant eye height to the ground could have given a cue for scale. In Experiment 1, we did find significant differences related to the texture of the ground surface, although these effects were small. We find the textured ground led to lower gains in the Move-To-Target and higher gains in the Adjust-Target task. Again, since these effects were small, we do not want to overemphasize these findings. Generally, we show that the differences previously reported in vection do not necessarily translate to differences in perceived travel distance.

### *Experiment 4 – The Effect of Starfield Density*

Experiment 4 was conducted with the hope of shedding light on why we did not find differences in perceived travel distance between different virtual environments. We thought that our manipulations over the first three experiments were perhaps not strong enough to overcome the fact that there was still enough optic flow information to accurately make these judgements. In Experiment 4, we were interested in whether there may be a ceiling effect on the ability to extract the appropriate amount of optic flow needed to accurately estimate travel distance and that the reason we found no effect with these other manipulations was because threshold had already been exceeded. To test this, we manipulated the density of stars in a starfield environment. Our results showed that travel distance could still be accurately estimated even with very little optic flow information, meaning that people might be very sensitive to optic flow information leading to a ceiling effect with how much optic flow is needed to accurately perceive travel distance. We hypothesize that this is why we did not find significant differences between many of the conditions in our first three experiments. The minor manipulations we made between structure, naturalism, and colour conditions did not integrally alter the environment enough to modulate the perception of travel distance because there was always enough optic flow information to make accurate judgements of travel distance, though we do not know exactly what the perceptual threshold for the amount of optic flow needed for travel distance estimation. In a future study, it would be interesting to add other movement cues e.g., a starfield in which some percentage of dots obey the optic flow rules and the others are moving in random direction, to obtain coherence thresholds of the system that calculates distance travelled from optic flow to fully understand how much optic flow is needed to accurately perceive travel distance, similar to Burr and Santoro (2001) who calculated the perceptual threshold needed to discern the direction of motion of a random dot pattern.

### *Conclusions*

Here, we show that many of the characteristics of a virtual scene have no effect on the perception of travel distance within the limits of how we varied them. This line of research provides insights into the effects of a ground surface on perceived travel distance. Together this series of experiments has implications for the design of virtual environments where estimating travel distance is important.

# CHAPTER 4: Differences in perceived travel distance from central versus peripheral optic flow are the same when standing and walking

*This chapter is under revisions at PLoS ONE. I am the first author, Hongyi Guo is the second author, Dr. Robert Allison is the third author, and Dr. Laurence Harris is the last author.*

## 4.1. Abstract

Continuously evolving ways in which people move challenge the brain's self-motion processing. Previous research from our lab has shown that when seated, optic flow presented in the far periphery results in people feeling they moved further than when the same motion was presented over the full field or in the central field only. The literature is mixed on the relative weightings of visual and non-visual cues when estimating travel distance, and it is unknown how non-visual cues might affect the use of optic flow in the far periphery. Here, we used a large-field edgeless display to either visually "move" participants while they were (i) physically stationary, (ii) performing a blind walking task on a treadmill, or (iii) visually "moving" while walking on a treadmill. Optic flow simulating forward self-motion was presented either full field, in the central field (central ±20°), or in the far periphery (beyond ±90°). Participants estimated travel distances by stopping at the location of a previously seen target (Move-To-Target Task) or adjusting a target to indicate the distance of a previous movement (Adjust-Target Task). In the Move-To-Target task, peripheral optic flow led to higher gains (perceived travel distance / actual travel distance) compared to the central field and full-field conditions during both the visual-only and visual-and-treadmill conditions. In the same task, the blind walking condition also led to higher gains than the visual-only or visual-and-treadmill conditions. In the Adjust-Target task, there were no significant differences between conditions. This implies that different processes might be used to estimate travel distance in the Move-To-Target and Adjust-Target tasks, and that the high sensitivity to optic flow in the far periphery is a general feature of perceptual odometry even when integrating non-visual cues with visual cues.

## 4.2. Introduction

Having an accurate perception of travel distance is essential for navigating and moving through the world. During natural self-motion, information from our sensory systems (visual, vestibular, proprioceptive, auditory) is integrated to create a coherent perceptual experience of self-motion (Laurienti et al., 2006). It is known that this redundant sensory information can be combined in a statistically optimal way based on their relative reliability (Ernst & Banks, 2002). In more modern forms of self-motion (e.g., driving a car, experiencing simulated self-motion in virtual reality, etc.), these sensory inputs can be conflicting. As the scenarios in which we experience modern forms of self-motion increase, so has the interest in understanding the sensory processes involved in estimating travel distance. In this study, we investigate the perception of travel distance using visual and non-visual self-motion cues. Within the visual self-motion cues, we were specifically interested in how the brain processes peripheral versus central optic flow to estimate travel distance.

Self-motion perception has primarily been studied under isolated individual sensory cue conditions. Investigations have typically used either visual self-motion cues or body-based cues alone. Past research has found that these reduced cue conditions result in similar travel distance estimations to those resulting when the same cue conditions are combined (Sun, Campos, Young, et al., 2004). Sun and colleagues (2004) showed that information can be extracted from one modality and responded to accurately in either the same or different sensory condition. A common test used to examine proprioceptive and vestibular contributions to perceived travel distance is the blind walking task, in which participants walk either freely or on a treadmill without visual information. Using this task, it has been established that humans are able to accurately reproduce the distance to a previously seen target with blind walking (Fukusima et al., 1997; Loomis et al., 1992; Mittelstaedt & Mittelstaedt, 2001; Rieser et al., 1990). It has been suggested that the mechanism responsible for the accuracy in the blind walking task is "step integration" (step length times step frequency times time) (Durgin et al., 2009). Evidence for using step integration as an odometric cue has also been seen in other animals, such as the desert ant (Thiélin-Bescond & Beugnon, 2005; Wittlinger et al., 2006, 2007).

Of course, step integration is only possible when making active movements. In these active movement scenarios, vestibular and proprioceptive inputs are often coupled. Harris and colleagues (2000) passively moved participants to uncouple these body-based cues and combined this with testing either with visual cues or in the dark to isolate the vestibular and visual contributions to the perception of travel distance. Participants experienced constant acceleration self-motion either visually (using a virtual reality display), physically (moving passively in the dark), or by a combination of both visual and passive physical motion. Perceived travel distance when receiving a combination of both visual and physical motion was more similar to experiencing only physical motion, compared to when experiencing only visual motion. These findings highlight the explicit importance of vestibular inputs in estimating travel distance.

It seems that the relative contributions of the different sensory systems to self-motion perception may be both task and stimulus dependent. During rotational movements, proprioceptive information generates the most consistent and accurate self-motion perception, followed by vestibular and then visual cues (Bakker et al., 1999). For translational motion, one study had participants compare travel distance when visual information provided through a head-mounted display was either congruent or incongruent with proprioceptive information generated from cycling on a stationary bike (Sun, Campos, & Chan, 2004). They found that when visual and proprioceptive information was inconsistent, participants responded as if optic flow were the dominant source of information, though the presence of proprioceptive information improved the visually specified distance estimates even when the cues were incongruent. An earlier study had participants walking on a treadmill at a constant speed, while manipulating the magnitude of optic flow (Prokop et al., 1997). Their results also showed participants changed their movements to align with the optic flow manipulations more so than with the constant speed of the treadmill, although they did not completely rely on optic flow. These studies provide evidence for a higher weighting of visual cues over non-visual cues during linear self-motion perception, in contrast to the proprioceptive dominance in rotational self-motion. More recent research integrating visual cues with either walking on a treadmill (Kopiske et al., 2023) or free walking (Campos et al., 2010, 2012) found that, as in the earlier experiments on rotational movements, non-visual cues were weighted higher than visual when estimating travel distance. Clearly the relative sensory contributions to the perception of linear travel distance is still an open question.

Previous research from our lab has shown that optic flow presented only in the far periphery (beyond 90°) resulted in people feeling they had moved further than when the same motion was presented full field or in only the central field (McManus et al., 2017a). For those experiments, however, participants were seated and received only visual stimuli about their movement. Harris and colleagues (2012) investigated the relative contributions of radial and laminar optic flow in the perception of travel distance, again while stationary. They found that laminar flow (corresponding to similar pattern of optic flow in the peripheral field) led to subjects feeling like they had moved further compared to radial flow (which correspond to optic flow presented in the central field when moving forward). Although these studies were investigating perceived travel distance, they align with earlier research that suggests that peripheral vision may be more effective than central vision in evoking self-motion (Brandt et al., 1973), sway (Delorme & Martin, 1986), and perception of a faster travel speed (Pretto et al., 2009). In the present study, we were not only interested in how the location of visual information would modulate the weightings of the visual contributions to perceived travel distance, but we were also interested in how the integration of visual and non-visual cues might affect the use of peripheral optic flow in self-motion perception. If non-visual cues are weighted higher than visual cues when estimating travel distance (Campos et al., 2010, 2012; Harris et al., 2000; Kopiske et al., 2023), the effects of visual field exposure might diminish when visual and non-visual cues are combined.

One model used to explain the perception of travel distance is the leaky spatial integrator, which accumulates perceived travel distance by integrating over space (Lappe et al., 2007a). There are two tasks that often used to test the perception of travel distance. The first is the Move-To-Target task, in which participants judge travel distances by stopping at the location of a previously seen target. The second is the Adjust-Target task, in which participants adjust a target to indicate the extent of a previous movement. In the Move-To-Target task people tend to make underestimations in which they stop before the previously seen target location, and in the Adjust-Target task people tend to make overestimations in which they adjust the target further away than the actual extent of their previous travel (Lappe et al., 2007a). The leaky spatial integrator model accounts for these seemingly inconsistent mis-estimations of travel distance as resulting from (1) the integration "leaking" as a function of distance moved, and (2) a gain factor involved in transforming visual motion to travel distance (Lappe et al., 2007a). This model can describe behaviour in both the Move-To-Target and Adjust-Target tasks, although few studies have used both tasks to measure perceived travel distance using non-visual cues. In this study, we examined the effectiveness of the leaky spatial integrator model to describe perceived travel distance using visual and non-visual information, both while these sensory cues were congruent and when they were incongruent. We did this by comparing the leaky spatial integrator model to a simple linear model that also fits both the Move-To-Target and Adjust-Target tasks. If there are no significant differences between the two models, we can assume that the “leakage” over distance is negligible. When visual and non-visual cues are congruent, we hypothesize that this decay found over distance may be diminished as well. We investigated the estimation of travel distance when optic flow was presented in the peripheral field compared to the central field. We predicted that, similar to McManus and colleagues (2017), participants would feel that they had moved further when receiving only peripheral optic flow, compared to when receiving optic flow in the full field or in the central field only. We also hypothesized that if non-visual cues were weighted higher than visual cues when estimating travel distance, the peripheral enhancement would diminish when visual and non-visual cues were combined.

## 4.3. Methods

### *Participants*

We collected data from 18 participants (8M, 10F; mean age 20.3 yrs, SD ±2.2). The recruitment period was between April 11$^{st}$, 2024 and September 23$^{rd}$, 2024. Participants were recruited using York's Kinesiology Undergraduate Research Participant Pool and given course credit. All participants had normal or corrected-to-normal vision. All participants gave prior informed written consent and were naive to the purpose of the study. The protocols used in this study were approved by the York Human Participants Review Sub-committee (#e2024-024) and were conducted in accordance with the principles of the Declaration of Helsinki.

### *Equipment*

Visual stimuli were presented on a large-field Edgeless Graphics Geometry display (EGG, Christie, Canada, field of view ±112° horizontally). Participants were strapped into a safety harness (LG 300, LiteGait Training) and walked or stood on a LifeSpan TR5000-DT5 treadmill (see Fig 4.1). Both the display and the treadmill received input from the same computer that was used to generate stimuli. Responses were made using a standard Xbox controller.

**Fig 4.1. Experimental Setup.** Participant stood or walked on a treadmill in front of the large-field Edgeless Graphics Geometry display, while strapped into a safety harness. Room lighting was extinguished during the experiments.

***Stimuli***

Participants experienced optic flow and/or physically walked on the treadmill at 1 m/s. They began either task while immersed in a simulated horizontal corridor (3.04 m tall x 3.04 m wide x 70 m long) displayed on the Edgeless Graphics Geometry screen. The walls of the corridor were white outlined with black edges and textured with 240 randomly placed black dots (radius 0.2 m to provide optic flow information. The block dots disappeared and reappeared at random intervals (0-6 s) and locations within 30 m from the observer's position such that they could not be used as landmarks. In both tasks, the target was a red square (3.04 m x 3.04 m) with a black cross (line width 0.14 m) on it that filled the full corridor (Fig 4.2A). This target square was removed during the optic flow stimulus and only present during distance adjustment (Adjust-Target Task) after the trial or target distance presentation (Move-To-Target Task) before the trial.

During the motion stimulus, participants received optic flow information over either the full field of view where the whole screen was visible (Fig 4.2A), the central field where optic flow was presented only within ±20° (Fig 4.2B), or the peripheral field where optic flow was only presented beyond 90° (Fig 4.2C). These optic flow field of view (FOV) conditions were combined with two sensory conditions: visual only and visual + walking. There was also another sensory condition of blind walking on the treadmill (no visual cues), resulting in a total of 7 conditions. The experiment was programmed in Python 3 with WorldViz Vizard VR toolbox (version 7.0).

**A) Full Field** | **B) Central Field (inside 40 deg)** | **C) Peripheral Field (outside 180 deg)**

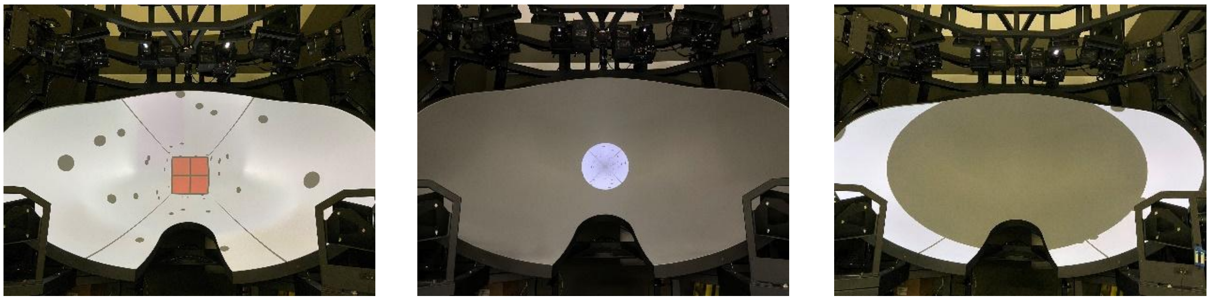


**Fig 4.2. Visual stimuli. A)** On the left is the simulated corridor and target square for the full field display (±112°). The target square was only present for distance responses (Adjust-Target Task) or before the trial (Move-To-Target Task) and was not present during the optic flow stimulus B) In the centre is the central field display (central ±20°). C) On the right is the peripheral field display (beyond ±90°).

***Move-To-Target Task***

Each trial started with a simulated red square target presented at a pre-specified distance in the full-field corridor (Fig 4.2A). Participants pressed a button triggering the target to disappear and simulated motion towards the target's position to commence. For the visual + walking condition, participants experienced optic flow on the screen while walking on the treadmill at the equivalent speed. For the visual-only condition, participants experienced optic flow on the screen while standing stationary on the treadmill. For the treadmill-only condition, participants first saw the target on the screen and then once the button was pressed, the visual display turned grey, and participants started walking on the treadmill. In all cases, participants indicated when they felt their nose had touched the previously seen target by pressing the button.

***Adjust-Target Task***

Participants stood in the same corridor as for the Move-To-Target task. They first experienced simulated movement forward through a pre-specified distance, again created using optic flow and/or by walking on the treadmill. Once they had traveled through the target distance, the motion stopped, and the target appeared at a random position in front of them. Participants then used the joystick on the controller to slide the target back and forth along the corridor until it appeared as far away as the distance through which they felt they had just moved. They pressed a button to end the trial and move on to the next trial.

