Active head rotations influence thresholds and perceived direction of visual motion.

Kate Margaret Pickard

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Faculty of Science
The University of Sydney
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Abstract

Self-motion signals must be accounted for such that an accurate and robust perception of object motion can be maintained. However, research in this area has been focused on translation self-motion, as well as often using passive or simulated self-motion cues. Active-self motion generates additional multi-sensory signals and it is therefor important to understand how we disambiguate motion signals while actively moving. Consequently, this thesis utilised virtual reality technology to examine the influence of active head rotations on visual motion perception, specifically on thresholds for perceiving visual motion, and perceived direction of visual motion. Study 1 compared thresholds for visual motion perception between congruent, incongruent and stationary self-motion conditions. The results indicate thresholds were significantly higher when subjects were turning their head, compared to stationary, though no significant difference was found between congruent and incongruent visual-self motion conditions. These findings contrast with prior research on the advantage of tracking and smooth-pursuit eye movement. Study 2 investigated the influence of active head rotations on perceived motion direction, finding perceived direction was pulled toward the direction of head rotation. This evidence supports the theory that visual-vestibular processing primarily exists to disambiguate confounding effects of self-rotation on visual motion perception. It is recommended that future research incorporate the active and passive generation of vestibular signals to develop a greater understanding of the role of rotational self-motion on visual motion perception.

Statement of Originality

This is to certify that to the best of my knowledge, the content of this thesis is my own work. This thesis has not been submitted for any degree or other purposes. I certify that the intellectual content of this thesis is the product of my own work and that all the assistance received in preparing this thesis and sources have been acknowledged.

Kate Pickard
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Chapter 1

Introduction

1.1 Visual motion perception

In most cases, navigating the distal world seems an effortless task, making it easy to imagine our visual system acting as a video camera, faithfully relaying information from our environment directly to our brain. However, visual perception in reality is far from analogous to a camera, existing rather, as most sensory systems do, to generate a "best guess" as to what actually exists in the world around us by utilising the visual information projected on our retinas. This is the fundamental difference between sensing and perceiving, and the current thesis seeks to better understand how we combine visual, vestibular, and other sensory signals associated with voluntary movement, to accurately perceive motion in the world around us.

Take for example crossing a street. As you approach the road, even without the presence of any moving cars, large motion signals will be registered across the retina as a result of your own motion through a stationary environment. This type of visual motion signal is known as optic flow, and is combined primarily with vestibular information in order to accurately perceive self motion and maintain the correct percept of a stationary environment (Britton & Arshad, 2019). Now imagine you have arrived at the edge of the road, and stare straight ahead as a car drives past. The car will generate a motion signal again registered on the retina, which can be treated as a faithful representation of the movement of the car, given the lack of any self-motion or eye-movements (Bridgeman, 1995). Alternatively, you could track the car with your eyes or head, meaning the car will remain stationary on the retina. Despite the absence of retinal motion, the motion of the eye or head itself can be used to estimate the motion of the car (Schütz et al., 2011). These simple examples already demonstrate how the perception of motion in the world is intrinsically linked to the motion of ourselves.

Now imagine the much more realistic scenario of walking up to a road that has cars moving in both directions, turning your head to the left and right to check for traffic as you approach, while also tracking an individual cars' movement with your eyes. How can our brains disentangle such a complex web of visual motion signals, generated by both self and distal motion, in order to accurately perceive our environment and cross the road safely? While much work has been done to answer this question, it has been primarily focused on specific sub-questions, such as how we gain an accurate heading perception—the sense of direction of self-motion—from optic flow (DeAngelis & Angelaki, 2012; MacNeilage et al., 2012; Royden et al.,

1994; W. H. Warren & Hannon, 1988; Zeng et al., 2023), or how eye-movements are accounted for in order to perceive moving objects (Arathorn et al., 2013; Greenlee et al., 2002; Souman et al., 2005; Spering & Montagnini, 2011). Further, this research has often been conducted on stationary participants, with self-motion either ignored, or simulated using optic flow or motion-platform like devices (e.g., Dyde and Harris, 2008; P. A. Warren and Rushton, 2007). While certainly insightful, simulated or passively-generated self-motion signals lack environmental validity, as active perception involves a much greater range of sensory signals (Cullen, 2012). In order to truly understand how we navigate our environments everyday, we must examine visual perception under active-sensory conditions—the fundamental motivation for this thesis.

1.2 Active perception

Active perception is a phrase which encompasses all cases of perceiving while voluntarily moving. Voluntary movement differs from simulated movement in the extra sensory signals it generates in addition to visual, and in the case of passive self-motion, vestibular information. One of these additional signals is what is known as sensory reafference. When planning movement, the motor signal required can be used to predict the sensory result of said movement, called reafference (Cullen, 2012). This prediction can then be subtracted from the resulting sensory input, leaving only externally-generated (exafferent) motion to be perceived (Cullen, 2012). Also present is proprioceptive input arising from the self-motion. These signals could potentially aid, or hinder, visual motion perception. While multisensory perception is often more robust (Ernst & Banks, 2002; Ernst & Bülthoff, 2004), in the case of motion perception, self-motion signals could add additional noise to a system already having to disambiguate many noisy motion signals. It remains unclear whether visual motion perception is more accurate or robust when actively moving, our natural state of being, or whether this additional movement increases the noise involved in motion processing such that motion perception is impaired.

Part of the barrier to investigating active perception till now has been technological. When working with stationary screens or monitors, an inherent difficulty in experimental design was always present as any motion of the subject would cause the screen itself to move across the retina, adding an additional visual motion signal and potentially changing the visual environment under investigation. With the advent and increased affordability of virtual reality (VR), this issue is removed. As the screen can now literally be strapped to a participant's head, participants can move around while allowing experiments to maintain absolute control of the visual environment being tested. This allows greater probing of how visual and action-vestibular signals are combined in motion perception. This thesis will utilise the opportunities afforded by VR technology to further our understanding of how we perceive motion in our environment while we ourselves are moving. As the incorporation of VR into psychophysics is still relatively new and evolving, the experiments included here will have the additional benefit of providing novel methods for the study of visual-vestibular interactions, and add to the growing body of evidence that VR technology is a reliable and useful tool for perceptual studies.

1.3 Thesis outline

This thesis utilises VR technology to investigate the interplay between visual and action-vestibular signals in visual motion perception. It does so by asking two fundamental questions. First, how might thresholds for visual motion perception be influenced by signals arising from active head rotations, and secondly, how might the perceived direction of visual motion be altered by active head rotations.

The background pertaining to such questions is discussed in Chapter 2. Chapter 3 addresses the first question by asking participants to judge the perceived direction of horizontal visual motion while rotating their heads to the right, left or remaining stationary. This allows investigation of whether visual action-vestibular interaction differs between cases where the visual motion is congruent or incongruent with the action-vestibular stimulation. Chapter 4 asks first whether our perceived direction of visual motion is influenced by task-irrelevant self-motion, and secondly whether this relationship differs depending on the strength of the visual motion signal. Implications of the findings in Chapters 3 and 4 are addressed in the general discussion found in Chapter 5.

Chapter 2

Background

2.1 Overview

This chapter provides a review of the relevant literature relating to visual motion perception during self-motion, highlighting the main justifications for this thesis. Due to the novelty of the current experiments, previous findings are drawn from a wide range of fields in order to provide a thorough theoretical base from which to predict results. The physiology that underlies visual-vestibular motion processing will be discussed first, followed by relevant findings from eye-movement research. Finally, results from studies utilising a variety of different methods to investigate visual and self-motion perception will be examined.

2.2 Physiology of visual-vestibular interactions

The primary aim of our sensory systems is to use information gained from ourselves and our environment to, as accurately as possible, determine what is occurring in the world around us. The signals registered across various senses can be ambiguous, or at least contain a high level of noise, meaning veridical perception is not guaranteed. It is well-known that combining signals from different sensory modalities can disambiguate cues and aid robust perception (Alais & Burr, 2004; Alais et al., 2010; Ernst & Banks, 2002; Ernst & Bülthoff, 2004). However, such combinations are governed by the physiological structure of the relevant multisensory system. As such, examination of the physiological mechanisms of visual-vestibular processing can give insight into the design and purpose of our motion processing system, and in turn help predict behavioural outcomes.

There are two types of self-motion: translation and rotation. Translation refers to movements that cause linear acceleration such as whole-body movements up, down, forward or backward. Rotation movements occur when the head tilts in one of three planes: yaw, pitch and roll. Visual-vestibular integration is thought to occur primarily in the dorsal medial superior temporal area (MSTd), and these neurons have different visual-vestibular cue preferences depending on whether the vestibular signal arose from translational or rotational self-motion (Gu et al., 2006; Takahashi et al., 2007). While studies of macaque monkeys have shown translational visual-vestibular neurons of the dorsal medial superior temporal area (MSTd) can have either congruent (visual and vestibular directions are aligned) or incongruent (preferred visual-vestibular signals are in opposite directions) directional tunings (Gu et

al., 2006), rotational visual-vestibular cells seem to occur solely with opposite tunings (Takahashi et al., 2007). Translational visual-vestibular integration is vital for accurate perception of self-motion direction, otherwise known as heading perception (Britton & Arshad, 2019). As such, congruent visual-vestibular cues are the norm when navigating through a stationary world, and therefore the combination of these cues to aid accurate heading perception is hypothesised to be the role of congruent translational cells (Gu et al., 2006; MacNeilage et al., 2012; Takahashi et al., 2007). In contrast, rotational movements of the head through a stationary world generate opposite visual motion signals on the retina to the direction of rotation. The lack of congruently-tuned rotational cells could indicate the primary function of rotational visual-vestibular integration being the disambiguation of confounding effects of optic flow arising from self-rotation across a stationary world (Morgan et al., 2008; Takahashi et al., 2007).

It seems then that these subtle physiological differences speak to the different functions of translational and rotational visual-vestibular processing, arising from the distinct occurrences of these types of movement in daily life. However, while heading is a behaviour commonly studied (DeAngelis & Angelaki, 2012; MacNeilage et al., 2012; Zeng et al., 2023), rotation is not, most likely due to technological difficulties in experimental design. It remains to be seen how the physiology of rotational visual-vestibular processing may influence perception of visual motion. Specifically, Experiments 1 & 2 (Chapter 3) seek to shed light on the perceptual outcomes of rotating while judging visual motion by investigating how thresholds for perceiving visual motion may differ between cases of congruent, incongruent and stationary head rotations.

2.3 Eye movements as predictors of head rotations

While there is little literature investigating effects of rotational head movements on visual motion perception, the same can not be said for eye movements. The study of how we successfully account for motion of the eyes when judging motion of an object has received ongoing attention (Spering & Montagnini, 2011), and can potentially provide a model for understanding larger head movements. Although head movements are much noisier signals involving different muscle groups, and most importantly activate the vestibular system, eye and head movements show similarities in the resultant confounding effects they have on visual motion perception, giving rise to the possibility they may be accounted for in similar ways. Indeed, in addition to learning about effects of head rotations on visual motion perception, the question of whether current results will mirror eye-movement findings is interesting in and of itself.

2.3.1 Smooth pursuit

Behaviourally, it is common to track objects moving through the environment in order to gain as much information about them as possible (Spering et al., 2011). This tracking, commonly referred to as smooth-pursuit in eye-movement literature, can be performed by moving the eyes, head or combination of both. When the eyes are

engaged in smooth-pursuit, the image of the moving object is held stationary on the retina, and perception of motion instead relies on known velocity of eye movement (Schütz et al., 2011). However, pursuit of an object is almost never perfect, with eyes lagging slightly behind, resulting in movement of the object across the retina known as 'retinal slip'. The true motion of the object can then be calculated by summing the velocity of the eye movement and retinal slip, predicted by the popular model of multisensory motion perception, Inferential Theory (von Holst, 1973; von Holst & Mittelstaedt, 1950; Wertheim, 1994). Specifically, Inferential Theory posits motion perception is derived from addition of retinal signals with extra-retinal signals, such as those derived from the muscles coordinating eye movement (Wertheim, 1994). Applied to head movements, the theory remains the same, with the extra-retinal signals now derived from head movements instead of eye-movements. Therefore if processed in a similar way, results from eye-movement studies may be used to predict those of head movements in the current thesis.

Smooth-pursuit eye movements can aid visual motion perception across a range of tasks, including direction and speed judgements, lowering perceived motion smear, and improving motion coherence (see Spering and Montagnini, 2011, 2011 for a review). Greenlee et al. (2002) also found they aided perception of coherent visual motion when compared to fixation. We could then expect head rotations in a direction congruent with visual motion, a proxy of smooth pursuit, to also aid perception of visual motion. However, Swanston and Wade (1988) found head movements to be more poorly compensated for than eye movements in a direction estimation task, suggesting this may not be the case. Indeed, eye-movements themselves have been found to impair speed and direction judgements in the Aubert-Fleischl phenomena (Dichgans et al., 1975) and Filehne (Mack & Herman, 1973)) phenomena. It is unclear then whether congruent, tracking-like, head movements will result in improved or impaired motion perception, and how these results may differ to incongruent motion. These effects are both investigated in Chapter 3.

2.3.2 Eye movements more broadly

In reality, deriving object motion from smooth-pursuit eye-movements is not the only ability necessary to perceive object motion every day. Eye-movements can occur in any direction relative to object motion, not least due to the saccadic movement present even when we are at rest (Rolfs, 2015). In the most simple situation, the eyes are steady and the retinal motion of an object is equal to its true physical motion (2.1 A). Conversely, when the eyes and/or are moving, the retinal motion is no longer a true representation of an object's physical motion (2.1 B). Rather, the retinal motion must be combined with the extra-retinal motion to derive true object motion. Studies have found this to be an imperfect process (Arathorn et al., 2013; Souman et al., 2005; Swanston & Wade, 1988). If instead the eyes (or possibly head) are engaged in smooth pursuit, assuming perfect pursuit and steady fixation of the eyes on the moving object, extra-retinal motion signals can become a substitute for the object's physical motion (2.1 C). In these cases, combining the extra-retinal and retinal signals is necessary for accurate motion perception. However, it remains unknown how a system designed to combine multisensory signals in order to account for them would process task-irrelevant self-motion. In Experiments 3 & 4 (Chapter 4), the visual motion appears within a head-centred aperture, such that the eyes can remain

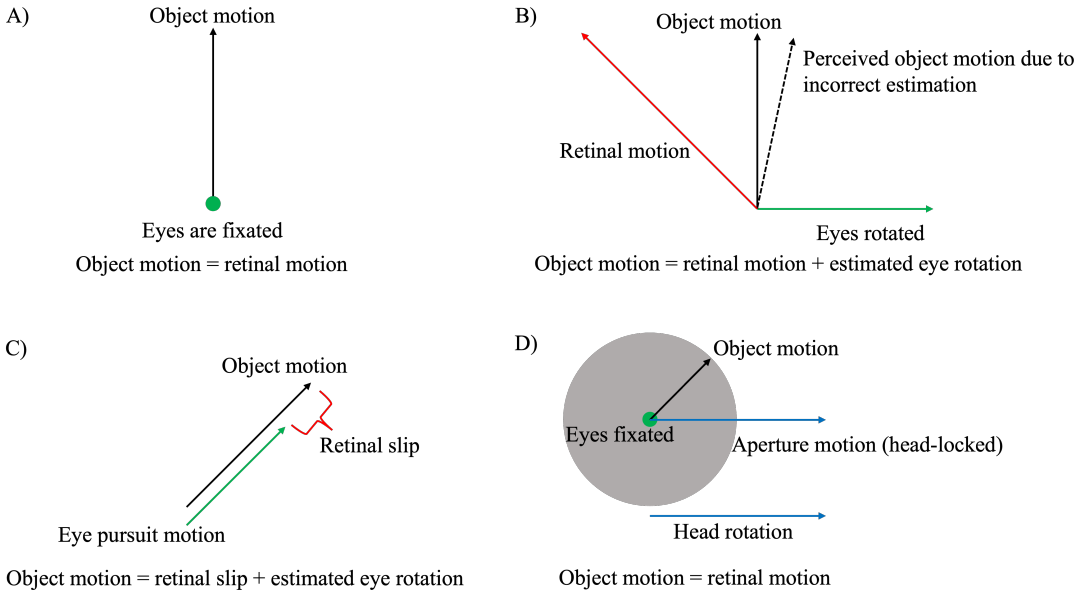

Figure 2.1: Multisensory motion processing as vector diagrams.
A) Object motion during fixation. B) Object motion during eye movements. C) Object motion during smooth pursuit. D) Object motion in the current thesis.

fixated centrally throughout rotation, and the retinal signal of object motion should theoretically equal its physically motion, rendering the self-motion signal generated from turning the irrelevant to perceiving the visual motion (2.1 D). The primary question we seek to answer is whether head rotations will alter direction perception in a systematic way that suggests the action-vestibular and visual signals are still being combined, regardless of necessity. Literature investigating the interplay between self and object motion may give some insight into what we can expect.

2.4 Motion processing during self-motion

2.4.1 Self-motion perception

Generally, motion signals can have one of two sources. Self-motion, or motion in the distal world. Almost always, accurate perception of one relies on accurate perception of the other. An example of when this goes wrong is the experience of illusory self-motion, otherwise known as vection (Britton & Arshad, 2019; Wann & Rushton, 1994). A well-known example is when you are sitting on a stationary train and the train outside the window starts to move, causing you to think you are moving until the train disappears and you suddenly perceive yourself as stationary again. In this case, the moving train creates such a huge motion signal on the retina that it is interpreted as optic flow, a visual signal caused by self-motion (Britton & Arshad, 2019). Your brain accordingly infers from the optic flow that you must be moving, and it is only when the visual signal stops (the train disappears from view), that you suddenly perceive yourself to be stationary. Illusions such as this give great insight into how we process self and distal motion signals, and indeed, how our visual motion influences our perception of self-motion has received much attention in the literature (e.g., Chen et al., 2011c; Fetsch et al., 2013). However, much less

is known about the reciprocal side of this relationship, namely the influence of self-motion on visual motion perception. This thesis seeks to fill part of this gap by investigating thresholds for both visual motion perception and perceived direction of visual motion.

2.4.2 Visual motion perception

Though caused by self-motion, optic flow is partially a result of the fact that the world around us is largely stationary (T. C. A. Freeman et al., 2010). So while we may well have a prior to perceive the world as stationary (T. C. A. Freeman et al., 2010), and subsequently attribute large visual motion signals to a self-motion source, our successful ability to navigate our everyday environments, let alone exceed at sports like soccer or tennis, is evidence of our ability to recognise motion of distal objects moving completely independently of ourselves. However, research has shown that the perception of object motion is not always accurate, and instead is often biased by our own self-motion.

For example, heading perception has been found to correlate with perceived object motion (Dyde & Harris, 2008; Wu et al., 2021; Xing & Saunders, 2022). The correlation between perceived heading, utilising both visual and vestibular cues, and judgments of object motion was established by Xing and Saunders (2022), whereas Dyde and Harris (2008) showed that, for an object to give the appearance of being stationary, it needed to move in sync with the observer's motion. Halow et al. (2023) also looked at stationarity perception, and found in order to perceive the world as stationary while being passively rotated, visual motion needed to be slower than would be naturally due to rotation. This suggests self-motion velocity may have been underestimated, influencing visual motion perception in turn. Such findings clearly show how self-motion perception often biases object motion due to incorrect accounting for the effects of self-motion on the visual landscape.

Finally, Alais et al. (2021) showed perceived motion direction during binocular rivalry between horizontally opposed motions matched the direction of self-rotation in cases of both active and passive perception. This suggests the influence of self-motion on object motion perception is not simply a higher-order perceptual process, but rather is driven by low-level physiological interactions. Specifically, it speaks to the congruent vs incongruent relationship found between visual-vestibular motion signals, as a suppression of incongruent motion due to self-rotation (driven by incongruent visual-vestibular cells) could be the driver for congruent visual motion to be consciously perceived (Alais et al., 2021). Priority processing of congruent visual motion is also consistent with findings of a boost of visual motion processing when paired with a congruent vestibular signal (Hogendoorn et al., 2016, 2017). Indeed, MacNeilage et al. (2012) found object discrimination thresholds were significantly lower when accompanied by congruent vestibular cues, compared to just visual cues from optic flow. Whether this will remain the case for active self-motion, and how it will compare to incongruent visual action-vestibular integration is the driving question behind Chapter 3 of this thesis.

