The Role of Peripheral Vision in Flow Parsing

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Summary

Identifying moving objects while we are moving is an important everyday skill. This ability allows us to monitor our surroundings, successfully interact with objects or people, and avoid potential hazards. Self-movement generates optical flow on the retina that complicates the recognition of moving objects from retinal motion alone. Rushton and Warren (2005) proposed a purely visual solution to this problem. They suggest that, in order to assess scene-relative object movement, the brain identifies and parses out (globally subtracts) patterns of visual flow that are consistent with self-movement. Existing research has demonstrated evidence of this flow parsing process in central vision (i.e. Warren & Rushton, 2008). This thesis aims to characterise the role of peripheral visual flow in this process.

Research from the wider self-motion literature has often distinguished between central and peripheral vision. Some researchers have claimed that peripheral vision is specialised for self-motion perception, whilst more recent studies have challenged this assertion. This thesis investigates whether peripheral visual motion, traditionally considered to be a strong cue to self-movement, also contributes to flow parsing.

The experimental work employed a simulated self-movement paradigm to isolate retinal motion from other non-visual cues. Thus, observers remained stationary whilst computer generated stimuli moved to produce patterns of retinal motion associated with actual self-movement. In the first set of experiments, I demonstrate that peripheral flow simulating forward or backward self-movement gives rise to characteristic flow parsing effects. This finding generalises to rotational observer motion (Chapter 3). Chapter 4 considers whether peripheral flow contributes to parsing for judgements of object size change. Finally, Chapter 5 investigates whether there is a benefit of peripheral information under conditions where central flow is potentially ambiguous. The results indicate that peripheral visual flow contributes to the flow parsing process. The contribution of flow in the near periphery appears to be maximally important.

Declaration

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List of Abbreviations

General

ACW	Anti-clockwise
AOR	Axis of Rotation
CW	Clockwise
DV	Dependent Variable
FOC	Focus of Contraction
FOE	Focus of Expansion
FPH	Flow Parsing Hypothesis
FSH	Functional Sensitivity Hypothesis
ISI	Inter Stimulus Interval
ITI	Inter Trial Interval
IV	Independent Variable
PDH	Peripheral Dominance Hypothesis
PSE	Point of Subjective Equality
RIH	Retinal Invariance Hypothesis

Statistical

ANOVA	Analysis of Variance
M	Mean
SD	Standard Deviation
SE	Standard Error

Units

cm	centimetres
hz	hertz
m	metres
s	seconds

Chapter 1. GENERAL INTRODUCTION

1.1 Chapter Overview

The central aim of this thesis is to probe the mechanism that underpins flow parsing. Specifically, I sought to establish whether peripheral visual flow contributes to flow parsing. This chapter introduces the problem of detecting moving objects whilst we ourselves are moving. I begin by outlining visual and non-visual sources of information about self-movement and explaining how they might be used to compensate for retinal motion arising from self-movement. The Flow Parsing Hypothesis (FPH; Rushton & Warren, 2005) presents a purely visual solution to the problem of detecting moving objects during self-movement. This hypothesis is explained and I review the existing research that indicates the existence of such a process, which has been demonstrated in central vision.

Then I explain how, due to variation in optic flow, different forms of self-movement produce patterns of visual flow that differ as a function of retinal eccentricity. A consequence of this is that central vision and peripheral vision are not always exposed to the same visual information about self-movement and therefore peripheral flow may provide information which is useful for detecting self-movement. Related literature on heading perception, vection, and postural control indicate that peripheral flow provides a reliable cue to self-movement. I propose that peripheral flow will contribute to the flow parsing process. The chapter concludes with an outline of the empirical work reported in this thesis.

1.2 Moving objects and moving observers

The ability to detect moving objects is a critical ability that allows us to interact with the environment and avoid potential hazards. For a stationary observer, the visual detection of a moving object in an otherwise stationary scene is a straightforward task (McLeod, Driver & Crisp, 1988), but during self-movement this task becomes more complex. When an observer is stationary[1],

---

[1] Here, stationary is considered to mean that the body, head, and eyes are not in motion.

moving objects in the world are indicated by motion in the image that is formed on the retina (retinal motion; Figure 1A). During observer movement objects that are stationary in the scene can also move within the retinal image (Figure 1B). Thus, during self-movement the brain must decompose a complex pattern of retinal motion (Figure 1C), to identify objects that are moving and objects that are stationary. Self-movement also complicates the estimation of the trajectory of a moving object from motion on the retina. Figure 1C shows how self-movement and object movement components combine to produce the retinal motion of a moving object during self-movement. The figure below demonstrates that the path of the object depicted on the retina may not reflect the veridical movement of the object in the scene.

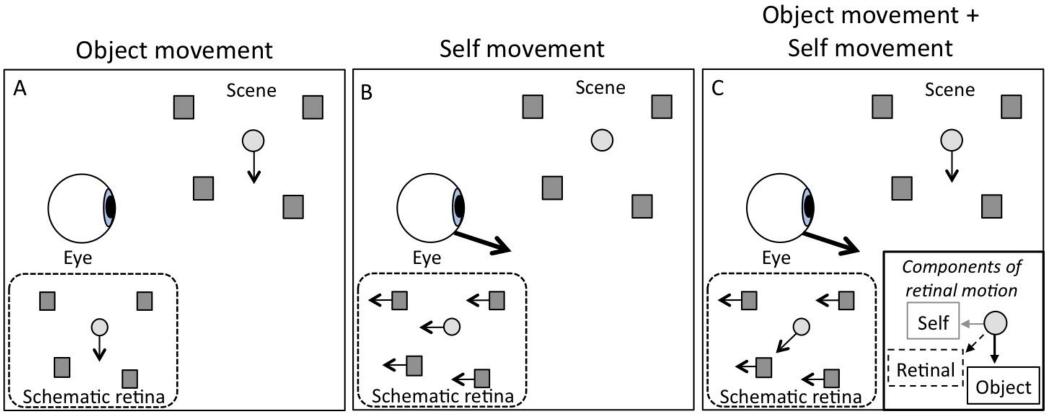

Figure 1 - Retinal motion associated with stationary objects (dark grey) and a moving object (light grey) in the scene, whilst stationary (Panel A) or during rightward self-movement (B and C). (Adapted from Warren, Rushton & Foulkes, 2012).

Knowledge of our own movement would allow us to predict the retinal motion of stationary objects as well as the inappropriate path of moving objects (Wallach, 1987; Gogel 1990). This prediction could then be used to compensate for retinal motion due to self-movement. The efferent signal, which is a copy of commands instigating self-movement, can be compared against the feedback from the sensory system in question, such as stretch receptors in the muscles and tendons around the joints (afference) or visual flow, to determine whether the signal matches the expected signal. This comparison process allows reafference (signals arising from self-movement) to be distinguished from exafference (signals arising from external sources) because any residual signal can be attributed to external factors. Such a compensation mechanism would restore stability to the retinal image – meaning objects that do not move in the world are correctly perceived to be stationary. By removing the confounding self-motion components from the retinal image, objects which do move in the scene could then be detected as though the observer was stationary.

1.3 Sources of information about self-movement

Both visual and non-visual cues provide potential sources of information about our own movement. A reliable neural signal from visual or non-visual sources that indicates self-movement would allow the brain to anticipate the pattern of retinal motion caused by self-movement. The brain could then maintain perceptual stability by “compensating” for this retinal motion.

1.3.1 Extra-retinal self-movement signals

In many situations, non-visual or extra-retinal signals provide information about self-movement (Wallach, 1987; Gogel, 1990). The vestibular system, located in the inner ear, is comprised of the otolith organs and semi-circular canals. The otoliths signal linear acceleration and deceleration as well as the orientation of the head with respect to gravity. The semi-circular canals indicate angular self-movement (Previc & Ercoline, 2004). Vestibular signals can be used to estimate self-movement and aid in the identification of components of retinal motion that arise from self-movement. Proprioceptive information, the relative position of parts of the body as well as the amount of effort exerted during movement, could also be utilised for estimating the visual flow arising from self-movement. von Holst and Mittelstaedt (1950) provided a variety of evidence that during self-movement a copy of the commands sent to the muscles is also sent to the sensory organs. This signal can then be compared to the afferent signals from the senses and any mismatch attributed to exafference.

Empirical studies have shown that together these non-visual cues provide an important source of information about self-movement which helps maintain perceptual stability. Wallach (1987) provides an indication of the utility of extra-retinal signals for estimating visual flow caused by self-movement. Wallach investigated the limitations of an extra-retinal estimate of self-movement by measuring how well these signals allowed observers to compensate for retinal motion due to self-movement. An observer’s forward translation was yoked to the rotation of a 3D object positioned to the side of the head in order to probe the limitations of perceptual stability. He varied the amount by which the visual stimulus rotated in relation to the movement of the observer. For example, a 1:1 ratio produced a visual stimulus identical to that which the observer would experience during a translation with a stationary object. Observers were asked to report if they perceived the object to rotate at all during their movement. If all visual motion were ignored during self-movement (discounted) then observers would not report any visual motion at all, regardless of the ratio. While discounting is a crude mechanism that essentially removes all retinal motion during self-movement, a more subtle mechanism could estimate visual motion arising from self-movement. A mechanism that estimated visual self-motion would allow any deviations from the expected visual flow, such as that produced by moving objects, to be readily detected. To test this, using a method of adjustment, Wallach gradually changed the visual stimulus towards a 1:1 ratio, approaching a veridical visual input that would be encountered by observers undertaking a forward movement. Wallach found that observers only reported visual motion when the visual stimulus differed from the associated head-movement by 40%. This suggests that the extra retinal self-movement signal did not provide a very accurate basis for the expected retinal motion because the rotation of the object differed substantially from what would normally be experienced and yet observers did not detect that the object had rotated. Thus, on the basis of extra-retinal cues to self-movement, it appears that the ability to detect scene-relative movement is somewhat limited.

Wexler, Lamouret, and Droulez (2001) demonstrated that extra-retinal information modifies the perception of ambiguous retinal motion. In their study, whilst the observer made a head-movement they presented a visual stimulus that had two possible interpretations; either that of a moving rigid object or a stationary but non-rigid object. When extra-retinal cues were available, observers tended to perceive an object that was stationary and non-rigid rather than a moving object that was rigid. Faced with ambiguous retinal motion, it appears that an extra-retinal cue to self-movement provides the visual system with information that biases observers to perceive objects as stationary during self-movement. This bias is useful for attributing retinal motion to self-movement rather than object movement. Wexler and colleagues have also demonstrated other instances where novel ambiguous stimuli are perceived to be stationary during self-movement, or simulated self-movement, of the observer but the same object is perceived to deform when the observer is not moving (van Boxtel, Wexler & Droulez, 2003; Wexler & Droulez, 2003; Wexler, 2003). These studies by Wexler et al. demonstrate that extra-retinal signals can provide an important source of self-movement information which can help to segregate retinal motion into components of self-motion and object-motion. If the visual system can interpret retinal motion as self-movement then this means that more retinal motion is accounted for and then any deviations from the expected pattern of retinal movement can be correctly identified as object movement relative to the scene.

Whilst Wexler et al.'s results show evidence of an extra-retinal input to the mechanisms which account or compensate for our own movements they do not provide information about the accuracy of the extra-retinal signal to self-movement. Wallach's findings suggest that there are limitations to the information from proprioceptive cues to self-movement. In certain conditions, extra-retinal signals may be imprecise or inaccurate, and sometimes they may be unavailable. One such situation is when travelling as a passenger in a car moving at a constant velocity, such as on a motorway. This scenario causes problems for afferent and efferent cues because as a passenger we would not be initiating any actions that are associated with self-movement and so there would be no corresponding motor command with which to anticipate and subsequently compare the experienced visual motion. Vestibular mechanisms only respond to changes in orientation or lateral acceleration and deceleration and therefore are unable to provide a reliable signal to self-movement during constant velocity (Gillingham & Previc, 1993). A reliance on extra-retinal cues to self-movement in this case would be likely to result in inaccurate or unreliable judgements of object movement during self-movement. In these situations especially, visual information about self-movement information is likely to be important for detecting object movement during self-movement.