***Procedure***

After providing informed consent, participants stood on the treadmill and were strapped into the safety harness that surrounded the treadmill, in front of the EGG display (Fig 4.1). After the instructions were explained, participants were given a practice session using the visual + treadmill condition, which included five trials at randomized distances between 5-32m. Once the practice was completed, participants ran the full version of each task.

This study was a within-subjects design such that every participant completed both the Move-To-Target and Adjust-Target tasks. The order in which the tasks were completed was counterbalanced, such that half completed the Move-To-Target first and the other half completed the Adjust-Target task first. Each task consisted of six target distances (5, 10, 15, 20, 25, 32 m), three field-of-view (FOV) conditions (full field, central field only, peripheral field only), and three sensory conditions (visual only, visual + treadmill, treadmill only). In all cases, the simulated self-motion speed and/or treadmill speed was 1 m/s. The sequence of distances presented was randomized to control for any order effects. The tasks were blocked by FOV condition and sensory condition, and the order in which these blocks were presented was randomized between participants. The whole experiment took about 1 hour (30 minutes for each of the two tasks).

### *Data Analysis*

Each participant completed 84 trials ([3 FOV conditions x 2 sensory conditions + 1 treadmill only sensory condition] x 6 distances x 2 tasks). First, an outlier removal was completed. The outlier removal was performed at the group level for each distance in every condition (7 sensory conditions x 2 tasks). Any data less than the 'Lower Quartile - 1.5 x Interquartile Range' or above the 'Upper Quartile + 1.5 x Interquartile Range' were removed. Out of 1552 data points (84 trials x 18 participants), 70 data points were removed.

The raw gains were then calculated for each trial for both tasks. In both tasks, raw gains were calculated by dividing the perceived travel distance by the actual travel distance. In the Move-To-Target task, this translates to:

| | |
|---|---|
| $Gain_{Move\text{-}To\text{-}Target}$ = Target Distance / Self-Motion Distance | (1) |

For the Adjust-Target task, this translates to:

| | |
|---|---|
| $Gain_{Adjust\text{-}Target}$ = Adjusted Target Distance / Self-Motion Distance | (2) |

Perfect performance in both tasks would result in a raw gain of 1. In both tasks, a raw gain greater than 1 would imply that participants felt that they had moved further than the simulated distance. We started by first testing whether any effects of FOV and sensory conditions differed between tasks. Since we did find differences between tasks, we analyzed them separately and did not pool the data from both tasks. We also found a significant difference in variability between the tasks. A Linear Mixed Model (LMM) analysis was then performed on the raw gains for each task (collapsing across distances) using the lme4 (Bates et al., 2015) for R (version 4.3.0). We started with a base model where the fixed-effect structure was chosen as a function of our hypotheses, in which we were interested in the main effects of FOV and sensory condition. We compared this base model to a model that included an interaction term between FOV and sensory condition. The interaction model in this case chooses which interactions exist and ignores the rest. Since the treadmill only condition did not include the FOV conditions, this study was not a crossed factorial design, and therefore the treadmill only condition and FOV interaction would be ignored. Since no significant differences were found between these two models, the interaction term was left out of the final model structure. Given that this study was not a crossed factorial design, we decided to test the main effects of sensory condition and FOV with two separate LMMs and compare the individual levels of each experimental variable against each other using the grand means of the other as intercept. For testing FOV we used the grand means of the sensory condition as intercept. For testing the sensory condition, we used the grand means of the FOV conditions as intercept. The final model structure for the LMM of the raw gains for FOV reads as follows:

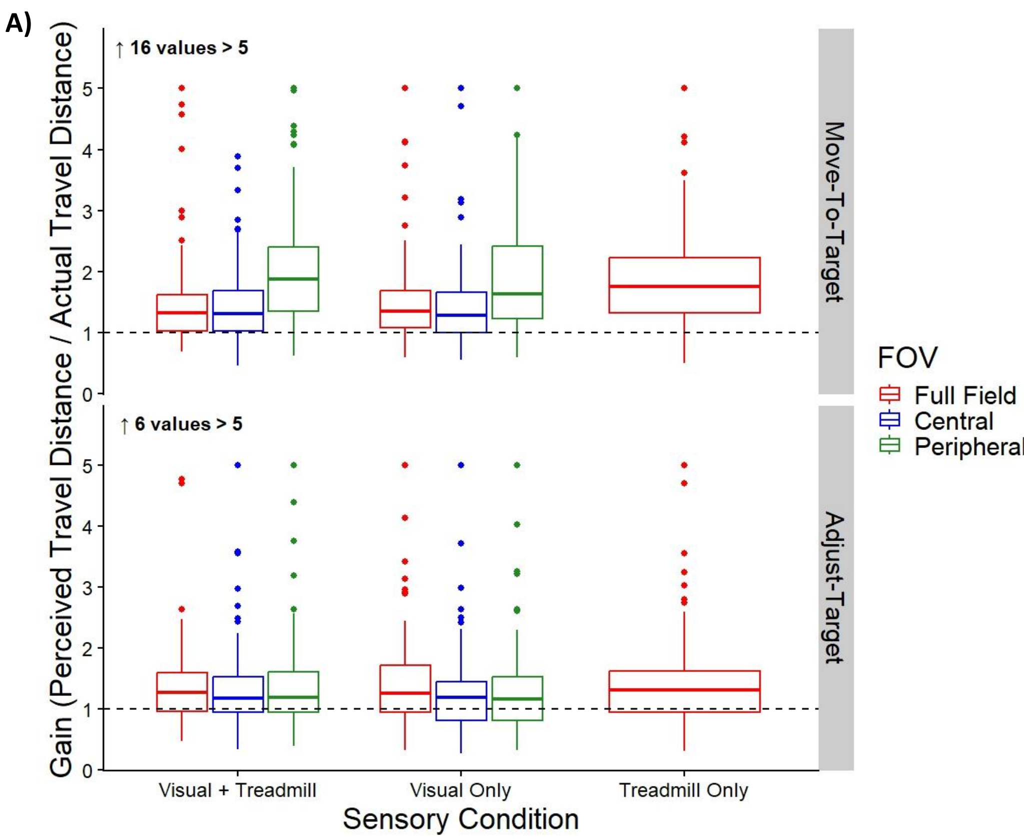
| | |
|---|---|
| Gain ~ FOV + Mean Sensory Condition + (FOV + Mean Sensory Condition \| Participant) | (3) |

The final model structure for the LMM of the raw gains for Sensory Condition reads as follows:

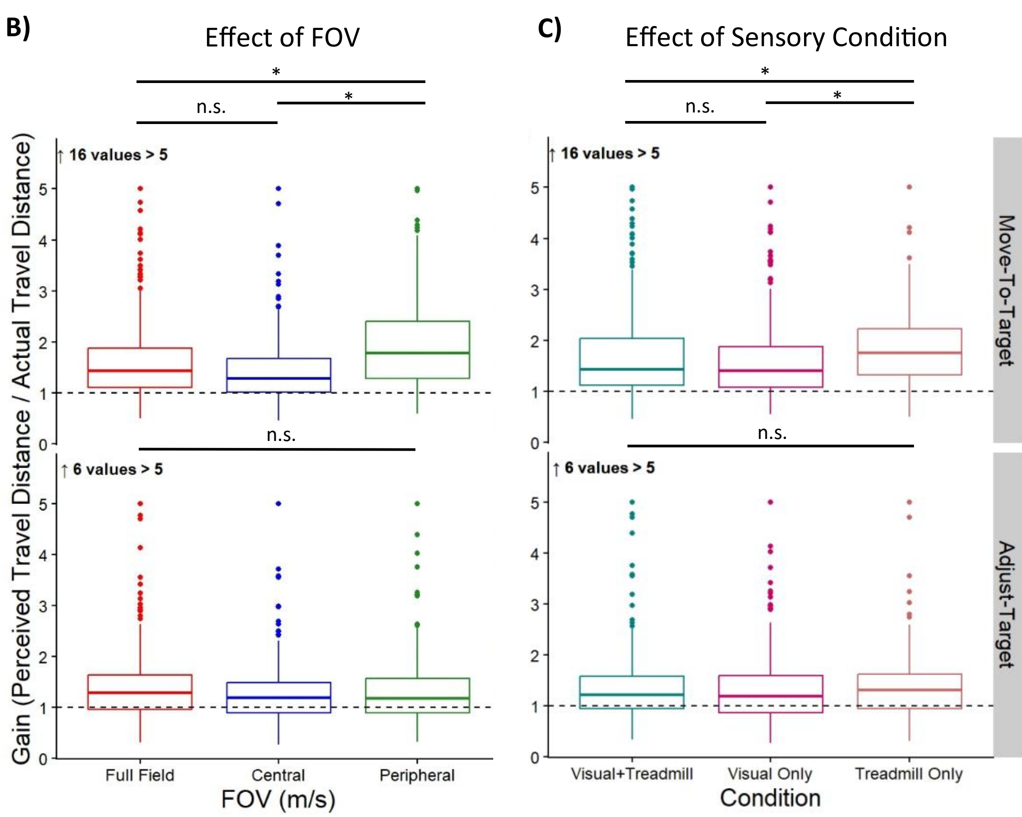
| | |
|---|---|
| Gain ~ Sensory Condition + Mean FOV + (Sensory Condition + Mean FOV \| Participant) | (4) |

To test for statistical significance, we then computed bootstrapped confidence intervals at an alpha level of 0.05 using the confint() function from the base R with the “boot” argument and default settings otherwise. All data was analyzed in R (version 4.3.0). All data and data analysis can be found at (https://github.com/ambikabansal/FOV_Treadmill).

## 4.4. Results



A)
↑ 16 values > 5
↑ 6 values > 5
Gain (Perceived Travel Distance / Actual Travel Distance)
Move-To-Target
Adjust-Target
FOV
Full Field
Central
Peripheral
Visual + Treadmill
Visual Only
Treadmill Only
Sensory Condition

B)
Effect of FOV
*
n.s.
*
↑ 16 values > 5
n.s.
↑ 6 values > 5
Gain (Perceived Travel Distance / Actual Travel Distance)
Full Field
Central
Peripheral
FOV (m/s)
C)
Effect of Sensory Condition
*
n.s.
*
↑ 16 values > 5
n.s.
↑ 6 values > 5
Move-To-Target
Adjust-Target
Visual+Treadmill
Visual Only
Treadmill Only
Condition

**Fig 4.3. Raw Gains.** (A) Box plots of the group raw gains for both the Move-To-Target (top row) and Adjust-Target (bottom row) tasks for each FOV and Sensory Condition. Data plotted here is from the full data set, with the y-axis restricted to gains below 5. The Move-To-Target task had 16 off-chart values. The Adjust-Target task had 6 off-chart values. The middle line represents the median, the boxes extend from the first quartile to the third quartile, the whiskers extend up to 1.5 times the interquartile range, and the outliers are shown as individual points beyond the whiskers. The full field is represented in red (left most), central field in blue (second from left), and peripheral field in green (right most). The black dashed line represents perfect performance (raw gain of 1). (B) Group raw gains collapsed across Sensory Condition to show the effect of FOV condition. (C) Group raw gains collapsed across FOV condition to show the effect of Sensory Condition. The Visual + Treadmill condition is represented in teal (left most), the Visual Only condition in pink (middle), and the Treadmill Only condition in tan (right most).

***Effect of Field-Of-View***

| | Full Field | Central Field | Peripheral Field |
|---|---|---|---|
| Move-To-Target Task | 1.67 ± 0.88 | 1.49 ± 0.75 | 2.12 ± 1.20 |
| Adjust-Target Task | 1.33 ± 0.61 | 1.23 ± 0.54 | 1.23 ± 0.54 |

Table 4.1: Means and standard deviations of the raw gains for the different FOV conditions.

*Move-To-Target Task*

Table 2 shows the results from the linear mixed model for the effect of FOV on the raw gains of the Move-To-Target task. The peripheral condition resulted in significantly higher raw gains than the full-field, or central conditions (see Table 1). However, we found no significant differences between the full-field and central conditions. The raw gains from the Move-To-Target task across FOV conditions are shown at the top of Fig 4.3B.

| | Regression Coefficient | Standard Error | 95% CI (lower) | 95% CI (upper) | Significance |
|---|---|---|---|---|---|

| | | | | | |
|---|---|---|---|---|---|
| Full Field vs. Central | -0.07 | 0.09 | -0.24 | 0.10 | n.s. |
| Full Field vs. Peripheral | 0.52 | 0.14 | 0.24 | 0.81 | * |
| Central vs. Peripheral | -0.59 | 0.13 | -0.85 | -0.34 | * |

Table 4.2: Results from the Linear Mixed Model run on data from the Move-To-Target task with the raw gain set as the dependent variable, with both FOV and Sensory Condition set as fixed effects. This table reports differences in FOV. This table reports unstandardized regression coefficients.

*Adjust-Target Task*

Table 3 shows the results from the linear mixed model for the effect of FOV on the raw gains of the Adjust-Target task. There were no significant differences between the full-field, central field, or peripheral conditions. The raw gains are from the Adjust-Target task across FOV conditions are shown at the bottom of Fig 4.3B.

| | Regression Coefficient | Standard Error | 95% CI (lower) | 95% CI (upper) | Significance |
|---|---|---|---|---|---|
| Full Field vs. Central | -0.10 | 0.05 | -0.21 | 0.002 | n.s. |
| Full Field vs. Peripheral | -0.09 | 0.05 | -0.19 | 0.0004 | n.s. |
| Central vs. Peripheral | -0.003 | 0.05 | -0.009 | 0.19 | n.s. |

Table 4.3: Results from the Linear Mixed Model run on data from the Adjust-Target task with the raw gain set as the dependent variable, with both FOV and Sensory Condition set as fixed effects. This table reports differences in the FOV. This table reports unstandardized regression coefficients.

***Effect of Sensory Condition***

| | Visual + Treadmill | Visual Only | Treadmill Only |
|---|---|---|---|
| Move-To-Target Task | 1.69 ± 0.82 | 1.69 ± 1.05 | 2.05 ± 1.15 |
| Adjust-Target Task | 1.26 ± 0.49 | 1.26 ± 0.61 | 1.36 ± 0.67 |

Table 4.4: Means and standard deviations of the raw gains for the different sensory conditions.

*Move-To-Target Task*

Table 5 shows the results from the linear mixed model for the effect of sensory condition on the raw gains of the Move-To-Target task. The treadmill condition resulted in significantly higher raw gains than the visual + treadmill, or visual only conditions (see Table 4). However, we found no significant differences between the visual + treadmill and visual only conditions. The raw gains from the Move-To-Target task across sensory conditions are shown at the top of Fig 4.3C.

| | Regression Coefficient | Standard Error | 95% CI (lower) | 95% CI (upper) | Significance |
|---|---|---|---|---|---|
| Visual + Treadmill vs. Visual Only | 0.04 | 0.11 | -0.17 | 0.24 | n.s. |
| Visual + Treadmill vs. Treadmill Only | 0.62 | 0.19 | 0.20 | 0.98 | * |
| Visual Only vs. Treadmill Only | -0.57 | 0.22 | -0.99 | -0.16 | * |

Table 4.5: Results from the Linear Mixed Model run on data from the Move-To-Target task with the raw gain set as the dependent variable, with both FOV and Sensory Condition set as fixed effects. This table reports differences in Sensory Condition. This table reports unstandardized regression coefficients.