2.4.3 Direction perception

Directional selectivity of mammalian visual systems begins with retinal ganglion cells themselves, that respond to preferred directions of motion due to inhibition from starburst amacrine interneurons (see Demb, 2007 for a review). This directional selectivity continues further up the hierarchy of the visual system, with neurons in both V1 and medial temporal (MT) areas of Macaque brains found to be directionally selective (Albright, 1984). As the MSTd specifically is known to be vital to visual-vestibular processing, the directional selectivity of these cells in particular is of interest when investigating how vestibular signals from action may influence perceived direction of visual motion, the primary focus of Experiments 3 & 4 (Chapter 4). Interestingly, a common finding when investigating direction perception is superior estimation for cardinal as opposed to oblique directions (Appelle, 1972; Gros et al., 1998; Karim & Kojima, 2010; Krukowski et al., 2003; Loffler & Orbach, 2001). These oblique effects may be driven by the greater occurrence of cardinal orientations throughout our natural environment (Appelle, 1972). It is unknown how our perception of motion while stationary may change when rotating, and how common effects like the oblique effect may or may not interact with the action vestibular motion signal.

It has been suggested visual and vestibular motion signals may be treated as vectors, and add together following all the same rules of vector addition (Hogendoorn et al., 2017; Verstraten et al., 1994). Hogendoorn et al. (2017) rotated participants on a motion platform and found direction perception to be pulled towards direction of rotation, providing supporting evidence that perceived direction of visual motion may rely on vector addition of multisensory motion signals (retinal and vestibular motion signals). If this is indeed the case, we would expect perceived direction to be pulled towards the direction of head rotation for both Experiments 3 & 4 (Chapter 4). Such results would give great insight into how we actively navigate a constantly moving environment.

2.5 Summary

In all, it is clear there is much to be learnt about the interaction between rotational self-motion and visual motion perception, specifically in the case of active self-motion. By investigating this relationship, we gain insights into everyday behaviour and the underlying functioning of the visual-vestibular multisensory system. In addition to studies on passive self-motion, eye movement studies provide a useful base from which to build predictions of the effects of head rotations on object motion perception. Chapter 3 first looks at perceptual thresholds for visual motion, investigating the potential differential processing of congruent and incongruent visual action-vestibular signals. Chapter 4 will then look at visual motion direction, and how active head rotations may bias perceived direction of object motion.

Chapter 3

Incongruent thresholds increase visual motion perception

This work has been submitted for publication in Neuroscience of Consciousness as: Pickard, K., Davidson, M.J., Kim, S., & Alais, D., Incongruent active head rotations increase visual motion detection thresholds.

It is available as a preprint at: 10.31234/osf.io/sxbu3.

Abstract

Attributing a visual motion signal to its correct source—be that external object motion, self-motion, or some combination of both—seems effortless, and yet often involves disentangling a complex web of motion signals. Existing literature focuses on either translational motion (heading) or eye movements, leaving much to be learnt about the influence of a wider range of self-motions, such as active head rotations, on visual motion perception. The current study investigated how active head rotations affect visual motion detection thresholds, comparing conditions where visual motion and head-turn direction were either congruent or incongruent. Participants judged the direction of a visual motion stimulus while rotating their head or remaining stationary, using a fixation-locked Virtual Reality display with integrated head-movement recordings. Thresholds to perceive visual motion were higher in both active-head rotation conditions compared to stationary, though no differences were found between congruent or incongruent conditions. Participants also showed a significant bias to report seeing visual motion travelling in the same direction as the head rotation. Together these results demonstrate active head rotations increase visual motion perceptual thresholds, particularly in cases of incongruent visual and active vestibular stimulation.

Keywords: active perception, multisensory, visual motion, self-motion, thresholds, bias

3.1 Introduction

Merging multiple streams of information from across different sensory systems results in a more robust perception of the world around us (Alais & Burr, 2004; Alais et al., 2010; Ernst & Banks, 2002; Ernst & Bülthoff, 2004). A key example is combining vestibular self-motion information with visual motion signals to correctly interpret the source and attributes of both our own self-motion and distal motion in the environment (Cullen, 2012; DeAngelis & Angelaki, 2012). However, many questions remain regarding how self-motion signals are accounted for such that an accurate and robust perception of object motion can be maintained. One key open question is how natural and realistic vestibular signals may contribute to visual perception of motion on the retina.

A well-studied example of visual and vestibular motion interaction is the study of optic flow and heading perception (e.g Gu et al., 2006, reviewed in DeAngelis and Angelaki, 2012). Heading refers to the perceived direction of one's translation, with the resulting global visual motion signal arising from relative motion of objects in the scene known as optic flow (Britton & Arshad, 2019; Zeng et al., 2023). Subtle changes in either the physical heading direction or cued direction from optic flow can be manipulated to determine overall perception of heading direction (see Britton and Arshad, 2019 for a review). Studies of macaque monkeys suggest integration of these signals involves visual-vestibular cells of the dorsal aspect of the medial superior temporal area (MSTd), where cells tuned to congruent translational movement (visual-vestibular direction preferences are aligned), or with opposite tunings occur in roughly equal proportions (Gu et al., 2006). While these cells are mostly reliant on visual cues when visual signals are strong (e.g. when measured in response to tasks with 100% visual motion coherence) (Gu et al., 2006), degrading the visual signal leads to an upweighting of vestibular input to maintain accurate perception (Morgan et al., 2008), with the congruent cells in particular aiding discrimination of small changes in heading direction (Gu et al., 2006; MacNeilage et al., 2012; Takahashi et al., 2007). In contrast to the findings for translation, Takahashi et al. (2007) found only oppositely tuned rotational cells in the MSTd. While congruent optic flow and heading movements occur regularly when moving through the world, and we would therefore benefit from a system designed to enhance congruent visual-vestibular signals in order to aid navigation, rotational movements of the head and body result in visual motion opposite to the direction of rotation, which must be accounted for in order to maintain robust motion perception (Takahashi et al., 2007). It has therefore been hypothesised that the role of the oppositely-tuned rotational cells in the MSTd is to disambiguate confounding effects of optic flow arising from self-rotation across a stationary world (Morgan et al., 2008; Takahashi et al., 2007) by providing an exafferent signal to be subtracted from the sensory response.

In these examples, the underlying neurophysiology for both translational and rotational motion systems are serving to maximise veridical motion perception in visual-vestibular conditions. However, just how active rotational head movements might affect thresholds for visual motion perception remains unknown. This is important to understand, as though both translational and rotational movements of the head occur when navigating the world everyday, rotations are far more frequent and common behaviours and fundamental to tracking objects or exploring a visual environment (Spering et al., 2011). Here we directly contrasted the visual motion

thresholds required to maintain $\tilde{7}5\%$ accuracy on a motion detection task during active head rotation. In two experiments we contrasted left/right motion detection thresholds with congruent and incongruent head rotations, as well as stationary conditions. We predicted that as both incongruent and congruent conditions may require increases in processing and attention due to the added self-motion signals, that these motion thresholds should be higher than stationary thresholds (Heinrich et al., 2020; Kinchla, 1992; Lavie et al., 2004; Swallow & Jiang, 2013). When comparing congruent and incongruent conditions, we predicted lower visual motion thresholds for congruent than incongruent rotations for two reasons. First, it is proposed that there is a sensory prior that the distal world is stationary (T. C. A. Freeman et al., 2010; Weiss et al., 2002; Welchman et al., 2008), and thus incongruent visual motion signals would be more likely attributed to a stationary object or background. A system designed to disambiguate optic flow arising from rotation, possibly driven by incongruent visual-vestibular cells (Morgan et al., 2008; Takahashi et al., 2007), could suppress these expected incongruent motion signals (thus raising thresholds) in order to highlight any independent motion in a scene. Second, as smooth-pursuit tracking is a common behaviour to gain as much information as possible about a moving object (Spering et al., 2011), we reasoned that congruent head rotations would similarly improve congruent motion-detection thresholds. While most previous research on tracking has focussed on smooth-pursuit eye movements, MacNeilage et al. (2012) found object discrimination thresholds were significantly lower when accompanied by congruent vestibular cues, compared to just visual cues from optic flow. Together, this suggests that tracking a moving object via congruent head rotations should aid visual perception.

The current experiments test these predictions using a virtual reality headset to maintain control of the visual environment, and to record head speed and rotation with high temporal resolution. To preview the results, we found increased visual motion thresholds for rotation conditions relative to stationary. There was some evidence for increased thresholds for incongruent rotation conditions when compared to both congruent and stationary conditions, though this result could be driven by participants' bias to respond in line with the direction of head rotation.

3.2 General Methods

3.2.1 Apparatus

A Vive Pro Eye head-mounted display (HMD) was used to present the stimulus. The HMD had a resolution of 2880 x 1600 pixels (1440 x 1600 per eye), a refresh rate of 90 Hz and a horizontal field of view (FOV) of approximately 110°. The virtual environment and stimuli was rendered with a NVIDIA GeForce RTX 2080 Ti graphic card and programmed in Unity version 2020.2.4f1 using the SteamVR Unity plugin (v1.21.12).

3.2.2 Data Analysis

All data was processed and visualised using Matlab R2022a. Statistical analyses were performed in JASP 0.17.1.0, and Matlab. Cumulative gaussian psychometric functions were fitted to the data for each condition and participant using the

maximum likelihood method (Watson, 1979), with a guess rate of 0.5. Individual participant signal-intensities required to achieve 75% accuracy were taken from their psychometric functions, and the mean of participants was used as our group measure of thresholds for visual motion perception in different conditions.

3.2.3 Linear Mixed Effects Analysis

We performed linear mixed-effects (LME) analyses to determine whether direction and congruence of visual-active vestibular signals had a significant effect on visual motion detection thresholds. Specifically, we performed linear mixed-effects model comparison in JASP, that fits models using the maximum likelihood method. We included fixed-effects for congruence and stimulus-direction, and random intercepts per participant. The goodness of fit was compared for each model using likelihood ratio tests, and significance reported when the goodness of fit significantly improved with the inclusion of fixed-effect parameters. We report the result of the likelihood ratio test (model improvement) and the Chi-squared value of the term tested.

3.2.4 Exclusion Criteria

An adaptive staircase procedure (Quest: Watson and Pelli, 1983) controlled the strength of the motion stimulus and maintained performance at 75% accuracy. Staircases from two sessions of six motion conditions (left/right motion directions x left/right/stationary rotation conditions) were plotted and inspected and any participant not attaining the required 75% accuracy threshold had their data for that condition removed. Trials across the two sessions were then combined to generate one psychometric function (PMF) for each of the six motion conditions for each participant. The means of these PMFs were the dependent measure of threshold.

3.3 Experiment 1: Visual motion detection thresholds

The first experiment measured visual motion detection thresholds by varying signal-to-noise ratio while observers were either stationary or making a head rotation that was congruent or incongruent with the direction of visual motion. Head rotation direction and speed was controlled by having subjects pursue a motion guide (see Figure 3.1).

3.3.1 Methods

Participants

Twenty-six individuals were recruited for this experiment. Six were removed from analysis due to technical issues during data collection (n = 2), incorrectly understanding task instructions (n = 3), or incorrectly performing rotations (n = 1) reducing the final number for analysis to 20. Participants had corrected-to-normal vision and no neck or vestibular conditions. They were recruited from the University of Sydney undergraduate Psychology cohort, with one participant a naive member

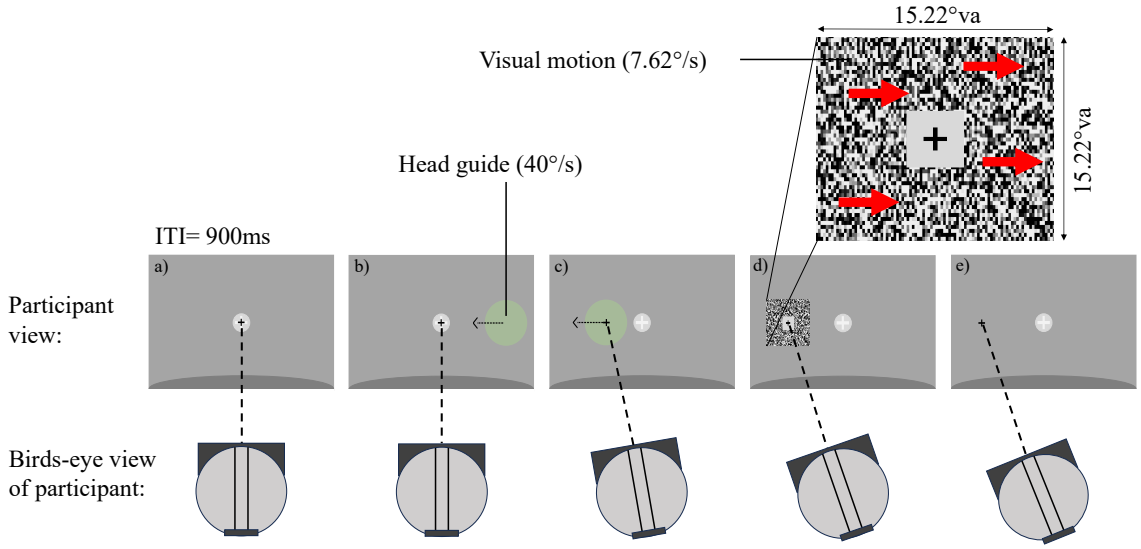

Figure 3.1: Example trial sequence with incongruent head rotation.
a) In VR, participants aligned their head-centred fixation cross with a world-centred forward marker (grey circular region with cross). b) Upon fixation, a coloured motion-guide entered their periphery and translated horizontally across the screen with a speed of 40 °/s, indicating the direction and speed of the required head rotation. Participants were instructed to monitor the guide as it approached their fixation point and prepare to make a head turn to follow it while keeping their head-centred fixation cross in the centre of the motion guide. c) The guide reached the world-centred marker after 1 second, which was when participants initiated a head turn to keep their head-centred fixation cross on the motion-guide and their eyes on the head-centred fixation cross. The head-centred cross provided live feedback as to how closely they were following the guide. The motion-stimulus would appear after 1.2 seconds, so 200ms after beginning the head rotation. Red arrows were not present but represent an example direction of motion. e) Participants indicated the perceived direction of motion using the left and right arrow keys, then returned to centre for the next trial (not shown), with an inter-trial interval (ITI) of 900 ms. The motion signal consisted of a black and white noise pattern drifting left or right, overlaid by stationary black and white noise, with the contrast ratio controlled by the adaptive staircase to maintain 75% correct performance. The speed of the visual motion was 7.62 °/s. View a short video of the procedure at https://osf.io/nf4uh and https://osf.io/r5t4e.

of the authors' laboratory. All participants were naïve to the purposes of the experiment and gave informed consent prior to participation. The study protocol was approved by the University of Sydney Human Research Ethics Committee (HREC 2021/048).

Stimuli

The motion signal consisted of a translating square aperture containing a patch of random luminance pixels whose average contrast (signal intensity) was controlled by an adaptive staircase (Quest: Watson and Pelli, 1983) to maintain performance at 75%. This pattern of 120 x 120 pixels would drift left or right at a speed of 7.62 °/s within the square aperture. The motion signal was generated using a luminance signal-to-noise ratio (LSNR) where varying the signal-to-noise ratio altered the strength of the motion signal while the mean contrast remained constant (Lankheet

et al., 2002; van der Smagt & van de Grind, 1999). The contrast value of individual pixels was drawn from a normal-distribution between 0 and 1, and their position was updated at 2 pixels a frame. The noise pattern was also 120 x 120 pixels, with a normal distribution of contrast values per pixel. The average contrast of the noise pixels was adjusted using the formula $\text{Contrast}_{noise} = \text{sqrt}(1\text{- Contrast}^2_{signal})$. As the adaptive staircase adjusted the contrast of the motion pattern, the motion and noise pixels were combined on each presentation frame by taking their average value per pixel. The noise was updated in synchrony with the movement of the motion signal, ensuring the noise and moving pattern could not be visually segregated based on temporal differences (Lankheet et al., 2002). The aperture subtended 15.22° x 15.22° and was locked to participants' head position such that when a participant turned their head, the aperture containing the stimulus always remained in the centre of participants' vision, and with the same relative orientation. As a result the retinally defined speed within the aperture was fixed at 7.62 °/s. Consequently there were no eye movements necessary to follow the stimulus and the stimulus aperture was not moving across the retina. A fixation cross of 1.2 °va surrounded by a grey square occupying 7.15 °va was presented in the centre of the stimulus to aid steady fixation and limit retinal motion stemming from confounding eye movements.

Procedure

Participants always saw a head-centred fixation cross which they could align with a world-centred forward marker so that each trial began from a central position. A circular head-guide was used to indicate required head movement. If the head guide was presented centrally, participants would keep their head stationary. Otherwise, the guide would enter from the edge of the display, travelling in a three-dimensional arc from one side of the display to the other at 40°/s, serving as a cue for the upcoming direction of rotation. Participants were instructed to start turning their head to follow the guide once it arrived in front of them at the fixation point, which was after 1 second. The guide would be replaced by the stimulus after 1.2 seconds, so 200 ms after participants began rotation (see Figure 3.1). The stimulus was presented for 400 ms. Participants would then press the left or right arrow key to indicate perceived direction of visual motion seen within the aperture, before returning their head to centre for the next trial. Participants completed a practice version of the experiment to coordinate following the head guide and responding to the stimulus. The practice experiment consisted of 30 trials in a fixed order without feedback (10 stationary, 10 with congruent motion and 10 with incongruent motion, with equal split of motion travelling left or right within each condition). In the subsequent experiment, each participant completed two blocks of 180 trials each (2 stimulus directions x 3 head rotations x 30 trials per condition) giving a total of 360 trials per participant and all trial types were randomly interleaved within a block. There were six visual-active vestibular motion signal combinations of interest in the current experiment, those being left-left, right-right, left-right, right-left, left-stationary and right-stationary (with the first in the pair referring to visual stimulus direction and the second head rotation direction). This allowed an analysis of whether cases of right or left visual motion impacted results. The data showed there was no left/right direction difference and these directional conditions were eventually collapsed to examine whether cases of congruent or incongruent head rotations had differential effects on visual motion perception, with the stationary

condition serving as a control.

3.3.2 Results

Incongruent head rotations increase visual motion detection thresholds

This experiment investigated motion perception thresholds in the presence of congruent, incongruent or no simultaneous head rotation. Using a 2 x 3 (left/right visual motion, congruent/incongruent/stationary head rotation) repeated-measures ANOVA, visual motion direction (left or right) was found to have no significant influence on thresholds for visual motion perception ($F(1,7) = 5.29$, $p = 0.06$). There was a significant main effect of rotation congruence on thresholds ($F(2,14) = 18.04$, $p < .001$, $\eta_p^2 = 0.72$), with no interaction ($F(2,14) = 3.64$, $p = 0.06$; Figure 3.2). Post-hoc pairwise comparisons with Bonferroni correction showed that incongruent visual-active vestibular motion signals resulted in significantly higher thresholds than both congruent or stationary conditions ($t(14) = 5.11$, $p < .001$, d = -1.37 and $t(14) = 5.29$, $p < 0.001$, $d = 1.42$, respectively). A linear-mixed-effects model (LME) was also run to quantify the strength of this main effect when modelling the contribution of individual participant data as a random effect. Likelihood ratio tests confirmed that congruence ($\chi^2(2) = 29.65$, $p < .001$) but not movement direction (p =.06) or the interaction ($p = .24$) were significant improvements to the linear mixed model.