1.3.2 Optic flow

An alternative source of information about self-movement is optic flow; the pattern of optical motion available at the eye during self-movement. A necessary distinction is drawn between the optic flow and retinal flow, with the former representing the pattern or structure of light at a particular vantage point whereas the latter denotes the pattern of light that falls on the retina during self-movement and is limited to the field of view and affected by gaze direction. To clarify these two terms, consider Gibson's classic drawing of optic flow (Figure 2).

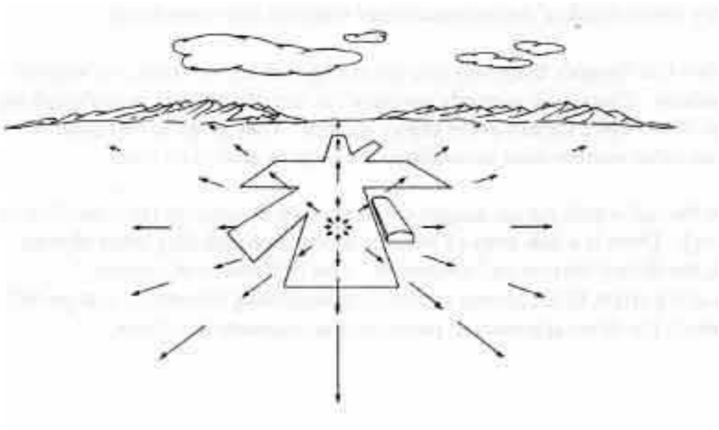

Figure 2 - An example of optic flow (Gibson, 1950).

Figure 2 depicts the optical flow produced by an observer translating forwards. When the observer is looking straight ahead, the pattern of retinal flow matches the pattern of optic flow with the focus of expansion (FOE) present at centre of the retinal and optic flow field. Yet if the observer's gaze direction is to their left and perpendicular to the direction of travel then the pattern of motion on the retina will not correspond to the optic flow because in the retinal flow the FOE will be shifted into peripheral vision whereas the optic flow remains fixed with respect to the observer. In addition, if the observer makes an eye movement during forward motion then this produces an additional component of optic flow. The optic flow due to the translation of the observer and the eye rotation will combine on the retina to produce a complex pattern of retinal flow. The next sub-section presents evidence that establishes human sensitivity to optic flow, and indicates that visual information about self-movement can be readily detected by the visual system. This detection is important if optic flow is to be utilised to compensate for retinal motion due to self-movement and aid in the detection of object movement during self-movement. The second sub-section then briefly outlines some alternative uses of optic flow that exist in the literature and provide useful background to the present work.

1.3.2.1 Sensitivity to optic flow

This section outlines some key studies that show convergent evidence from neurophysiology, psychophysics and imaging research that the brain is sensitive to global patterns of optic flow. The corroboration of data across these three methodologies indicates not only that there are neural regions sensitive to visual flow consistent with self-movement but also that we can utilise this information to make perceptual judgements. Human sensitivity to optic flow supports the hypothesis that this visual information plays a role in compensating for retinal motion during self-movement.

1.3.2.2 Neurophysiology

Neurophysiology work in primates provided the first indication of cells that selectively respond to visual self-motion (e.g. Graziano, Andersen, & Snowden, 1994; Siegel & Read, 1997). One notable example is the work of Duffy and Wurtz (1991, 1995) who reported evidence of cells in the medial superior temporal area (MST) of macaque monkeys that show a preferential response to either expanding and contracting radial motion or clockwise and anti-clockwise circular motion (Figure 3).

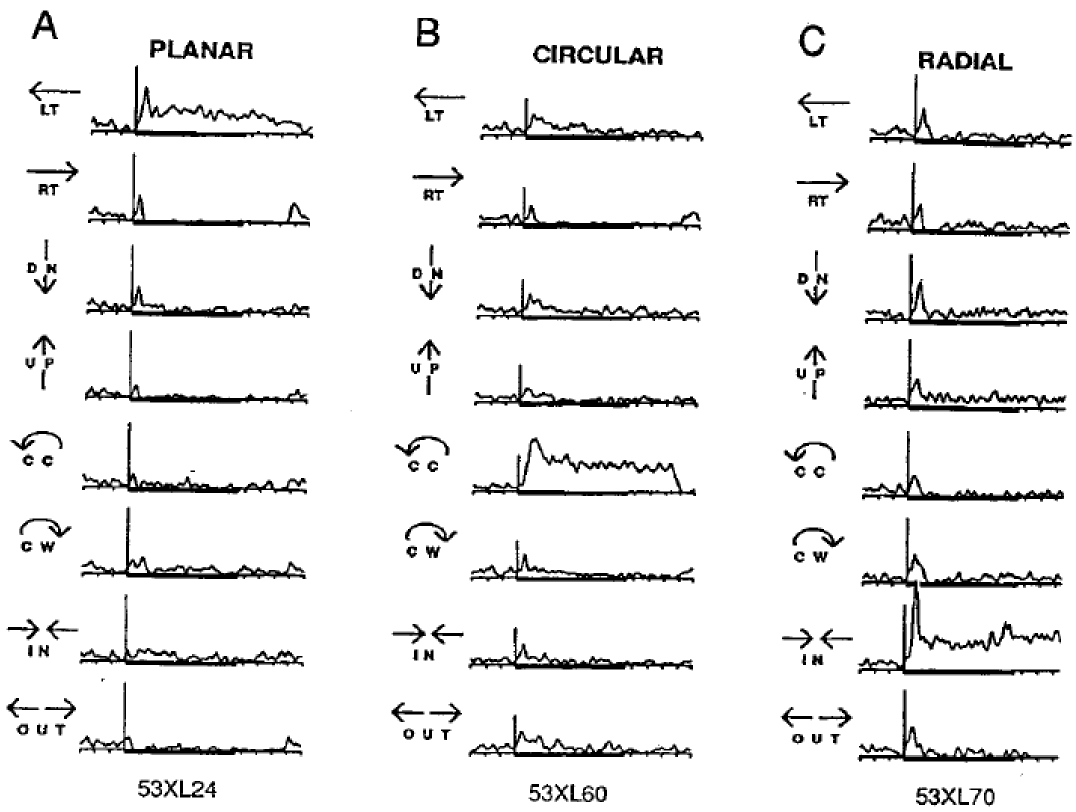

Figure 3 – Preferential responding of three cells in MST to planar (a), rotary (B) or radial (C) flow (Figure 4; Duffy & Wurtz, 1991).

Other researchers have also demonstrated similar findings in primates (Tanaka & Saito, 1989; Siegel & Read, 1997; Anderson & Siegel, 1999; Paolini, Distler, Bremmer, Lappe & Hoffman, 2000).

1.3.2.3 Psychophysical data

Snowden and Milne (1997) probed whether neurons like those that had been identified in non-human primates (i.e. Duffy and Wurtz, 1991) for detecting large field motion were also present in humans. They looked for evidence of neurons with large retinal fields sensitive to rotation, translation and expansion/contraction. If such neurons exist then it should be possible to adapt them to global motion and, following adaptation, demonstrate a motion after effect (MAE). Furthermore, if the adapting neurons have large receptive fields then the MAE should not only be present in the same location as the adapted stimulus but also in other locations within the same receptive field. Snowden and Milne termed the latter a ‘phantom’ MAE because if motion was not in this location during adaptation then any illusory motion experienced in this location would not be ‘after’ physical motion.

To test these predictions, they adapted observers to motion presented in two segments located on the left and right of fixation. Participants were adapted to global patterns of radial, rotary, translation motion or a second rotation condition in which opposing upward translation was presented on the left of fixation and downward translation presented on the right of fixation (or vice versa). Following adaptation, test segments were then presented either in the same location as the adapting stimulus or in the segments where the adapting stimulus had not been present (above and below fixation) to test for a classic MAE and a phantom MAE respectively. Observers reported motion after effects in both test conditions. The phantom MAE is particularly interesting because it demonstrates that motion presented in one area of the retina is sufficient to activate and subsequently adapt neurons that respond to global motion even though no there is no physical motion across the retina. This suggests that the detection of global motion consistent with self-movement would be relatively robust because even discrete areas of flow would likely activate these neurons and lead to the identification of self-movement. In sum, the global adaptation in this study is strong evidence for the existence of neurons with large receptive fields that are sensitive to global patterns of flow, such as those present on the retina during self-movement.

This work is also supported by that of Freeman and Harris (1992) who demonstrated that the processing of global flow appears to be independent for expansion and rotation. They presented observers with expanding or rotating (roll) flow fields, or modified destructured versions of these two patterns; generated by randomly rotating the trajectory of each dot in the original stimulus such that they no longer formed a coherent flow pattern. In their first study, they presented random dot stimuli in two intervals of 650 ms. One interval contained a stationary dot pattern and the other contained a moving stimulus. Observers were asked to detect which interval contained the moving pattern. The results revealed that observers had lower thresholds for the detection of structured patterns than destructured patterns. The authors interpreted their findings as an indication of specialised detectors for coherent motion patterns but not for random motion, arguing that coherent motion activated neurons that detect global flow leading to an enhanced perceptual sensitivity to these patterns compared to destructured motion.

In a second experiment, Freeman and Harris demonstrated that the ability to detect expanding flow was not affected by the presence of a rotating mask and similarly, detection of rotation was not affected by an expanding mask. If these two patterns of motion had interacted then this would suggest the same neurons were responding to both types of motion rather than separate populations of neurons being activated by different types of motion. The dissociation that Freeman and Harris found between expansion and rotation suggests that the visual system is selectively and independently tuned for these two patterns of motion. This demonstration of human sensitivity to optic flow supports the idea that retinal flow which is consistent with self-movement could be rapidly identified by the visual system. Once identified it could then be used to compensate for retinal motion due to self-movement and allow observers to detect object movement.

Bex, Metha, and Makous (1998) have provided further evidence that supports the existence of neurons that selectively respond to global patterns of motion and demonstrated a hierarchy of motion processing whereupon these neurons pool information from local motion signals. They investigated the perceived speed and speed discrimination thresholds for moving gratings presented in four apertures. The location of the apertures remained fixed but their orientation, and thus the direction of motion, was manipulated as in Figure 4. This created three distinct patterns of global motion (radial, rotation and translation) that were composed of the same local elements.

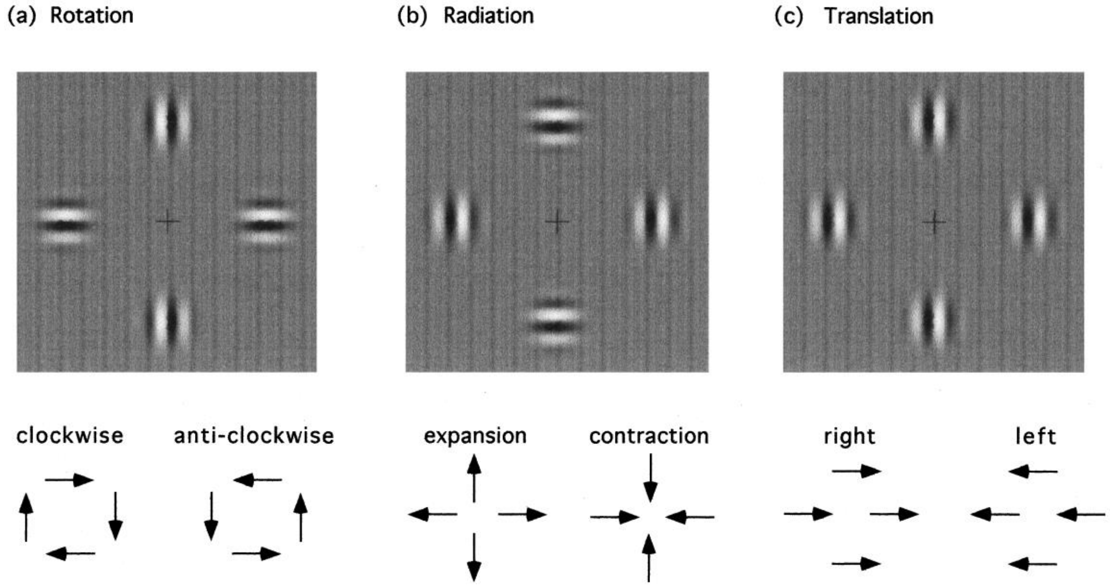

Figure 4 - Stimuli used by Bex et al. (1998).