*Adjust-Target Task*

Table 6 shows the results from the linear mixed model for the effect of sensory condition on the raw gains of the Adjust-Target task. There were no significant differences between the visual + treadmill, visual only, or treadmill only conditions. The raw gains from the Adjust-Target task across sensory conditions are shown at the bottom of Fig 4.3C.

| | Regression Coefficient | Standard Error | 95% CI (lower) | 95% CI (upper) | Significance |
|---|---|---|---|---|---|
| Visual + Treadmill vs. Visual Only | -0.0008 | 0.07 | -0.14 | 0.14 | n.s. |
| Visual + Treadmill vs. Treadmill Only | 0.05 | 0.08 | -0.10 | 0.21 | n.s. |
| Visual Only vs. Treadmill Only | -0.05 | 0.11 | -0.26 | 0.17 | n.s. |

Table 4.6: Results from the Linear Mixed Model run on data from the Adjust-Target task with the raw gain set as the dependent variable, with both FOV and Sensory Condition set as fixed effects. This table reports differences in Sensory Condition. This table reports unstandardized regression coefficients.

## 4.5. Modeling

*Leaky Spatial Integrator Model*

Now that we have analyzed the raw gains to answer our primary research questions, we were interested in how this behaviour could be best modeled. The mis-estimations that occur when estimating travel distance can be modeled as the consequences of a leaky spatial integrator (Lappe et al., 2007a). Few studies have used this model to describe perceived travel distance using visual and non-visual cues. As a secondary objective for this study, we were interested in the effectiveness of the leaky spatial integrator model to describe perceived travel distance using visual and non-visual information, both while these sensory cues were congruent and when they were incongruent.

With this model, a single equation has been shown to account for both the underestimations typically seen with the Adjust-Target task, and the overestimations typically seen with the Move-To-Target task. The model assumes that there is a state variable (the current distance from the start), that is incremented as the movement progresses by a constant gain factor. This state variable is reduced in proportion to a leak factor (alpha) that occurs as the movement progresses. In the Adjust-Target task, the leakage reduces the current estimate of travel distance and in the Move-To-Target task, reduces the current estimate of the target distance. This is why the model predicts that the further one travels, the larger these errors in distance estimates will be. Perfect performance corresponds to a gain of 1, and an alpha of 0 (no leakage). The larger errors at the further distances are represented by a higher alpha. A prerequisite of the model is that alpha cannot be lower than 0.

Equation 5 is used to fit the data from the Adjust-Target task.

| | |
|---|---|
| $p(d_0) = (gain/alpha) * (1 - exp(-d_0*alpha))$ | (5) |

Equation 6 is used to fit the data from the Move-To-Target task.

| | |
|---|---|
| $p(d_0) = (log(d_0+gain/alpha)-log(gain/alpha))/alpha$ | (6) |

P($d_0$) is the perceived distance travelled, “gain” is the gain factor, “alpha” is the leak factor, and $d_0$ is the target distance. These two equations were fitted to the data obtained from both the Adjust-Target task (eq 5) and the Move-To-Target task (eq 6) simultaneously by minimizing the combined sum-of-square errors (see Fig 4.4) to obtain a single estimate of gain and decay for each subject in each condition.

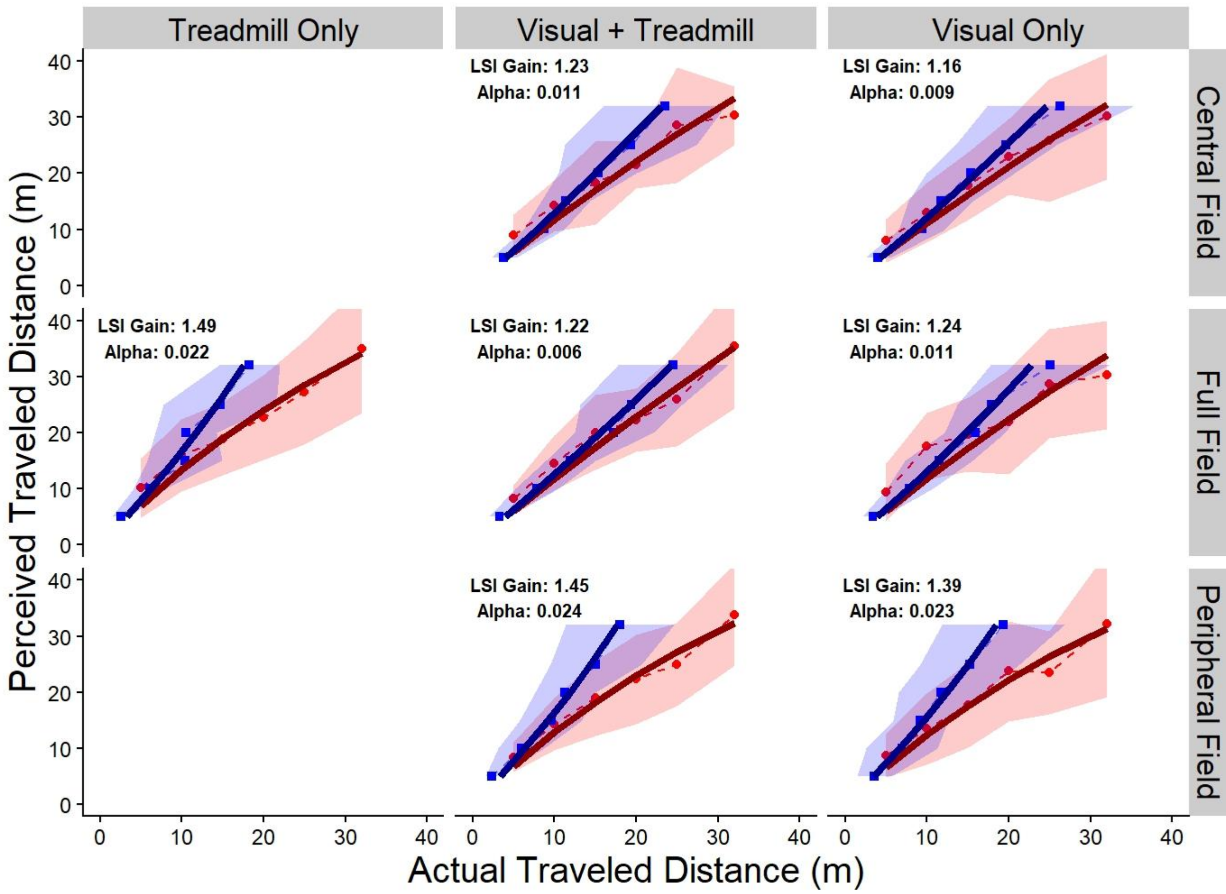



**Fig 4.4. Leaky spatial integrator model fits.** Leaky spatial integrator model fitted to through the mean of all data across all participants. Each column of panels corresponds to a different sensory condition (treadmill only, visual + treadmill, visual only) and each row of panels corresponds to a different FOV condition (central field, full field, peripheral field). The red symbols represent mean data from the Adjust-Target task, and the blue symbols represent the mean data from the Move-To-Target task. The dashed lines represent the raw data averaged across participants for both tasks, whereas the solid lines represent the model fits (dark red for Adjust-Target, eq 5, and dark blue for Move-To-Target, eq 6). The LSI gains and alphas reported here are averaged across participants for each FOV and sensory condition. The shaded areas represent one standard deviation above and below the mean of the raw data. Note that for the Adjust-Target task the response (dependent variable) is plotted on the abscissa, so the error bands extend horizontally rather than vertically around the data points.

In order to examine the effectiveness of the leaky special integrator model, for all sensory conditions, we compared the leaky spatial integrator model fits to a simple linear model that also fits both Move-To-Target and Adjust-Target tasks. Like the leaky spatial integrator model fit, the linear model was fit by minimizing the combined sum-of-square errors from both tasks to obtain a single estimate of gain for each subject in each condition. This resulted in one slope for each Move-To-Target and Adjust-Target tasks. If there were no significant difference between the two models, we could assume that the decay over distance is negligible, and therefore the simpler linear model should be used. For the visual + treadmill condition, there were no significant differences between the two models (likelihood ratio $p > 0.05$). However, the leaky spatial integrator model was a significantly better fit than the simple linear model for the visual only (likelihood ratio $p < 0.01$) and treadmill only (likelihood ratio $p < 0.001$) conditions (see Fig 4.5).

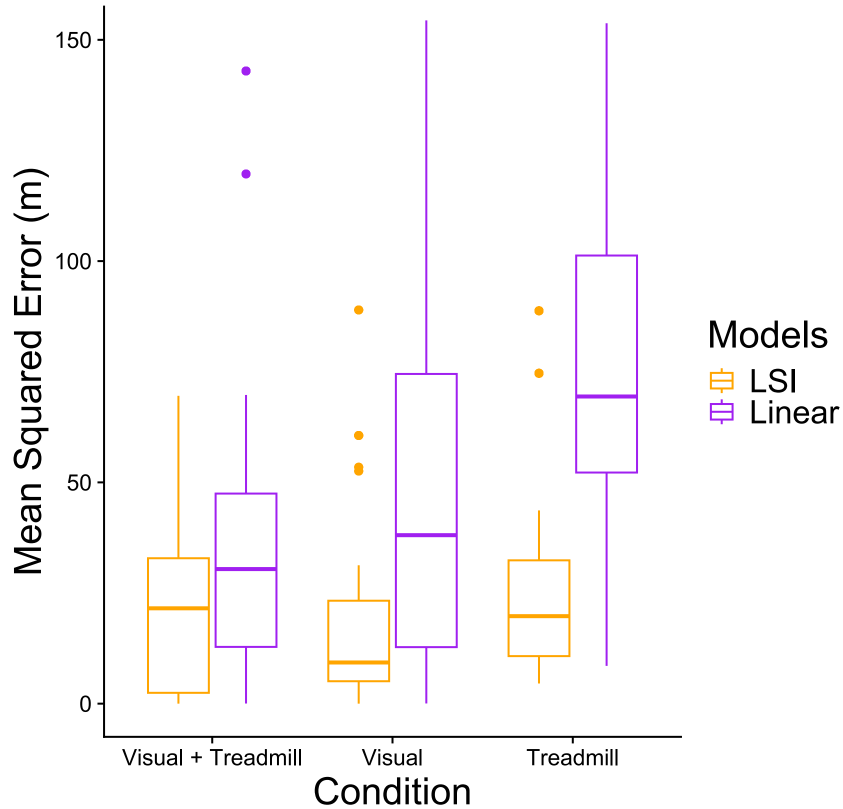



**Fig 4.5. Model comparisons for each sensory condition.** Mean square error for each fit collapsed across FOV conditions. The leaky spatial model fits are in yellow, and the linear model fits are in purple.

## 4.6. Discussion

This study investigated how the presence of both visual and non-visual cues affected the estimation of travel distance when optic flow was presented in the far peripheral field (beyond 90°) compared to when it was presented over the full-field or in just the central field (within ±20°). We found that optic flow presented in the periphery led to people feeling they had moved further than when optic flow was presented to either the central field or the full field in the Move-To-Target task. For the same Move-To-Target task, we found that blind treadmill walking led to people feeling they had moved further than when they were treadmill walking with optic flow information or receiving optic flow information while stationary. However, we found no significant differences between any of our conditions with the Adjust-Target task. The greater variability in the results of the Move-To-Target task compared to the Adjust-Target task imply that different processes may be involved in perceiving travel distance for these different Move-To-Target and Adjust-Target tasks.

### ***Effect of FOV Condition***

Similar to McManus et al.'s (2017) seated observers, our participants responded earlier on the Move-to-Target task in the peripheral FOV condition compared to the full field or central field. This was true for both the visual only and visual + treadmill conditions. However, we found no significant differences between these conditions in the responses to the Adjust-Target task (not tested by McManus et al. 2017). Our findings also align with previous research from our lab that investigated perceived travel distance using laminar and radial optic flow (Harris et al., 2012a). That study found that laminar flow (found only in the peripheral field when moving forwards) led to higher raw gains compared to radial flow (corresponding to optic flow presented in the central field when moving forward). These higher gains found when only peripheral optic flow was available also supports previous research that suggests that peripheral vision may be more effective than central in evoking self-motion (Brandt et al., 1973), and sway (Delorme & Martin, 1986). When experiencing forward self-motion, the angular velocities of objects in a scene are dependent on their position relative to the heading of the observer, their distance and on the speed of the moving observer (Gibson, 1950). Information in the peripheral visual field is associated with higher angular velocities, while information from the central visual field are associated with lower angular velocities. Similarly features on the walls in our stimulus had the smaller egocentric radial distance and thus increased velocity when they were in the coronal plane through the eyes (i.e., at 90º eccentricity). Previous research has found that perceived travel speed was higher when visual information was only present in the peripheral FOV compared to when it was available in the central FOV or over the full field (Pretto et al., 2009; Pretto & Chatziastros, 2006). This remained true when optic flow was provided with a less realistic random dot pattern (Pretto et al., 2009) or with a more realistic driving simulator (Pretto & Chatziastros, 2006). Across both studies, these authors hypothesized that during forward self-motion, the availability of lower angular velocities from the central FOV directly decreases the overall estimation of speed. In the present study, this would explain the lower raw gains in both the central FOV and full field conditions, compared to the peripheral-only FOV. The greater sensitivity to optic flow in the periphery also makes sense from an evolutionary standpoint, as movement seen only in the far periphery may signal a greater threat. This potential danger may have driven the evolution of an increase in our general motion sensitivity in the periphery, thereby enhancing our sensitivity to optic flow. Overestimating movements in the far periphery could provide a survival advantage by promoting more caution.

Although the human field of view is close to ±110° (Strasburger et al., 2011), most research studies investigating the effects of central and peripheral optic flow have not been able to examine optic flow in the far periphery due to their limitations in display size. Here, we were able to examine the less researched far periphery using a large-field Edgeless Graphics Geometry display (field of view ±112°). McManus and colleagues (2017) using this same display, but in a non-stereoscopic mode, found that there was a significant difference between using the far periphery (beyond 90°) and the less far periphery (beyond 40°) when estimating travel distance, which is why we were specifically interested in examining optic flow in the far periphery. This display however did not have stereoscopic depth cues, which would have introduced a conflict between the monocular and binocular depth cues in the central field. Although earlier studies have found stereoscopic cues to enhance vection (Palmisano, 1996, 2002), later research has shown that there is no effect on stereoscopic depth cues on estimating travel distance (Frenz et al., 2007). Although binocular cues would not have played a role in the far periphery which is only monocularly visible, this disparity between monocular and binocular depth cues in the central field could have also contributed to the differences we see between the FOV conditions.

### *Effect of Sensory Condition*

We found that for the Move-To-Target task, blind treadmill walking led to higher raw gains than treadmill walking with visual information or when physically stationary viewing visual information alone. However, we found no significant differences between the visual +

treadmill condition and the visual only condition. We also found no significant differences with the Adjust-Target task. In the treadmill only condition of the Move-To-Target task, where we find larger raw gains, the target distance was presented visually, and participants were required to transform that visual distance information into treadmill walking distance. In the visual only and visual + treadmill conditions, the visual motion information could be used to estimate the visual target distance. Previous research has shown that a visually presented target can be more accurately matched when making visual travel distance estimates, compared to when making estimates using a passive physical movement (Harris et al., 2000; Israel et al., 1993). This is true for both short (Israel et al., 1993) and long travel distance estimates (Harris et al., 2000). Our findings from the Adjust-Target task also align with Sun and colleagues (2004), who found no differences in travel distance estimates between isolated visual only and body-based only conditions and sensory combined conditions. These findings are however contrary to previous research that has provided evidence that body-based cues can be weighted higher than visual cues when estimating travel distances using active physical movement, both when free walking (Campos et al., 2010, 2012) and walking on a treadmill (Kopiske et al., 2023). The current study taken in combination with the previous literature suggests that the sensory contributions to the perception of travel distance might be task and stimulus dependent. Previously, our group has also investigated the visual and vestibular contributions to the perception of travel distance during long-term exposure to microgravity using the Move-To-Target task (Jörges et al., 2024a). We found that there were no significant differences between the perception of travel distance on Earth compared to in space during long-term exposure to microgravity. Although, we did find small differences in perceived travel distance on Earth when completing the task in a supine position compared to a seated one. This study also provides mixed evidence as to the sensory weightings and sensory integration when perceiving travel distance.