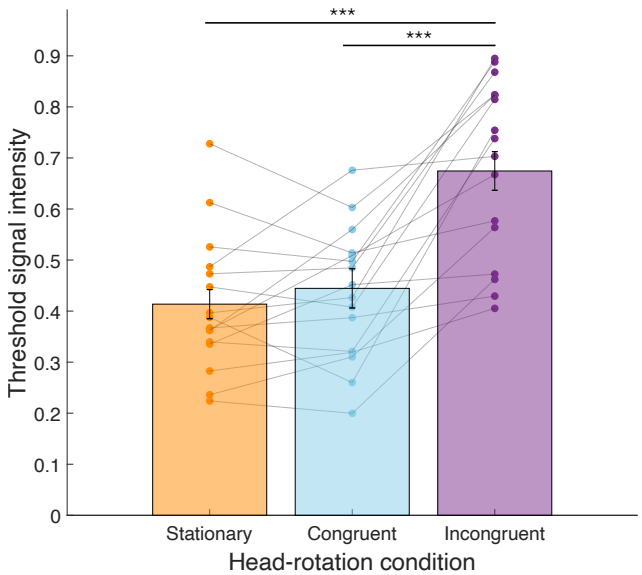

Figure 3.2: Average thresholds for head rotation conditions (collapsed across left/right stimulus motion directions).
Each dot is a participant (participants with missing data not shown) and columns show group means with error bars showing standard error of the mean. An ANOVA and LMM both showed a significant difference in motion thresholds based on head-rotation condition. Post-hoc comparisons revealed significantly higher thresholds in the incongruent than congruent and stationary conditions. *** denotes $p < .001$, Bonferonni corrected.

Speed of head rotation

We analysed participants' ability to follow the head guide and any potential effects of head-speed on visual motion detection thresholds. One participant was found to have not turned their head in rotation conditions and made significant movements while stationary, so was removed from analysis. Rotations were also checked on a trial by trial basis so trials containing incorrect movement (i.e., turning during a stationary trial or vice versa) were removed. Participants were on average slightly slower than the guide but consistent between both rotation conditions. Figure 3.3a shows the specific time course of head rotation, including when stimuli were presented. Figure 3.3b shows the average absolute rotation across all participants, separated by trials when participants correctly or incorrectly judged motion direction. Figure 3.3c shows the average speeds and variability for each rotation condition. These averages could be slightly lower than the target speed as they were calculated over the entirety of the rotation, including the initial acceleration and ending deceleration periods. When fitting a linear model to each participant's average speed and threshold value when turning left and right, there was no significant correlation between rotation speed and threshold (*right*, R^2_{Adj} = -0.002, $F(1,16) = 0.96$, $p = 0.34$; *left* ,$R^2_{Adj} = 0.11$, $F(1,17) = 3.25$, $p = 0.09$). This suggests that differences in head speed rotation did not drive any difference in thresholds we report. It is clear participants could follow the guide close to the target speed and with minimal variability with acceleration during the presentation of the stimulus was close to linear. This gives confidence that the current method of following a head guide in a VR scene is a valid method of studying the influence of active head rotations on visual motion perception.

Head rotation direction biases perceived motion direction

In addition to the condition-average effects (see Figure 3.3), we additionally calculated the point-of-subjective equality (PSEs) after fitting psychometric functions (PMFs) to the motion signal intensities of each condition (see Methods). For this analysis, signal intensities were re-coded to be negative if the response direction was leftward and positive if rightward. PMFs were then fitted for each participant to show responses as percentages of rightward responses, with leftward and rightward threshold values plotted against each other, as shown in Figure 3.4a. As the average PSE seemed to cluster off the diagonal, potentially signifying a bias in participant responses, we performed a supersubject analysis to investigate the presence of this bias in our sample. Figure 3.4b shows the PMFs generated for the super subject for each rotation condition. The statistical reliability of these differences in supersubject thresholds were investigated via a bootstrapping procedure using full resampling of the data with replacement. Data was bootstrapped 1000 times and mean bootstrapped thresholds are shown in Figure 3.4c. Error bars represent 95% confidence intervals, suggesting there is a significant bias for participants to answer in line with the direction of head rotation. Together, these results indicate a cost imposed upon motion detection thresholds by incongruent visual motion/head rotation such that thresholds are higher for detection in incongruent compared to congruent or stationary conditions. In addition, a bias to respond to left/right motion congruently with head-rotation was observed, and became the focus of Experiment 2.

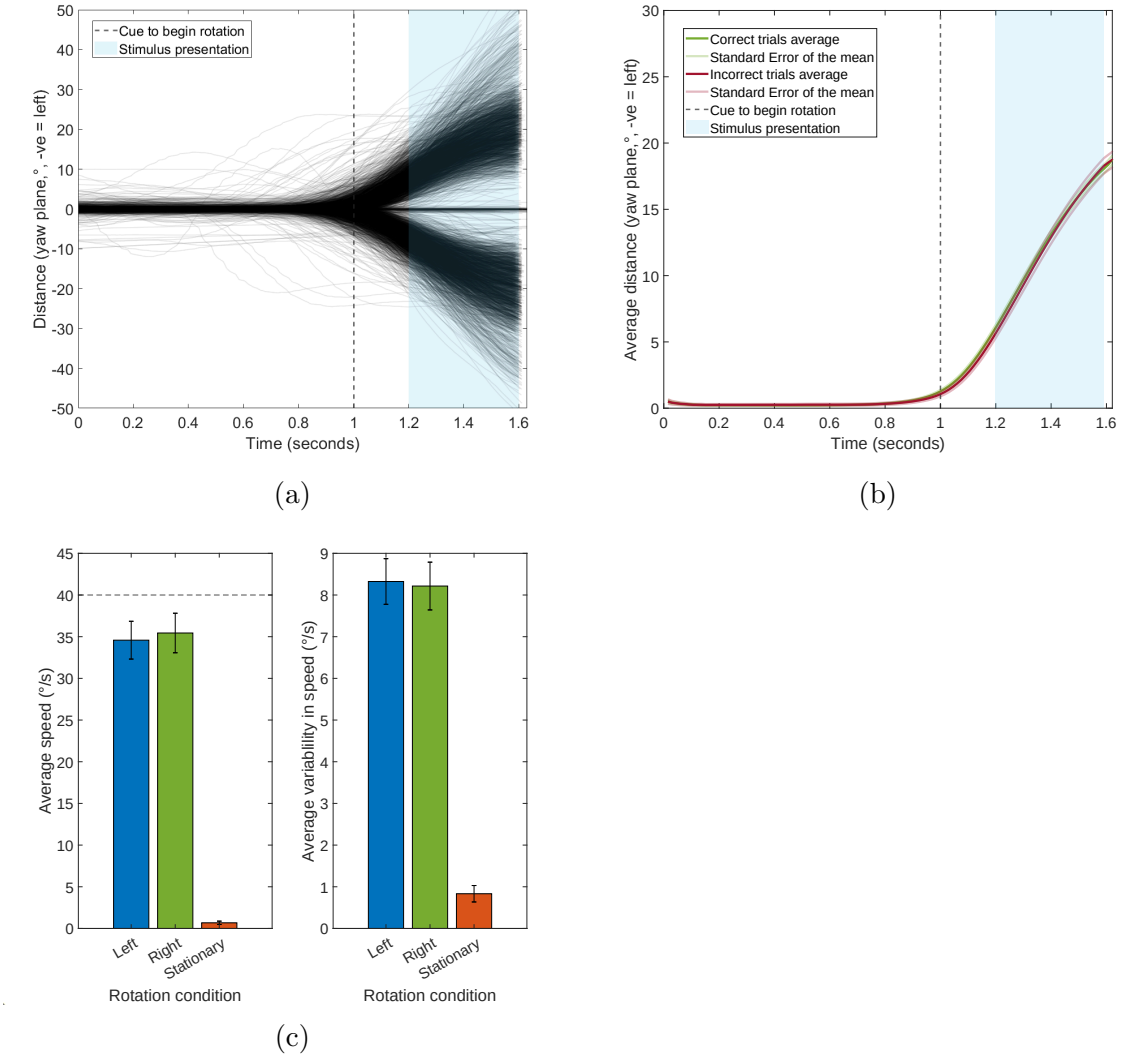

Figure 3.3: Head rotations Experiment 1.
Head rotation for each rotation trial of every participant. (a) The cue to begin the turn came from the head guide (travelling st 40°/s) reached a centre marker. Trials with erroneous rotations were removed before analysis.Red represents trials that had incorrect responses, green trials with correct direction judgements. (b) Average absolute value of trajectories across participants for trials that were correct or incorrect. Shaded lines represent SEM. (c) Average speed and variability of head rotations across each participant, error bars represent SEM. A dashed line at 40°/s indicates speed of head guide.

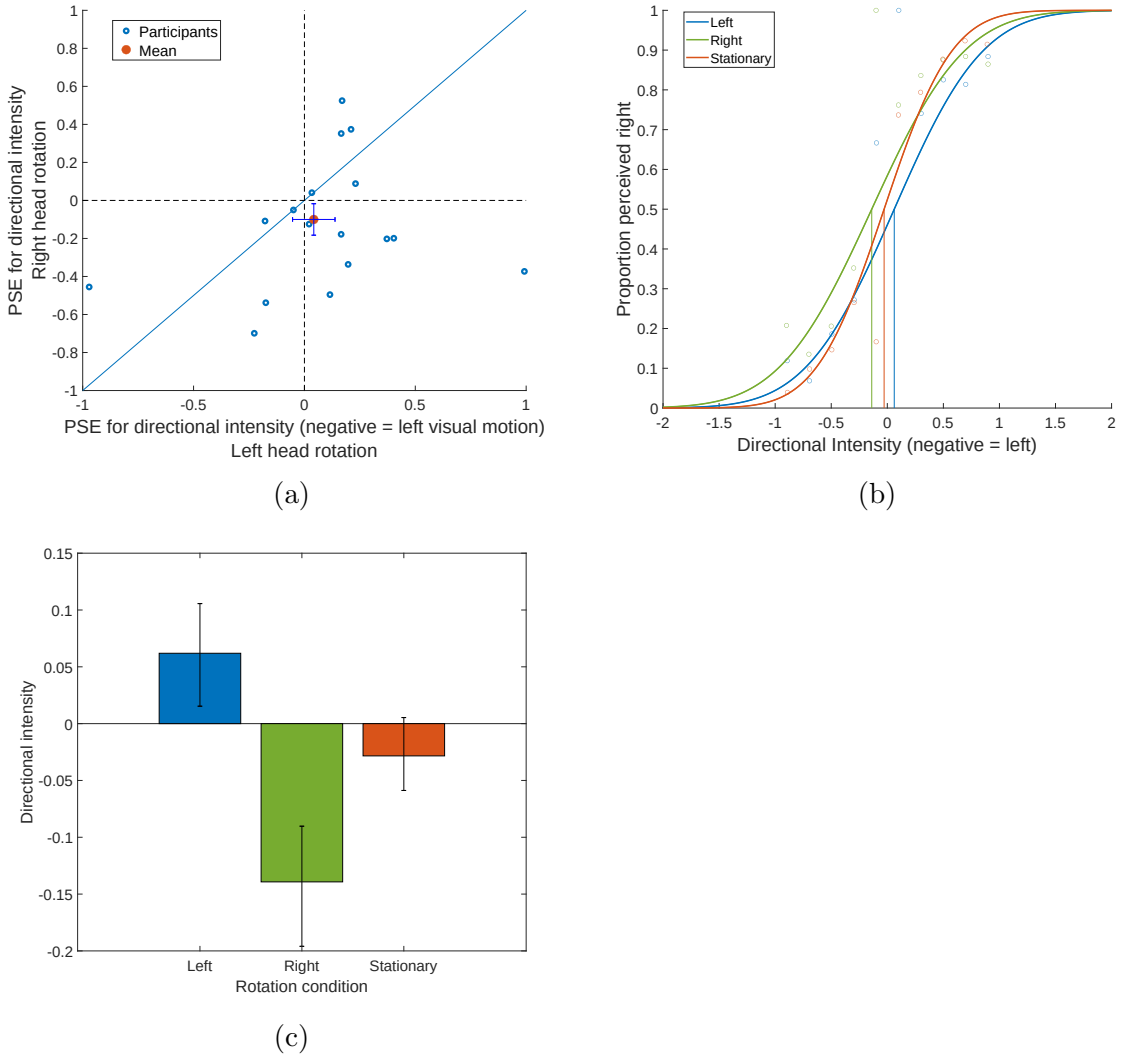

Figure 3.4: Bias to follow head rotations.
(a) PSEs for directional intensity with left visual motion coded as negative. Threshold values for leftward-rotation trials for each subject were plotted against the corresponding threshold values for rightward-rotation trials and the dashed line shows the equality line. The group mean is off the diagonal in the lower half and suggests a bias to make visual motion responses consistent with the direction of head rotation. Participants with missing data not shown. (b) PMFs generated for a super participant showing a shift in average threshold value for each rotation condition. (c) Average threshold value for each rotation condition after super participant data was bootstrapped 1000 times. Error bars show 95% confidence intervals.

3.4 Experiment 2: Further investigation of congruence bias

Experiment 1 found that incongruent visual-active vestibular motion impaired motion detection thresholds. Interestingly, participants also exhibited a significantly increased likelihood to report left or right perceived motion when performing the same direction of head-turn. In Experiment 2 we removed the mapping of left/right response options in a revised version of our task to investigate this bias to report congruent motion in the absence of overlapping left/right response criteria.

3.4.1 Methods

Participants

Twelve participants were recruited from the University of Sydney undergraduate Psychology cohort, and one was removed for failing to achieve 75% accuracy. The remaining 11 had corrected-to-normal vision and no neck or vestibular conditions, were naïve to the purposes of the experiment and gave informed consent prior to participation. The study protocol was approved by the University of Sydney Human Research Ethics Committee (HREC 2021/048).

Stimuli

The motion signal was generated following the same method as in Experiment 1. The aperture occupied 10.00 x 10.00 °va. To aid fixation the stimulus contained a central inner grey square and fixation cross, occupying 2.29 and 1.17 °va respectively. In this experiment, however, the stimulus was split into an upper and lower half, with the motion occurring in one half only, again moving either leftward or rightward (see Figure 3.5). Participants responded using the up or down arrow keys to indicate which half of the stimulus (upper or lower) contained the motion, regardless of its direction. The task thus emphasised motion detection.

Procedure

Procedure for motion cueing was the same as Experiment 1 (following a head guide). Judged from head rotation data in Experiment 1, the presentation of the stimulus in the current experiment was delayed slightly to better ensure the stimulus was viewed during linear acceleration. The stimulus was therefore presented 1.2 seconds after the arrival of the motion guide with 400 ms duration. Participants indicated which half of the stimulus contained the visual motion using the up and down arrow keys. Participants completed a practice version of the experiment to get used to following the head guide and responding to the stimulus. The practice experiment consisted of 30 trials (10 stationary, 10 with congruent motion and 10 with incongruent motion, with equal split of motion travelling left or right within each condition). In the experiment proper, each participant completed two back-to-back sessions of 180 trials each (2 stimulus directions x 3 head rotations x 30 trials per condition) giving a total of 360 trials per participant. Presentation of the stimulus in the upper or lower hemifield was equally distributed in each condition. All trial types were presented

in a random order within each session. A Quest adaptive staircase controlled the stimulus intensity for each trial to maintain 75% correct performance.

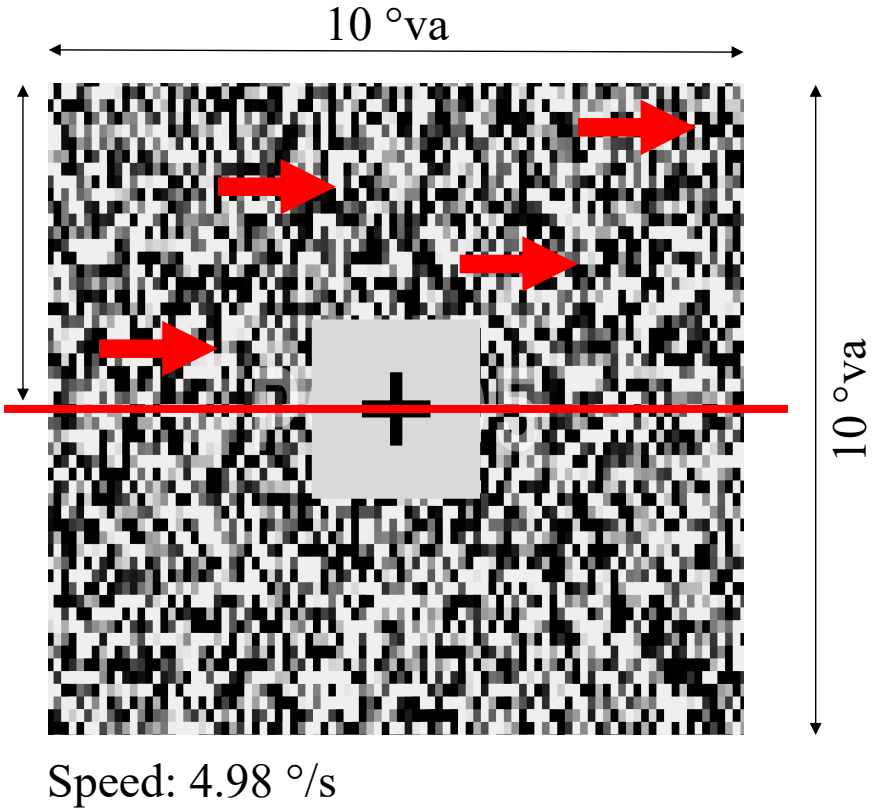

Figure 3.5: Stimulus for Experiment 2.
The motion signal was only presented in the upper or lower half (with the other half stationary). The task became a two-alternative forced-choice: which half (upper or lower) contained the motion? This removed the possibility of response bias and isolated sensitivity to the motion task. The red line and arrows are for illustration purposes only and were not present in the actual experiment.

3.4.2 Results

All head rotations increase visual motion detection thresholds

A 2x3 repeated-measures ANOVA (stimulus motion vs head rotation) showed that visual motion direction (left/right) did not significantly affect motion-detection thresholds ($F(1,9) = 0.26$, $p = .62$). In contrast, a significant main effect of head congruency was observed ($F(2,18) = 10.68$, $p < .001$, $\eta_p^2 = 0.54$). The interaction between congruence and direction was also non-significant ($F(2,18) = 2.24$, $p = .14$). Post-hoc pairwise comparisons (Bonferroni corrected) showed both congruent and incongruent conditions resulted in significantly higher thresholds than the stationary condition ($t(9) = 3.24$, $p = .01$, $d = 1.03$ and $t(9) = 4.47$, $p < .001$, $d = 1.41$, respectively). Unlike in experiment 1, congruent and incongruent conditions were found not to differ significantly from each other ($p = .70$, see Figure 3.6). We performed an additional linear mixed effects analysis to confirm our main results

while accounting for the influence of individual participants as random effects. Including congruence ($\chi^2(2) = 16.62$, $p < .001$), but not direction ($\chi^2(1) = 0.61$, $p = 0.44$), or their interaction ($\chi^2(1) = 2.90$, $p = 0.23$), significantly improved upon the model fit.

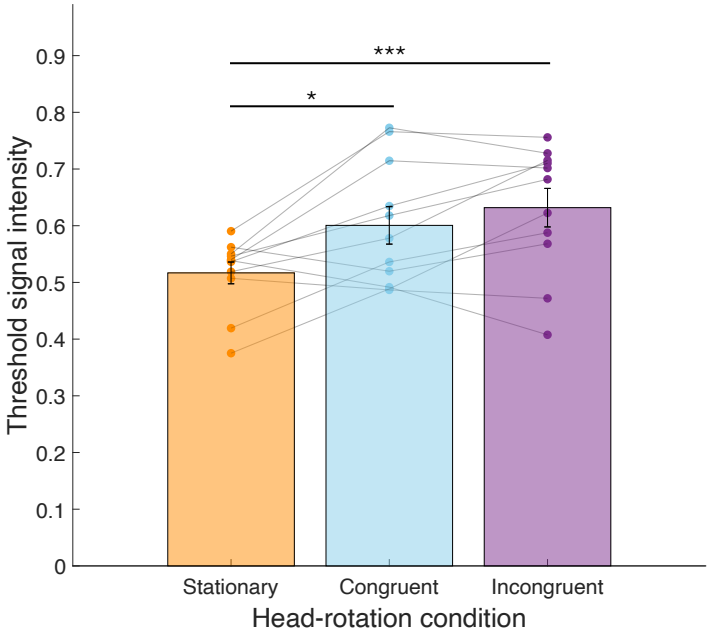

Figure 3.6: Average thresholds for visual-active vestibular motion conditions (collapsed across left/right stimulus motion directions).
A repeated-measures ANOVA with post-hoc comparisons indicated motion thresholds when stationary were significantly lower than during both congruent and incongruent head rotations. Dots indicate individual participants, columns show the group mean with error bars showing standard error of the mean. * denotes $p < 0.05$, *** $p < 0.001$.