Even though the speed of each local motion element was always the same they found that when they were arranged to produce a radial pattern the perceived speed of this stimulus was 32% higher than for the rotation or translation patterns. Despite this difference in apparent speed there were no differences in speed discrimination between the patterns of motion. Access to speed information in the local process is not compromised by the global processing of the stimulus. This would explain why the ability to discriminate speed is unaffected by the apparent speed of the stimulus. It is therefore the global processing of speed that leads to the higher apparent speed in the radial condition compared to rotation and translation conditions. One possible reason that Bex et al. suggest for the higher apparent speed in the radial formation is that if the patterns represented real observer movement through the world then due to perspective projection the flow vectors in radial flow are foreshortened. This means that for radial flow a motion vector of the same length on the retina equates to a larger forward displacement in the world than if the same motion vector was present on the retina during rotation or translation. If the visual system were to take account of this foreshortening then the rate of displacement in the radial condition would necessarily be faster than during the other two conditions, which would explain the higher apparent speed for radial flow.

Taken together these psychophysical studies suggest that humans, like primates, are sensitive to global patterns of optic flow and that this processing is distinct from simple local motion processing.

1.3.2.4 Functional imaging

The work of Morrone, Tosetti, Montanaro, Fiorentini, Cioni and Burr (2000) has also extended the primate findings to humans using imaging techniques and found selective activation of MT+ to optic flow stimuli using functional magnetic resonance imaging (fMRI). They presented coherent radial, rotation, and translation flow patterns or incoherent patterns with the same local motion components. The coherent stimuli produced a stronger response in the V5/MT+ complex for radial and rotation motion. The three patterns of activation produced by radial, rotary and translation motion were distinct from the activation seen during in the incoherent motion displays, mirroring the psychophysical data presented by Freeman and Harris (1992) which implied an enhanced neural sensitivity to coherent patterns of optic flow but not to destructured versions of the same stimuli. Morrone et al.'s results built upon the psychophysical research and provided evidence that MT+ is the neural locus of these effects.

Smith, Wall, Williams and Singh (2006), like Morrone et al. (2000) also investigated the human response to optic flow using fMRI and found evidence of optic flow sensitivity in MST. They found that activation was greater for complex structured flow patterns, such as expansion and rotation, than for random motion. In contrast to MST, MT did not appear to show selectivity for flow consistent with self-movement as this area responded equally to structured and random patterns of motion. This suggests that MT is responsible for processing motion, whereas MST is designated for processing optic flow. A more detailed discussion of neural sensitivity to retinal flow across the retina is found later in this General Introduction.

The combined findings from psychophysical studies, neurophysiology and imaging demonstrate that the brain is sensitive to patterns of flow indicative of self-movement. The next section explores some potential roles for optic flow that have been suggested in the literature, before moving on to consider how optic flow might aid in detecting moving objects during self-movement.

1.3.2.5 The role of optic flow

Several potential roles of optic flow have been put forward. Gibson (1950) initially suggested optic flow might aid observers in navigating through their environment. For example, forward movement of the observer produces a radial pattern of motion with the centre of the radial pattern (the FOE) indicating the direction of movement in retinal coordinates. Gibson suggested the FOE could be utilised as an indicator of self-direction, or heading. Experimental work revealed that observers are capable of judging their heading from radial flow to within 1 degree (Warren & Hannon, 1988). Although it has been questioned whether observers actually utilise optic flow for guiding locomotion in this way (Rushton, Harris, Lloyd & Wann, 1998). In spite of this controversy, it is clear that observers are able to identify the FOE from within retinal flow with a high degree of accuracy. Heading from optic flow is revisited later in the General

Introduction. Another possible role for optic flow concerns the spatial representation of the environment. Lepecq, Jouen and Dubon (1993) found evidence that the presentation of peripheral optic flow caused stationary observers to update the perceived direction of a world stationary target with respect to themselves, as if they had physically moved forwards in the world. This indicates that visual self-motion in peripheral vision feeds into mechanisms that maintain the spatial representation of objects in the surrounding environment.

Optic flow has been implicated in a range of other tasks. These include the visual control of reflexive eye movements (Busettini, Masson & Miles, 1997), as well as the ability to maintain balance or control posture during standing (Lee & Aronson, 1974) or locomotor activities (Bardy, Warren & Kay, 1999). Visual flow has also been shown to play an important role in the control of flight in insects (i.e. Kirchner & Srinivasan, 1989; Wagner, 1982) and birds (Lee & Reddish, 1981; Lee, Reddish, & Rand, 1991; Lee, Davies, Green, & van der Weel, 1993). Similarly, aircraft pilots must utilise visual information to control their flight path (Beall, & Loomis, 1997; Loomis, & Beall, 1998).

Until recently, research on optic flow has mainly investigated its role in the visual estimation of heading rather than with regards to maintaining perceptual stability. The next section introduces the Flow Parsing Hypothesis which suggests that optic flow provides a visual cue to self-movement which can be used to compensate for associated retinal motion.

1.4 The Flow Parsing Hypothesis (FPH)

Rushton and Warren (2005) have suggested that that optic flow feeds in to a visual mechanism to compensate for retinal motion due to self-movement and that the parsing of this optic flow from the retinal image allows observers to detect moving objects during self-movement. The FPH argues that global patterns of retinal motion that are characteristic of self-movement are identified and then parsed (or "globally subtracted"[2]) out. Figure 5 illustrates this process during forward movement. Figure 5A shows the pattern of retinal motion that

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[2] Note, subtraction is a mathematical description of the process but many mechanisms are possible. For example self-movement information can be used to generate a prediction of the retinal motion at a given location which can be compared against the perceived motion.

results when an observer views an object that is moving vertically upwards in the world whilst they themselves are moving forward.

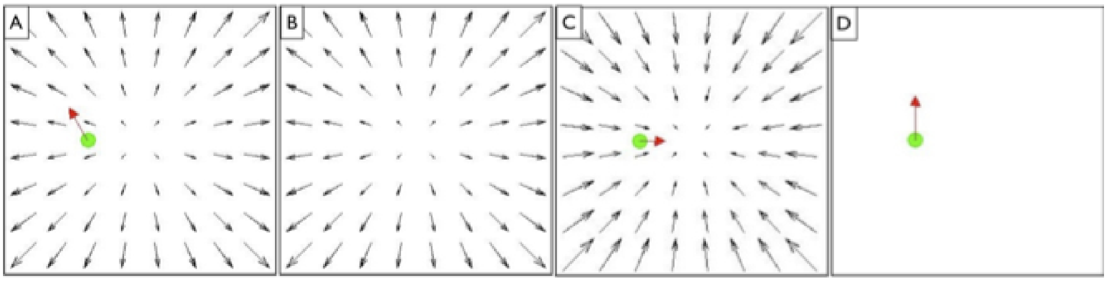

Figure 5 - Flow Parsing Hypothesis (Rushton & Warren, 2005). A) Retinal motion of a vertically moving probe viewed during forward self-movement. B) Brain identifies self-motion components. C) Self-motion components are subtracted/parsed from the scene (equivalent to adding a contraction field. D) Any remaining motion is attributed to object movement within the scene.

The global component of retinal motion due to self-movement, is illustrated in Figure 5B. The reader should note the naming convention adopted throughout; motion refers to motion on the retina whereas movement refers to movement in the world. This radial optic flow field is identified and then globally subtracted from the retinal image, which is equivalent to adding a contracting flow field (Figure 5C). The result of this subtraction is shown in Figure 5D; the remaining motion can then be attributed to the movement of an object relative to the scene. In this example the object is consequently perceived to move vertically upward, rather than along the oblique trajectory found in the retinal image.

Since proposing the FPH in 2005, Rushton and Warren have conducted a series of experiments to establish whether human behaviour is compatible with their theory. They simulated self-movement, which allowed them to isolate the visual cues to self-movement. As observers were instructed to remain stationary, extra-retinal signals to self-movement were minimised meaning that the visual parsing process could be examined largely in isolation. This paradigm also allows the experimenter to control the speed and duration of the simulated self-movement to ensure that the properties of the stimulus are held constant across observers. In their experiments they have tested the FPH by presenting stationary observers with a computer-generated pattern of visual motion that would be produced by actual self-movement of the observer within a stationary scene.

In the majority of Rushton and Warren's flow parsing experiments observers viewed visual motion depicting an object moving within a stationary scene that moved to simulate with self-movement and reported the trajectory of the moving object. In accordance with the FPH (see Figure 5), Rushton and Warren hypothesised that perceived trajectory of the object would be affected by two factors: the optic flow components that were presented and the position of the probe within the flow field or with respect to the observer.

Different types of self-movement (e.g. forward translation versus roll) produce different patterns of retinal flow. These differences mean that when flow is parsed from the retinal image, the effect of the subtracted flow component upon the target will also be different. For example, a vertically moving target positioned to the left of the FOE that is viewed during forward movement and expanding radial flow will, as a result of global parsing, have an additional rightward (globally contracting) component of motion applied to its trajectory. This will bias the trajectory to be perceived as tilting towards the FOE, rather than moving vertically. The same target trajectory viewed during backwards translation and contracting radial flow will, under flow parsing, have an additional leftward component of motion applied to it (global expansion) and therefore the trajectory will be perceived as tilting away from the FOE.

The position of the probe is predicted to influence perceived trajectory because the magnitude and direction of motion vectors differ depending upon the depth of the probe in the scene and also with retinal eccentricity. Therefore, when these flow components are parsed, the additional component added to the trajectory of the probe will be equal to the magnitude of the flow vector for that specific location in the scene. During forward translation, the greater the distance of the probe from the FOE the larger the magnitude of the flow vector. This means that when the probe is positioned further from the FOE then the motion vectors to be parsed from the retinal image will be larger than for a target located nearer to the FOE. The same principle applies when the probe is located at different distances from the observer. For example, during a lateral translation a probe located near to the observer would have a larger component of motion subtracted from it than a probe which was positioned further away. Thus, it can be seen that the predictions of the FPH with respect to perceived target trajectory are dependent upon the type of self-movement, which dictates the pattern of flow to be parsed from the scene, and the specific 3D location of the target within the scene.

1.4.1 Overview of sub-sections

To empirically test whether the flow components and position of the probe affect perceived object trajectory Rushton and Warren have simulated different types of self-movement and manipulated probe position across a number of experiments. After demonstrating evidence of a parsing process, Rushton and Warren have since begun to investigate the nature of the flow parsing mechanism. The research presented in the following section has been subdivided. The first two sub-sections (1.4.2 & 1.4.3) detail the evidence in support of a flow parsing mechanism. In Section 1.4.4, the global nature of this process is demonstrated which is critical to establish for the present hypothesis that visual flow from the peripheral retina will contribute to flow parsing. Section 1.4.5 considers evidence that flow parsing contributes to the perception of size change during self-movement. The subsequent section outlines additional evidence for flow parsing and the mechanisms which are thought to underpin this process. Finally, the flow parsing literature is summarised with reference to how it supports the present research.