Lappe's leaky spatial integrator model has been used to describe behavior in both the Move-To-Target and Adjust-Target tasks (Lappe et al., 2007a). Although a previous study (Lappe & Frenz, 2009) used the leaky spatial integrator model to explain the perception of travel distance when walking and receiving optic flow information, this study did not compare the model to a simple linear fit. Lappe and Frenz (2009) showed that the errors in travel distance estimates in the real world were similar to the estimations made in virtual environments, although they had participants free walking instead of treadmill walking like we did here. It has also been found that the leaky integrator model was not the best at modeling behaviour when moving in non-forward directions (backward, up, down) (Bansal et al., 2024). Here, we show that the leaky spatial integrator model can be used to model data from blind treadmill walking and visual only conditions, but its decay was not consistent across conditions, and it does not model our results significantly better than a simple linear fit when modeling data from our visual + treadmill conditions. This implies that when visual and non-visual cues are integrated, the decay that is found over distance (Lappe et al., 2007a) and time (Bansal et al., 2024) tends to disappear. Adding congruent treadmill walking to the optic flow information introduces step integration, which may contribute to this diminished spatial decay. Congruent visual and non-visual information may also allow for continuous calibration that rectifies some of the sensory conflicts associated with a virtual reality display that may compound over distance and time. This should be taken into consideration when modelling the perception of travel distance under these multisensory conditions.

### *Conclusions*

These findings support the idea that when estimating travel distance, non-visual cues may not be weighted higher than visual cues. These findings also highlight the importance of the far periphery in self-motion processing. However, the differences in perceived travel distance were only found in the Move-To-Target task and not in the Adjust-Target task, which implies that different processes may be used to estimate travel distance in these two Move-To-Target and Adjust-Target tasks.

# CHAPTER 5: General Discussion

This dissertation examined the perception of travel distance using visual and non-visual self-motion cues. Self-motion perception, and accurate navigation, is essential for our survival. As mentioned in Chapter 1, path integration requires both direction (heading) and distance components. Many who have studied the perception of self-motion have focused on heading perception. The perception of travel distance has been much less studied, and it is travel distance that I focus on in this dissertation. In all the experiments across this dissertation, I use both the Move-To-Target and Adjust-Target tasks to get estimates of travel distance. In Chapter 2, I demonstrated that, as I hypothesized in Chapter 1, the perception of travel distance depends on the speed and direction of self-motion. In Chapter 3, I used a series of four experiments to test how the characteristics of a virtual environment affect the perception of travel distance through it. I originally predicted that the variability in travel distance estimates we see across studies could be a result of the different virtual environment used. Contrary to what I hypothesized however, in Chapter 3 I show that many characteristics of a virtual environment (structure, naturalism, colour) in fact do not affect the perception of travel distance through it, and that travel distance can still be reliably estimated even with limited optic flow information. Therefore, this question of where the variability across studies comes from remains open. In Chapter 4, I examined how integrating non-visual cues may contribute to the optic flow from different visual fields. Originally, I hypothesized that the peripheral enhancement seen in travel distance estimates would diminish when visual and non-visual cues were combined. Again however, contrary to my hypothesis, I found that the high sensitivity to optic flow in the far periphery is a general feature of perceptual odometry even when integrating non-visual cues with visual cues.

Although it was not the focus of my dissertation, I also found large differences in travel distance when using both the Move-To-Target and Adjust-Target tasks. Though more research needs to be done to fully understand these differences and the different processes involved in these two tasks. Together, my studies contribute to our overall understanding of our perception of travel distance and aid in our ability to test this odometic system.

## 5.1. The Leaky Spatial Integrator Model

One common model used to describe the perception of travel distance is the leaky spatial integrator model. The leaky spatial integrator model predicts that the distance traveled for a given target distance can be described by a gain factor along with a distance-dependent decay factor where, for each "step" a person takes there is a decrease in the remembered distance that they still must travel (for formulas, see 'Modeling' sections of Chapter 2 and 4). This decay results in a non-linear performance 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 Chapters 2 and 4, I fit my data using this model. This model assumes that the perception of travel distance requires an integration over space, but in Chapter 2, I propose that it might also require an integration over time as well. The findings described in Chapter 2 provide evidence that the decay factor may be time-dependent as well as distance-dependent. In other words, it may not just be the further you move the worse you are at being able to gauge the distance travelled, but it may also be that the longer you are moving the worse you are as well. There are other studies which have found similar differences in travel distance estimates when moving participants at different visual speeds (Redlick et al., 2001; Harris et al., 2012; McManus et al., 2017) and different accelerations. In Chapter 2, I also show that the leaky spatial integrator model can be used to model the perception of travel distance in the backward, upward, and downward directions, although the data from these directions are a significantly less good a fit than they are when modelling the forward direction. This study further suggests the model should be expanded to include a speed term and should be modified to better model self-motion perception in non-forward directions. I am currently working with the creator of the leaky spatial integrator model, Dr. Markus Lappe, on potentially modifying the leaky spatial integrator model. In Chapter 4, I show that the leaky spatial integrator model can be used to model data from blind treadmill walking and visual only conditions, but its decay is not consistent across conditions, and it does not model my results significantly better than a simple linear fit when modeling data from the visual + treadmill conditions. This implies that when visual and non-visual cues are integrated, the decay that is found over distance (Lappe et al., 2007a) and time (Bansal et al., 2024) tends to disappear and the results become more linear. Adding congruent treadmill walking to the optic flow information introduces step integration, which may have contributed to the diminished spatial decay. When using virtual reality, there is a sensory conflict where visual cues send information that you are moving but body-based cues, such as vestibular and proprioceptive cues, are sending information that you are stationary. Congruent visual and non-visual information, as seen in the visual + treadmill condition, may also allow for continuous calibration that rectifies some of the sensory conflicts associated with a virtual reality display and that may compound over distance and time. Such continuous recalibration should be taken into consideration when modelling the perception of travel distance under multisensory conditions.

## 5.2. Variability in the Data

Across studies, I have found a high variability in travel distance estimates (see Fig 5.1). This is true for the three studies that comprise this dissertation, and for others studying the perception of travel distance (e.g., McManus et al., 2017; Harris et al., 2012; Bury et al., 2021). Originally, I hypothesized that some of this variability in travel distance estimates may be explained by the variation in virtual environments used across studies. We have found differences between the perception of travel distance, where participants felt like they had moved further, when using a virtual corridor (Bansal et al., 2024) compared to studies using less structured environments (e.g., Bury et al., 2020; McManus & Harris, 2021). These "less structured environments" included a star field stimulus and a "lollipop field". The star field environment is the least structured because it contained no sense of orientation, and although the "lollipop field" provided orientation cues, the objects in both environments were arranged with no sense of systematic organization and these environments were thus considered more abstract and less realistic than a virtual corridor. In Chapter 3, I investigated how the characteristics of a virtual environment may affect the perception of travel distance through it. Though since I find that manipulating many of the characteristics of a virtual environment (structure, the ground floor, naturalism, colour) did not affect travel distance estimates, the question of why we find high variability across studies remains open.

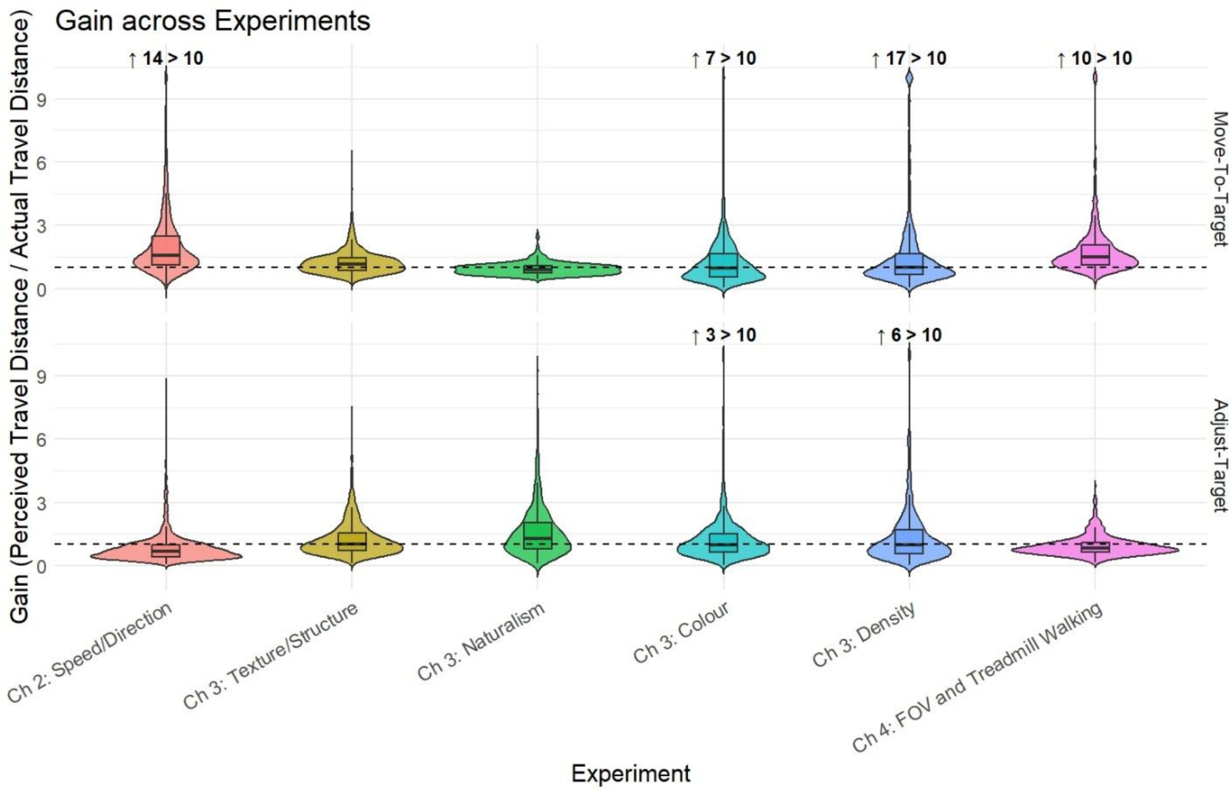



**Fig 5.1. Distribution of Gains Across Experiments.** Data from the Move-To-Target task is on top and data from the Adjust-Target task is on the bottom. Perfect performance corresponds to a gain of 1indicated by the dashed horizontal lines in each graph. The gains are clipped at a gain of 10.

The use of stereoscopic cues and whether the display was dynamic might lead to better depth perception for near (stereopsis) and far (motion parallax) target distances, which might lead to variations in gain. In Chapter 4, where I use York University's large-field edgeless graphic display, I did not have stereoscopic cues. The stereoscopic glasses that would allow us to include these cues, also limited the peripheral field-of-view unacceptably. Given the fact that I was comparing the effect of visual field, I made the decision to not use these glasses. Though these stereo cues could have led to better distance perception, and therefore more accurate estimates of the travel distance required. Research using virtual reality to investigate self-motion perception is also mixed as to whether the visual display is head-fixed (the visual environment seen by the participant does not move with the participant's head movement) or world-fixed (the visual environment moves with the participants head). Since the data in Chapter 2 were collected remotely, I decided to make the virtual environment head-fixed to ensure all participants received the same visual stimuli. Though, to make the visual displays more naturalistic and introduce motion parallax, I made the virtual environments world-fixed in Chapters 3 and 4. These differences in depth cues could have also introduced some variability in travel distance estimates. I also did not limit where participants looked during a trial for any experiment. In all experiments, participants were asked to keep their head straight and try to not fixate on any one area for too long. Since I did not monitor eye movements I could not confirm where my participants were actually looking. Thus, potential differences in participants' eye movements could have contributed to the large variability I see across studies.

Another potential contributor to the variability in our data could be individual demographic differences. For example, I did not control for how much VR experience participants had. We could predict that if one had more experience visually moving through virtual environments, that they could be more accurate at perceiving their travel distance through it. I also did not control for any gender or social factors, including socioeconomic status, sports experience, music experience, etc. Generally, the large variability in gains we see across studies imply that there are some clear individual differences in perceiving travel distance, though more research needs to be done to understand what these individual differences may be.

## 5.3. Vection

Vection is the illusion of self-motion. Many researchers studying self-motion perception have used vection as a measure. While vection can indicate whether someone feels like they are moving, it does not necessarily reflect how visual motion cues are used to judge self-motion. For example, people can accurately estimate travel distance without experiencing vection or the illusion that they are actually moving. This distinction is supported by research showing that vection speed increases in microgravity (Oman et al., 2003; Young & Shelhamer, 1990), yet travel distance judgments remain unchanged (Jörges et al., 2024a). Similarly, while optic flow speed has been shown to influence vection (De Graaf et al., 1990), evidence is mixed regarding its effect on perceived travel distance (Bansal et al., 2024; Frenz et al., 2007; Harris et al., 2012; Lappe et al., 2007; McManus et al., 2017). Although it might seem intuitive that vection and travel distance perception should be linked, these studies suggest otherwise. In other words, you can perceive self-motion without feeling like you are moving. Optic flow may be interpreted not only as self-motion through space, but alternatively as the environment moving past a stationary observer. While many virtual reality studies have examined how visual scene components influence the perception of vection (Bubka & Bonato, 2010; Seno et al., 2010; Tamada & Seno, 2015; Vaziri-Pashkam & Cavanagh, 2008), no one has directly tested their impact on perceived travel distance. Across Experiments 1–3 of Chapter 3, I found no significant effects on travel distance estimates when manipulating various virtual scene components such as structure, naturalism, or colour. Thus, I show here that these differences found in vection do not translate to travel distance estimates. Though, one limitation is that we did not test for whether participants experienced vection in any of my experiments.

## 5.4. Interaction between Speed, Time, and Distance

The perception of travel distance requires one to integrate travel speed with the time spent moving. As mentioned in Section 5.1., my findings from Chapter 2 imply that there is a decay of perceived travel distance over time, as well as over distance. One key variable to take into consideration is memory. In both the Move-To-Target and Adjust-Target tasks, participants must "remember" either the target location (in the Move-To-Target task) or their previous travel distance (in the Adjust-Target task) to accurately perform these tasks. The longer they move, the more likely it is that their memory of the target location and travel distance would fade. Therefore, this decay factor might be a decay in memory as a function of time and not just of distance. In a future study, I could examine whether it was possible that instead of continuously using optic flow cues, participants could instead be at least partially relying on a time estimate. If so, the participant would estimate the distance to the target object and the speed they are moving based on the optic flow cues provided and could then use this to estimate when they should stop and could just ignore the rest of the stimulus. In a future experiment, participants could attempt to perform both the Move-To-Target and Adjust-Target tasks without receiving optic flow information at all (i.e., no information on the speed of movement), where the only information they could use was time. With this data, I could then see whether participants may possess a default speed prior of how fast they feel like they are moving using only their imagination. Previous research has shown that humans carry an implicit default expectation, or *prior,* about speed in both perception and action. This prior is plastic, continuously shaped by experience, and influential in how we interpret sensory input and execute movements. In vision, it has been shown that observers have a default prior that objects move slowly, which biases motion perception under uncertainty (Sotiropoulos et al., 2011). Crucially, repeated exposure to faster stimuli can shift this prior, leading to long-lasting changes in perceived motion direction. In locomotion, it has been demonstrated that walking speed and prior practice affect distance estimation when walking without vision, suggesting that the temporal dynamics of movement are internally represented and that prior experience calibrates these representations (Elliott, 1987). Extending this to motor control, Hammerbeck et al. (2014) found that after training at either fast or slow speeds, participants' subsequent reaching movements were biased toward the training speed, even under new task constraints. This reflects a habitual, modifiable prior for preferred movement speed. This future line of research would examine whether there might be a speed prior when estimating travel distance.