Speed of head rotation

We analysed participants' ability to follow the head guide and any potential effects of rotation speed on visual motion detection thresholds. As in Experiment 1, Figure 3.7 clearly shows participants' ability to follow the head guide accurately and precisely. A linear model showed when turning right, there was no significant correlation between rotation speed and threshold ($R^2_{Adj} = 0.015$, $F(1,9) = 1.15$, $p = 0.31$). The same was found for leftward head rotations ($R^2_{Adj} = 0.14$, $F(1,9) = 2.67$, $p = 0.14$).

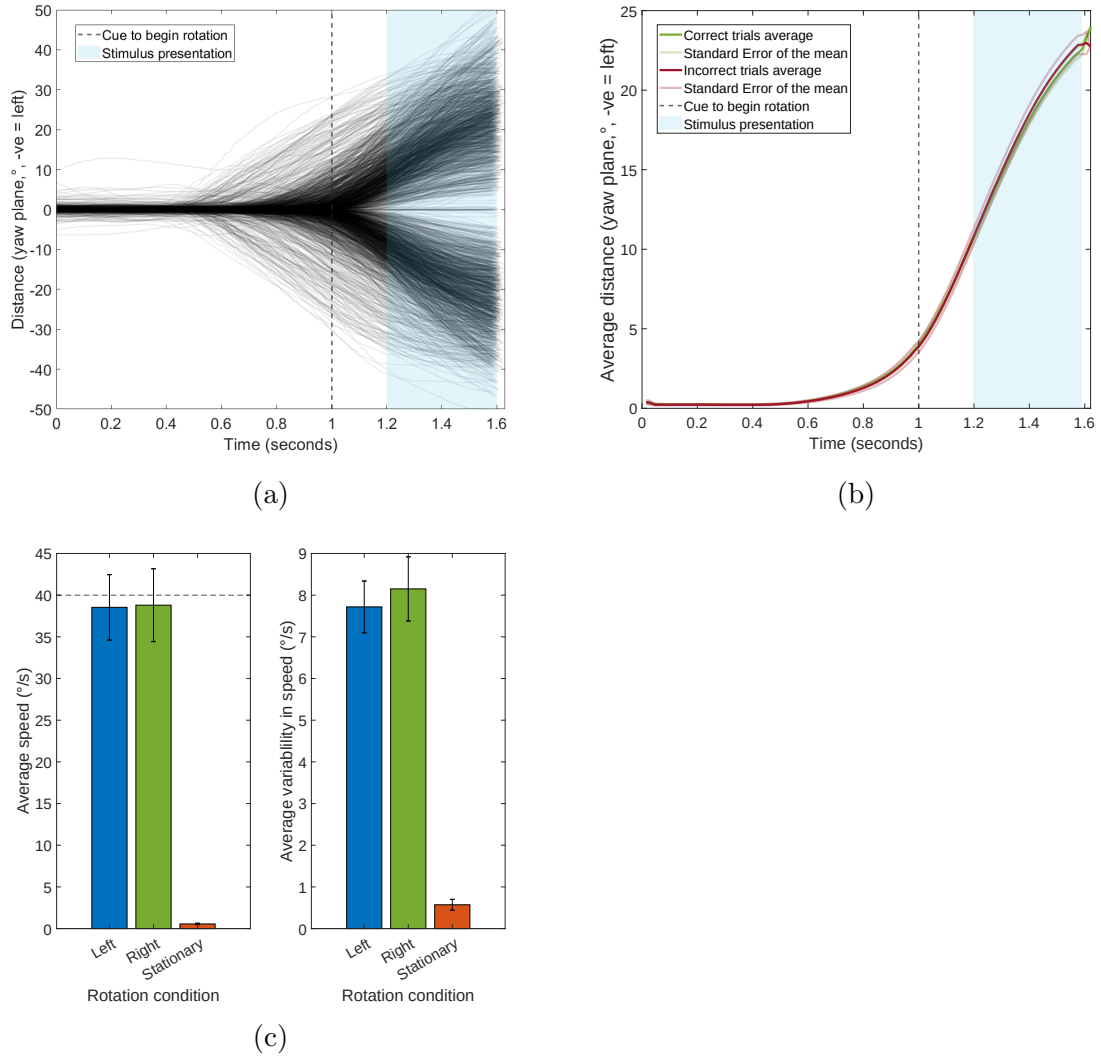

Figure 3.7: Head rotations Experiment 2.
(a) The cue to begin the turn came from the head guide (travelling st 40°/s) reached a centre marker. Trials with erroneous rotations were removed before analysis. (b) Average absolute value of trajectories across participants for trials that were correct or incorrect. Shaded lines represent SEM. (c) Average speed and variability of head rotations, error bars represent SEM. A dashed line at 40°/s indicates speed of head guide.

3.5 Discussion

In this study we tested visual motion detection thresholds in the presence of congruent and incongruent head rotation. In two experiments, participants were tasked with performing brief rotational head movements in a VR environment and to indicate whether the retinal motion of a stimulus presented in a fixation-centred display was moving leftward or rightward (Experiment 1) or whether motion (in either direction) was present in the upper or lower hemifield (Experiment 2). We discovered elevated motion thresholds for active head rotations, in particular during incongruent visual-active vestibular stimulation.

Analysis of subjects' ability to follow the head guide across both experiments showed participants, while on average a little slower (but not significantly) in turning their head than the speed of the guide, can accurately and precisely follow the guide to perform active head rotations. This validates the current method as a viable paradigm for studying the influence of head rotation on visual motion perception. In addition, the ability to track the entire course of each rotation allows analysis of the true speed of each participant, if desired.

It therefore unclear whether a low-level physiologically-driven perceptual effect or higher-level directional bias accounts for the results in Experiment 1, given lack of replication in Experiment 2. The increased motion threshold during head rotation may result from an increased likelihood of attributing motion signals to self-motion during incongruent head rotations, owing to a world-stationarity prior (T. C. A. Freeman et al., 2010; Weiss et al., 2002; Welchman et al., 2008). Specifically, as most incongruent visual motion signals are frequently attributed to self-motion in everyday activities, this strong prior could result in significantly higher thresholds for perceiving incongruent visual motion, as found in Experiment 1. This supports the hypothesis that visual motion viewed while turning the head in an opposite direction must be stronger than when viewed while turning in a congruent direction (or remaining stationary), in order to overcome the bias to perceive such visual motion as "normal" scene-shift resulting from self-motion (T. C. A. Freeman et al., 2010; Weiss et al., 2002; Welchman et al., 2008). This could be driven by cells tuned selectively for incongruent visual-vestibular rotation in MSTd (Takahashi et al., 2007). However, participants were also found to have a bias to report the same direction of motion as their head rotation, potentially resulting in a higher rate of incorrect responses for cases of incongruent motion, and a higher correct rate for congruent motion. To test this, Experiment 2 used a two-alternative forced-choice task to remove this potential response bias to better determine whether the results were driven by low-level differences in visual motion sensitivity, or by a response-level directional bias. Interestingly, the motion threshold results showed that congruent head rotations did not produce better performance than incongruent rotations. This finding can be contrasted with results of analogous eye tracking studies which show that smooth pursuit eye movements produce a benefit for the tracked stimulus (e.g., Greenlee et al., 2002; Spering et al., 2011. We suggest that functional benefit may not apply to tracking achieved via active head rotation once response confounds are controlled to isolate threshold sensitivity.

3.5.1 Self-motion bias in visual motion perception

The demonstration of a self-motion bias is intriguing and could represent a low-level bias that upweights vestibular cues when visual stimuli are close to threshold in an attempt to gain a more reliable percept of veridical motion after multisensory integration (Ernst & Banks, 2002; Ernst & Bülthoff, 2004; Morgan et al., 2008). On the other hand, the fact that participants were biased to report the direction of head rotation could also be explained by a higher-level response bias to answer in line with head rotation when stimulus uncertainty is high. This is supported by other findings of correlated heading and object motion biases (Dyde & Harris, 2008; Wu et al., 2021; Xing & Saunders, 2022). For example, Xing and Saunders (2022) found that perceived heading based on both visual and vestibular cues positively correlated with judgements of object motion, akin to the correlated rotation-direction decisions in the current study. Dyde and Harris (2008) found that for an object to appear stationary, it had to move with the motion of an observer, to counteract the effect of observers perceiving the object to be moving away from them when truly earth stationary. This could be an example of an incorrect accounting of motion signals, which could also be driving the higher rotational thresholds in the current experiment.

In other related work, Wu et al. (2021) used context trials of random-dot kinematograms (RDK) travelling in a certain direction within a trial block to build an expectation of direction. When shown a low-coherence RDK and asked to indicate perceived direction, participants showed a perceptual repulsion bias such that direction judgements were made in a direction opposite the expected direction. If an opposite visual signal is expected when a rotation of the head is made, then a similar repulsion bias in the current experiment would result in greater numbers of responses in the direction of the head turns. These prior findings could explain the bias in the current experiment and the subsequent differences in threshold for congruent and incongruent conditions. Further, Wu et al. (2021) showed by manipulating the coherence of a motion signal in a RDK that the repulsive effect was not due to low-level adaptation but rather to a perceptual bias. It was also present when eyes were fixated so also could not be attributed to eye movements themselves but rather a system that prioritises processing of novel or "unexpected" stimuli. The perceptual bias and priority processing supports the favoured explanation of the current results. Namely, if oppositely-tuned visual-vestibular rotation cells in the MSTd suppress the expected incongruent motion of a shifting stationary scene due to self-rotation, an "unexpected" congruent motion signal, which is more likely therefore to signal object motion, could be more easily perceived. This is supported by Alais et al. (2021) findings that during binocular rivalry between competing leftward and rightward visual motions, the direction congruent with the direction of active or passive self-rotation is perceived. Priority processing of congruent visual motion is also consistent with findings of a vestibular boost of visual motion processing (Hogendoorn et al., 2016, 2017).

It is therefore unclear whether a low-level physiologically-driven perceptual effect or higher-level directional bias accounts for the results in Experiment 1. In an attempt to at least partially answer what is the driving force behind these results, Experiment 2 decoupled the perception of motion from direction judgement, so the possible low-level effects of visual-active vestibular motion perception could be explored. In Experiment 2, instead of responding with a left-right arrow press to

indicate perceived direction, participants instead indicated whether they detected motion at all, regardless of leftward or rightward direction, in the upper or lower half of the stimulus. Interestingly, this method showed no significant difference between motion thresholds for incongruent and congruent head turns, and both were significantly higher than thresholds for viewing motion while stationary. This pattern of results lends favour to bias driving the differences between congruent and incongruent thresholds observed in Experiment 1. Moreover, the finding that motion thresholds were elevated in a way that was not selective for visual motion/head rotation congruence supports the idea that it might arise from increased attentive, cognitive, or task demands associated with active movements and thus elevated thresholds (Heinrich et al., 2020; Lavie et al., 2004; Swallow & Jiang, 2013). Specifically, requiring participants to follow a head guide while also judging stimulus motion direction could be considered a dual-task paradigm, which is known to have performance costs (Bourke et al., 1996; Lavie et al., 2004), especially for dual-tasks of common modalities as in the current case (Treisman and Davies, 1973, as cited in Bourke et al., 1996).

3.5.2 Smooth-pursuit comparisons

It was hypothesised that congruent head rotations in the current experiment could mirror results of MacNeilage et al. (2012), where object discrimination thresholds were significantly lower when accompanied by congruent vestibular cues, compared to just visual cues from optic flow. However, no such benefit was found in Experiment 2 as congruent and incongruent rotations showed no significant difference for visual motion detection thresholds, and both were significantly increased from stationary. An explanation might be found in smooth-pursuit eye-movement literature. While such movements have been found to aid perception of coherent visual motion when compared to fixation (Greenlee et al., 2002) in addition to direction and speed judgements, lowering perceived motion smear, and improving motion coherence (see Spering and Montagnini, 2011 for a review), smooth pursuit has also been found to worsen motion perception (Spering & Montagnini, 2011), with two well-known examples being the Filehne (Mack & Herman, 1973) and Aubert-Fleischl phenomena (Dichgans et al., 1975), where direction and speed judgements respectively are impaired, again in comparison to fixation. More recently, Arathorn et al. (2013) found whenever retinal image motion was opposite to eye motion, the perception of the relative motion was reduced. Finally, Krukowski et al. (2003) found no difference in direction perception between fixation and smooth pursuit conditions.

It seems then that current results from tracking achieved via active head rotation may align more closely with findings suggesting perceptual costs of smooth-pursuit eye movements, rather than those reporting perceptual benefits. Whether this is due to the active nature of the movement, with potentially noisy motor and proprioceptive signals to be processed in addition to vestibular signals, or a worse ability to account for vestibular signals when processing visual stimuli, remains unknown without a passive case comparison.

3.5.3 Active vs Passive perception

The difference in ability to accurately perceive visual motion while rotating the head compared to the head-stationary condition could also signal a general effect of imperfect estimates of the self-motion signal (Britton & Arshad, 2019; Dupin & Wexler, 2013; Dyde & Harris, 2008; Garzorz et al., 2018; MacNeilage et al., 2012; Xing & Saunders, 2022; Zeng et al., 2023). In essence, robust visual motion perception during self-motion relies on accurate accounting of such self-motion so that object motion can be disambiguated and veridically perceived. It is often theorised that this calculation relies on an efference copy of a motor command being used to predict the sensory outcome, with the prediction then used to subtract motion generated by self-motion from the incoming signal (reafference), leaving only motion generated from external sources (exafference) to be perceived (Cullen, 2012; Roy & Cullen, 2001). In the current study, this would mean trials requiring a head rotation would generate an expected visual signal in an opposite direction to the head turn, which in an ideal system would be accounted for when assessing the presence of any exafferent motion. However, it is widely thought that this accounting is not perfect, and resulting errors in motion perception are common (Britton & Arshad, 2019; Dupin & Wexler, 2013; Dyde & Harris, 2008; Garzorz et al., 2018; MacNeilage et al., 2012; Xing & Saunders, 2022; Zeng et al., 2023). These errors are thought to arise from an incorrect subtraction of eye-movement from retinal motion, resulting in an over or under estimation of target motion (Dupin & Wexler, 2013; Rushton & Warren, 2005). In particular, Swanston and Wade (1988) found pursuit movements of the head were less effectively compensated for than movement of the eyes. Our eyes are specialised to make fast, precise movements, whereas our heads are much heavier and would take a greater effort to turn. This increased resistance could lead to greater variability in head rotations which in turn could increase the variability in the theorised subtraction process for veridical motion perception. Further, high variability can lead to an increased reliance on priors, which as discussed above, would in the current case translate to an increased expectation for the world to be stationary (T. C. A. Freeman et al., 2010; Weiss et al., 2002; Welchman et al., 2008). These fundamental differences could explain why congruent rotations of the head did not provide any benefit to perceiving visual motion, in contrast to what was predicted based on findings in smooth pursuit eye movements.

Sensory reafference is only possible in cases of active self-motion, as passively stimulating the vestibular system would not generate any prior motor commands. Active perception also involves proprioceptive signals for self-motion, in addition to vestibular ones and without comparison to a passive case, disambiguating the effect of each component is impossible. Since vestibular nuclei show a reduced responsiveness to vestibular afferent signals when motion was generated by an active head turn (Roy & Cullen, 2001), investigating the effect of active vs passive interactions on visual motion thresholds should be a key focus for future studies. For example, a motion platform could be used to passively rotate an observer at a rate matching the active head rotations used in these experiments and thus isolate the vestibular contribution to the effects reported here. It is important to differentiate between cases of active and passive perception as a growing body of literature is finding that active movement can have significant effects on our sensory functions (Alais et al., 2021; Davidson et al., 2023).

3.5.4 Foreground vs background motion

Another limitation of the current study was the fact that the depth of the visual stimulus was somewhat ambiguous. Swanston and Wade (1988) suggest that different to eye movements, head movements need a 3D compensation that accounts for perceived egocentric distance of an object of interest, so judgements of object distance could affect compensation of self-motion when judging object motion. If different participants were perceiving the current stimulus at different depths, perception of visual motion could have been impaired and thus masked any underlying effect of congruence. Dupin and Wexler (2013) highlight that motion of a scene's background does affect perceived motion of a foreground object. Dyde and Harris (2008) found that errors in depth, while not fully explaining impairment in motion perception, do influence results. In addition to this literature, it follows common sense that our motion processing system might treat foreground and background motion differently, given the background as a whole is more likely to be stationary, causing an opposite visual motion signal to self-rotation. On the other hand, objects in the immediate foreground of a scene may be more likely to be attached to the body in some way (e.g. a tea cup being carried) and therefore generate motion signals congruent with the body. Either way, object motion would not take up the entire scene like a scene-shift signal would, and therefore could be highlighted as a potential object of interest. Future studies should investigate the potential differential processing of congruent and incongruent self-motion signals on perceptual thresholds for foreground and background motion.

3.5.5 Conclusion

The direction of active rotational head movements do not appear to influence visual motion thresholds other than to increase thresholds when compared to viewing motion while stationary. These findings contrast with prior research on the advantage of tracking and smooth-pursuit eye movement. It is recommended that future research incorporate the active and passive generation of vestibular signals to develop a greater understanding of the role of rotational self-motion on visual motion perception.

3.6 Acknowledgements

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Chapter 4

Perceived direction of visual motion is pulled towards direction of head rotation

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It is available as a preprint at: 10.31234/osf.io/5ay2s.

Abstract

In order to effectively navigate the world around us, we must be able to correctly attribute motion signals to a wide variety of sources, including ourselves. Previous research has examined how we accurately split visual motion signals into those caused by self-motion or object motion, however this misses the key fact that we are active observers in our environment. To understand how we successfully disentangle complex motion signals, we must investigate how active components of self-motion signals might influence visual motion perception. The current study utilises virtual reality (VR) technology to investigate perceived direction of visual retinal motion across two experiments during active head rotations. Experiment 1 investigates the influence of horizontal active head rotations on the perceived direction of motion for 16 motion angles spaced equally around 360°. Experiment 2 additionally manipulated the strength of visual motion signals in order to examine how vestibular and visual signals might be weighted when one sensory signal is unreliable. In both experiments, perceived direction of visual motion was consistently biased toward the direction of head rotation, demonstrating an influence of active movement on vision. In addition, directions of motion that were adjacent to the cardinal axes (e.g. ±22.5° from vertical/horizontal) were repelled away from the cardinal reference during head rotations and stationary conditions, indicating an additional effect of reference repulsion.

Keywords: active perception, multisensory, visual motion, self-motion, direction perception

4.1 Introduction

Our capacity to effectively navigate everyday environments relies heavily on our ability to accurately judge both self-motion, and motion of objects in the environment. Without this, actions such as crossing the street – which require judgements as to the source, speed and direction of multiple motion signals – would be impossible. Much of the research that has examined our ability to split motion in a scene into self and object motion has relied on simulation of self-motion using optic flow, rather than having subjects physically move themselves (e.g. Rushton et al., 2018; P. A. Warren and Rushton, 2007; Xing and Saunders, 2022). While understanding how we differentiate visual signals arising from simulated self-motion and object motion is important, relying on simulated movement lacks environmental validity as active movement involves a much more complex self-motion signal. Active self-motion consists of motor predictions and re-afferent sensory signals, and proprioceptive and vestibular input, in addition to self-motion induced optic flow (Cullen, 2012; Roy & Cullen, 2001). It is currently not well understood how these additional signals, which are ubiquitous in natural behaviour, may influence the perceived direction of visual motion.

One impediment to incorporating active behaviour into studies of visual perception has been the conflicting demands of enabling free-movement while maintaining experimental control. The current study utilised virtual reality (VR) technology in order to mitigate these demands, as VR allows the total control of the visual environment while simultaneously allowing natural movement of subjects. By using visual stimuli that are tightly controlled within the head-mounted display (HMD) this technology can enable a better understanding of how our brain integrates motion signals arising from everyday self-motion with object motion, and therefore provide greater insight into how we accurately and effectively perceive our moving surroundings. We focus on the perceived visual motion direction during active head rotations either to the horizontal left or right, and compare performance to stationary conditions (Experiments 1 and 2), across a wide range of visual motion angles (Experiment 1) and with different levels of visual signal intensity (Experiment 2).