1.4.2 Detecting object movement during self-movement

The first aspect of the FPH that Rushton and Warren sought to confirm was whether observers are able to detect relative movement between an object and the scene during simulated self-movement (Rushton & Warren, 2005). Observers were presented with 24 cubes depicting a rigid scene, viewed stereoscopically on a CRT monitor (Figure 6B). On 50% of trials, the scene moved in a manner consistent with a leftward translation and counter head-rotation of the observer, in the other 50% of trials the scene was consistent with a rightward translation and counter rotation. Within this scene, a stationary target was placed in a fixed location in the centre of the screen at one of three disparity defined distances (see Figure 6A) and observers were asked to report its direction as quickly as possible once the motion began.

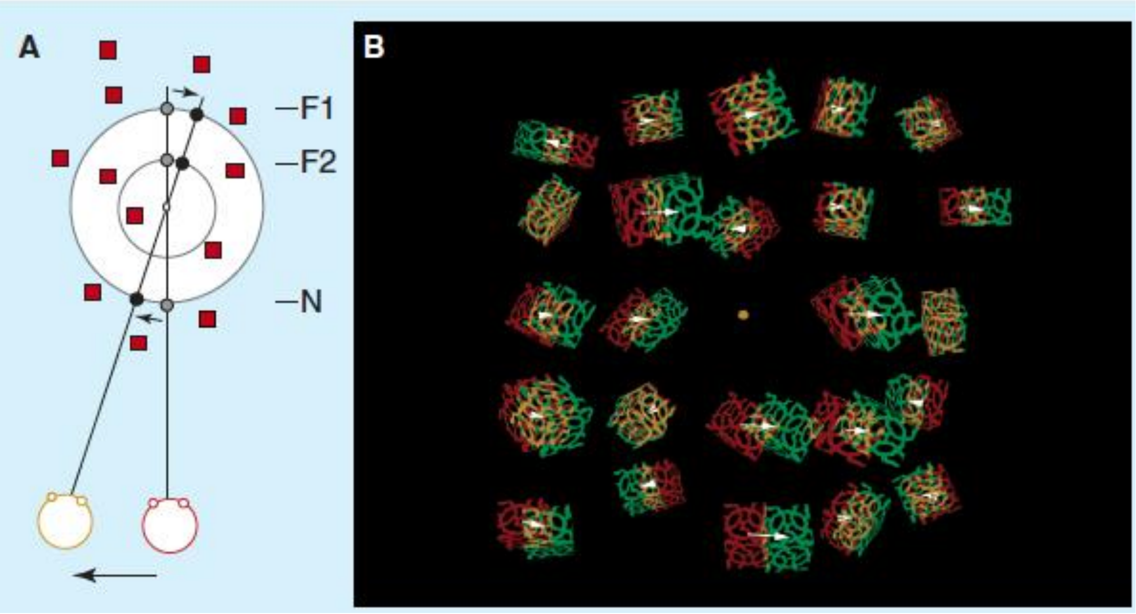

Figure 6 - A) Plan view of 3D cube scene used by Rushton and Warren (2005) with three target distances (F1, F2, & N) indicted. B) Visual stimulus used by Rushton and Warren (2005), arrows indicate the direction of motion of each cube.

Given the geometry of the scene, and therefore the flow components present on the retina, Rushton and Warren were able to predict the perceived direction and speed of the probe for each target location on the basis of the FPH. They predicted that, due to the geometry of the scene, targets positioned closest to the observer (position N in Figure 6A; defined by stereopsis), and in front of fixation would appear to move in the same direction as the observer. Conversely, targets beyond the centre of fixation (F1 & F2) were expected to be perceived to move against the flow (Figure 6A). The data was in line with each of these predictions, and provided strong evidence that observers could utilise retinal motion to make scene-relative judgements of object movement. This research suggested that observers are able to decompose these complex patterns of retinal motion into object motion and self-motion components in order to make judgements of object movement with respect to a stationary scene. The results of this study suggest that optic flow facilitates perceptual stability by parsing out retinal motion due to self-movement, and consequently, affords observers a scene-relative perception of object movement.

In 2007, Rushton, Bradshaw and Warren investigated whether observers could detect a moving object within an array of moving objects that simulated self-movement as readily as they could detect a moving object whilst stationary. Observers viewed an array of cubes set within a 3D volume and were asked to identify whether any of the cubes moved relative to the scene and to respond as quickly as possible whether that cube moved to the left or right. They varied the number of cubes in the scene to see whether the number of elements affected reaction time. A visual search paradigm was used and observers were asked to indicate if the object was moving to the left or the right relative to the scene. In a classic visual search task, a target item is placed within a number of distractor items which to not share the same visual feature. In Rushton et al.'s study, the motion of the target cube differed from the motion of the distractors. For stationary and simulated self-movement conditions they argued that if reaction times slowed as the number of potential targets increased then this would suggest that observers were actively searching the scene for an object which moved differently to the rest. Thus, on average, it would take longer to perform this search as the number of objects in the scene increased. If this was the case then it would suggest that the presence of distractor items which moved in a manner consistent with self-movement did not facilitate the detection of object movement. On the other hand if reaction times were not affected by the number of distractors in the scene then this would indicate that the coherent motion of the distractors enabled observers to rapidly segregate the target from the other elements in the scene and would provide support for the FPH.

The results showed that in both the stationary and the self-movement conditions participants were able to rapidly report whether a moving cube was present and reaction times were not affected by the number of cubes in the scene. This 'pop-out' of the moving object in the self-movement condition suggests that the visual system was able to identify and segregate the cubes which moved in a manner consistent with self-movement and that this parsing enabled observers to easily and rapidly detect the movement of the target cube.

The two flow parsing studies described in this section both support Rushton and Warren's notion of a purely visual mechanism for disaggregating retinal motion into components due to self-movement and object movement. This segregation of retinal motion permits observers to detect object movement during self-movement. The next sub-section considers whether observers can also discriminate the trajectory of a moving object during self-movement.

1.4.3 Discriminating object trajectory during self-movement

The FPH claims that the perceived trajectory of an object during self-movement will depend upon the optic flow components present on the retina and the location of the object in the scene. To investigate this claim, and build upon their initial two studies demonstrating that observers are able to *detect* scene-relative object movement, Rushton and Warren adopted a new paradigm to test for differences in object trajectory during different types of self-movement.

To test whether observers could discriminate object trajectory during self-movement Warren and Rushton (2007) simulated lateral translation and observer rotation and hypothesised that relative tilt would vary as a function of the type of optic flow and the depth of a target object placed in the scene. This study utilised a 3D display similar to Rushton and Warren (2005), which consisted of 24 randomly orientated 3D cubes (see Figure 7). A target was placed in the centre of the screen at one of three distances (80 cm, 95 cm, 110 cm) and moved upwards as the scene moved to simulate either lateral translation or yaw rotation.

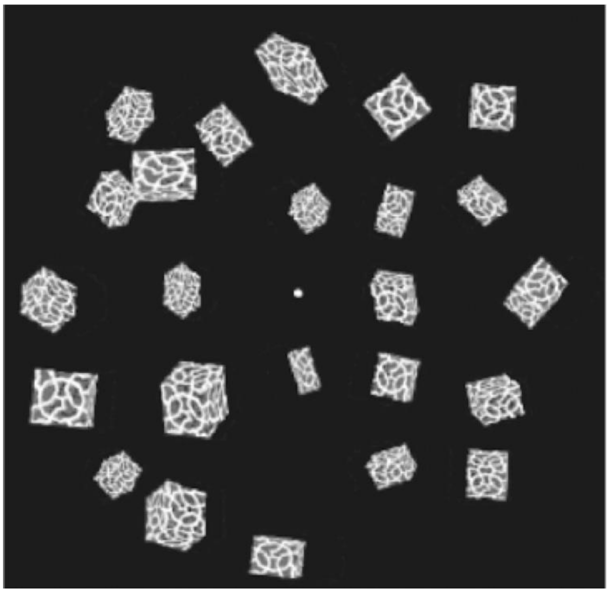

Figure 7 - Stimulus used by Warren and Rushton (2007).

The geometry of the scene differs during these two self-movements; during lateral translation the cubes that are further from the observer, and beyond fixation, will move less than the cubes which are closer but during yaw rotation the cubes will move across the retina by the same visual angle regardless of their distance. Thus, translation produces a pattern of flow that is dependent on depth but rotation produces a flow structure that is independent of depth.

Figure 8 visualises these differences.

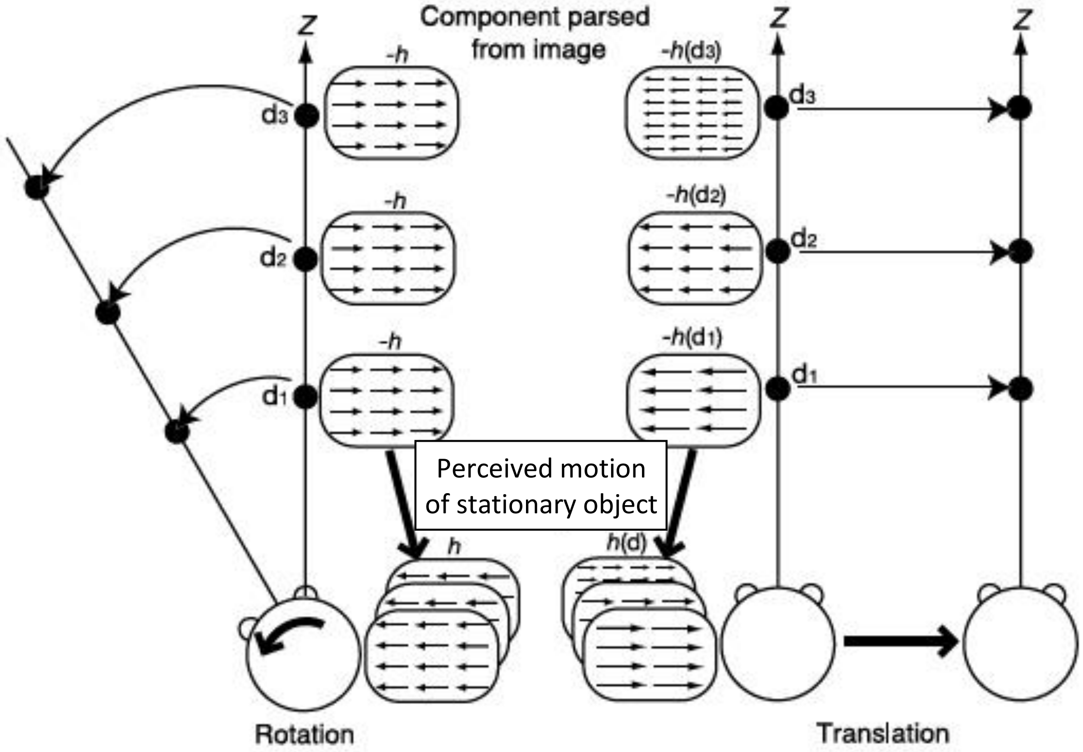

Figure 8 - An observer viewing a stationary object at one of three distances (d1, d2, d3) during yaw rotation (left) or lateral translation (right). The flow components to be parsed from the retinal image (-h) are independent of depth for rotation and dependent on depth

for translation. Due to the parsing process, the perceived motion of the stationary object is also independent of depth during rotation and dependent on depth during translation. Figure from Warren and Rushton (2007).