One confounding variable to be taken into consideration when examining the relationship between travel time and travel distance is participant boredom. Like other cognitive variables, such as effort (Proffitt et al., 2003), we can assume that the more bored one is, the longer one feels like they have moved. This would just be the beginning of examining the integration of travel speed and time in the perception of travel distance. In all three studies, I visually moved participants at a constant velocity. Although not seen in the real world, one way of interpreting the optic flow information I provided is not just experiencing movement through the world, but it could also be interpreted as remaining stationary while the world moves past. In this scenario, our Move-To-Target task could be interpreted as you remaining stationary while the target location was moving closer to you.

As mentioned earlier, estimating travel distance requires the integration of travel speed and travel time. For the Move-To-Target task, you must first perceive the distance of the target before beginning the movement, and in the Adjust-Target task you must perceive the distance of the target you are adjusting. In other words, both tasks require an extra component on top of travel speed and travel time, which is distance perception. During my PhD, I was part of collaborative project in which we investigated the perception of travel distance (Jörges et al., 2024a) and distance perception (Jörges et al., 2024b) in astronauts in long term microgravity, and on earth. We found that there were no significant differences between the perception of travel distance on Earth compared to in space during long-term exposure to microgravity. In the second experiment, we performed a psychophysics task investigating the perception of size and distance, where participants had to respond to whether a virtual square was larger or smaller than a reference stick (Jörges et al., 2024b). For both controls and astronauts, the virtual square had to be set larger to appear the same size as the reference stick. If participants underestimate their initial distance to the target, they should also scale down the distance to other objects in the environment that induce optic flow (such as the walls or stars in our experiments). Any biases in distance perception should thus cancel out.

## 5.5. Neurophysiology of Travel Distance Perception

As we navigate through space, place cells in the hippocampus become active at specific locations, forming an allocentric (world-centered) map that helps track our position (O'Keefe & Dostrovsky, 1971; O'Keefe & Nadel, 1978). These cells respond to local sensory cues (e.g., sights, smells) and even distant landmarks. Some are influenced by the direction the individual faces, though head direction cells are primarily responsible for encoding orientation. These place cells depend on both visual and vestibular input, and in rodents, respond only to horizontal directions (for review, see Ekstrom et al., 2018). As one moves, different place cells activate in their respective "fields," collectively creating a cognitive map of the space. The medial entorhinal cortex also contains grid cells that fire in a regular, periodic pattern across environments, forming a metric system for spatial navigation. Grid cell activity is thought to be crucial for odometric estimation, as their firing reflects accumulated movement and displacement (Doeller et al., 2010).

Research on self-motion perception has systematically advanced our understanding of how vestibular signals are transformed across neural systems to support perception and action. Foundational work by Volker Henn demonstrated how semicircular canal and otolith inputs are integrated in the vestibular nuclei and cerebellum to stabilize gaze and orientation during both rotational and translational motion (Henn, 1988). David Robinson has also developed influential computational models of the oculomotor system and the neural integrator, showing how vestibular inputs are converted into motor commands that ensure accurate gaze stabilization and spatial constancy (Robinson, 1968). Building on this foundation, others have extended the scope of vestibular research into cortical domains, identifying how vestibular and visual inputs converge in parietal and frontal eye fields to support not only reflexive stabilization but also spatial perception, attention, and voluntary eye movement control (Bremmer et al., 1999; Goldberg & Bruce, 1990). This work provided a bridge from basic reflex pathways to higher-order cortical processes of self-motion perception.

More recent advances have emphasized multisensory integration and context-dependent coding. Dora Angelaki and colleagues demonstrated that vestibular, visual, and proprioceptive signals are combined in a statistically optimal manner, consistent with Bayesian principles, within cortical and cerebellar circuits to generate robust estimates of heading and self-motion under conditions of sensory noise and conflict (Angelaki et al., 2009; Gu et al., 2008). Kathy Cullen showed that vestibular signals in brainstem and cerebellar neurons are dynamically modulated depending on behavioral context, enabling the system to distinguish between active, self-generated movements and passive, externally applied perturbations (Brooks & Cullen, 2009;

Cullen, 2012). Together, these contributions reveal a hierarchical framework in which vestibular signals are transformed from reflexive motor commands into multisensory estimates of self-motion that inform perception and guide action. Although much is now understood about how vestibular and visual cues are integrated for self-motion perception, the specific neural substrates of perceived travel distance remain largely unexplored.

At the cortical level, studies by Frank Bremmer and Charles Duffy have further detailed how self-motion cues are represented in parietal and temporal areas. Bremmer investigated how areas like the ventral intraparietal area (VIP) and medial superior temporal area (MST) of the macaque brain encode different aspects of optic flow (e.g., expansion, rotation) (Bremmer, 2005; Bremmer et al., 2000; Duffy, 1998) and how this supports judgments of heading direction and motion through space (Bremmer, Duhamel, et al., 2002). Neuronal responses in MST and VIP have been shown to accumulate over time during sustained motion stimulation (Duffy & Wurtz, 1997). This suggests a potential mechanism for temporal integration, which is essential for estimating travel distance. VIP and MST neurons have also been shown to be multisensory, meaning they respond not just to visual motion, but also to inertial motion from vestibular input (Schlack et al., 2003). These neurons combine visual motion and vestibular acceleration signals to build a coherent sense of movement. VIP integrates visual and vestibular input (Bremmer, Klam, et al., 2002), and many neurons here have been found to be tuned to linear translation, not just rotation (Bremmer et al., 1999; Schlack et al., 2002). Much of Frank Bremmer's neurophysiological work on self-motion perception has been done on macaque brains, though in one study he did show strong evidence for structural and functional homologies between the human and macaque brains in how multisensory motion information is processed (Bremmer, Schlack, Duhamel, et al., 2001). This study confirmed that ipsilateral human intraparietal sulcus

(IPS) is functionally analogous to macaque VIP, supporting its role in perceiving motion from multiple sensory sources (Bremmer, Schlack, Shah, et al., 2001). Cells in the depth of the intraparietal sulcus (IPS) responded robustly to visual, auditory and tactile motion, indicating true multisensory motion processing (Fig 5.2). Motion-related activation was also observed in ventral premotor cortex and lateral inferior postcentral gyrus, suggesting these areas integrate motion cues across senses, much like in non-human primates. Although these studies all focus on self-motion perception, no one has investigated the brain areas involved specifically in perceived travel distance.

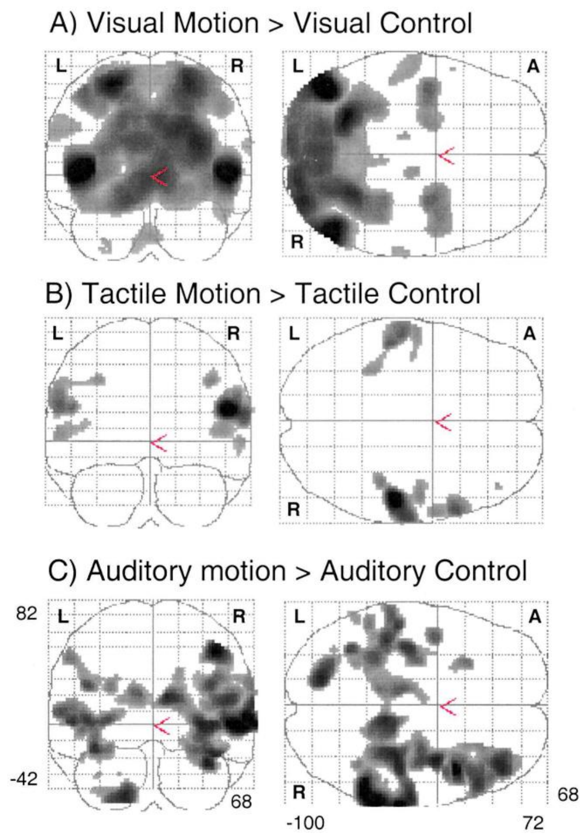



**Fig 5.2.** from Bremmer et al., 2001. Modality-Specific Activation Pattern (A–C) The activation patterns (motion stimulus response minus no motion control response) for visual (A), tactile (B), and auditory (C) stimulation. Visual motion information increased neural activity in the primary and secondary visual cortex, the lateral temporooccipital region, posterior parietal cortex, lateral inferior postcentral cortex, and lateral premotor cortex bilaterally (A). Tactile motion information showed increased neural activity in the primary and secondary somatosensory cortex bilaterally,

posterior parietal cortex bilaterally, and right lateral premotor cortex (B). Auditory motion stimulation led to increased neural activity in primary and secondary auditory cortex, posterior parietal cortex, lateral premotor cortex bilaterally, and left cerebellar hemisphere (C).

## 5.6. Limitations

One potential limitation that may have caused inconsistent and less reliable data is the nature of our participant groups. I used York University's Undergraduate Participant Pool (URPP) to recruit participants for both Chapters 3 and 4. These are all subjects who received class credit for their participation. Anecdotally, I can say that there was a wide range of motivation across participants, and this likely affected the variability in our data as well. The URPP also provides only a limited selection of the population of about 18-22 years old and from a restricted range of backgrounds. In Chapter 2, data were collected fully remotely due to the COVID-19 lockdown. Although there were clear instructions sent before with a combined practice done beforehand, there was no way of validating whether the participants were completing the tasks correctly.

Although this dissertation focuses on providing data-driven research to understand our perception of travel distance, it is natural to think how this research may be applied to scenarios in the real world. One limitation is that all of these experiments in this dissertation were performed using VR. Another limitation of applying this research is the fact that these tasks do not exist in the natural world. In the Move-To-Target task, the target disappears before translational movement in that direction occurs. Again, in the real world, objects would not disappear as you approach them. In the real world, you would have visual information as to the distance between yourself and the object. Although, as described in Section 5.2., this would be a Time-To-Contact task, in which the observer can use the optical variable tau to understand where to stop before reaching the object. This would not be a task in which I could evaluate their perception of travel distance, specifically. Another aspect of our tasks that does not exist in naturally is the fact that participants are only moving visually (for Chapters 2 and 3). Although "moving only visually" occurs in video games, in the natural world, the perception of travel distance is a multisensory process, meaning that you are integrating information from all your different senses into understanding how far you have moved. Even in Chapter 4, where I introduce non-visual cues from treadmill walking, this is still not a truly natural movement. Participants are harnessed in place and therefore are not receiving vestibular inputs consistent with forward movement. Although the Move-To-Target and Adjust-Target tasks do not exist naturally, that was not the primary goal in the design of these tasks. These tasks are specifically designed to test perceived travel distance, and I believe that they are still valid tests to do just that.

## 5.7. Future Directions

The line of research examined in this dissertation can be continued in many different directions. When it comes to modelling the perception of travel distance, the leaky spatial integrator model is clearly still a strong way of understanding the non-linear behaviour of estimating travel distance. Though as mentioned in Section 5.1., the model fits in Chapter 2 provide evidence for the fact that the leaky spatial integrator model should be modified when modelling travel distance estimates in non-forward directions. In Chapter 2, I simulated the visual experience of moving participants in the forward, backward, upward, and downward directions. In future studies, I would like to examine self-motion in the left and right directions, as well as the angles in between. In the forward and backward directions, the pattern of optic flow is radial, and the pattern of optic flow when moving left and right is similar to that of moving upward and downward in the sense that the visual motion information is predominantly laminar orthogonal to the direction of travel (see Section 1.1., Chapter 1). It would be interesting to see how left/right travel distance estimates might differ when experiencing lateral self-motion compared to up-and-down. Investigating the angles in between would allow us to understand how one integrates both radial and laminar optic flow when perceiving travel distance. Understanding self-motion perception when moving in the directions, beyond the ones examined in Chapter 2, can help us model perceived travel distance when moving in all directions. As it stands currently, the leaky spatial integrator model assumes an integration over space, though our findings from Chapter 2 show that there is likely an integration over time as well. We are currently working on modifying the model to include a speed term. In Chapter 4, I show that the leaky spatial integrator model can be used to model data from blind treadmill walking and visual only conditions, it does not model my results significantly better than a simple linear fit when modeling data from the visual + treadmill conditions. Future research should apply and test these modifications to the leaky spatial integrator model so that it can generalize to include these different scenarios.

Many researchers that have tested the perception of travel distance have used a version of either the Move-To-Target (where participants estimate travel distances by stopping at the location of a previously seen target) or Adjust-Target tasks (where participants adjust a target to indicate the distance of a previous movement). In all experiments across the studies described in this dissertation, I use both the Move-To-Target and Adjust-Target tasks to test the perception of travel distance. Though in all cases, I find differences in travel distance estimates between these two tasks. This implies that different processes might be used to estimate travel distance in the Move-To-Target and Adjust-Target tasks beyond those that are captured by the LSI model. The mixed findings of travel distance judgements we find could be a result of differences in the tasks being used to measure perceived travel distance. When interpreting results between studies, the method used to measure perceived travel distance must be taken into consideration. Clearly, there are different processes involved in making these judgements during these two tasks, though more research needs to be done to fully understand these perceptual differences. In a future study, we could use a 2-Alternative-Forced-Choice task that included both the Move-To-Target and Adjust-Target as a way of seeing where these differences may be. This task would involve first showing participants the target in front of them (as done in the Move-To-Target task), then moving them to a specific distance (as done in the Adjust-Target task), and then asking them in which condition they felt like they moved further. This would also be done in the reverse order as well, to account for any order effects. To gain some more clarity, a future neurophysiological study could also investigate the differences in the specific brain processing used to estimate travel distances in these two tasks. This series of neurophysiological studies would start with first understanding the exact brain areas involved in perceiving travel distance. As mentioned in Section 5.4., Frank Bremmer has done a lot of work to understand the cortical brain areas involved in self-motion perception, although no one has studied the brain processes involved in perceived travel distance specifically. After understanding the general brain areas involved, it would be interesting to investigate whether these behavioural differences I see between the Move-To-Target and Adjust-Target tasks translate to the neural processes happening in the brain as well. Along similar lines of understanding the brain processes involved in perceiving travel distance, a future study should also investigate how the perception of travel distance is altered with loss of vision or in the presence of vestibular disorders. If the perception of travel distance is altered with loss of vision or vestibular disorders, then it would also be worthwhile knowing whether perceived travel distance can be recalibrated using a training paradigm. Another future study should investigate how age affects the perception of travel distance. Together, this series of experiments will allow us to understand plasticity the perception of travel distance.

Moving in the real world is multisensory process, though this dissertation focuses mainly on the visual component to self-motion perception. In Chapter 4, I examine how integrating walking may affect the optic flow processing in different areas of the visual field. I found that a high sensitivity to optic flow in the far periphery is a general feature of perceptual odometry even when integrating non-visual cues with visual cues. Here, I used a treadmill to get participants to physically walk in place while receiving optic flow information. Though participants were not really getting vestibular cues consistent with moving forward. A future study could use a longer conveyer belt and have participants move more naturally while receiving both proprioceptive and vestibular cues. A conveyer belt would allow for the experimental control of manipulating walking speed. Though to get more ecological validity, we could also have participants walk in the real world, either controlling for the visual stimuli using VR, or in an open field as Lappe & Frenz (2009) did. As mentioned earlier, virtual reality leads to a sensory cue conflict where participants visually see that they are moving, though they are not receiving any body-based cues that they are moving. In Chapter 2, I assessed the effect of *visual* self-motion direction on travel distance estimates. Though, the role of the missing multisensory components on this question remains open. In future studies, one could use an omnidirectional treadmill (a treadmill where participants can walk in all directions) to assess how these effects of moving in different directions might change travel distance estimates when sensory cues are congruent versus incongruent (Fig 5.3). Again, an omnidirectional treadmill would allow for the experimental control of manipulating walking speed. One clear distinction that should be born in mind when interpreting the studies mentioned above is whether participants are moving actively (a movement initiated by the participant) or passively (movement initiated by an external force). A future line of research should investigate how active versus passive self-motion affects perceived travel distance.