We focused on visual direction perception during active head rotations for several reasons: first, in all cases apart from smooth-pursuit movements, self-motion signals arising from eye or larger head movements cause the retinal signal of object motion to differ from the true physical motion, and consequently the self-motion must be compensated for in order to accurately perceive the physical motion of an object (Halow et al., 2023; Souman et al., 2005; Swanston & Wade, 1988). Previous research has indicated that the compensation for eye and head movements may distinctly contribute to object motion perception. Souman et al. (2005) found that eye-movements are incorrectly compensated for, resulting in perceived object motion pulled towards direction of eye movement, and Swanston and Wade (1988) compared head and eye movements and found head movements resulted in poorer estimates of motion direction. However, when testing participants' direction perception of retinally-stable visual motion while being passively rotated on a motion platform, Hogendoorn et al. (2017) found direction perception was pulled towards the direction of the head turn. They theorised this was due to a left-over compensation from a system designed to discount self-motion from retinal motion to perceive true physical motion, as discussed in the eye movement studies above. Indeed,

Krukowski et al. (2003) found direction discrimination thresholds to be equal, regardless of whether the eyes were fixated or engaged in smooth-pursuit of the motion target. However, the critical influence of active head rotations has not been investigated. In the present study, we have fixed the visual stimulus to head position, to reduce the influence of retinal motion on visual motion perception, and isolate the influence of active-head rotations. We hypothesised that although the additional action-vestibular signal is task-irrelevant, it will nevertheless be compensated for by a system designed to discount self-motion, resulting in direction perception being pulled towards the direction of the head turn, in line with findings from both eye movement (Souman et al., 2005) and whole-body rotation studies (Hogendoorn et al., 2017).

Multisensory integration is known to rely on the cue reliability of individual sensory modalities (Alais & Burr, 2004; Alais et al., 2010), enabling a test in our paradigm of how active-head rotations interact with the reliability of visual motion signals. Physiological studies of multisensory visual-vestibular cells have found visual signals to be weighted in cue-combination paradigms differently depending on their reliability (Chen et al., 2011c; Morgan et al., 2008). To test the potential weightings of visual and action-vestibular signals in direction perception, we manipulated visual motion signal strength in Experiment 2. It was hypothesised that as the visual motion signal degrades, the influence of the vestibular signal would increase (Alais & Burr, 2004; Alais et al., 2010), resulting in a greater error in perceived direction, towards the direction of head rotation. Generally, we predicted the error in perceived motion direction would be greatest for motion viewed while rotating, compared to the stationary control condition, due to increased task demands and noise stemming from the head rotations (Lavie et al., 2004; Swanston & Wade, 1988). Additionally, direction perception was predicted to be most accurate for cardinal motion direction conditions, in line with well-reported oblique effects in motion direction perception (Appelle, 1972; Gros et al., 1998; Karim & Kojima, 2010; Krukowski et al., 2003; Loffler & Orbach, 2001).

To preview our results, across both experiments perception of visual motion direction was pulled in the direction of head rotation. Perceived direction error was greatest for angles adjacent to the cardinal (horizontal and vertical) axes and always in a direction repulsed away from the nearest cardinal reference. The amount of error in perceived direction during head turns decreased as visual motion intensity increased, suggesting a decreased reliance on the action-vestibular signal on motion direction judgements.

4.2 General Methods

4.2.1 Apparatus

The head-mounted display (HMD) used to present the stimulus was a Vive Pro Eye. This had a resolution of 2880 x 1600 pixels (1440 x 1600 per eye), a refresh rate of 90 Hz and a horizontal field of view (FOV) of approximately 110°. The virtual environment and stimuli was rendered with a NVIDIA GeForce RTX 2080 Ti graphic card and programmed in Unity version 2020.2.4f1 using the Steam VR plugin (v1.21.12), running on Windows 11 version 10.0.22621 on an Alienware Aurora R8.

4.2.2 Data Analysis

All data was processed and visualised using Matlab R2022a. Statistical analyses were completed using JASP 0.17.1.0.

4.3 Experiment 1: Direction perception

The first experiment measured visual motion direction perception by varying the angle of stimulus motion, while observers were either stationary or making a head rotation to the right or left on the horizontal plane. The direction and speed of head rotation were controlled by having subjects pursue a motion guide (see Figure 4.1).

4.3.1 Methods

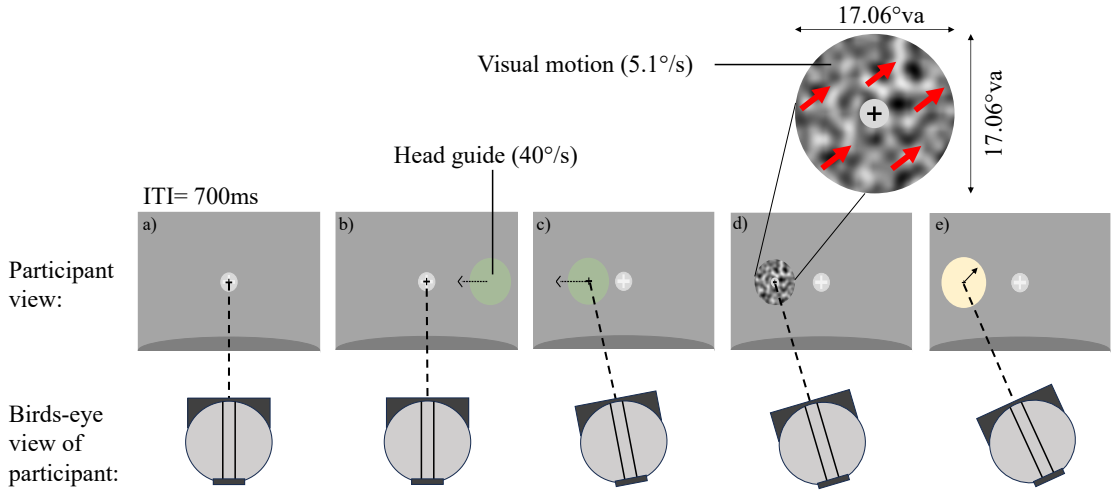


Figure 4.1: Example trial sequence with leftward head rotation (not to scale). a) The VR scene displayed a world-centred marker (grey circular region with cross) which participants would align with their head-centred fixation cross. b) The trial began with a coloured motion-guide entering participants' periphery and translating horizontally across the screen at 40 °/s. This indicated the direction and fixed-speed of the required head rotation. Participants were instructed to monitor the guide as it approached their fixation point and prepare to make a head turn to follow it. c) Once the guide reached the world-centred marker, participants initiated a head turn at a rate which kept their head-centred fixation cross centred on the motion-guide, while keeping their eyes on the head-centred fixation cross. In this way the head-centred cross provided live feedback as to how closely they were following the guide. The motion-stimulus would appear after 1.2 seconds, approximately in the middle of the head-rotation. Red arrows represent an example direction of motion and were not present during the actual experiment. e) After 400 ms the stimulus was replaced by the response display, which was a plain circle with a radial arrow. Participants indicated the perceived direction of motion by using the left and right arrow keys to orient the on-screen arrow to the perceived direction of the stimulus. The motion signal consisted of Perlin noise drifting at one of 16 angles spaced at 22.5° intervals around the circle, starting at right horizontal (0°). The speed of the visual motion was 5.1 °/s. View a short video of the procedure at https://osf.io/ar3yx/. https://osf.io/ar3yx/.

Participants

Twenty-two individuals participated in the experiment. Participants had no vestibular conditions or neck issues and had corrected-to-normal vision. They were recruited via the University of Sydney SONA psychology undergraduate pool, and were each compensated with one percent of their course mark for the one-hour study. All participants were naïve to the purposes of the experiment and gave informed consent prior to participation. The study protocol was approved by the University of Sydney Human Research Ethics Committee (HREC 2021/048).

Stimuli

The motion signal consisted of a translating circular aperture containing a patch of Perlin noise (Perlin, 1985) drifting at a speed of 5.1°/s. Perlin noise is a pseudo-random alternative to white or Gaussian noise that is preferable for its more natural appearance, owing to apparent structure at low spatial frequencies. The generated pattern travelled in one of sixteen directions spaced at 22.5° intervals around the circle, starting at horizontal to the right (0°). The aperture occupied 17.06 °va and was locked to participants' head position such that when a participant turned their head, the aperture containing the stimulus always remained in the centre of participants' vision so that the retinally defined speed within the aperture was fixed at 5.1 °/s and orientation of motion remained constant. Consequently there were no eye movements necessary to follow the stimulus and the stimulus aperture was not moving across the retina. To limit retinal motion stemming from confounding eye movements, a fixation cross of 0.60 °va surrounded by a grey circle occupying 1.00 °va was presented in the centre of the stimulus to aid steady fixation.

Procedure

To begin each trial, participants aligned a head-centred fixation cross with a world-centred forward marker so the eyes and head were fixated centrally. The spawning position of a circular head-guide indicated the required upcoming head movement. Specifically, when the head guide appeared centrally, participants would keep their head stationary. Otherwise, the guide would enter from the edge of the display, appearing in participants' peripheral vision and travelling in a three-dimensional arc from one side of the display to the other at 40 °/s, thereby cueing the upcoming direction of rotation. After approximately 800 ms, the guide reached the central fixation point and participants would start turning their head to follow its motion. The guide was replaced by the stimulus after 1.2 s, which was roughly in the middle of the head turn (see Figure 4.1). The stimulus was presented for 400 ms after which a plain circle with an arrow (spawning at a random position around the circle) appeared on screen. Participants used the left and right arrow keys to point this arrow in the direction they perceived the stimulus to have moved, pressing the space-bar to record the desired orientation. Participants would then return their head to centre for the beginning of the next trial. Participants completed a practice experiment to ensure correct understanding of following the head guide and responding to the stimulus. The practice experiment consisted of 15 trials (3 rotations x 5 angles x 1 trials per condition). In the subsequent experiment, each subject participated in one session of 240 trials (16 angles x 3 head rotations x 5

trials per condition). Trial order was randomised. Participants were offered a chance to take a break from the experiment once completing each third of trials.

4.3.2 Results

Exclusion criteria

Absolute error in perceived motion direction was calculated by taking the absolute difference between displayed motion direction and angle of motion indicated. Absolute error was plotted for a super-subject and it was noticed there were some responses indicating close to 180° error in perceived direction, across all motion and rotation conditions. Using the stationary condition as a control, the probability of indicating a "reversal" of direction (> 90° error) was calculated for each participant by dividing the number of reversal responses in the stationary condition by the number of stationary trials total and multiplying the result by 100 to get a percentage indication of reversal trials. The average percentage of stationary trials classed as reversals was 18.75%, however with an individual minimum of 0% and maximum of 95%.

The significant error in direction estimation present even while stationary was taken as evidence of lack of attention or understanding from some participants, and they were therefore removed from analysis. The participants to be removed were decided using the isoutlier.m function, median method in Matlab. Eight participants were identified as outliers and removed, reducing the final sample size to 14.

As response reversal (error > 90°) indicated incorrect understanding or lack of attention, it was decided exclusion of data would also be performed on a trial-by-trial basis. Specifically, any trial with a response error > 90° was removed from analysis on the assumption the participant was not engaged with the task.

Head movements

Head position in three planes (yaw, pitch, roll) was recorded for every trial using the 3D head-tracking provided by the Vive Pro Eye HMD (90 Hz resolution). The time-course of head position in the yaw plane for every trial is shown in Figure 4.2 a). Before the exclusion of trials as described above, trials were classed as "correct within range" (response error < 90°) or "reversal" (response error > 90°), and the time-course of head rotations for each type of trial was visualised to assess the potential influence of changes in head trajectory on ability to judge motion direction. Figure 4.2 b) shows no difference in the average head rotations for correct and reversal trials. Figure 4.2 c) shows slightly increased movement during reversals on stationary trials, further justifying the exclusion of data on a trial-by-trial basis.

Direction perception

Error is greatest when rotating compared to remaining stationary

A 16 x 3 repeated-measures ANOVA (angle x head direction) showed a significant effect of head direction on absolute response error ($F(2,24) = 10.07$, $p < .001$, $\eta_p^2 = 0.46$). Bonferroni-corrected post-hoc analysis shows both right and left rotations resulted in significantly greater response error when compared to stationary ($t(25) = 4.04$, $p = .001$, $d = 0.58$ and $t(25) = 3.72$, $p = .003$, $d = 0.53$ respectively).

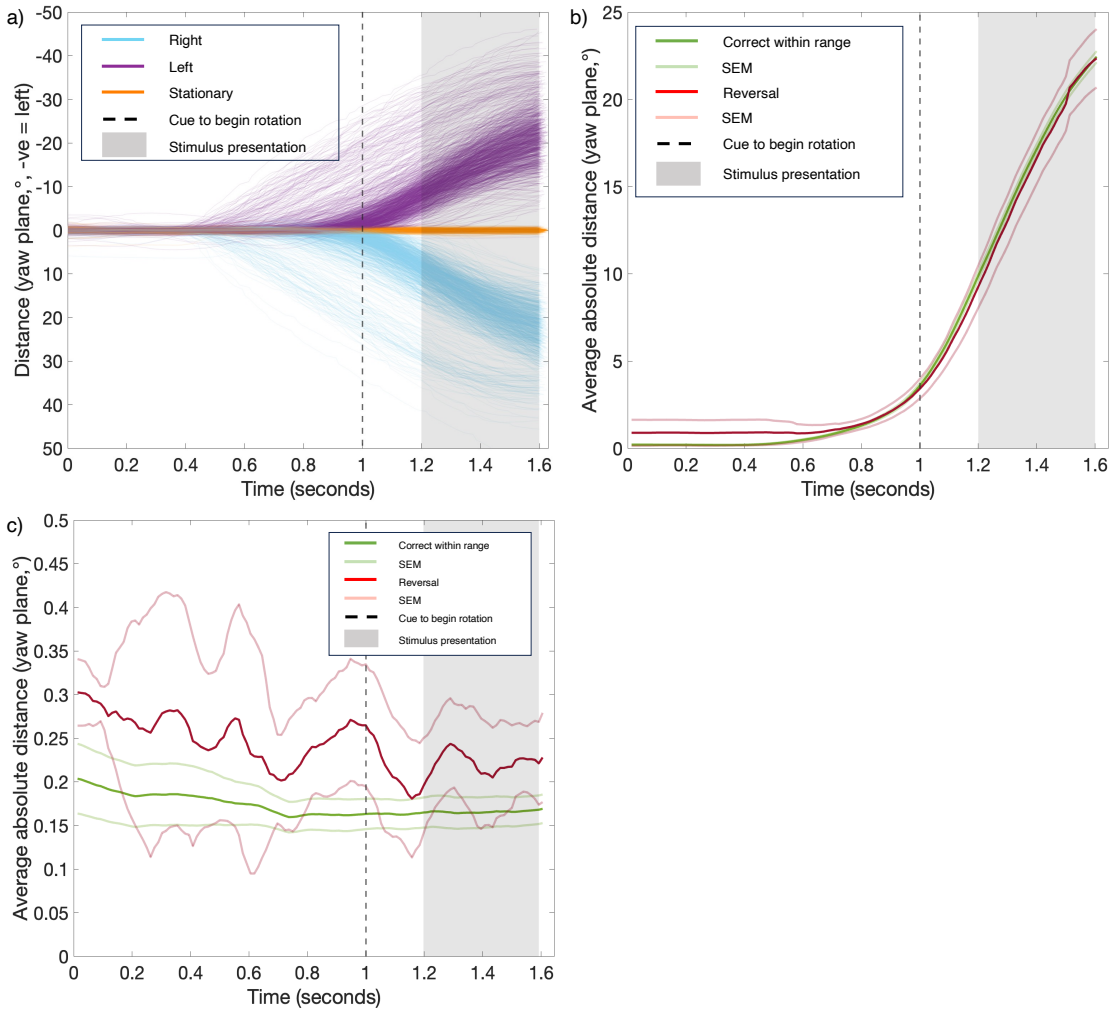


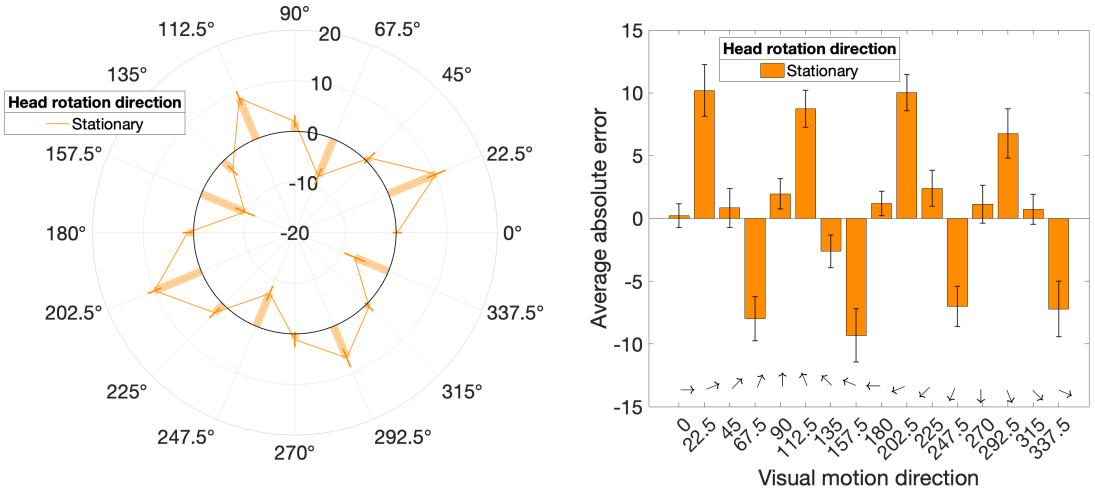
Figure 4.2: Head rotations Experiment 1.
(a) Trajectory of head position in the (horizontal) yaw plane for all trials across all participants. Each line represents an individual trial. The cue to begin rotation was when the head guide reached the world-centred forward marker. For stationary trials the guide would appear centrally and remain in place until replaced by the stimulus. (b) Average absolute value of trajectories across participants for rotation trials that were correct within range (error $< 90°$) or reversals (error $> 90°$). Note though that reversal trials were excluded from subsequent analysis. Shaded lines represent SEM. (c) Average absolute value of trajectories across participants for stationary trials that were correct within range or reversals.

There was no significant difference between right and left rotation conditions ($t(25) = 0.32$, $p = 1.00$).

Error in perceived direction when stationary depends on angle of visual motion

Relative error in perceived motion direction was calculated by subtracting the true angle of motion from perceived angle of motion, resulting in a relative error range between -180° and +180°. For all results, negative error represents an underestimation (responding clockwise to actual direction) and positive relative error captures an overestimation of true motion angle (with responses counter-clockwise to the actual direction). Figure 4.3 shows average relative error for each angle condition

when subjects were stationary. A pattern emerges such that very low relative error is reported for the cardinal directions of motion (horizontal and vertical), and for perfectly oblique angles (±45° from cardinal). For the remaining angles adjacent to the cardinal angles (i.e., ±22.5°, relative error increased, and in a direction that was repulsed away from the nearest cardinal reference. A 1 x 16 repeated-measures ANOVA on the average relative error for each motion condition showed a significant effect of true angle motion on perceived motion direction ($F(15,195) = 16.10$, $p < .001$, $\eta_p^2 = 0.55$).



(a) (b)

Figure 4.3: Stationary condition: average relative error in perceived motion direction.
(a) Relative error for each direction of motion displayed. Note the interior black circle marks 0° of relative error, with positive relative error values representing a counterclockwise error bias. Negative relative error values represent a clockwise error bias. Error bars denote ±1 SEM. (b) The same circular data unwrapped to visualise the consistent pattern of repulsion away from the cardinal axes.