In light of these differences, Warren and Rushton predicted that the perceived trajectory of the target would differ as a function of the depth of the target in the scene and the type of self-movement. Critically, because the movement of the target was scaled with distance (such that its onscreen movement was less when it was placed further away in depth), the intuitive predictions of the translation and rotation conditions are reversed (Chapter 5 describes this study and these predictions in more detail).

Warren and Rushton's results supported the predictions of the FPH and demonstrated that perceived target trajectory differed with the depth of the target in the scene and the type of self-movement. This study added to Warren and Rushton's prior findings that had indicated observers are able to detect object movement within simulated self-movement. By employing two different types of self-movement, they provided evidence that observers can utilise patterns of visual flow to segregate retinal motion into components of self- and object-motion in order to discriminate perceived target trajectory. Together, these findings demonstrate compelling evidence that observers can effortlessly detect and discriminate scene-relative object movement on the basis of visual flow. If peripheral vision also contributes to flow parsing then peripheral flow should also facilitate the detection and discrimination of object movement during self-movement.

1.4.4 A global flow parsing mechanism

In two subsequent experiments Warren and Rushton sought to establish that their results were not driven by alternative accounts such local motion contrast (described below) and also to demonstrate that the effects were due to global motion processing. For the present work, it is important to establish that the parsing of self-motion from the retinal image is a global process because it is of particular relevance to the likely role of peripheral vision in flow parsing. For example, if flow parsing is not a global process then the presence of flow on the retina that is spatially separated from a moving object is unlikely to be effective in identifying self-movement and subsequently is also unlikely to contribute to retinal motion due to self-movement being parsed from across the retina. Rushton and Warren have tested the effects of discrete areas of visual flow upon the perception of object trajectory. This work was motivated by a desire to disentangle the predictions of the FPH from alternative local motion processing explanations of their earlier results. However their findings are presented here because they suggest that the presentation of visual flow in distinct retinal regions does give rise to flow parsing. In the experiments in this thesis, visual flow was also presented in similar discrete regions in peripheral vision and therefore these results provide an indication of the likely outcome of the current investigation.

Induced motion (Duncker, 1929) is a well-known effect that is typically reported when a stationary object is placed in-front of a directionally moving background. The stationary object then appears to move in the opposite direction to the background motion. The motion of the background induces this apparent, or illusory, motion in the stationary object. To dissociate the predictions of the FPH and the phenomenon of induced motion and to further investigate the global nature of flow parsing, Warren and Rushton (2008) presented a 2D radial flow field comprised of limited-lifetime dots that simulated forward observer movement. They varied the flow field in two key ways; the symmetry of the flow and the amount of noise present in the flow field. These manipulations placed the predictions of flow parsing and induced motion in competition. In all conditions, a probe was placed at the centre of the radial flow field (at the FOE) and moved vertically upwards.

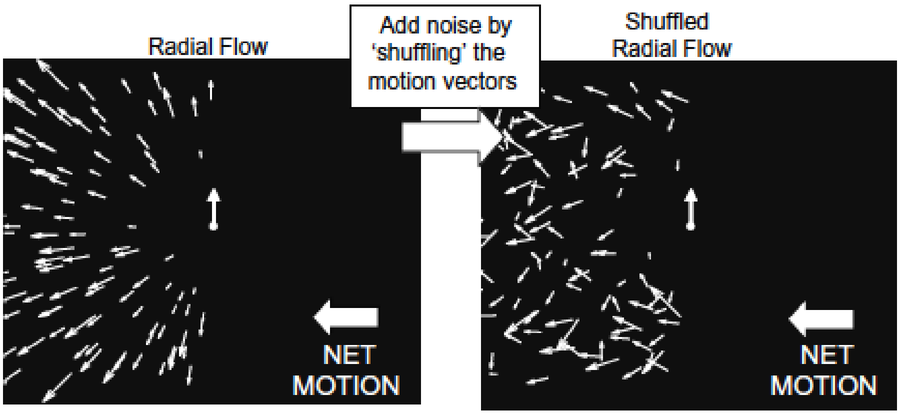

Figure 9 - Stimuli used by Warren and Rushton (2008)

The symmetry of the flow field was manipulated by changing the proportion of dots that were presented on each side of the screen. Under the

FPH, the ability to detect the radial flow field should be unaffected by the symmetry of the flow. Thus, for all symmetry conditions, it was hypothesised that radial flow would be detected and parsed from the scene. As the probe was initially located at the FOE and moved vertically upwards, the global subtraction of radial flow should mean that the probe is perceived to move vertically upwards with no trajectory bias. However, an induced motion account would predict that the probe trajectory would vary as a function of the symmetry of the flow field. For example, if all dots are placed on the left of the screen then there is a net leftward motion present in the display which, in the classic illusion, should cause induced motion of the probe in the opposite direction. Therefore when more dots are on the left of the display, induced motion would predict that probe trajectory would be biased towards the right, and when more flow is on the right the probe trajectory would be biased to the left.

The second aspect of the flow field that Warren and Rushton (2008) manipulated was the flow structure. The robustness of the self-motion signal was manipulated by shuffling the motion vectors in the radial flow field (as in Figure 9). In the half noise condition, 50% of the motion vectors were shuffled, and in the full noise condition 100% were shuffled. This shuffling ensured that the motion vectors present in the image were the same as in the no noise condition but in were not in a formation consistent with forward translation. In the no noise condition, Warren and Rushton predicted that forward self-movement would be identified and parsed from the retinal image, so that regardless of symmetry, the centrally located probe would always be perceived as moving vertically upwards. They made differing predictions for symmetric and asymmetric flow fields with an expected interaction between noise and symmetry. For asymmetric flow, in the half noise and full noise conditions, where either 50% of 100% of the motion vectors were shuffled respectively, they expected the flow field would no longer be identified as purely radial and this would mean that perceive trajectory was no longer in line with the parsing of only a radial flow field. They predicted that when the flow field was asymmetric, i.e. a higher percentage of points on the left-hand side of the screen, the net motion of the shuffled motion vectors would be interpreted as a gaze rotation rather than forward translation. When the majority of points were on the left of the screen (as in Figure 9), this would lead to global leftward flow being identified and parsed, subsequently resulting in perceived object trajectory that was rightward of vertical and vice-versa for when more points were on the right-hand side. In contrast, simple induced motion would not predict any differences in probe trajectory as a function of the amount of noise in the display because induced motion relies upon the net motion of the dots which remains the same across the noise conditions used in this study. To recap, flow parsing predicts an interaction between noise and symmetry with noise influencing probe trajectory only in asymmetric conditions but induced motion predicts that the symmetry of the flow field will influence probe trajectory but that noise will not.

As predicted by the flow parsing, Warren and Rushton (2008) found that when there was no noise in the flow field the asymmetry of the flow did not affect perceived probe trajectory. Yet when noise was introduced by shuffling the motion vectors the probe trajectory was perceived as tilted in the opposite direction to the net motion of the flow field. On trials where the flow field was symmetric, the perceived trajectory did not vary with the amount of noise suggesting that the symmetry of the flow field did not affect the ability to detect self-movement, and indicates that flow parsing mechanisms are equally adept at detecting self-movement from a partial flow-field as from a full flow-field.

This study placed the predictions of the FPH against those of an induced motion account. The interaction between symmetry and noise matched the predictions of the FPH and cannot be accounted for by induced motion. Importantly, the introduction of noise to the self-motion stimulus shows that if the self-movement signal is noisy then the brain will identify lamellar components rather than radial then observers' judgements of object movement may be compromised as self-motion components are not appropriately parsed from the retinal image meaning that it is harder to identify objects which are moving in the world from those that have retinal motion due to self-movement but are part of the stationary scene. According to the FPH a more accurate cue to self-movement will result in an increased ability to identify and subtract self-motion components from the retinal image. However, if the visual flow indicating self-movement is noisy then this may mean that self-motion is detected as lamellar rather than radial. If radial flow is misidentified as translating flow (for sideways movement) or yaw rotation then during the subtraction process not all elements of self-motion would be parsed out from total retinal motion leading observers to erroneously perceive stationary objects as moving. Thus, the correct identification of self-movement from retinal flow is a key step which Warren and Rushton state must occur before self-motion can be effectively parsed out from retinal motion.

To examine whether a global subtraction process drives the perception of object movement observed in their earlier studies, Warren and Rushton (2009a) moved the location of the probe away from the FOE. The central aim of this paper was to ascertain the relative contribution of local and global motion to flow parsing. In the first experiment, a 2D display presented expanding radial flow centred in the middle of the screen and observers were asked to report the perceived trajectory of a moving probe that was situated to the left or right of the FOE (Figure 10A). The FPH predicts that the subtraction of self-motion from retinal flow (the radial flow field) would mean the trajectory of the probe would have a contracting component of motion applied to it and subsequently the perceived trajectory would be biased towards the FOE, located in the centre of the screen. The results supported these predictions.

However these results could also be driven by a mechanism such as simple local motion contrast between the probe and the surrounding flow (Frost & Nakayama, 1983). A local motion contrast mechanism would compare the movement of the probe with the movement of the flow that surrounds the probe and this comparison could potentially indicate that the probe was moving in the opposite direction to the background flow. Thus, because the relative tilt predicted by the FPH is also in the direction opposite the flow (towards the FOE) then the bias in perceived trajectory could arise from either flow parsing or from the local motion contrast.

In the first experiment, three conditions were employed to test the relative contribution of local and global motion processing to the flow parsing process; a full field condition, local motion only presented within a circular aperture, and global motion only where an aperture obscured the local motion (Figure 10B).

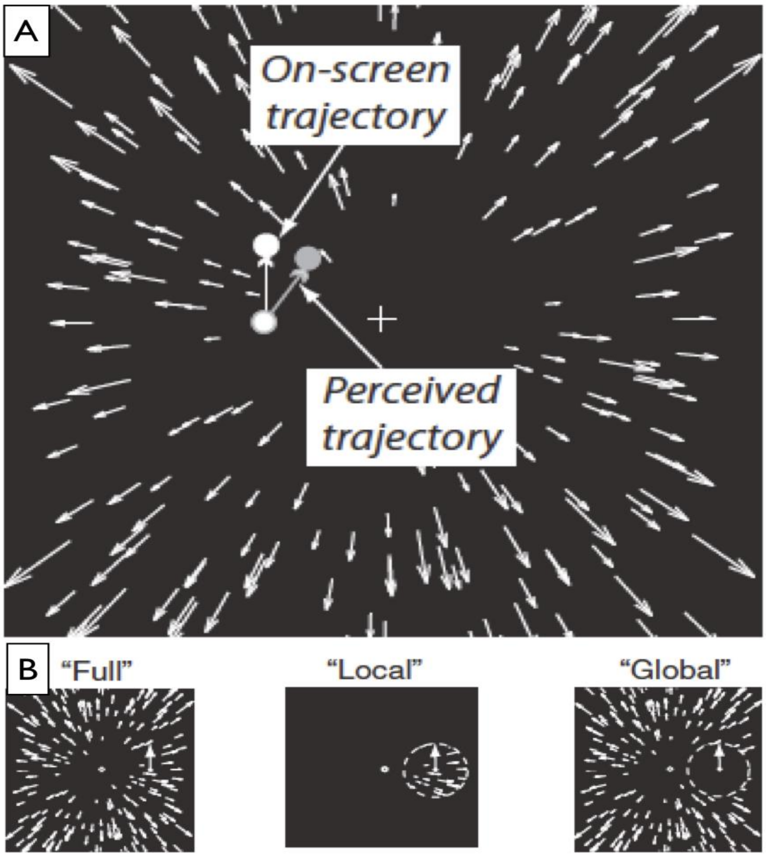

Figure 10 - Stimuli used by Warren and Rushton (2009a) A) Experiment 1 B) Experiment 2

The results revealed a significantly larger relative tilt was present in the full field and global only conditions than in the local only condition. This suggests that global motion processing is predominantly responsible for the identification of self-motion components from retinal flow, supporting a further aspect of the FPH.