**Fig 5.3.** from Ekstrom et al., 2018. Example of an omnidirectional setup, with an HMD to control the visual stimuli.

In Chapter 3, Experiment 4 was conducted as a means of understanding why I did not find differences in perceived travel distance between these different virtual environments. I thought that the manipulations I tried over the first three experiments were not strong enough to overcome the fact that there was still enough optic flow information to accurately make these judgements. To test this, I manipulated the density of stars in a starfield environment. Our results show that travel distance can still be accurately estimated with very little optic flow information, meaning that there may be a ceiling effect with how much optic flow is needed to accurately perceive travel distance. In a future study, we could add other movement cues e.g., a starfield in which just more than 50% of the dots obey the optic flow rules and the other just less than 50% are moving in the opposite direction. Although our study in Chapter 3 shows that little optic flow is needed to accurately estimate travel distance, this new study would allow us to titrate exactly how much optic flow is needed. I predict this is why I do not find significant differences between any conditions in my first three experiments of Chapter 3. The minor manipulations I made between structure, naturalism, and colour conditions did not integrally alter the environment enough to modulate the perception of travel distance because there was always enough optic flow information to make accurate judgements of travel distance. As mentioned earlier, a future study should also examine the relationship between travel distance and travel time by administering the Move-To-Target and Adjust-Target tasks without any optic flow during the movement phases. As mentioned earlier, across all the studies reported here, I visually move participants at a constant velocity, though I find differences in travel distance estimates when moving at different speeds (Bansal et al., 2024), in line with previous research (Redlick et al., 2001; McManus et al., 2017; Harris et al., 2012) that has also found differences in travel distance estimates when visually moving at difference accelerations. In Chapter 2, I show that moving at 1 m/s leads to people feeling like they had moved further than when moving at 3 or 5 m/s. Although, we do not know how one estimates travel distance between these different speeds. In a future study, one could systemically compare how different rates of acceleration and different constant velocities might change travel distance estimates. This could extend from slow walking speeds to faster driving speeds.

## 5.8. Potential Applications

Though this dissertation focuses on theory-based data-driven research, there are many important applications of this research. One implementation of this research done to understand visual odometry has been in the evolution of robotics. A single camera moving through the world does not provide enough information for a fully effective odometric system. Like our human bodies, these machines need scale information as well as optic flow information to properly estimate travel distance. Understanding the navigational systems from a biological perspective regarding how we solve these problems can aid in the design of terrestrial and aerial autonomous vehicles. One study equipped a mobile robot with a visually driven odometer, resulting in the ability to accurately move through a corridor and stop after it had reached the fixed distance, travelling with an error of less than 2% (Weber et al., 1996). Building on these smaller terrestrial vehicles, another group showed how visual odometry from optic flow information could be used in larger autonomous vehicles, including an industrial forklift and a Toyota Prado SUV (Nourani-Vatani et al., 2009). With a single downward-facing camera and the appropriate scale information, these authors show a promising replacement for the more typical wheel encoder based odometry that has been used previously. Although the field of biologically inspired autonomous robotics has come a long way, there are many possibilities for where these advancements can still go.

Another important application of my research on the perception of travel distance is in developing virtual reality applications, not only for gaming and entertainment purposes, but also for rehabilitation and training. Perceiving travel distance in VR relies primarily on visual motion cues, corresponding to their importance as a crucial component of how users experience and navigate through virtual environments. In gaming, there are multiple ways in which a player can be visually moved. You can move naturally (i.e., where the player has control, as you would in the real world), or be teleported (where you disappear and reappear in a different location), you can be moved at different speeds or natural walking speeds, or different accelerations. In all these scenarios, players can understand the location to which they have moved, and using this location information, can understand how far they have moved. Although the environments used in my experiments are different than those of most gaming environments (e.g., the objects in the environments do not disappear), our findings suggest that the further (and longer) you move, the worse you are at gauging how far they have moved. Understanding visual odometry in these virtual environments will help users build a mental map of their virtual space. Military or pilot training using virtual reality must also require accurate travel distance perception to ensure safe simulation.

## 5.9. Conclusions

Having an accurate perception of travel distance is essential for navigating and moving through the world. To accurately navigate through the world, one must both perceive the direction and distance of movement. The experiments described in this dissertation focus on the distance component of navigation. In my first study (Chapter 2), I show that the speed and direction of self-motion can affect your perception of travel distance. One major contribution to the field that this dissertation provides is highlighting the time component in perceiving travel distance. Previously, the literature has shown a decay in perceived travel distance that happens over distance, meaning, the further you move the worse you are at being able to gauge how far you have moved. Here, I provide evidence that it may not just be the *further* you move, but also the *longer* you move the worse you are being able to make these travel distance estimates. I also show that the leaky spatial integrator model can be used to model the non-linear behaviour of estimating travel distance. However, I do show that the model should be expanded to include a speed term, which I am in the process of doing. One question I attempted to answer in this dissertation was why we find such high variability in travel distance estimates across studies. I hypothesized that it might be due to the differences in virtual environments used across studies. Since I found no significant differences in travel distance estimates when using a selection of different virtual environments, the question of why we see such high variability across studies remains open (Chapter 3). The continuously evolving ways in which people move challenges the brain's self-motion processing ability. In more modern forms of self-motion (e.g., driving a car, experiencing simulated self-motion in virtual reality, etc.), the sensory inputs involved can be conflicting. In my last study (Chapter 4), I show that the high sensitivity to optic flow in the far periphery is a general feature of perceptual odometry even when integrating non-visual cues with visual cues.  Although this dissertation just scratches the surface of our understanding how we perceive travel distance, these studies aid our understanding of the processes involved in making travel distance estimates and helps us more accurately model this complex odometric system.

# References

Ache, B. W., Hein, A. M., Bobkov, Y. V., & Principe, J. C. (2016). Smelling Time: A Neural Basis for Olfactory Scene Analysis. *Trends in Neurosciences*, *39*(10), 649–655. https://doi.org/10.1016/j.tins.2016.08.002

Allison, R. S., Ash, A., & Palmisano, S. (2014). Binocular contributions to linear vertical vection. *Journal of Vision*, *14*(14(5)), 1–23. https://doi.org/10.1167/14.12.5.doi

Angelaki, D. E., Gu, Y., & DeAngelis, G. C. (2009). Multisensory integration: Psychophysics, neurophysiology, and computation. *Current Opinion in Neurobiology*, *19*(4), 452–458. https://doi.org/10.1016/j.conb.2009.06.008

Apthorp, D., & Palmisano, S. (2014). The Role of Perceived Speed in Vection: Does Perceived Speed Modulate the Jitter and Oscillation Advantages? *PLoS ONE*, *9*(3), e92260. https://doi.org/10.1371/journal.pone.0092260

Bakker, N. H., Werkhoven, P. J., & Passenier, P. O. (1999). The Effects of Proprioceptive and Visual Feedback on Geographical Orientation in Virtual Environments. *Presence: Teleoperators and Virtual Environments*, *8*(1), 36–53. https://doi.org/10.1162/105474699566035

Bansal, A., McManus, M., Fiehler, K., & Harris, L. R. (2023). The Effects of Environmental Structure and Texture on Perceived Travel Distance. *Journal of Vision*, *23*(9), 5075. https://doi.org/10.1167/jov.23.9.5075

Bansal, A., McManus, M., Jörges, B., & Harris, L. R. (2024). Perceived travel distance depends on the speed and direction of self-motion. *PLOS ONE*, *19*(9), e0305661. https://doi.org/10.1371/journal.pone.0305661

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using **lme4**. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Baumberger, B., Isableu, B., & Fl□ckiger, M. (2004). The visual control of stability in children and adults: Postural readjustments in a ground optical flow. *Experimental Brain Research*. https://doi.org/10.1007/s00221-004-1930-1

Bian, Z., Braunstein, M. L., & Andersen, G. J. (2005). The ground dominance effect in the perception of 3-D layout. *Perception & Psychophysics*, *67*(5), 802–815. https://doi.org/10.3758/BF03193534

Bonato, F., & Bubka, A. (2006). Chromaticity, Spatial Complexity, and Self-Motion Perception. *Perception*, *35*(1), 53–64. https://doi.org/10.1068/p5062

Bossard, M., & Mestre, D. R. (2018). The relative contributions of various viewpoint oscillation frequencies to the perception of distance traveled. *Journal of Vision*, *18*(2), 3. https://doi.org/10.1167/18.2.3

Brandt, Th., Dichgans, J., & Koenig, E. (1973). Differential effects of central versus peripheral vision on egocentric and exocentric motion perception. *Experimental Brain Research*, *16*(5), 476–491. https://doi.org/10.1007/BF00234474

Bremmer, F. (2005). Navigation in space – the role of the macaque ventral intraparietal area. *The Journal of Physiology*, *566*(1), 29–35. https://doi.org/10.1113/jphysiol.2005.082552

Bremmer, F., Duhamel, J.-R., Ben Hamed, S., & Graf, W. (2000). Stages of Self-Motion Processing in Primate Posterior Parietal Cortex. In *International Review of Neurobiology* (Vol. 44, pp. 173–198). Elsevier. https://doi.org/10.1016/S0074-7742(08)60742-4

Bremmer, F., Duhamel, J.-R., Ben Hamed, S., & Graf, W. (2002). Heading encoding in the macaque ventral intraparietal area (VIP): Heading encoding in area VIP. *European*

*Journal of Neuroscience*, *16*(8), 1554–1568. https://doi.org/10.1046/j.1460-9568.2002.02207.x

Bremmer, F., Klam, F., Duhamel, J., Ben Hamed, S., & Graf, W. (2002). Visual–vestibular interactive responses in the macaque ventral intraparietal area (VIP). *European Journal of Neuroscience*, *16*(8), 1569–1586. https://doi.org/10.1046/j.1460-9568.2002.02206.x

Bremmer, F., Kubischik, M., Pekel, M., Lappe, M., & Hoffmann, K. -P. (1999). Linear Vestibular Self-Motion Signals in Monkey Medial Superior Temporal Area. *Annals of the New York Academy of Sciences*, *871*(1), 272–281. https://doi.org/10.1111/j.1749-6632.1999.tb09191.x

Bremmer, F., & Lappe, M. (1999). The use of optical velocities for distance discrimination and reproduction during visually simulated self motion. *Experimental Brain Research*, *127*(1), 33–42. https://doi.org/10.1007/s002210050771

Bremmer, F., Schlack, A., Duhamel, J.-R., Graf, W., & Fink, G. R. (2001). Space Coding in Primate Posterior Parietal Cortex. *NeuroImage*, *14*(1), S46–S51. https://doi.org/10.1006/nimg.2001.0817

Bremmer, F., Schlack, A., Shah, N. J., Zafiris, O., Kubischik, M., Hoffmann, K.-P., Zilles, K., & Fink, G. R. (2001). Polymodal Motion Processing in Posterior Parietal and Premotor Cortex. *Neuron*, *29*(1), 287–296. https://doi.org/10.1016/S0896-6273(01)00198-2

Brooks, J. X., & Cullen, K. E. (2009). Multimodal Integration in Rostral Fastigial Nucleus Provides an Estimate of Body Movement. *The Journal of Neuroscience*, *29*(34), 10499–10511. https://doi.org/10.1523/JNEUROSCI.1937-09.2009

Bubka, A., & Bonato, F. (2010). Natural Visual-Field Features Enhance Vection. *Perception*, *39*(5), 627–635. https://doi.org/10.1068/p6315

Bubka, A., Bonato, F., & Palmisano, S. (2008). Expanding and Contracting Optic-Flow Patterns and Vection. *Perception*, *37*(5), 704–711. https://doi.org/10.1068/p5781

Burr, D. C., & Santoro, L. (2001). Temporal integration of optic flow, measured by contrast and coherence thresholds. *Vision Research*, *41*(15), 1891–1899. https://doi.org/10.1016/S0042-6989(01)00072-4

Bury, N.-A., Jenkin, M., Allison, R. S., Herpers, R., & Harris, L. R. (2023). Vection underwater illustrates the limitations of neutral buoyancy as a microgravity analog. *Npj Microgravity*, *9*(1), 42. https://doi.org/10.1038/s41526-023-00282-3

Bury, N.-A., Jenkin, M. R., Allison, R. S., & Harris, L. R. (2020). Perceiving jittering self-motion in a field of lollipops from ages 4 to 95. *PLOS ONE*, *15*(10), e0241087. https://doi.org/10.1371/journal.pone.0241087

Campos, J. L., Butler, J. S., & Bülthoff, H. H. (2012). Multisensory integration in the estimation of walked distances. *Experimental Brain Research*, *218*(4), 551–565. https://doi.org/10.1007/s00221-012-3048-1

Campos, J. L., Byrne, P., & Sun, H. (2010). The brain weights body-based cues higher than vision when estimating walked distances. *European Journal of Neuroscience*, *31*(10), 1889–1898. https://doi.org/10.1111/j.1460-9568.2010.07212.x

Clark, B., & Stewart, J. D. (1968). Comparison of sensitivity for the perception of bodily rotation and the oculogyral illusion. *Perception & Psychophysics*, *3*(4), 253–256. https://doi.org/10.3758/BF03212740

Clément, G., Bukley, A., Loureiro, N., Lindblad, L., Sousa, D., & Zandvilet, A. (2020). Horizontal and Vertical Distance Perception in Altered Gravity. *Scientific Reports*, *10*(1), 5471. https://doi.org/10.1038/s41598-020-62405-0

Crowell, J. A., & Banks, M. S. (1993). Perceiving heading with different retinal regions and types of optic flow. *Perception & Psychophysics*, *53*(3), 325–337. https://doi.org/10.3758/BF03205187

Crowell, J. A., & Banks, M. S. (1996). Ideal observer for heading judgments. *Vision Research*, *36*(3), 471–490. https://doi.org/10.1016/0042-6989(95)00121-2

Cullen, K. E. (2012). The vestibular system: Multimodal integration and encoding of self-motion for motor control. *Trends in Neurosciences*, *35*(3), 185–196. https://doi.org/10.1016/j.tins.2011.12.001

Cutting, J., Springer, K., Braren, P., & Johnson, S. (1992). *Wayfinding on foot from information in retinal, not optical, flow. 121*(1), 41–72.

D'Amour, S., Harris, L. R., Berti, S., & Keshavarz, B. (2021). The role of cognitive factors and personality traits in the perception of illusory self-motion (vection). *Attention, Perception, & Psychophysics*, *83*(4), 1804–1817. https://doi.org/10.3758/s13414-020-02228-3

Day, B. L., & Fitzpatrick, R. C. (2005). The vestibular system. *Current Biology*, *15*(15), R583–R586. https://doi.org/10.1016/j.cub.2005.07.053

De Graaf, B., Wertheim, A. H., Bles, W., & Kremers, J. (1990). Angular velocity, not temporal frequency determines circular vection. *Vision Research*, *30*(4), 637–646. https://doi.org/10.1016/0042-6989(90)90074-U

Dearing, R. R., & Harris, L. R. (2011). The contribution of different parts of the visual field to the perception of upright. *Vision Research*, *51*(20), 2207–2215. https://doi.org/10.1016/j.visres.2011.08.018

Delorme, A., & Martin, C. (1986). Roles of retinal periphery and depth periphery in linear vection and visual control of standing in humans. *Canadian Journal of Psychology / Revue Canadienne de Psychologie*, *40*(2), 176–187. https://doi.org/10.1037/h0080091

Dichgans, J., & Brandt, T. (1978). Visual-Vestibular Interaction: Effects on Self-Motion Perception and Postural Control. In R. Held, H. W. Leibowitz, & H.-L. Teuber (Eds.), *Perception* (pp. 755–804). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-46354-9_25

Doeller, C. F., Barry, C., & Burgess, N. (2010). Evidence for grid cells in a human memory network. *Nature*, *463*(7281), 657–661. https://doi.org/10.1038/nature08704

Duffy, C. J. (1998). MST Neurons Respond to Optic Flow and Translational Movement. *Journal of Neurophysiology*, *80*(4), 1816–1827. https://doi.org/10.1152/jn.1998.80.4.1816

Duffy, C. J., & Wurtz, R. H. (1997). Multiple temporal components of optic flow responses in MST neurons: *Experimental Brain Research*, *114*(3), 472–482. https://doi.org/10.1007/PL00005656

Durgin, F. H., Akagi, M., Gallistel, C. R., & Haiken, W. (2009). The precision of locomotor odometry in humans. *Experimental Brain Research*, *193*(3), 429–436. https://doi.org/10.1007/s00221-008-1640-1

Edwards, M., & Ibbotson, M. R. (2007). Relative Sensitivities to Large-Field Optic-Flow Patterns Varying in Direction and Speed. *Perception*, *36*(1), 113–124. https://doi.org/10.1068/p5626

Ekstrom, A. D., Spiers, H. J., Bohbot, V. D., & Rosenbaum, R. S. (2018). *Human spatial navigation*. Princeton University Press.