Perceived direction of visual motion is pulled toward direction of head turn

As results from the stationary control condition clearly show baseline error rates across direction of motion are not equal, each participants' relative error at each angle for the stationary condition was subtracted from the active head rotation conditions, to investigate the influence of active head-rotations on motion perception relative to a stationary control. This allowed direct comparison between right and left head-rotations on direction perception. Figure 4.4a shows perceived direction before normalisation, panels 4.4b and 4.4c show responses after normalisation. It is clear after normalisation to stationary baselines that perceived direction of visual motion is pulled toward the direction of head rotation. For example, when rotating their heads to the right, participants' responses to angles in the upper hemisphere were pulled clockwise, and responses to angles in the lower hemisphere were pulled counterclockwise. This effect was strongest for vertical directions of motion, and absent for horizontal directions of motion (see Supplementary Figure 4.10). A 2 x 16 repeated-measures ANOVA (angle x head direction) therefore showed no significant effects for angle ($F(15,180) = 1.12$, $p = 0.34$) or head direction ($F(1,12) = 3.42$, p

= 0.22), but a significant interaction between the two ($F(15,180) = 8.54$, $p < .001$, $\eta_p^2 = 0.42$). Simple main effects testing showed there was a significant difference in relative response error depending on angle condition when rotating both right ($F(15,180) = 4.07$, $p < .001$, $\eta^2 = 0.32$) and left ($F(15,180) = 3.67$, $p < .001$, $\eta^2 = 0.29$). Simple main effects testing also showed there was a significant difference in relative response error depending on whether participants rotated to the left or right for half of the angle conditions. Supplementary Figure 4.10 displays the relative error for the cardinal (vertical and horizontal) directions of motion, which demonstrates systematic biases in visual motion perception for vertical directions of motion based on head turns, with no such effects found for horizontal motion.

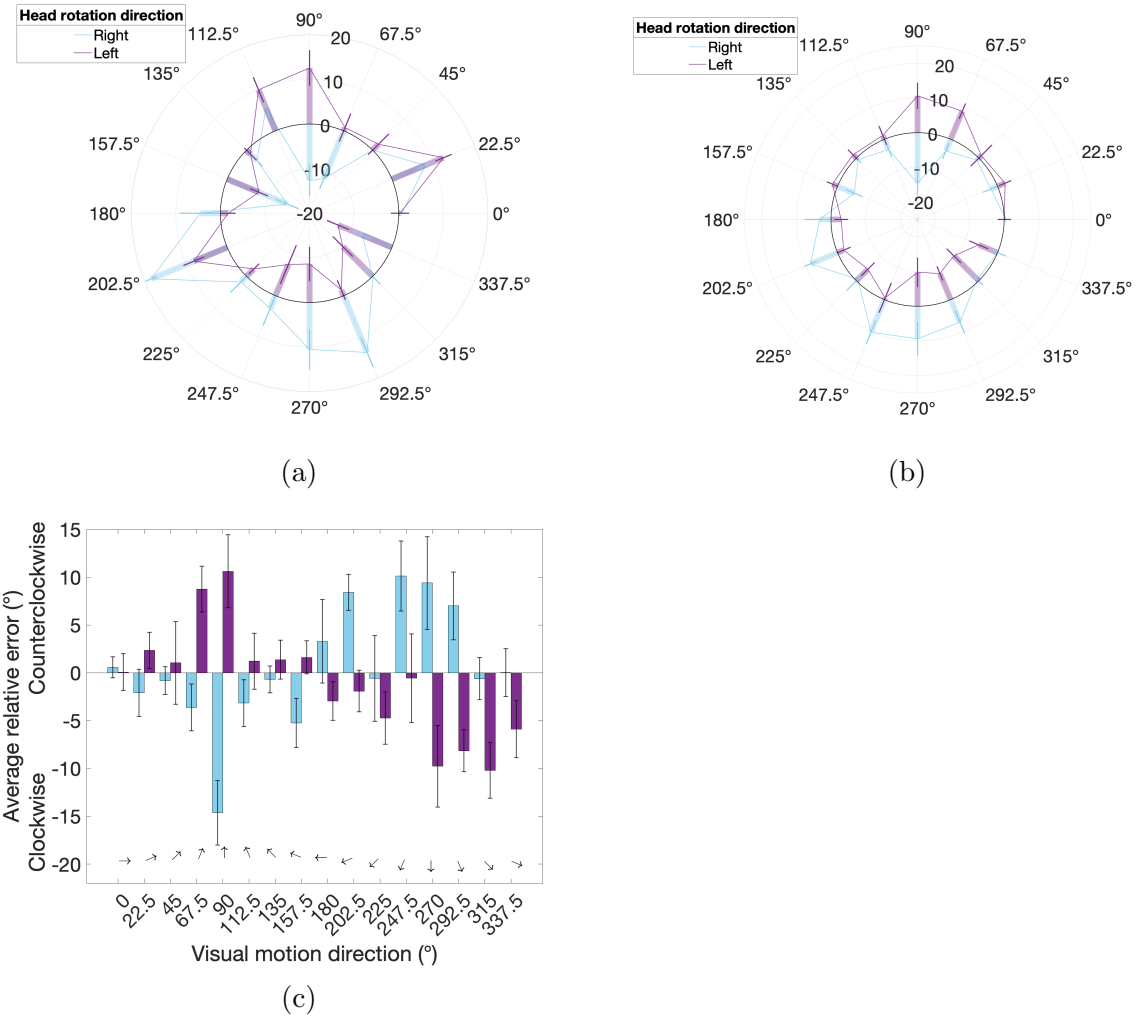


Figure 4.4: Head rotation condition: average relative error in perceived motion direction.
(a) Relative error for rotation conditions. (b) Relative error for rotation conditions normalised to participants averages for stationary condition. (c) Relative error for rotation conditions normalised to participants averages for stationary condition. Lines on ends of bars represent ±1 SEM.

4.4 Experiment 2: Manipulating strength of visual motion

Experiment 2 sought to replicate results from Experiment 1 while additionally investigating the influence of visual motion strength on the perception of visual motion direction and integration of action-vestibular signals. As such the method remains mostly the same, though the stimulus itself was changed to allow manipulation of visual signal strength. As the same pattern of results were found between upper and lower hemispheres in Experiment 1, angle conditions were reduced to just the upper hemisphere for Experiment 2.

4.4.1 Methods

Participants

Eighteen individuals participated in the experiment. Participants had no vestibular conditions or neck issues and had corrected-to-normal vision. They were recruited via the University of Sydney SONA psychology paid subject pool, with each subject being paid $AU20 for the one hour study. All participants were naïve to the purposes of the experiment and gave informed consent prior to participation. The study protocol was approved by the University of Sydney Human Research Ethics Committee (HREC 2021/048). Two participants were removed due to incomplete datasets which reduced the number for analysis to 16.

Stimuli

In order to control the signal intensity, the motion stimulus in Experiment 2 was generated using a luminance signal-to-noise ratio (LSNR) method as described in Lankheet et al. (2002) (see Figure 4.5). The motion signal consisted of an 80 x 80 pixel pattern (approximate pixel size was 0.2 °va), with individual pixel contrast values drawn from a normal-distribution between 0 and 1. Luminance was added to the signal pixel-by-pixel such that the signal was masked to varying degrees, depending on the signal-to-noise ratio. The average contrast of the noise pixels was adjusted using the formula $\text{Contrast}_{noise} = \text{sqrt}(1 - \text{Contrast}^2_{signal})$. This method allows the total contrast of the combined noise and signal values to remain constant while varying signal strength (Lankheet et al., 2002; van der Smagt & van de Grind, 1999).

The motion signal was presented at one of three intensity levels: low ($\text{Contrast}_{signal} = 0.5$), medium ($\text{Contrast}_{signal} = 0.75$) and high ($\text{Contrast}_{signal} = 0.99$). The motion signal travelled in one of 16 directions spaced at 22.5° intervals around the circle, starting at perfectly horizontal to the right (0°). The aperture occupied 17.06 °va and was locked to participants' head position such that when a participant turned their head, the aperture containing the stimulus always remained in the centre of participants' vision so that the retinally defined speed within the aperture was fixed at 12.8 °/s and orientation remained constant. Consequently there were no large eye movements necessary to follow the stimulus and the stimulus aperture was not moving across the retina.

Procedure

The method used to cue head rotation and record participant response was the same as that used in Experiment 1 (participants followed a head guide and oriented a bar to indicate perceived direction of motion). Participants completed a practice version of the experiment to get used to following the head guide and responding to the stimulus. This consisted of 30 trials (3 rotations x 5 angles x 2 trials per condition). In the experiment proper, each participant completed one session of 324 trials (9 angles x 3 intensities x 3 head rotations x 4 trials per condition). Trial order was randomised. Participants were offered a chance to take a break from the experiment once completing each third of trials.

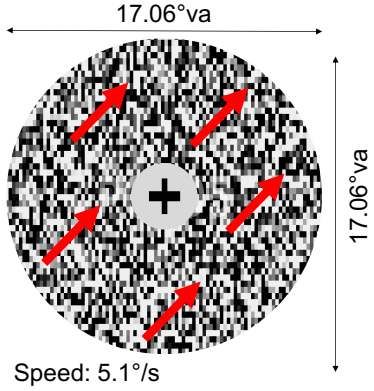


Figure 4.5: Motion stimulus for Experiment 2.
Motion strength was manipulated by varying the contrast ratio between signal and noise dots to titrate signal-to-noise (see Methods). It was presented at one of three signal intensities, low, medium or high. The red arrows are for illustration purposes only and were not present in the actual experiment.

4.4.2 Results

Exclusion criteria

As in Experiment 1, absolute error between perceived motion direction and actual motion direction was plotted for a super-subject and probability for indicating a reversal of direction ($> 90°$ error) was calculated for the stationary condition for each participant. Again using the isoutlier.m matlab function, two participants were removed, reducing the final number for analysis to 14. Exclusion of outliers was not performed on a trial-to-trial basis, as the low visual intensity condition could have resulted in large errors in perceived direction due to an intentionally difficult experimental design.

Head movements

Head position in three planes (yaw, pitch, roll) was monitored for every trial, with the time-course of head position in the yaw plane for every trial shown in Figure 4.6 a). As in Experiment 1, prior to exclusion trials were then classed as "correct within range" (error $< 90°$) or "reversals" (error $> 90°$) to examine the relationship between head trajectory and motion direction perception. As seen in Figure 4.6

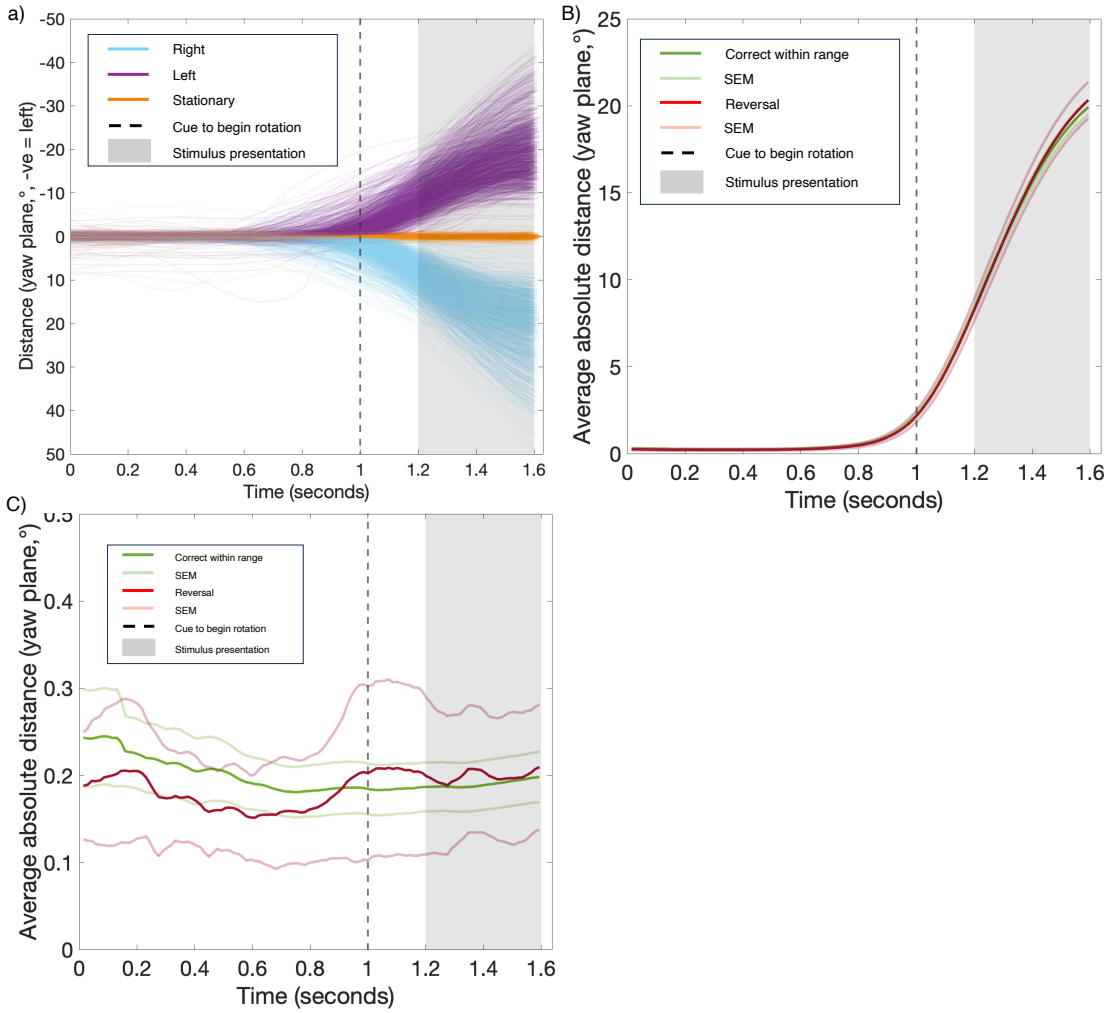


Figure 4.6: Head rotations Experiment 2.
(a) Trajectory of head position in the (horizontal) yaw plane for all trials across all participants. Each line represents an individual trial. The cue to begin rotation was when the head guide reached the world-centred forward marker. For stationary trials the guide would appear centrally and remain in place until replaced by the stimulus. (b) Average absolute value of trajectories across participants for rotation trials that were correct within range (error $< 90°$) or reversals (error $> 90°$). Shaded lines represent ± 1 SEM. (c) Average absolute value of trajectories across participants for stationary trials that were correct or reversals.

b) and c), no differences in speed were found for correct and reversal trials across rotation and stationary conditions.

Direction perception

Absolute error in perceived direction increase with visual intensity

Absolute error in perceived motion direction was calculated by subtracting the true angle of motion from perceived angle of motion and wrapping responses between 0° and 180°. Absolute error was calculated to compare size of error between different levels of visual intensity and head rotation condition. A 9 x 3 x 3 repeated-measures ANOVA (angle x intensity x head rotation) showed a significant main effect of inten-

sity ($F(2,26) = 70.21$, $p < .001$, $\eta_p^2 = 0.84$). Bonferroni-corrected post-hoc t-tests showed the low visual intensity condition to have significantly increased error when compared to both medium ($t(27) = 8.81$, $p < .001$, $d = 0.80$) and high visual intensity conditions ($t(27) = 11.27$, $p < .001$, $d = 1.02$) (see Figure 4.7). The difference in error between medium and high conditions was not significant ($t(27) = 2.46$, $p = .06$). There was also a significant effect of head rotation condition ($F(2,26) = 23.05$, $p < .001$, $\eta_p^2 = 0.64$). Bonferroni-corrected post-hoc t-tests showed absolute response error was significantly greater when turning right and left than remaining stationary ($t(27) = 6.08$, $p < .001$, $d = 0.79$ and $t(27) = 5.66$, $p < .001$, $d = 0.74$ for right and left comparisons, respectively). There was no significant difference between rightward and leftward rotation conditions ($t(27) = 0.41$, $p = 1.00$).

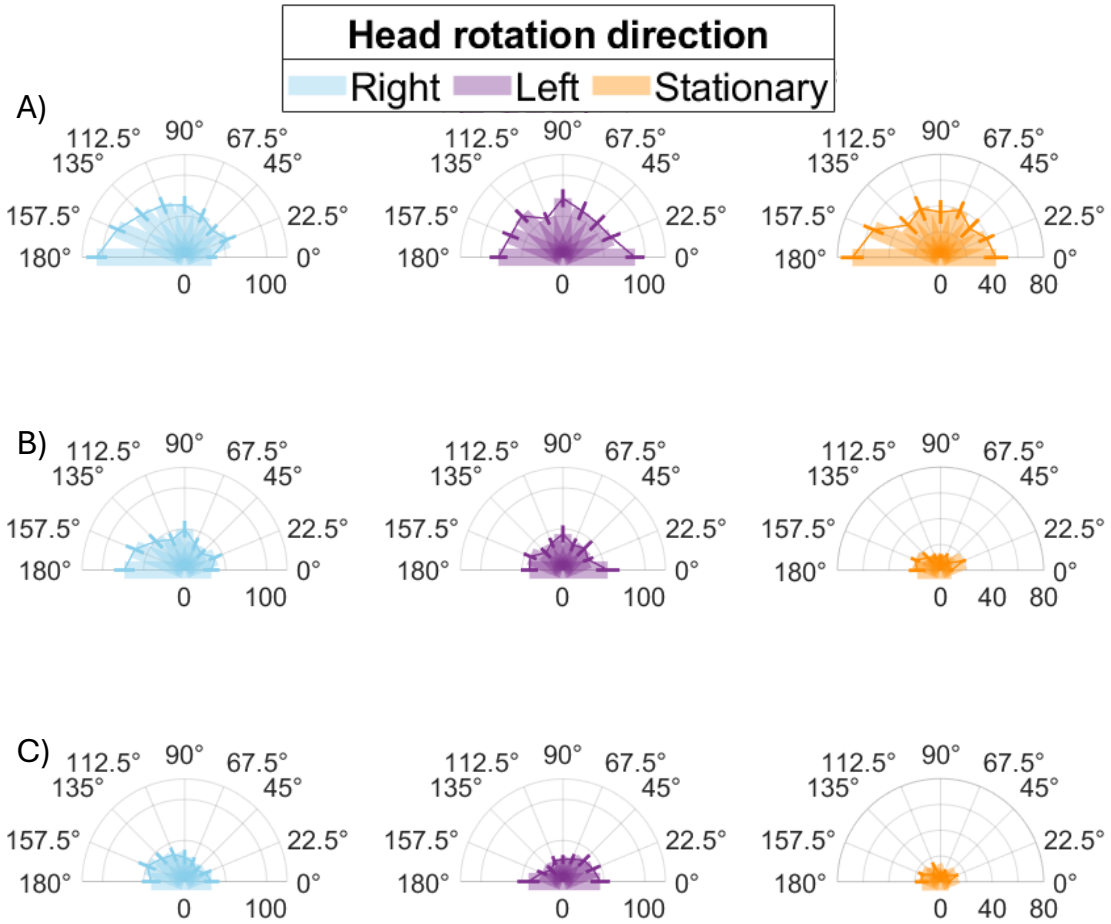


Figure 4.7: Mean absolute response error for rightward (blue) and leftward (purple) head rotations. The stationary condition is shown at right in yellow.
(a) Low visual intensity, all rotations. (b) Medium visual intensity, all rotations. (c) High visual intensity, all rotations. All error bars represent ±1 SEM. Stationary condition scale was adjusted to better display results.

Relative Error when stationary depends on angle of visual motion

We next investigated the relative error in perception. In stationary conditions, similar to Experiment 1, relative error was repelled away from the cardinal directions

of stimulus motion (Figure 4.8). This effect was preserved across visual stimulus intensities. A 9 x 3 repeated-measures ANOVA (angle x intensity) on the average relative error for each motion condition showed a significant effect of true angle motion on perceived motion direction ($F(8,104) = 2.72$, $p = .009$, $\eta_p^2 = 0.17$). The effect of visual intensity on relative error was not significant ($F(2,26) = 0.92$, $p = .41$) meaning the same pattern of cardinal-repulsion was present regardless of the strength of visual motion (see Figure 4.8). Again, it was decided to normalise the rotation responses to the stationary condition as it was clear the baseline was not equal to 0° response error across angle conditions.