To further separate the predictions of the FPH from those of local motion contrast and the induced motion phenomenon they conducted a second study in which they relocated the probe so that the FPH predicted a bias in a different direction to any potential induced motion of the flow field (Figure 11). In three conditions they presented either a full radial flow field, one half of a radial flow field with the probe placed in the same visual hemi-field, or half a radial flow field with the probe placed the opposite visual hemi-field (see Figure 11).

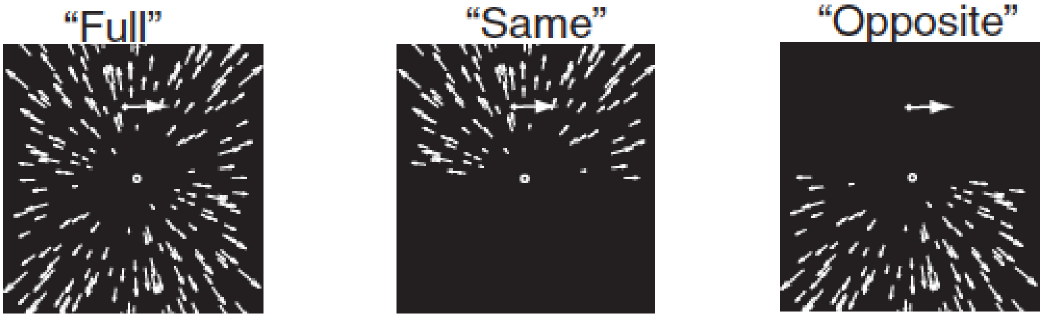

Figure 11 - Stimuli used in Experiment 2 of Warren and Rushton (2009a)

As in the first experiment, participants were asked to report the perceived trajectory of a probe placed either 2 degrees or 4 degrees from fixation. If the subtraction of self-motion occurs across the visual field then a relative tilt towards fixation would be expected in all three conditions. Furthermore, if the effects are due to flow parsing rather than induced motion then relative tilt should be larger for targets located further from fixation. The results supported this prediction, with a relative tilt towards fixation in the three stimulus conditions. Most importantly, even when the probe was spatially separated from the flow field the same pattern of results was maintained and relative tilt also increased with target eccentricity. Critically, an induced motion account would only predict induced motion to be in the opposite to the direction of the flow field and the effect would not increase with target eccentricity. Thus, induced motion cannot account for the relative tilt towards fixation or the increase in relative tilt with target eccentricity that was identified in the condition where the flow and probe were in opposite hemi-fields.

The two experiments presented in Warren and Rushton (2009a) clearly indicate that self-motion is globally subtracted across the visual field. Despite the fact that only half of the radial flow field was present (Experiment 2) this did not prevent the identification and parsing of self-motion from retinal motion. This suggests that the flow parsing process is relatively robust to a reduction in the amount of visual flow and that even small areas of self-motion on the retina are sufficient to drive the parsing mechanism.

1.4.5 Judgements of object size change during self-movement

Thus far, the studies I have presented by Rushton and Warren have considered either the detection of scene-relative movement or judgements of object trajectory during simulated self-movement. Judgements of object trajectory when stationary are a simple task, but this task is complicated during self-movement. The work outlined above suggests that when flow consistent with self-movement is present on the retina, observers can detect and discriminate object movement as though they were stationary. Equally, judgements about objects that change in physical size are simple when the observer is stationary but the same retinal motion becomes ambiguous during self-movement because changes in the retinal size of an object can arise from a number of events in the world. Rushton and Warren have suggested that visual self-movement information enables observers to disentangle changes in retinal size that are due to self-movement from those that are the result of a change in the physical size of the object.

Rushton and Warren (2011) presented preliminary evidence that suggests flow parsing also assists in judgements of an object's size during self-movement. They extended the predictions of the FPH in order to empirically test whether observers could detect an object changing in size during simulated self-movement. Observers viewed an array of wireframe objects with a sphere placed in the middle of the screen at fixation (Figure 12).

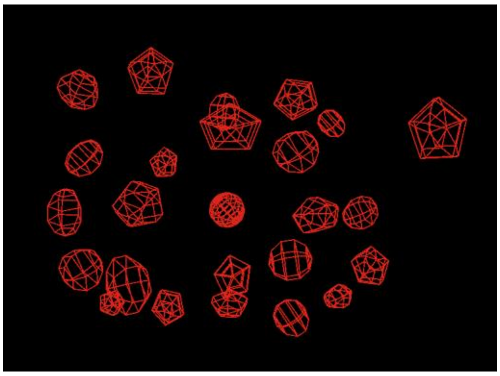

Figure 12 - Stimulus used by Rushton and Warren (2011)

In two separate experiments participants reported whether a sphere that moved in depth was also changing in physical size. Only on half of the trails did the object change in size. When the sphere was placed within a stationary scene of wireframe shapes, observers performed at chance level when asked to identifying whether the sphere changed in size. When the background scene also moved with the object this created a pattern of optic flow consistent with the observer moving towards a stationary object. In this instance, performance was greatly improved, and observers could detect whether the object changed in size with more than 90% accuracy. The addition of visual flow indicating self-movement facilitated judgements of object size because retinal motion could be parsed into self-movement and object-movement components. In the absence of visual flow the retinal motion could not be decomposed in this manner and observers were unable to differentiate between an object that moved in depth and an object which changed in size. This study extended Rushton and Warren's earlier findings and demonstrated that observers can also detect changes in object size during self-movement as well as detecting and discriminate object trajectory.

1.4.6 Further evidence for flow parsing

The research presented in Sections 1.4.2 to 1.4.5 provides compelling evidence for a flow parsing process. However the mechanisms which underpin this process are still somewhat unclear. More recent work has begun to explore the contribution of different visual features to parsing as well the integration of visual flow with non-visual cues in the perception of object movement during self-movement.

Warren and Rushton, alongside other researchers working independently, have begun to explore these mechanisms that might underpin this process by manipulating critical features of the flow field (Warren et al., 2012; Foulkes, Rushton & Warren, 2013a). Additionally, they have also presented evidence which suggests that although heading and flow parsing appear to rely on common processing (Foulkes, Rushton & Warren, 2013b) flow parsing does not rely on obtaining a prior estimate of heading from standard heading recovery mechanisms (Warren et al., 2012).

Another key study by Warren and Rushton demonstrates the importance of stereoscopic and monocular cues to depth for flow parsing (Warren & Rushton, 2009b). They tested whether, in the absence of stereo disparity, monocular cues to depth including motion parallax contribute to flow parsing. If flow parsing depends upon the depth information in the scene then results would show that flow parsing ability improves with the addition of depth cues. As in their first study (Rushton & Warren, 2005), they presented observers with displays of textured cubes simulating an observer translation and counter-rotation of thehead and asked them to report whether a centrally located probe at one of three distances (N, F1, F2) appeared to move to the left or right. As before they predicted that the perceived direction and speed of the probe would be affected by its position relative to the centre of the array (as in Figure 6, Page 17). Motion parallax was present in all displays. Monocular depth information in the scene was manipulated by adding relative size, linear perspective and occlusion clues (as in Figure 13) and examining how well the results matched the predictions of the FPH as each cue was added to the display. The results of these monocular conditions were compared against performance when depth was defined stereoscopically but the monocular cues (except for motion parallax) were absent.

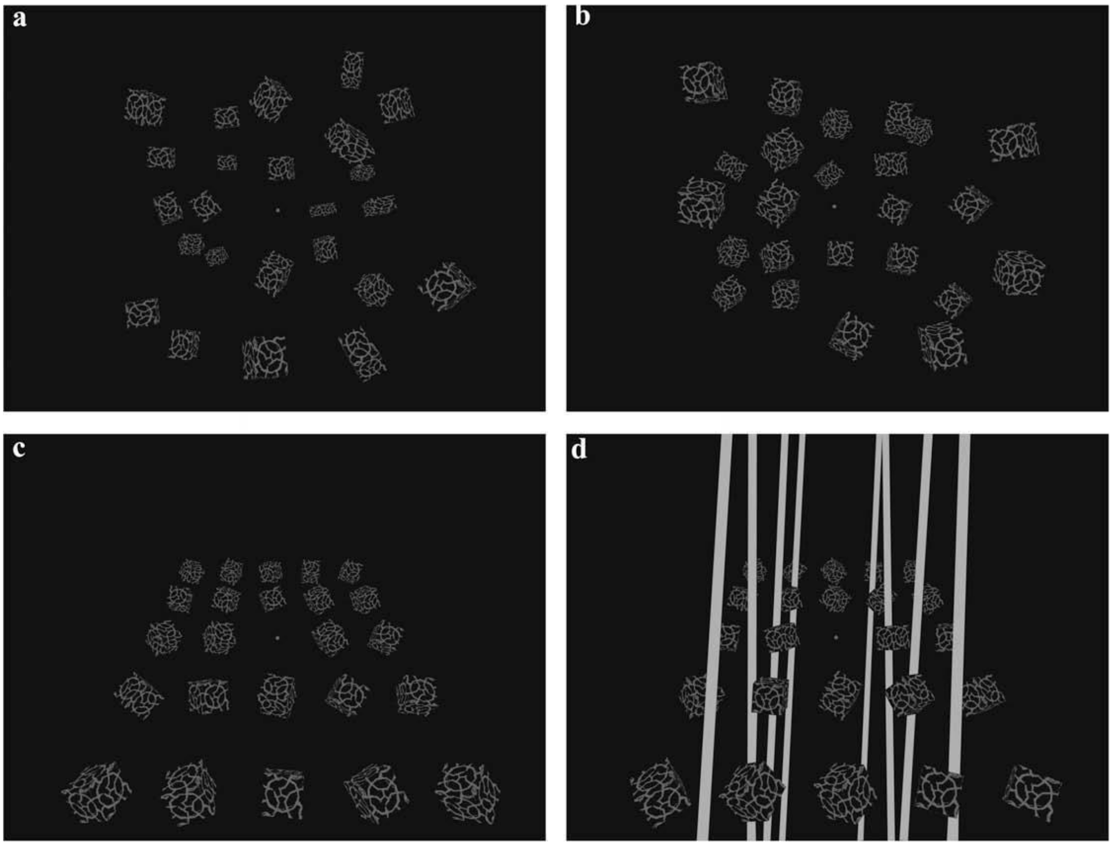

Figure 13 - Monocular stimuli used by Warren and Rushton 2009b. a) Motion parallax cues only b) Motion parallax and relative size cues c) Motion parallax, relative size, and linear perspective d) Motion parallax, relative size, linear perspective and occlusion.

The results showed that when stereoscopic depth information was present in the display a clear flow parsing effect was present. When stereo cues were absent and depth was defined only by motion parallax the results were no longer consistent with a flow parsing account. The addition of monocular cues to the display appeared to improve the ability to detect the movement of the probe relative to the scene and when all monocular cues were present performance was almost as good as when stereo information was available.

This study demonstrates that the availability of depth cues in central vision is important for flow parsing. When stereoscopic cues to depth are absent the perception of object trajectory is less in line with a flow parsing account. In Chapter 5, I utilise these findings to design an experiment where I reduced the reliability of central visual flow by removing stereoscopic cues to depth. The results of Warren and Rushton (2009b) indicate that this should result in a reduced ability to detect scene-relative movement. I propose that the addition of peripheral flow will offset the reduction in parsing ability when only monocular depth cues are available.