Elliott, D. (1987). The Influence of Walking Speed and Prior Practice on Locomotor Distance Estimation. *Journal of Motor Behavior*, *19*(4), 476–485. https://doi.org/10.1080/00222895.1987.10735425

Ellmore, T. M., & McNaughton, B. L. (2004). Human Path Integration by Optic Flow. *Spatial Cognition & Computation*, *4*(3), 255–272. https://doi.org/10.1207/s15427633scc0403_3

Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, *415*(6870), 429–433. https://doi.org/10.1038/415429a

Fitzpatrick, R. C., Wardman, D. L., & Taylor, J. L. (1999). Effects of galvanic vestibular stimulation during human walking. *The Journal of Physiology*, *517*(3), 931–939. https://doi.org/10.1111/j.1469-7793.1999.0931s.x

Flückiger, M., & Baumberger, B. (1988). The Perception of an Optical Flow Projected on the Ground Surface. *Perception*, *17*(5), 633–645. https://doi.org/10.1068/p170633

Frenz, H., & Lappe, M. (2005). Absolute travel distance from optic flow. *Vision Research*, *45*(13), 1679–1692. https://doi.org/10.1016/j.visres.2004.12.019

Frenz, H., Lappe, M., Kolesnik, M., & Bührmann, T. (2007). Estimation of travel distance from visual motion in virtual environments. *ACM Transactions on Applied Perception*, *4*(1), 3. https://doi.org/10.1145/1227134.1227137

Fujii, Y., & Seno, T. (2020). The Effect of Optical Flow Motion Direction on Vection Strength. *I-Perception*, *11*(1), 2041669519899108. https://doi.org/10.1177/2041669519899108

Fukusima, S. S., Loomis, J. M., & Da Silva, J. A. (1997). Visual perception of egocentric distance as assessed by triangulation. *Journal of Experimental Psychology: Human Perception and Performance*, *23*(1), 86–100. https://doi.org/10.1037/0096-1523.23.1.86

Gagliardo, A. (2013). Forty years of olfactory navigation in birds. *Journal of Experimental Biology*, *216*(12), 2165–2171. https://doi.org/10.1242/jeb.070250

Gibson, J. J. (1950). *The Perception of the Visual World*. Cambridge: Riverside Press.

Gibson, J. J. (1979). *The ecological approach to visual perception*. Houghton, Mifflin and Company.

Gibson, J. J., & Gibson, E. J. (1955). Perceptual learning: Differentiation or enrichment? *Psychological Review*, *62*(1), 32–41. https://doi.org/10.1037/h0048826

Glasauer, S., Amorim, M.-A., Vitte, E., & Berthoz, A. (1994). Goal-directed linear locomotion in normal and labyrinthine-defective subjects. *Experimental Brain Research*, *98*(2). https://doi.org/10.1007/BF00228420

Goldberg, M. E., & Bruce, C. J. (1990). Primate frontal eye fields. III. Maintenance of a spatially accurate saccade signal. *Journal of Neurophysiology*, *64*(2), 489–508. https://doi.org/10.1152/jn.1990.64.2.489

Gu, Y., Angelaki, D. E., & DeAngelis, G. C. (2008). Neural correlates of multisensory cue integration in macaque MSTd. *Nature Neuroscience*, *11*(10), 1201–1210. https://doi.org/10.1038/nn.2191

Guterman, P. S., Allison, R. S., Palmisano, S., & Zacher, J. E. (2012). Influence of head orientation and viewpoint oscillation on linear vection1. *Journal of Vestibular Research*, *22*(2–3), 105–116. https://doi.org/10.3233/VES-2012-0448

Hammerbeck, U., Yousif, N., Greenwood, R., Rothwell, J. C., & Diedrichsen, J. (2014). Movement speed is biased by prior experience. *Journal of Neurophysiology*, *111*(1), 128–134. https://doi.org/10.1152/jn.00522.2013

Harris, L. R., Herpers, R., Jenkin, M., Allison, R. S., Jenkin, H., Kapralos, B., Scherfgen, D., & Felsner, S. (2012). The relative contributions of radial and laminar optic flow to the perception of linear self-motion. *Journal of Vision*, *12*(10), 7–7. https://doi.org/10.1167/12.10.7

Harris, L. R., Jenkin, M., & Zikovitz, D. C. (2000). Visual and non-visual cues in the perception of linear self motion. *Experimental Brain Research*, *135*(1), 12–21. https://doi.org/10.1007/s002210000504

Harris, L. R., Sakurai, K., & Beaudot, W. H. A. (2017). Tactile Flow Overrides Other Cues To Self Motion. *Scientific Reports*, *7*(1), 1059. https://doi.org/10.1038/s41598-017-01111-w

Henn, V. (1988). Motion Sense. In J. A. Hobson, *States of Brain and Mind* (pp. 59–59). Birkhäuser Boston. https://doi.org/10.1007/978-1-4899-6771-8_23

Israel, I., Chapuis, N., Glasauer, S., Charade, O., & Berthoz, A. (1993). Estimation of passive horizontal linear whole-body displacement in humans. *Journal of Neurophysiology*, *70*(3), 1270–1273. https://doi.org/10.1152/jn.1993.70.3.1270

Jahn, K., Strupp, M., Schneider, E., Dieterich, M., & Brandt, T. (2000). *Differential effects of vestibular stimulation on walking and running*. *11*(8), 1745–1748.

Jörges, B., Bury, N., McManus, M., Bansal, A., Allison, R. S., Jenkin, M., & Harris, L. R. (2024a). The effects of long-term exposure to microgravity and body orientation relative to gravity on perceived traveled distance. *Npj Microgravity*, *10*(1), 28. https://doi.org/10.1038/s41526-024-00376-6

Jörges, B., Bury, N., McManus, M., Bansal, A., Allison, R. S., Jenkin, M., & Harris, L. R. (2024b). The impact of gravity on perceived object height. *Npj Microgravity*, *10*(1), 95. https://doi.org/10.1038/s41526-024-00430-3

Kano, C. (1991). The Perception of Self-Motion Induced by Peripheral Visual Information in Sitting and Supine Postures. *Ecological Psychology*, *3*(3), 241–252. https://doi.org/10.1207/s15326969eco0303_3

Kapralos, B., Zikovitz, D. C., Jenkin, M., & Harris, L. R. (2004). Auditory Cues in the Perception of Self Motion. *Audio Engineering Society Convention*.

Kim, J., & Palmisano, S. (2008). Effects of active and passive viewpoint jitter on vection in depth. *Brain Research Bulletin*, *77*(6), 335–342. https://doi.org/10.1016/j.brainresbull.2008.09.011

Kopiske, K., Heinrich, E.-M., Jahn, G., Bendixen, A., & Einhäuser, W. (2023). Multisensory cues for walking in virtual reality: Humans combine conflicting visual and self-motion information to reproduce distances. *Journal of Neurophysiology*, *130*(4), 1028–1040. https://doi.org/10.1152/jn.00011.2023

Kruijff, E., Marquardt, A., Trepkowski, C., Lindeman, R. W., Hinkenjann, A., Maiero, J., & Riecke, B. E. (2016). On Your Feet!: Enhancing Vection in Leaning-Based Interfaces through Multisensory Stimuli. *Proceedings of the 2016 Symposium on Spatial User Interaction*, 149–158. https://doi.org/10.1145/2983310.2985759

Lappe, M., & Frenz, H. (2009). Visual estimation of travel distance during walking. *Experimental Brain Research*, *199*(3–4), 369–375. https://doi.org/10.1007/s00221-009-1890-6

Lappe, M., Jenkin, M., & Harris, L. R. (2007a). Travel distance estimation from visual motion by leaky path integration. *Experimental Brain Research*, *180*(1), 35–48. https://doi.org/10.1007/s00221-006-0835-6

Lappe, M., Jenkin, M., & Harris, L. R. (2007b). Travel distance estimation from visual motion by leaky path integration. *Experimental Brain Research*, *180*(1), 35–48. https://doi.org/10.1007/s00221-006-0835-6

Laurienti, P. J., Burdette, J. H., Maldjian, J. A., & Wallace, M. T. (2006). Enhanced multisensory integration in older adults. *Neurobiology of Aging*, *27*(8), 1155–1163. https://doi.org/10.1016/j.neurobiolaging.2005.05.024

Lepecq, J.-C., Giannopulu, I., & Baudonniere, P.-M. (1995). Cognitive Effects on Visually Induced Body Motion in Children. *Perception*, *24*(4), 435–449. https://doi.org/10.1068/p240435

Liechti, F. (1995). Modelling Optimal Heading and Airspeed of Migrating Birds in Relation to Energy Expenditure and Wind Influence. *Journal of Avian Biology*, *26*(4), 330. https://doi.org/10.2307/3677049

Loomis, J. M., da Silva, J. A., Fujita, N., & Fukusima, S. S. (1992). Visual space perception and visually directed action. *Journal of Experimental Psychology: Human Perception and Performance*, *18*(4), 906–921. https://doi.org/10.1037/0096-1523.18.4.906

Mccarley, J. S., & He, Z. J. (2000). Asymmetry in 3-D perceptual organization: Ground-like surface superior to ceiling-like surface. *Perception & Psychophysics*, *62*(3), 540–549. https://doi.org/10.3758/BF03212105

McManus, M., D'Amour, S., & Harris, L. R. (2017a). Using optic flow in the far peripheral field. *Journal of Vision*, *17*(8), 3. https://doi.org/10.1167/17.8.3

McManus, M., D'Amour, S., & Harris, L. R. (2017b). Using optic flow in the far peripheral field. *Journal of Vision*, *17*(8:3), 1–11. https://doi.org/10.1167/XX.XX.XX.doi

McManus, M., & Fiehler, K. (2025). The effect of vection on the use of optic flow cues. *Royal Society Open Science*, *12*(7), 250364. https://doi.org/10.1098/rsos.250364

McManus, M., & Harris, L. R. (2021). When gravity is not where it should be: How perceived orientation affects visual self-motion processing. *PLOS ONE*, *16*(1), e0243381. https://doi.org/10.1371/journal.pone.0243381

Mittelstaedt, M.-L., & Mittelstaedt, H. (2001). Idiothetic navigation in humans: Estimation of path length. *Experimental Brain Research*, *139*(3), 318–332. https://doi.org/10.1007/s002210100735

Morimoto, Y., Sato, H., Hiramatsu, C., & Seno, T. (2019). Material surface properties modulate vection strength. *Experimental Brain Research*, *237*(10), 2675–2690. https://doi.org/10.1007/s00221-019-05620-0

Murata, K., Seno, T., Ozawa, Y., & Ichihara, S. (2014). Self-Motion Perception Induced by Cutaneous Sensation Caused by Constant Wind. *Psychology*, *05*(15), 1777–1782. https://doi.org/10.4236/psych.2014.515184

Murovec, B., Spaniol, J., Campos, J. L., & Keshavarz, B. (2021). Multisensory Effects on Illusory Self-Motion (Vection): The Role of Visual, Auditory, and Tactile Cues. *Multisensory Research*, *34*(8), 869–890. https://doi.org/10.1163/22134808-bja10058

Nakamura, S., Seno, T., Ito, H., & Sunaga, S. (2010). Coherent Modulation of Stimulus Colour Can Affect Visually Induced Self-Motion Perception. *Perception*, *39*(12), 1579–1590. https://doi.org/10.1068/p6793

Nordahl, R., Nilsson, N. C., Turchet, L., & Serafin, S. (2012). Vertical illusory self-motion through haptic stimulation of the feet. *2012 IEEE VR Workshop on Perceptual Illusions in Virtual Environments*, 21–26. https://doi.org/10.1109/PIVE.2012.6229796

Nourani-Vatani, N., Roberts, J., & Srinivasan, M. V. (2009). Practical visual odometry for car-like vehicles. *2009 IEEE International Conference on Robotics and Automation*, 3551–3557. https://doi.org/10.1109/ROBOT.2009.5152403

Ogawa, M., & Seno, T. (2014). Vection is Modulated by the Semantic Meaning of Stimuli and Experimental Instructions. *Perception*, *43*(7), 605–615. https://doi.org/10.1068/p7639

O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Research*, *34*(1), 171–175. https://doi.org/10.1016/0006-8993(71)90358-1

O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Clarendon Press ; Oxford University Press.

Oman, C. M., Howard, I., Smith, S. T., Beall, A., Natapoff, A., Zacher, J., & Jenkin, H. (2003). *The Role of Visual Cues in Microgravity Spatial Orientation*.

Palmisano, S. (1996). Perceiving self-motion in depth: The role of stereoscopic motion and changing-size cues. *Perception & Psychophysics*, *58*(8), 1168–1176. https://doi.org/10.3758/BF03207550

Palmisano, S. (2002). Consistent Stereoscopic Information Increases the Perceived Speed of Vection in Depth. *Perception*, *31*(4), 463–480. https://doi.org/10.1068/p3321

Palmisano, S., Burke, D., & Allison, R. S. (2003). Coherent Perspective Jitter Induces Visual Illusions of Self-Motion. *Perception*, *32*(1), 97–110. https://doi.org/10.1068/p3468

Palmisano, S., & Chan, A. Y. C. (2004). Jitter and Size Effects on Vection are Immune to Experimental Instructions and Demands. *Perception*, *33*(8), 987–1000. https://doi.org/10.1068/p5242

Palmisano, S., Gillam, B. J., & Blackburn, S. G. (2000). Global-Perspective Jitter Improves Vection in Central Vision. *Perception*, *29*(1), 57–67. https://doi.org/10.1068/p2990

Palmisano, S., Pinniger, G. J., Ash, A., & Steele, J. R. (2009). Effects of Simulated Viewpoint Jitter on Visually Induced Postural Sway. *Perception*, *38*(3), 442–453. https://doi.org/10.1068/p6159

Pretto, P., & Chatziastros, A. (2006). Changes in optic flow and scene contrast affect the driving speed. *Europe Driving Simulation Conference*, 263–272.