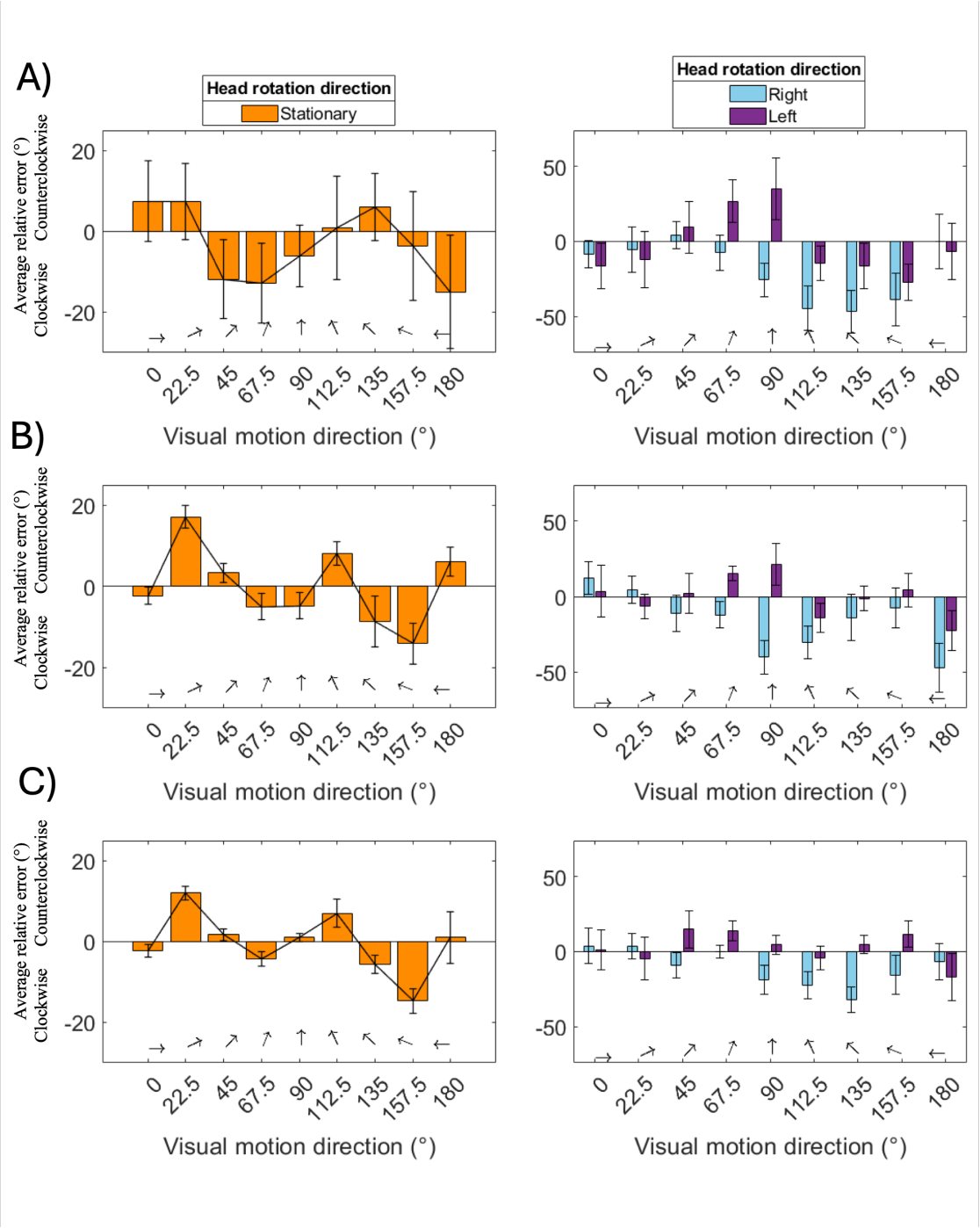


Figure 4.8: Mean relative response error.
Rotation conditions are normalised to stationary averages. (a) Low visual intensity. (b) Medium visual intensity. (c) High visual intensity. Error bars represent ±1 SEM.

Perceived direction of visual motion is pulled toward direction of head turn across intensity levels

As was the case in Experiment 1, a comparison between the effects of left and right head-rotation conditions on relative error demonstrates that perceived direction of visual motion is pulled toward the direction of head rotation (Figure 4.8). A 9 x 3 x 2 repeated-measures ANOVA (angle x intensity x head rotation) on relative response error showed a significant effect of head rotation on relative response error ($F(1,13)$

= 5.99, $p = .03$, $\eta_p^2 = 0.32$). As seen in Figure 4.8, relative response error during rightward head rotations was significantly biased clockwise from the actual direction of motion. There was no significant effect of angle ($F(8,104) = 1.49$, $p = .17$) or intensity ($F(2,26) = 2.51$, $p = .10$). There was however a significant interaction between the direction of head rotation and angle on relative error ($F(8,104) = 3.59$, $p = .001$, $\eta_p^2 = 0.22$). This replicates the 'pull' effect from Experiment 1, as depicted in Figure 4.8.

Finally, to test whether the strength of the pull effect differed across signal intensities, we performed repeated- measures ANOVAs within each signal intensity, in order to compare the strength of the interaction between the direction of head-rotation and angle. Relative error in response at low-intensity had a significant interaction effect between angle and head rotation ($F(8,104) = 2.10$, $p = .04$, $\eta_p^2 = 0.14$). The medium intensity condition was also found to have a significant interaction between angle and head direction ($F(8,104) = 3.13$, $p = .003$, $\eta_p^2 = 0.19$). Finally, there was a significant interaction between angle and head direction at the highest intensity visual signal ($F(8,104) = 2.68$, $p = .01$, $\eta_p^2 = 0.17$), meaning the medium intensity condition had the strongest interaction effect. Supplementary Figure 4.11 displays the relative error for the cardinal (vertical, left- and right-horizontal) directions of motion, which demonstrates systematic biases in visual motion perception for vertical directions of motion based on head turns, with no such effects found for horizontal motion, as in Experiment 1.

4.5 Discussion

In this study we tested participants' perceived direction of visual motion, comparing between a wide range of motion directions, during stationary conditions, as well as active left and right head rotations. The stimulus was presented in a VR environment and locked to participants' head position such that participants would judge the angle of retinal motion arising from translating Perlin noise (Experiment 1) or a translating LSNR motion signal at varying signal strengths (Experiment 2). Accuracy of perceived direction while stationary depended on the angle of visual motion, with perceived direction of cardinally-adjacent angles repelled away from the nearest cardinal reference. Head rotations were found to increase error in perceived direction, with perceived angle of motion consistently pulled towards the direction of head rotation.

4.5.1 Oblique Effects

Oblique effects, where judgements on visual motion and orientation are significantly better for cardinal than oblique directions, have been well-reported throughout the literature (Appelle, 1972; Gros et al., 1998; Karim & Kojima, 2010; Krukowski et al., 2003; Loffler & Orbach, 2001). The current study also found, in the stationary condition, clear evidence of increased error in direction estimations for oblique angle conditions, though most notably for those angles which were cardinal-adjacent. Here we saw the direction of error indicated a repulsion away from the nearest cardinal point, otherwise known as "reference repulsion" (Rauber & Treue, 1998). Rauber and Treue (1998) found estimates of visual motion direction to be repelled away from the angle of a comparison line, which they suggest is due to a general tendency

for overestimation of distance between a stimulus and reference. In the current case, as the cardinal adjacent angles are close to the cardinal directions, participants may have been using an internal measure of cardinal direction with which to compare the displayed direction, and in line with Rauber and Treue's (1998) hypothesis, subsequently overestimate that distance. These oblique effects were present in both experiments.

4.5.2 Effects of Rotation

Given the results from the stationary control condition suggest our baseline perception of direction is not equal for all angle conditions, and could be influenced by the strength of an internally held reference prior (Rauber & Treue, 1998), error in perceived motion for the stationary condition was subtracted from error in rotation conditions so that rotation responses were normalised to the stationary control. This allowed direct comparison between rightward and leftward head rotations.

In line with findings from eye movement studies (Souman et al., 2005; Swanston & Wade, 1988), head rotations caused perceived direction of motion to be pulled towards the direction of rotation, across angle conditions. This finding was replicated in Experiment 2. Also found in both experiments was an increased error in estimated direction of visual motion while rotating when compared to stationary. This is line with prior literature (Pickard et al., 2023) and is most likely due to the increased task demands of following a head guide while also judging motion, a split of attention that is known to have performance costs in dual-task paradigms (Bourke et al., 1996; Lavie et al., 2004). In addition to the increased attentive demands most likely present during rotation trials (Kinchla, 1992; Lavie et al., 2004), active head rotations are known to comprise a noisy motion signal due to the proprioceptive, motor, reafferent, visual and vestibular signals all associated with active movement ((Cullen, 2012) and accordingly could have introduced noise to visual-vestibular motion processing, increasing error in perceived visual direction, as hypothesised. This could also explain why tracking-like active-head rotations do not align with the perceptual benefits sometimes reported in smooth pursuit eye-movement studies (Spering and Montagnini, 2011 for a review). During binocular rivalry between opposed horizontal motions, Alais et al. (2021) found both active and passive self-rotation caused visual motion in a direction congruent to rotation to be perceived, though with a stronger entrainment and lesser time lag for the active condition. This suggests a greater influence of active rotations on visual motion perception, possibly due to the additional efference copy signals present (Alais et al., 2021), leaving the current findings of increased error for active head rotations unsurprising.

4.5.3 Manipulation of visual strength

In Experiment 2, at all levels of visual intensity, response error was in the direction of head rotation, as seen in Experiment 1. Individual repeated-measures ANOVAs were compared for each intensity level and it was found the weakest effect was in the lowest-intensity condition, followed by the high intensity condition, with medium intensity visual motion resulting in the greatest pull of perceived direction toward head rotation. This was somewhat surprising, as it was initially hypothesised error would increase as visual intensity decreased. However, as the visual motion in the

low-threshold condition was purposely designed to be close to participants' perceptual threshold, the task may have been too difficult resulting in noise masking any effect present. The increased effect size between medium and high intensity conditions supports the original idea that a decrease in visual intensity would result in a greater influence of the vestibular motion signal. This is in line with prior studies finding as one sensory signal is degraded, another can be up-weighted when being combined into one percept (Alais & Burr, 2004; Alais et al., 2010). Specifically, it could reflect the findings of Morgan et al. (2008) and Chen et al. (2011c), where visual-vestibular cells of the MSTd alter the weighting of visual signals depending on their reliability.

4.5.4 Compensation regardless of necessity

Regardless of specific effects, it is clear across both experiments that the action-vestibular signals generated from head rotations in the current experiment, while technically task-irrelevant, are nevertheless being integrated with visual motion signals such that perception of motion direction is pulled toward the direction of head rotation. While many cases of multi-sensory integration prove to enhance accuracy and veracity of perception (Ernst & Banks, 2002; Ernst & Bülthoff, 2004), the current combination of visual and action-vestibular signals could be argued to worsen, or mislead our perception of true direction of motion. Why then do we combine these signals? The head-fixed display is a somewhat unnatural case of visual-vestibular processing, so could result in erroneous perception due to lack of appropriate visual-vestibular processing. However, this reasoning would suggest the signals are being treated like more common cases of visual-vestibular interactions, such as natural tracking-like head movements, and as such results could give insight into the fundamental purpose of visual-vestibular processing, and indeed these results give insight in the design and workings of such a system.

While other senses can be combined to help overcome ambiguities inherent in unisensory information, for example combining visual signals with auditory information to better localise the source of a sound (L. C. A. Freeman et al., 2018), self-rotation often generates confounding visual motion signals that must be accounted for in order to accurately maintain perception of a mostly-stationary world, with objects moving within it. It has therefore been hypothesised that the primary function of the brains visual-vestibular areas is to account for these confounding visual signals arising from self motion (Morgan et al., 2008; Takahashi et al., 2007), leaving perception of motion, or lack thereof, in the distal world as accurate as possible. Unimodal cues are often combined into one percept, with loss of access to individual cues as they become superfluous (Prsa et al., 2012). Visual and vestibular cues for self-motion have also been found to undergo mandatory fusion, where individual sensory signals are lost and only the combined signal remains, the first time this process was found across different sensory modalities (Prsa et al., 2012 cf. Hillis et al., 2002). It was hypothesised this was due to both visual and vestibular cues arising from the same source, self-motion, and as such maintaining individual cues from each sense, in addition to the combined percept, is unnecessary (Prsa et al., 2012). In the current case then, forced-fusion may also be occurring, which could explain why even "task-irrelevant" action-vestibular signals influence perceived direction. Halow et al. (2023) explain forced-fusion of visual-vestibular signals during

rotation as a natural result of smooth-pursuit, as the vestibulo-ocular reflex when turning the head is not present during pursuit. Indeed, when studying the dynamic re-weighting of visual-vestibular cues during heading perception, Fetsch et al. (2009) found some monkey and human subjects over-weighted vestibular input. They theorised this was due to visual motion always having potentially two sources, self or external motion, whereas vestibular signals have a single source. This could have led to an imbalance in certainty of causation between the two modalities and subsequent over-weighting of vestibular cues (Fetsch et al., 2009). The same ambiguity as to the source of the visual motion could have been present in the current experiment, leading to over-weighting of the more certain vestibular cues and resulting in direction perception pulled towards the direction of the head rotation.

In essence, the findings and explanation speak to a system designed to account for action-vestibular signals, rather than rely on them for improved perception. This could be a unique property of the vestibular system, and also hint at why there is no vestibular cortex, an area of the brain purely dedicated to interpreting vestibular signals (Prsa et al., 2012), as is seen for other senses such as touch or vision. Instead, vestibular signals travel across many regions of the brain, often to areas known to combine multi-sensory information, such as area MST in the case of visual-vestibular signal integration. If vestibular activation must primarily be accounted for, rather than integrated for more robust perception, it makes sense for the process to be multisensory. This reasoning is even evident at a physiological level, with only oppositely-tuned visual-vestibular rotational cells being found in the MSTd (Takahashi et al., 2007), whose role is suspected to be one of accounting for optic flow signals arising from self-motion across a stationary world (T. C. A. Freeman et al., 2010). This theory is supported by other findings of visual action-vestibular integration from both eye and head movements (Hogendoorn et al., 2017; Krukowski et al., 2003).

Compensation regardless of necessity was also found in Hogendoorn et al.'s (2017) study of perceived visual motion direction during passive, whole-body rotations. Active as opposed to passive movement is known to significantly affect perception (Alais et al., 2021; Davidson et al., 2023). Using passive rotation, Hogendoorn et al. (2017) also found perceived direction of visual motion to be pulled in the direction of rotation. Given these similar findings, it is tempting to conclude the results of both are driven by the vestibular rotational signal, as it is the only sensory signal common across both active and passive perception. This is interesting, as much of the influence of active sensory signals is thought to come from reafference (Alais et al., 2021; Cullen, 2012), which could still be the case here. A direct comparison study between passive and active cases would allow for greater insight into the role of different rotational signals in multisensory visual processing.

4.5.5 Conclusion

Perceived direction of visual motion is pulled toward direction of head rotation, across multiple angles of motion and visual signal intensities. This evidence supports the theory of visual-vestibular processing primarily existing to disambiguate confounding effects of self-rotation on visual motion perception. Future research should further investigate differences between passive and active self-rotation as well as how eye and head movements together influence visual motion perception.

4.6 Acknowledgements

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4.7 Supplementary Material

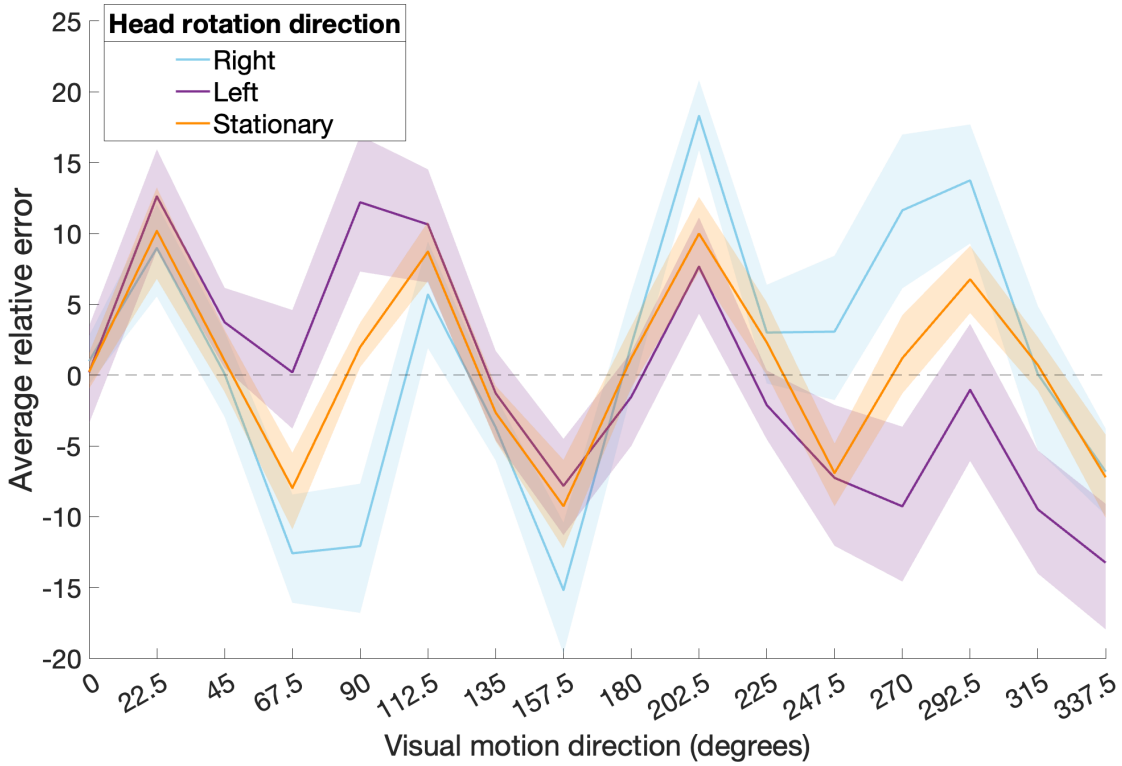
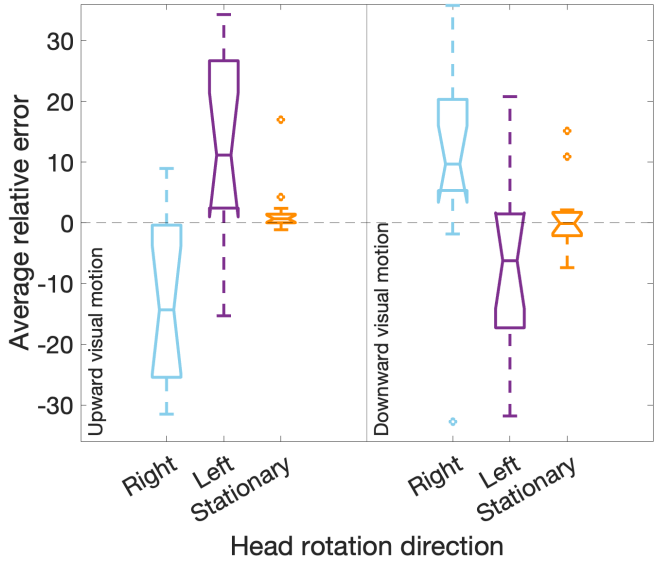
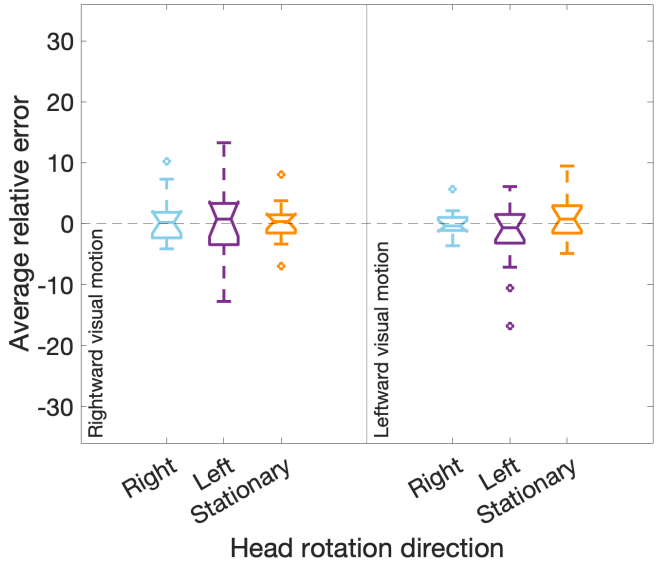


Figure 4.9: Bootstrapped relative error in perceived motion direction Experiment 1. Relative error in perceived motion direction from a super subject in Experiment 1, negative representing an underestimation and positive an overestimation. Shaded regions represent 95% CI from bootstrapping.