In addition to Warren and Rushton's work, several other labs have conducted studies that corroborate the existence of the flow parsing mechanism (Calabro, Soto-Faraco & Vaina, 2011; Calabro & Vaina, 2011; Royden & Connors, 2010; Fajan & Matthis, 2011; Fajen & Matthis, 2013; Fajen, Parade & Matthis, 2013; Matsumiya & Ando, 2009; Royden & Moore, 2012; Royden & Holloway, 2014). Related work by Glennerster and colleagues have utilised virtual reality in order to probe the contribution of visual and non-visual cues to self-movement estimation and the maintenance of perceptual stability; providing further evidence that visual information plays a role in the compensation of retinal motion due to self-movement (i.e. Tcheang, Gilson & Glennerster, 2005). In addition, Wexler and others (Wexler et al., 2001; van Boxtel et al., 2003; Wexler & Droulez, 2003; Wexler, 2003; Fajen & Matthis, 2013; MacNeilage, Zhang, DeAngelis & Angelaki, 2012) have demonstrated that the availability of both visual and non-visual cues influences our perception of object movement, indicating that the processing of object movement is not independent from the processing of self-movement.

Matsumiya and Ando (2009) used a similar experimental design to the ones used by Rushton and Warren, except that the observer was placed within an immersive virtual reality system which significantly increased the field of view of the flow stimulus that was projected on to 2 m x 2 m walls, three of which surrounded the observer and the other which served as the floor. In their first experiment, they simulated forward self-movement towards a plane that was defined using yellow dots, which was rotating about the horizontal. If participants based their judgement purely on the retinal motion of the plane, they would perceive the plane to rotate about the vertical axis. However, if they could extract the movement due to their own movement from the retinal image then they would perceive the plane to rotate about the horizontal axis. Four rooms were generated: a dark room, a stationary room, a moving floor, and a moving room. In all rooms the central 10 degrees was obscured by a black surface, which contained the yellow dots that indicated the movement of the rotating plane. They found that when observers were viewing a moving room, the addition of self-movement information to the scene altered the perception from ego-centric to world-centric and therefore the plane appeared to rotate around the horizontal axis.

In their second experiment, Matsumiya and Ando investigated 3D object trajectory in the same environment. In the dark and stationary rooms trajectory judgements matched those predicted by an observer-centred reference frame. In contrast, when presented with a moving room, observers' judgements were more in line with a world-centric reference frame. These findings provide additional evidence to suggest that observers are able to utilise visual self-movement information in order to extract a scene-relative (or world-centric) percept of object movement. Moreover, this work is the first to demonstrate flow parsing within a rich immersive virtual reality environment. Their study presented visual flow across the visual field, which extends the work of Warren and Rushton who utilised either a CRT monitor or large projection screen for their self-movement stimuli. Existing research has only demonstrated flow parsing process using central visual flow and whereas this study was the first that included both central and peripheral flow. The self-motion stimuli used by Warren and Rushton have never exceeded 52 degrees of visual angle (26 degrees either side of fixation). Matsumiya and Ando (2009) presented flow in the peripheral visual but this was always paired with central flow. They found that performance improved with a display that included a ground plane in the peripheral visual field. However, because this study never presented peripheral flow in isolation it is not possible to determine whether there is a unique peripheral contribution to flow parsing.

Expanding upon Warren and Rushton's work some investigators have employed alternative paradigms to investigate the contribution of visual and non-visual self-movement cues to flow parsing. Fajen and Matthis (2013) asked observers wearing a head mounted display and walking through a virtual environment to judge whether or not they would be able to pass between two moving obstacles. They sought to identify whether non-visual cues generated by the observer's active locomotion dominated over visual cues to self-movement or whether both contributed equally to the detection of object motion during self-movement. In order to isolate the contribution of visual information about self-movement from the actively generated extra-retinal information they increased speed of the visual stimulus by 50% on 24 out of 120 trials. This manipulation meant that the non-visual cues still gave observers veridical information about their own movement but the visual information was no longer providing accurate visual information about their movement through the world. They found that the manipulation of visual information still influenced observers' judgements despite the incongruence between their own movement through the world and the visual information indicating their self-movement. These results indicate that even in the presence of extra-retinal information visual information still makes a notable contribution to the perception of scene-relative object movement. This study highlights that there are interactions between visual and non-visual sources of information about self-movement and demonstrates that they do not operate in isolation. In terms of the present work this promotes the idea that central and peripheral visual flow might play complementary roles in flow parsing which support the perception of object movement during self-movement.

MacNeilage et al. (2012) investigated how vestibular information affects the parsing of optic flow. They presented participants with visual flow depicting a certain heading and asked observers to detect the movement of an object within the scene; a standard flow parsing display and task. In addition, they ran a condition in which the participant was physically moved in the heading direction for the corresponding visual flow. This generated vestibular information about self-movement. They hypothesised that the addition of vestibular information would improve the ability to detect object movement. They varied the heading of the optic flow (0, 30, 60, 90 degrees) and measured object movement discrimination thresholds with and without vestibular cues. Forward motion (0 degrees) showed no significant change in threshold with the addition of vestibular information. However, more eccentric headings revealed a significant improvement in detection when vestibular information was available. They suggested that vestibular information is more reliable than vision with large heading eccentricities, but that visual information is more reliable when heading is less eccentric. This suggests that different cues to self-movement do not make a fixed contribution to flow parsing but instead that some cues are more important in certain situations. The changing contribution of centrally presented visual information in the presence of extra-retinal sources of information about self-movement suggests that in some circumstances the availability of peripheral flow could improve the ability to detect scene-relative movement.

1.4.7 Flow parsing summary

To summarise, optic flow is key source of information about our own movement through the world. Rushton and Warren (2005) have suggested that human sensitivity to visual flow consistent with self-movement facilitates a visual parsing process that allows observers to detect scene-relative object movement. Empirical evidence supports the existence of a flow parsing mechanism that operates globally to remove self-motion components from the retinal image and permits the detection and discrimination of object movement during self-movement.

Critically, the presentation of flow in a small portion of the visual field appears to drive a global subtraction of self-motion components from the retinal image. For the present work, this suggests that a peripheral flow stimulus would be capable of contributing to flow parsing process despite a large angular separation between the visual flow and a centrally located target. Rushton and Warren have successfully demonstrated that central visual flow is sufficient to drive a scene-relative percept of object trajectory and also assists in the discrimination between objects that change in size and objects that move in depth. If peripheral vision contributes to this process then it should be possible to demonstrate the same signature flow parsing effects when self-movement information is *only* available in peripheral vision.

Researchers investigating the contribution of visual and non-visual self-movement cues to flow parsing have indicated that the contribution of each cue may vary depending upon the type of self-movement and reliability of the cue for estimating self-movement (Fajen & Matthis, 2013; MacNeilage et al., 2012). This suggests that when additional visual information about self-movement is available this is likely to contribute to flow parsing. In the next section I explore reasons why peripheral flow might also provide an input to the flow parsing process.

1.5 Flow parsing in peripheral versus central vision

The main focus of this research is to probe the mechanism that underpins flow parsing. Specifically, I seek to establish whether self-movement information in peripheral vision contributes to flow parsing.

1.5.1 Hypothesis and motivating factors

Due to variation in optic flow, central and peripheral vision are often exposed to different patterns of flow and consequently provide different visual information about self-movement. My overall hypothesis is that when peripheral vision provides different or complementary information to central vision, peripheral flow will make a unique contribution to flow parsing. This hypothesis is informed by evidence that:

1. flow parsing is a global process (see Section 1.4.4, above)
2. humans show a neural sensitivity to peripheral flow
3. peripheral flow is important for the perception and control of self-movement.

Section 1.5.2, below, formally defines what is meant by peripheral vision in the context of this thesis. I then move on to discuss the differences in optic flow with eccentricity, prior to presenting evidence that humans can detect peripheral flow (Section 1.6.2) and that this information is important for the perception and control of self-movement (Section 1.7).

1.5.2 Defining peripheral vision

Near to the inner surface of the eye, the retina is a layer of retinal ganglion cells (RGCs). These cells each receive input from photoreceptors in a specified region of the retina; the cell's receptive field. The presentation of a stimulus within this receptive field will raise the firing rate of the cell, transmitting information along the optic nerve and on to the visual cortex. The size of the receptive field of a RGC corresponds to the number of photoreceptors that input to the cell and will determine the resolution of vision. For example, a RGC that receives input from only a handful of photoreceptors will provide information about the light falling on the retina that is highly localised. If a number of RGCs occupy a very small region of the retina, with overlapping receptive fields, then it becomes possible to discriminate visual features with very fine detail because the same region is sampled multiple times. This sampling provides multiple localised information points and also allows the firing rate to be compared between cells. When a large number of photoreceptors project to a single RGC the receptive field size is larger and consequently the resolution is, in comparison, greatly reduced.

In central vision receptive field size is small (Hubel & Wiesel, 1974). This allows fine details in the world to be discriminated, especially within the fovea, the small pit in the retina with maximum visual acuity. Receptive field size increases with retinal eccentricity (Hubel & Wiesel, 1974) resulting in a lower angular resolution further from the fovea (Weymouth, 1958).

Although resolution decreases with eccentricity, RGCs with larger receptive fields are more sensitive to small changes in the pattern of light on the retina than those in the centre of vision. For example, suppose RGCs respond when the input from photoreceptors reaches a given threshold and each photoreceptor output provides an equal output that is below that threshold. When the receptive field is large and many photoreceptors converge to a single RGC, a small change on the retina which activates only a small proportion of the photoreceptors will still cause a response in the RGC because information is pooled from a larger area. This explains why flicker is more readily detected in peripheral rather than central vision (Tyler, 1981). However, if a RGC only receives input from a single photoreceptor, the same change on the retina will not cause a response in the RGC because it is sub-threshold. Thus, the size of the receptive fields across the retina results in a trade-off between resolution and sensitivity.

RGCs can be divided into two classes; ON-centre and OFF-centre. The former responds when only the centre of the receptive field is stimulated with no excitation in the inhibitory surround. OFF-centre RGCs show the opposite preference, preferring a stimulus to be present in the surround but not the centre. The size of the centre spot within the receptive field of a RGC therefore dictates the preferred spatial frequency of the cell. Figure 14 illustrates this relationship between receptive field size and preferred spatial frequency in ON-centre RGCs.

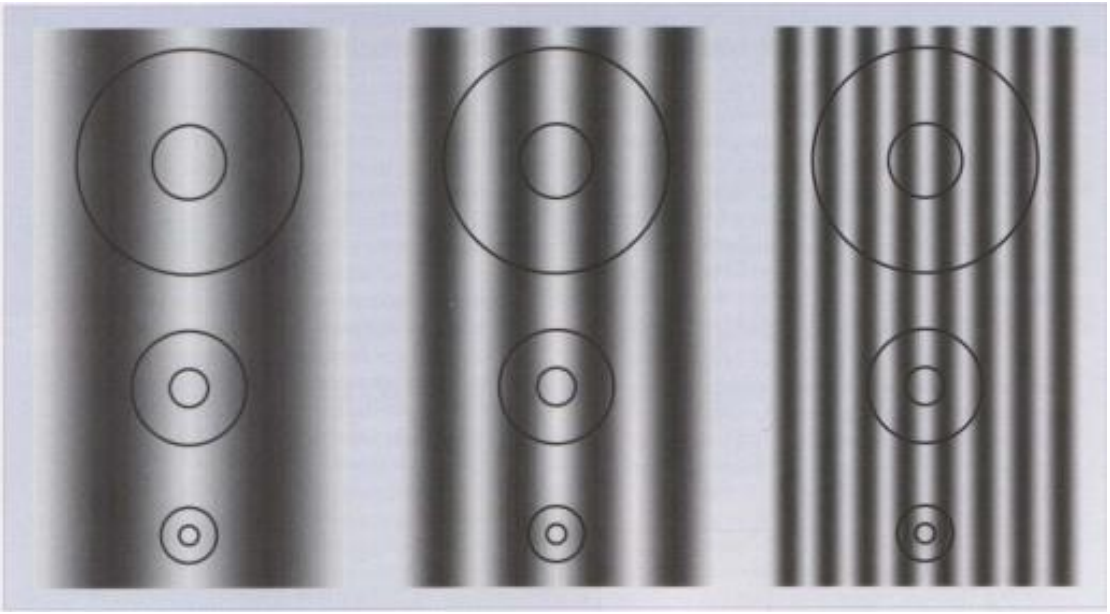

Figure 14 - Three sinewave gratings of increasing spatial frequency from left to right. The receptive fields of three ON-centre RGCs are superimposed on each grating. From Meese (2002).