Pretto, P., Ogier, M., Bülthoff, H. H., & Bresciani, J.-P. (2009). Influence of the size of the field of view on motion perception. *Computers & Graphics*, *33*(2), 139–146. https://doi.org/10.1016/j.cag.2009.01.003

Proffitt, D. R., Stefanucci, J., Banton, T., & Epstein, W. (2003). The Role of Effort in Perceiving Distance. *Psychological Science*, *14*(2), 106–112. https://doi.org/10.1111/1467-9280.t01-1-01427

Prokop, T., Schubert, M., & Berger, W. (1997). Visual influence on human locomotion Modulation to changes in optic flow: Modulation to changes in optic flow. *Experimental Brain Research*, *114*(1), 63–70. https://doi.org/10.1007/PL00005624

Redlick, F. P., Jenkin, M., & Harris, L. R. (2001a). Humans can use optic flow to estimate distance of travel. *Vision Research*, *41*(2), 213–219. https://doi.org/10.1016/S0042-6989(00)00243-1

Redlick, F. P., Jenkin, M., & Harris, L. R. (2001b). Humans can use optic flow to estimate distance of travel. *Vision Research*, *41*(2), 213–219. https://doi.org/10.1016/S0042-6989(00)00243-1

Reinhardt-Rutland, A. H. (1982). Asymmetry in Forward and Backward Vection. *Perceptual and Motor Skills*, *54*(3), 870–870. https://doi.org/10.2466/pms.1982.54.3.870

Riecke, B. E., Schulte-Pelkum, J., Avraamides, M. N., Heyde, M. V. D., & Bülthoff, H. H. (2006). Cognitive factors can influence self-motion perception (vection) in virtual reality. *ACM Transactions on Applied Perception*, *3*(3), 194–216. https://doi.org/10.1145/1166087.1166091

Riecke, B. E., Schulte-Pelkum, J., Avraamides, M. N., von der Heyde, M., & Bülthoff, H. H. (2005). Scene consistency and spatial presence increase the sensation of self-motion in virtual reality. *Proceedings of the 2nd Symposium on Applied Perception in Graphics and Visualization*, 111–118. https://doi.org/10.1145/1080402.1080422

Riecke, B. E., Väljamäe, A., & Schulte-Pelkum, J. (2009). Moving sounds enhance the visually-induced self-motion illusion (circular vection) in virtual reality. *ACM Transactions on Applied Perception*, *6*(2), 1–27. https://doi.org/10.1145/1498700.1498701

Riecke, L. (2016). Physiology, Psychoacoustics and Cognition in Normal and Impaired Hearing. In *Physiology, Psychoacoustics and Cognition in Normal and Impaired Hearing* (Vol. 894, pp. 371–379). Cham: Springer International Publishing.

Rieser, J. J., Ashmead, D. H., Talor, C. R., & Youngquist, G. A. (1990). Visual Perception and the Guidance of Locomotion without Vision to Previously Seen Targets. *Perception*, *19*(5), 675–689. https://doi.org/10.1068/p190675

Robinson, D. A. (1968). Eye Movement Control in Primates: The oculomotor system contains specialized subsystems for acquiring and tracking visual targets. *Science*, *161*(3847), 1219–1224. https://doi.org/10.1126/science.161.3847.1219

Roditi, R. E., & Crane, B. T. (2012). Suprathreshold asymmetries in human motion perception. *Experimental Brain Research*, *219*(3), 369–379. https://doi.org/10.1007/s00221-012-3099-3

Rupert, A., & Kolev, O. (2008). *The Use Of Tactile Cues To Modify The Perception Of Self-Motion*.

Rushton, S. K., Bradshaw, M. F., & Warren, P. A. (2007). The pop out of scene-relative object movement against retinal motion due to self-movement. *Cognition*, *105*(1), 237–245. https://doi.org/10.1016/j.cognition.2006.09.004

Sasaki, K., Seno, T., Yamada, Y., & Miura, K. (2012). Emotional Sounds Influence Vertical Vection. *Perception*, *41*(7), 875–877. https://doi.org/10.1068/p7215

Schlack, A., Hoffmann, K., & Bremmer, F. (2002). Interaction of linear vestibular and visual stimulation in the macaque ventral intraparietal area (VIP). *European Journal of Neuroscience*, *16*(10), 1877–1886. https://doi.org/10.1046/j.1460-9568.2002.02251.x

Schlack, A., Hoffmann, K., & Bremmer, F. (2003). Selectivity of macaque ventral intraparietal area (area VIP) for smooth pursuit eye movements. *The Journal of Physiology*, *551*(2), 551–561. https://doi.org/10.1113/jphysiol.2003.042994

Schwarz, M., & Hamburger, K. (2023). Implicit versus explicit processing of visual, olfactory, and multimodal landmark information in human wayfinding. *Frontiers in Psychology*, *14*, 1285034. https://doi.org/10.3389/fpsyg.2023.1285034

Seno, T. (2013). Social Inhibition of Vection. *Psychology*, *04*(08), 619–621. https://doi.org/10.4236/psych.2013.48088

Seno, T., & Fukuda, H. (2012). Stimulus Meanings Alter Illusory Self-motion (Vection)—Experimental Examination of the Train Illusion. *Seeing and Perceiving*, *25*(6), 631–645. https://doi.org/10.1163/18784763-00002394

Seno, T., Ogawa, M., Ito, H., & Sunaga, S. (2011). Consistent Air Flow to the Face Facilitates Vection. *Perception*, *40*(10), 1237–1240. https://doi.org/10.1068/p7055

Seno, T., Sunaga, S., & Ito, H. (2010). Inhibition of vection by red. *Attention, Perception, & Psychophysics*, *72*(6), 1642–1653. https://doi.org/10.3758/APP.72.6.1642

Seya, Y., Yamaguchi, M., & Shinoda, H. (2015). Single stimulus color can modulate vection. *Frontiers in Psychology*, *6*. https://doi.org/10.3389/fpsyg.2015.00406

Shik, M. L., & Orlovsky, G. N. (1976). Neurophysiology of locomotor automatism. *Physiological Reviews*, *56*(3), 465–501. https://doi.org/10.1152/physrev.1976.56.3.465

Sotiropoulos, G., Seitz, A. R., & Seriès, P. (2011). Changing expectations about speed alters perceived motion direction. *Current Biology*, *21*(21), R883–R884. https://doi.org/10.1016/j.cub.2011.09.013

Strasburger, H., Rentschler, I., & Jüttner, M. (2011). Peripheral vision and pattern recognition: A review. *Journal of Vision*, *11*(5), 13. https://doi.org/10.1167/11.5.13

Sun, H.-J., Campos, J. L., & Chan, G. S. W. (2004). Multisensory integration in the estimation of relative path length. *Experimental Brain Research*, *154*(2), 246–254. https://doi.org/10.1007/s00221-003-1652-9

Sun, H.-J., Campos, J. L., Young, M., Chan, G. S. W., & Ellard, C. G. (2004). The Contributions of Static Visual Cues, Nonvisual Cues, and Optic Flow in Distance Estimation. *Perception*, *33*(1), 49–65. https://doi.org/10.1068/p5145

Tamada, Y., & Seno, T. (2015). Roles of Size, Position, and Speed of Stimulus in Vection with Stimuli Projected on a Ground Surface. *Aerospace Medicine and Human Performance*, *86*(9), 794–802. https://doi.org/10.3357/AMHP.4206.2015

Thiélin-Bescond, M., & Beugnon, G. (2005). Vision-independent odometry in the ant Cataglyphis cursor. *Naturwissenschaften*, *92*(4), 193–197. https://doi.org/10.1007/s00114-005-0609-1

Tinga, A. M., Jansen, C., Van Der Smagt, M. J., Nijboer, T. C. W., & Van Erp, J. B. F. (2018). Inducing circular vection with tactile stimulation encircling the waist. *Acta Psychologica*, *182*, 32–38. https://doi.org/10.1016/j.actpsy.2017.11.007

Trutoiu, L. C., Mohler, B. J., Schulte-Pelkum, J., & Bülthoff, H. H. (2009). Circular, linear, and curvilinear vection in a large-screen virtual environment with floor projection. *Computers & Graphics*, *33*(1), 47–58. https://doi.org/10.1016/j.cag.2008.11.008

Väljamäe, A. (2009). Auditorily-induced illusory self-motion: A review. *Brain Research Reviews*, *61*(2), 240–255. https://doi.org/10.1016/j.brainresrev.2009.07.001

Vaziri-Pashkam, M., & Cavanagh, P. (2008). Apparent speed increases at low luminance. *Journal of Vision*, *8*(16), 9–9. https://doi.org/10.1167/8.16.9

Warren, W. H., & Hannon, D. J. (1988). Direction of self-motion is perceived from optical flow. *Nature*, *336*(6195), 162–163. https://doi.org/10.1038/336162a0

Weber, K., Venkatesh, S., & Srinivasan, M. V. (1996). Insect inspired behaviours for the autonomous control of mobile robots. *Proceedings of 13th International Conference on Pattern Recognition*, 156–160 vol.1. https://doi.org/10.1109/ICPR.1996.546010

Wittlinger, M., Wehner, R., & Wolf, H. (2006). The Ant Odometer: Stepping on Stilts and Stumps. *Science*, *312*(5782), 1965–1967. https://doi.org/10.1126/science.1126912

Wittlinger, M., Wehner, R., & Wolf, H. (2007). The desert ant odometer: A stride integrator that accounts for stride length and walking speed. *Journal of Experimental Biology*, *210*(2), 198–207. https://doi.org/10.1242/jeb.02657

Wood, R. M., Harvey, M. A., Young, C. E., Beedie, A., & Wilson, T. (2000). Weighting to go with the flow? *Current Biology*, *10*(15), R545–R546. https://doi.org/10.1016/S0960-9822(00)00606-0

Wright, W. G., DiZio, P., & Lackner, J. R. (2006). Perceived self-motion in two visual contexts: Dissociable mechanisms underlie perception. *Journal of Vestibular Research*, *16*(1–2), 23–28. https://doi.org/10.3233/VES-2006-161-202

Yoder, R. M., & Taube, J. S. (2014). The vestibular contribution to the head direction signal and navigation. *Frontiers in Integrative Neuroscience*, *8*. https://doi.org/10.3389/fnint.2014.00032

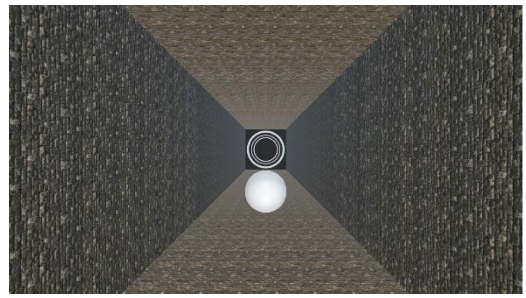
Young, L. R., & Shelhamer, M. (1990). Microgravity enhances the relative contribution of visually-induced motion sensation. *Aviation, Space, and Environmental Medicine*, *61*(6), 525–530.

**S1 APPENDIX**

## MOVE TO TARGET TASK

INSTRUCTIONS:

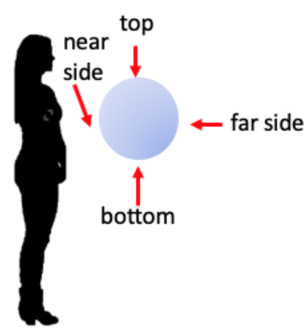
1. You will begin in a horizontal corridor with a reference ball directly in front of you and a target in the distance.



2. To begin moving, press the **RIGHT** mouse button. Depending on the experimental block you are in, the environment around you will rotate, such that you are either facing backward, upward, downward, or remain looking forward. The target will then disappear and you will start moving towards the target's location.

3. When you feel like the ball in front of you has arrived at the target's location, press the **RIGHT** mouse button to stop and move to the next trial.

NOTES:

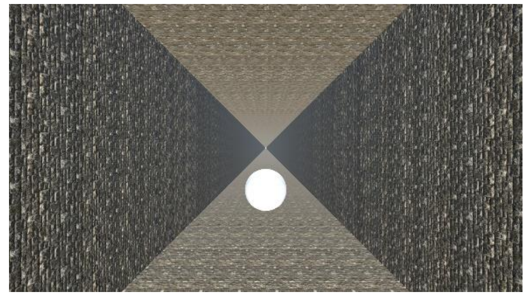



- There are 4 blocks in total: forward, backward, upward, downward.
- For each direction you use a different side of the ball as a reference. When you are moving forward, stop when the far side of the ball reaches where the target used to be. When you are moving backward use the near side. When moving upward use the top, and when moving downward use the bottom.
- When you complete all 4 blocks, the program will automatically shut down, and you should see a data file in the 'moveToTarget_Data' folder called 'participantData_MTT'.
- When you have read these instructions, please proceed to the practice (2 mins). After you complete the practice, you may begin.

THANK YOU FOR PARTICIPATING! GOOD LUCK!

## ADJUST TARGET TASK

INSTRUCTIONS:



1. You will begin in a horizontal corridor with a reference ball in front of you.

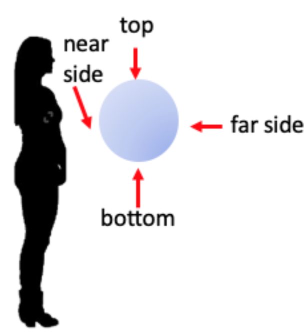
2. To begin moving, press the **RIGHT** mouse button. This will trigger the environment around you to rotate and depending on the direction, you will begin moving either upward, downward, backward or forward through the corridor and stop at randomized location.

3. After you stop, you will be moved back to the original position and a target will appear in front of you.

4. You will then use the **UP** and **DOWN** arrow keys to move the target towards and away from you until it matches the distance you just moved through.

5. Press the **SPACEBAR** to start the next trial.

NOTES:




- There are 4 blocks: forward, backward, upward, downward.
- For each direction you use a different side of the ball as a reference. After moving forward, you adjust the target to the location of where the far side of the ball reached. After moving backward, you adjust the target to where the near side reached. After moving upward you use the top of the ball, and after moving downward you use the bottom of the ball.
- When you complete all four blocks, the program will automatically shut down, and you should see a data file in the 'adjustTarget_Data' folder called 'participantData_ATT'.
- When you have read these instructions, please proceed to the practice (2 mins). After you complete the practice, you may begin.

THANK YOU FOR PARTICIPATING! GOOD LUCK!

**S2 APPENDIX**

## Linear Mixed Model Comparisons

Since the gains had a roughly normal distribution, a Linear Mixed Model was performed using the lme4 (Bates et al., 2015) for R (version 4.3.0.). To determine the most appropriate model structure, we started with a maximal model including all relevant experimental variables as slopes per participant and compared to simpler models until no significant differences were found between models (Barr et al., 2013). The R script used to compare the two models can be found here (https://github.com/ambikabansal/Speed_Direction).

### MOVE-TO-TARGET TASK

The maximal model reads as follows:

lmer(Gains ~ Direction + Speed + Distance + (Speed + Direction | Participant)

This maximal model was compared to a simpler model where we removed random slopes for direction per participant, which reads as follows:

lmer(Gains ~ Speed + Distance + (Speed | Participant)

These models were found to be significantly different from one another ($p < 0.001$), so we knew we needed to include direction as a random effect.

The maximal model was compared to a simpler model where we removed random slopes for speed per participant, which reads as follows:

lmer(Gains ~ Direction + Distance + (Direction | Participant)

These models were found to be statistically significant ($p < 0.001$), so we used the maximal model structure with direction, speed, and distance set as random effect to analyze the gains.

Although we did not have any specific hypotheses about the interaction between speed and direction, and did not expect any population-wide effects, for completion's sake we did test the model structure including the interaction compared to the maximal model. The interaction model reads as follows:

lmer(Gains ~ Direction * Speed + (1 + Speed + Direction | Participant)

We also found no significant difference ($p > 0.173$), which is why we chose to omit the interaction from the fixed effects.

The maximal model reads as follows:

lmer(Gains ~ Direction + Speed + Distance + (Speed + Direction | Participant)

This maximal model was compared to a simpler model where we removed random slopes for direction per participant, which reads as follows:

lmer(Gains ~ Speed + Distance + (Speed | Participant)

These models were found to be significantly different from one another ($p < 0.001$), so we knew we needed to include direction as a random effect.

The maximal model was compared to a simpler model where we removed random slopes for speed per participant, which reads as follows:

lmer(Gains ~ Direction + Distance + (Direction | Participant)

These models were not found to be statistically significant ($p < 0.001$), so we used the simpler model structure with speed removed as a random effect to analyze the alphas.

Although we did not have any specific hypotheses about the interaction between speed and direction, and did not expect any population-wide effects, for completion's sake we did test the model structure including the interaction compared to the maximal model. The interaction model reads as follows:

lmer(Gains ~ Direction * Speed + (1 + Speed + Direction | Participant)

We also found no significant difference ($p > 0.216$), which is why we chose to omit the interaction from the fixed effects.