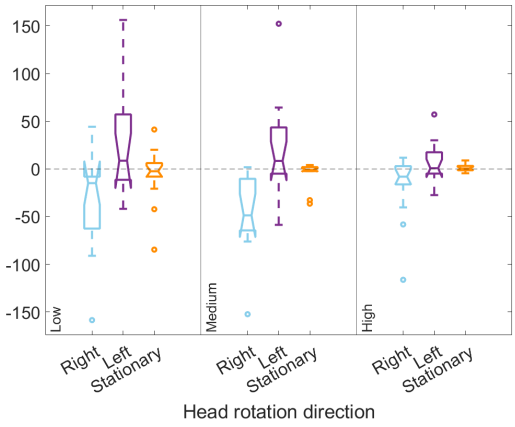


(a)

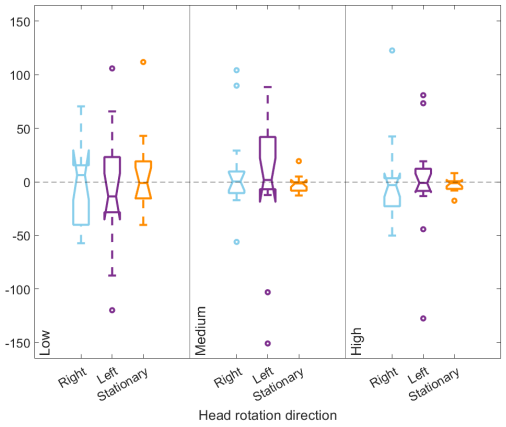


(b)

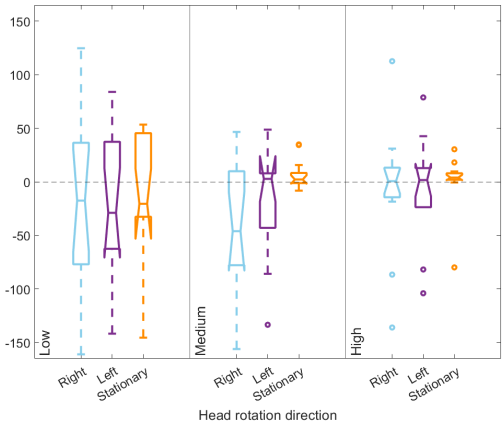
Figure 4.10: Relative error in perceived motion direction.
(a) vertical and (b) horizontal motion in Experiment 1. The "pull" of perceived motion orientation towards direction of head turn is clearly evident in the case of vertical motion and unsurprisingly lacking from horizontal motion conditions.



(a)



(b)



(c)

Figure 4.11: Relative error in perceived motion direction.
(a) vertical (b) leftward and (c) rightward motion in Experiment 2. The "pull" of perceived motion orientation towards direction of head turn is evident in the case of vertical motion and again lacking in horizontal motion conditions.

Chapter 5

Discussion

5.1 Overview

The aim of this thesis was to investigate the influence of active-head rotations on visual motion perception. While there has always been a strong scientific interest in how we successfully attribute motion signals received on the retina to their correct source in the world, this research has been somewhat limited in the types of self-motion investigated. Partly due to technological limitations, rotational self-motion has received much less focus than translational movements, such as those found in heading perception studies. Additionally, studies that do investigate rotation often do so passively, using motion-platforms or similar devices to rotate participants without motor activation. While passive studies are important for understanding, for example, how additional vestibular signals may influence motion perception, they lack environmental validity as the active movement we perform every day comprise many additional sensory signals that may affect motion perception. Additionally, the motion-type focus of prior studies on either self-motion or visual motion perception is unbalanced, with the larger portion of the literature focusing on the influence of visual motion on self-motion perception, rather than the other way around.

Therefore the primary objective of this thesis was to utilise VR technology to allow investigation of active, rotational head movements on visual motion perception. In doing so, much can be learned about the way we account for the movement of our heads when judging motion (or lack thereof) in our everyday environments. This thesis first asked whether our fundamental thresholds for perceiving visual motion are affected by active-rotations of the head, and specifically whether thresholds may differ between cases of congruent or incongruent visual action-vestibular stimulation (Chapter 3). We then chose to investigate direction perception. How active head rotations might influence perceived direction of visual motion depending on the relationship between direction of motion and head rotation, as well as strength of visual motion was the focus for Chapter 4. The findings and implications of these experiments are discussed below.

5.2 Summary of findings

5.2.1 Incongruent thresholds increase visual motion perception (Chapter 3)

Across two experiments, participants completed brief rotational head movements in a VR environment after which they indicated whether the retinal motion of the fixation-centred stimulus was moving leftward or rightward (Experiment 1) or whether motion (in either direction) was present in the upper or lower hemifield (Experiment 2). Head-rotations were found to increase thresholds for perceiving visual motion, especially when the head was rotated in a direction opposite to the visual signal, i.e., incongruent conditions.

In Experiment 1, as participants were directly reporting if they saw the stimulus motion travelling left or right, a bias was found that participants would be more likely to report perceived motion in the direction of head turn. This left two alternative explanations for the significantly increased thresholds for incongruent visual-rotational motion. First, the bias to answer in line with head direction could have been the sole driver behind increased rates of correct responses for congruent trials, and decreased rates of incongruent trials, driving the subsequent difference in thresholds. Alternatively, the increased thresholds for incongruent visual-rotational motion could have reflected a fundamental difference in the way congruent and incongruent visual action-vestibular signals are processed and interpreted. As the world is most often stationary (T. C. A. Freeman et al., 2010; Weiss et al., 2002; Welchman et al., 2008), rotating the head usually results in a visual motion signal across the whole retina in a direction opposite to that of the head turn. We proposed that our prior to perceive the world as stationary (T. C. A. Freeman et al., 2010; Weiss et al., 2002; Welchman et al., 2008) increases the likelihood of attributing incongruent visual signals experienced while rotating to the normal scene-shift of a stationary world across our retina. Stronger visual motion signals may then be needed to perceive object motion in a direction incongruent to head rotations, like those seen in Experiment 1. However, while both thresholds for both congruent and incongruent motion were significantly elevated when compared to stationary in Experiment 2, no difference was found between the two themselves, suggesting this was not the case. The findings of Experiment 2 instead suggest rotation thresholds increase visual perceptual thresholds due to the attentive, cognitive, and task demands associated with active movements (Heinrich et al., 2020; Lavie et al., 2004; Swallow & Jiang, 2013).

Interestingly, these seem to align more closely with findings suggesting perceptual costs of smooth-pursuit eye movements (Arathorn et al., 2013; Dichgans et al., 1975; Mack & Herman, 1973). Though head-rotations are tracking-like movements, the potentially noisy motor and proprioceptive signals to be processed in addition to vestibular signals, or a worse ability to account for vestibular signals when processing visual stimuli, may serve to limit perceptual benefits seen in some smooth-pursuit eye movement studies (Greenlee et al., 2002; Spering & Montagnini, 2011).

5.2.2 Perceived direction of visual motion is pulled towards direction of head rotation (Chapter 4)

Accuracy of perceived direction during stationary conditions was influenced by the angle of visual motion, with cardinal-adjacent angles notably repelled away from the nearest cardinal reference. Head rotations consistently heightened error in perceived direction, drawing the perceived angle of motion towards the head rotation direction. This effect was amplified as visual motion intensity decreased.

Though generally worse performance was expected for oblique angles, in line with commonly found oblique effects (Appelle, 1972; Gros et al., 1998; Karim & Kojima, 2010; Krukowski et al., 2003; Loffler & Orbach, 2001), the increased error in cardinal-adjacent angles (found across both experiments) as opposed to perfectly oblique angles was surprising. It is thought this result is driven by reference repulsion, where perceived direction is repelled away from an internal reference (Rauber & Treue, 1998). This, like the world-stationarity prior relevant to Chapter 3 (T. C. A. Freeman et al., 2010; Weiss et al., 2002; Welchman et al., 2008), clearly displays how even at rest, our internal priors for motion can have a significant influence on our conscious perception. This is an important finding, as it clearly demonstrates the need for control conditions in perceptual studies. Specifically, any effects of experimental manipulation will be clearer when normalisation of responses to our actual perceptual baseline occurs.

Applied to the current case, normalisation of rotation-condition responses to stationary averages resulted in a clear trend for perception of visual motion direction to be pulled towards direction of head rotation. This is a fascinating result, as since the stimulus was locked to the participants' head such that the retinal motion signal was theoretically equal to the stimulus motion, it suggests a system designed to disambiguate effects of self-motion on visual motion perception, most often by combining signals across these senses. Halow et al. (2023) suggest that the forced fusion of visual-vestibular signals for self-motion found by Prsa et al. (2012) occur during smooth-pursuit rotations of the head, as the usual counter-rotation of the eyes is suppressed. As the world is mostly stationary, the visual signal arising from rotation is just an additional cross-modal signal for the same rotation, and as such does not need to be processed separately (Prsa et al., 2012). This forced fusion thought to be present during eye-fixated head rotations could be the main driver behind the pull of perceived direction towards head direction in the current experiments. This speaks to a visual-vestibular system designed to account for confounding self-motion, rather than combine signals for more robust perception, as found in other multisensory interactions (Ernst & Banks, 2002; Ernst & Bülthoff, 2004).

5.3 Limitations and future directions

5.3.1 Bimodality of responses in Chapter 4

The near 180° error present in direction estimates across both studies in Chapter 4 caused data to be removed as no explanation could be found for these responses. While results were replicated between the two experiments, giving confidence the removal of data did not significantly alter any effects of head rotation on perceived

direction of visual motion, the question of what caused these reversals in perceived direction remains.

As these reversals occurred across all conditions, and no correlation between head movements (position, velocity or acceleration) and reversals of direction could be found, it is suspected these reversals occurred due to erroneous eye movements during stimulus presentation. Though participants were instructed to keep their eyes fixated on a head-centred cross throughout all trials, eye data from Experiment 1 shows that for those who experienced reversals there was an increase in the y displacement of their gaze direction on reversal trials as compared to their 'normal' trials. Further, participants who reported reversals had similar levels of eye movement on their normal trials to the average movement for participants who experienced no reversals. These graphs are shown in Appendix A.

These additional eye movements could have caused a reversal in perceived direction due to the change in retinal information gained about the stimulus motion. According to Souman et al. (2005), who also found bi-modality in perceived direction, these reversals could have been caused by variation in gain ratio of eye movement signal gain to retinal signal gain. The same could have occurred in the current experiments, further justifying the removal of erroneous data.

5.3.2 The need for greater collaboration between physiology and behavioural approaches

Further exploration of the underlying physiology of visual-vestibular interactions—particularly for rotational movement —may also give insight into the lack of difference found between congruent and incongruent visual motion thresholds found in Chapter 3. It was originally hypothesised that the oppositely-tuned rotational cells of macaque MSTd would highlight visual motion signals congruent with self-motion by suppressing incongruent signals generated from rotating across a stationary world (Alais et al., 2021; Gu et al., 2006; Takahashi et al., 2007). However, Chen et al. (2011a) suggested that the cortical hierarchy of vestibular heading signal processing means signals are projected from the parietoinsular vestibular cortex (PIVC) to VIP and MSTd. Given optic flow signals are upweighted as they travel through the different brain areas towards MSTd (Chen et al., 2011c), and PIVC itself is non-responsive to optic flow (Chen et al., 2011b), the location that the visual-vestibular signals generated in the current experiment were combined could have a significant effect on the subsequent perception of both self and object motion. Indeed, many studies finding differences in congruent/incongruent visual-self-motion interactions (Arathorn et al., 2013; Dyde & Harris, 2008; MacNeilage et al., 2012; Morgan et al., 2008; Souman et al., 2005) were looking at supra-threshold interactions. These interactions may be processed in a higher-order brain area rather than the presumably low-level sub-threshold interactions driving perceptual measurements in the current experiment, potentially explaining the unexpected results of the current study. It must be noted however that most published findings investigate translational self-motion, and with known differences existing between rotational and translational physiological processing, findings from heading studies may not apply to rotation. Focussing on rotational self-motion should be a focus for future studies so the mechanisms behind these interactions can be better understood.

Indeed, closer collaborations between behavioural psychology and neuroscience

would greatly benefit our understanding of visual-vestibular interactions. Both fields are interested in how our brain processes multisensory information to determine what we perceive but employ two different approaches for doing so. While neurophysiological studies focus on the cellular-level interactions between neurons, behavioural studies are primarily interested in how the outcomes of these interactions shape our conscious experience. If more studies could be designed that combined the two, inferences made from behavioural results would be more likely to be proved or refuted from complementary physiological investigation.

As an alternative to studying the cells themselves, incorporation of neural networks into behavioural studies could achieve a similar result. Behavioural data can be used to predict how our brains process information, with these predictions then being tested on neural network models, allowing actual feedback on theories derived from behavioural results. For example, Rideaux et al. (2021) used a neural network model to show the balance of activity between congruent and opposite visual-vestibular motion cells, cells that have been discovered in neurophysiological studies (Gu et al., 2006; Takahashi et al., 2007), to determine whether visual and vestibular cues should be separated or integrated. Combining neurophysiology, neural network modelling and behavioural study methodologies through collaborations between researchers in each field will further our understanding of multisensory perception, the united goal of each discipline.

5.3.3 Active vs passive comparisons

In order to truly understand which sensory signals are driving conscious perception, comparison of active studies to passive controls is crucial. While the signals involved in active rotations in the current studies have been classed as "action vestibular" signals, and results interpreted as such, a precise understanding of the vestibular sensory processes at play is unattainable without passive replication. Passive movement of subjects activates the vestibular system, giving direct insight into the vestibular component of this process. Active movement, however, also involves motor planning, execution, resulting sensory reafference, and proprioceptive input in addition to vestibular activation. By comparing the two, the role of vestibular vs other self-motion signals can be scrutinised. This is important as motor reafference is thought to play an important part in active perception. For example, Alais et al. (2021) found both passive and active self-rotations caused perceived visual alternations in binocular rivalry to become entrained to the rate of rotation, although the entrainment was stronger for the active condition. They theorised that while the vestibular component may be enough for perceived visual direction to oscillate congruently with rotation, the stronger effect in the active case indicated that efference copies of motor signals could be used to predict sensory outcomes (Cullen, 2012) and thereby better account for self motion. This is supported by the finding that vestibular nuclei show a reduced responsiveness to vestibular afferent signals when motion was generated by an active head turn (Roy & Cullen, 2001). Given these known differences between active and passive perception, future studies should seek to replicate studies similar to those reported here using passive rotation, so that the individual roles of vestibular and efference copy sensory signals can be better segregated.

5.4 Conclusions

In conclusion, it is clear active head rotations increase thresholds for perceiving visual motion, and subsequently pull perceived motion direction towards the direction of head rotation. This is the first time such effects have been found, increasing our understanding of how self-motion signals are accounted for in order to maintain veridical perception of motion in the world around us. VR technology made these studies possible and is a useful tool for psychophysics that should be increasingly utilised to study the consequences of action on visual perception. There is still much to be learnt about how we actively perceive our world, and as such studies which combine neurophysiological, modelling and behavioural approaches in order to investigate the differences between the more traditional passive perceptual studies and active perception should be prioritised.

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Appendix A

Supplementary material

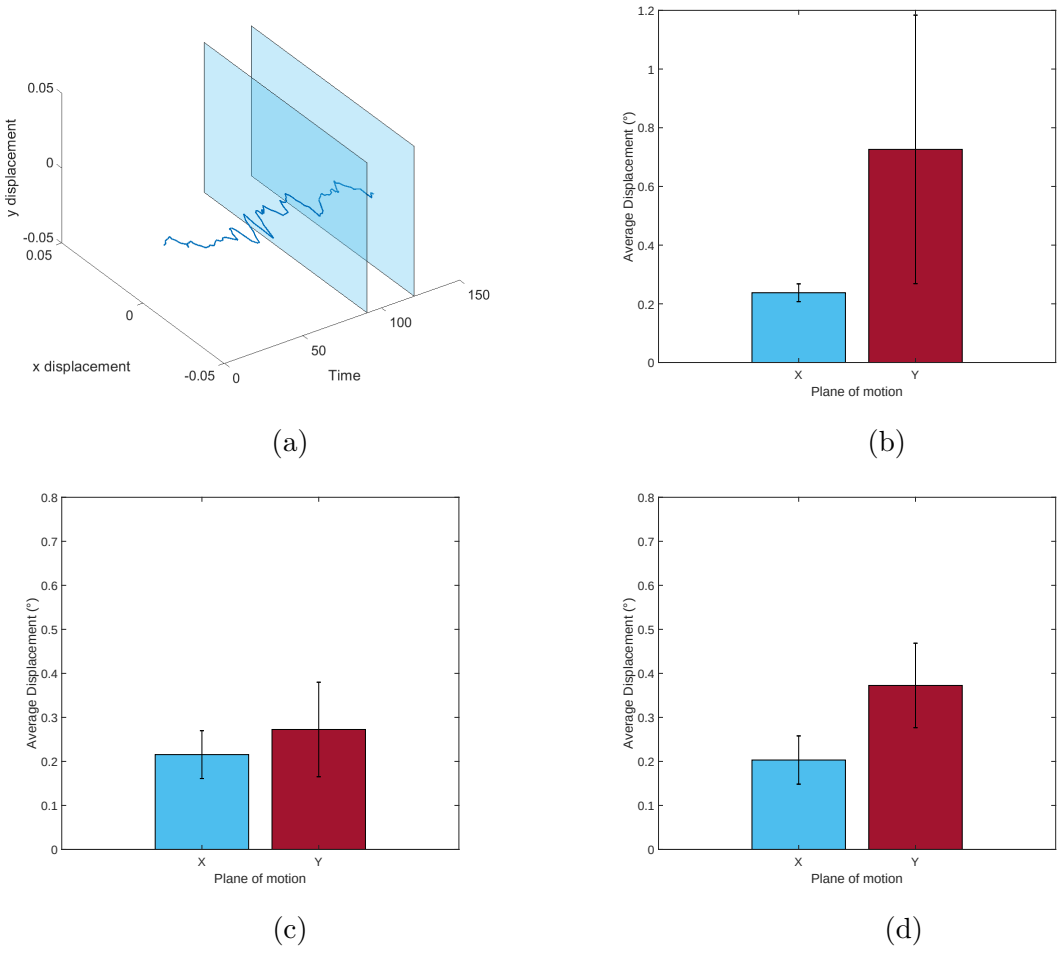

Figure A.1: Eye movements during stimulus presentation.
(a) Eye trajectory from an example trial. Blue windows represent the onset and end of stimulus presentation. (b), (c), (d) Average X-Y displacement for stationary trials. (b) Average across trials that were reversed. (c) Average across trials that were correct, for participants who did have reversals. (d) Average across trials that were correct, for participants who did not have any reversals.

Appendix B

Statement of author contributions to work submitted for publication

Chapter 3 of this thesis was submitted for publication as:

Pickard, K., Davidson, M.J., Kim, S., & Alais, D., Incongruent active head rotations increase visual motion detection thresholds.

Kate Pickard

1. Research design
2. Programmed experiments
3. Data collection and analysis
4. Wrote the manuscript

Matthew Davidson

1. Advised data analysis
2. Edited and advised on the manuscript

Sujin Kim

1. Study conception
2. Programmed experiments

David Alais

1. Study conception
2. Advised data analysis
3. Edited and advised on the manuscript

Chapter 4 of the thesis was submitted for publication as:

Pickard, K., Davidson, M.J., & Alais, D., Visual direction perception is pulled toward direction of head rotation.

Kate Pickard

1. Study conception
2. Research design
3. Programmed experiments
4. Data collection and analysis
5. Wrote the manuscript

Matthew Davidson

1. Advised data analysis
2. Edited and advised on the manuscript

David Alais

1. Study conception
2. Advised data analysis
3. Edited and advised on the manuscript

In addition to the statements above, in cases where I am not the corresponding author of a published item, permission to include the published material has been granted by the corresponding author.

Kate Pickard
December 2023

As supervisor for the candidature upon which this thesis is based, I can confirm that the authorship attribution statements above are correct.

David Alais
December 2023