Small receptive fields show preferential responding to high spatial frequency information while large receptive fields are tuned to lower spatial frequencies. The increase in receptive field size of RGCs with retinal eccentricity therefore means that the centre of vision is specialised for detecting high spatial frequencies and more eccentric cells are more readily able to detect low spatial frequencies.

The change in receptive field size with retinal eccentricity helps to define the extent of central vision and peripheral vision. Osaka (1994, as cited in Berencsi, Ishihara, & Imanaka, 2005) assessed the distribution of cones and rods across the retina and defined the central 2 to 4 degrees of vision as ‘central’ with everything beyond this being classed as peripheral vision. Trevarthen (1968) classified peripheral vision as beyond the central 4-5 degrees of vision. However many experimental studies consider central vision to cover a much larger portion of the central retina, typically extending up to 15 degrees from fixation (a 30 degree region in the centre of vision). Table 1 lists the central and peripheral distinctions that have previously been adopted by other researchers. This prior literature informed a suitable definition of peripheral vision for this thesis.

Table 1 – Details of the central and peripheral stimuli used in a sample of previous studies investigating the role of central and peripheral vision.

Study	**Central stimulus (diameter)**	**Peripheral stimulus**
Brandt, Dichgans and Koenig (1973)	30 degrees / 60 degrees	beyond central 60 degrees
Paulus, Straube, and Brandt (1984)	30 degrees	beyond central 30 degrees
Delorme and Martin (1986)	40 degrees	beyond central 80 degrees
Post (1988)	30 degrees	beyond central 60 degrees
Warren and Kurtz (1992)	10-25 degrees	beyond central 10/25 degrees to 40 degrees

On the whole, it seems that central vision is generally regarded to the central 30 degrees of vision, that is, 15 degrees either side of fixation. Beyond this central portion, most researchers adopt the term peripheral vision to describe the area being stimulated.

In this thesis, central vision is defined as a circular region that extends 15 degrees from fixation. Peripheral vision is defined as anything beyond the central 30 degrees of vision. The peripheral region is further subdivided into Near peripheral and Far peripheral. The near periphery is defined as a ring, or annulus of 30 degrees width that surrounds central vision. The maximum eccentricity of the Near periphery was chosen because it is exactly 45 degrees either side of straight ahead. The Far periphery surrounds the near periphery and extends ~60 degrees to the limits of the visual field. Figure 15 shows the extent of each region; Near peripheral between 30-90 degrees and Far peripheral beginning at 90 degrees and extending to the limits of the visual field. Separate near and far peripheral displays were defined because the flow structure present in these regions during self-movement is distinctively different. As such, the role of each region may not be the same in terms of flow parsing. The apparatus used to display visual flow is described later in the General Introduction (Section 1.9).

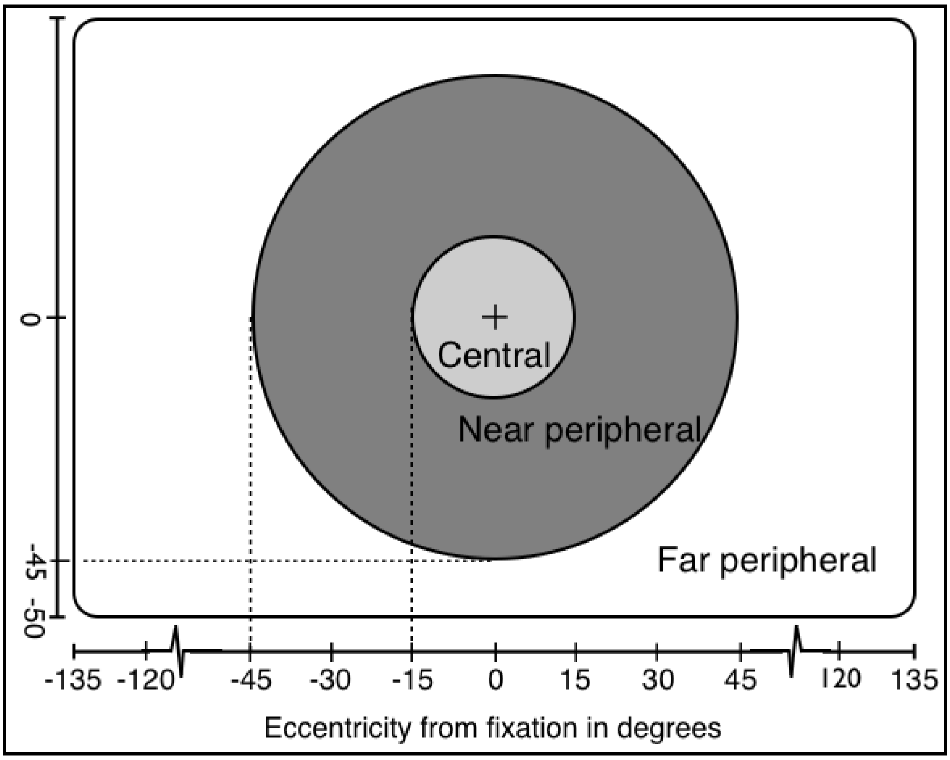

Figure 15 - Near and Far peripheral regions used in experiments.

1.6 Optic flow as a function of eccentricity

> *'When a perceiver moves forward in the world...the optical flow that is generated does not have the same geometrical structure everywhere (Gibson, 1979)'*
>
> (Stoffregen, 1985, p555)

This quote highlights an important motivation for this thesis; during locomotion, optical flow differs as a function of eccentricity meaning that central and peripheral vision are often exposed to different flow structures. Figure 16 shows the optical flow field produced during observer translation and observer rotation. Translation through the world generates a FOE which corresponds to the direction of motion through the world, and a focus of contraction (FOC) on the opposite side of the optical sphere, with lamellar flow in-between. Rotation about any axis produces two identical patterns of circular flow that surround the axis of rotation (AOR) on either side of the sphere and lamellar flow in-between.

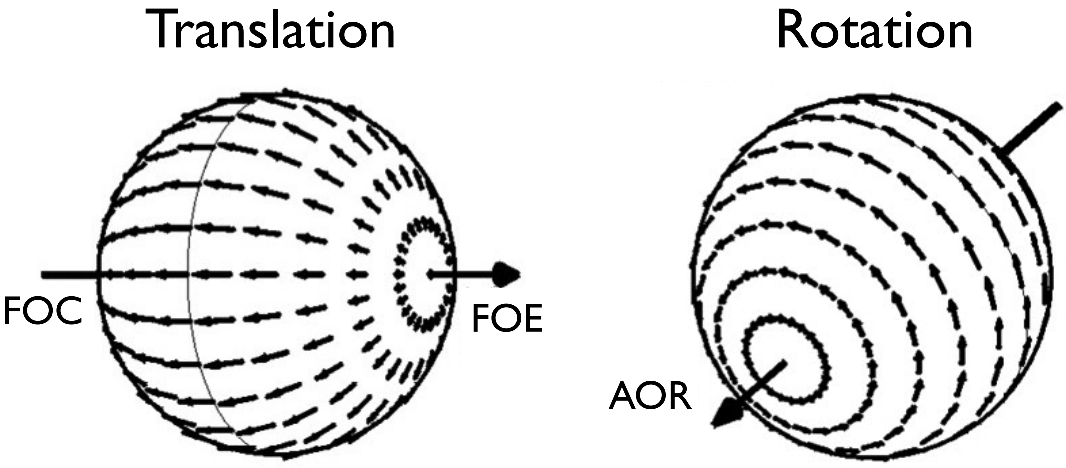

Figure 16 - Optic flow for translation and rotation movements projected onto an optical sphere (Adapted from Karmeier, Krapp & Egelhaaf, 2003; Figure 1).

1.6.1 Differences in flow structure as a function of retinal eccentricity

Depending upon where the observer is looking, different parts of the flow field will project to different parts of the retina. As the optic flow field is not a uniform pattern of motion this means that the structure of the flow that is present in central vision and peripheral vision will often differ. For example, during translation with gaze in the direction of travel, an expanding radial flow structure is present in central vision but a predominantly lamellar flow structure in the periphery (i.e. at 90 degrees eccentricity). When gaze is perpendicular to the direction of travel (or equally, if translation is lateral with gaze straight ahead) this relationship is reversed, with the FOE and FOC present in the peripheral visual field and lamellar flow present centrally. Thus, the retinal motion due to self-movement differs as a function of retinal eccentricity.

A key consideration of this thesis is whether the visual system can utilise the information present in peripheral vision to detect self-movement for flow parsing. Figure 17 shows the four flow patterns that are examined with respect to flow parsing in the empirical chapters of this thesis, assuming that gaze is straight ahead in all cases.

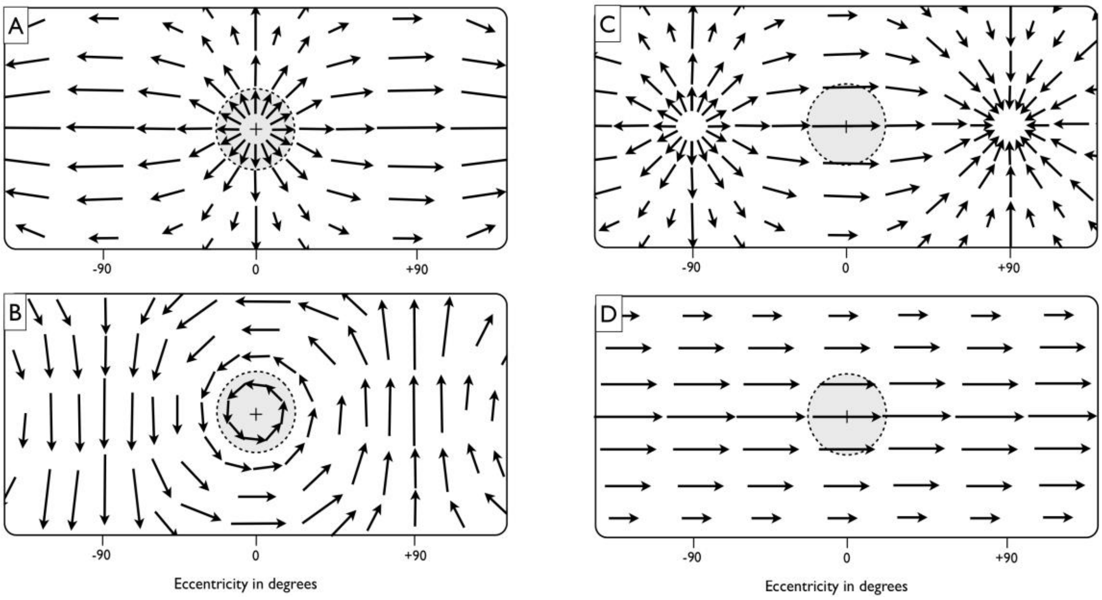

Figure 17 - Perspective projection of flow fields demonstrating the geometric differences in 2D flow as a function of eccentricity during the following observer movements: A) forward translation with gaze in the direction of motion B) roll rotation C) translation to the left with gaze perpendicular D) yaw rotation. These diagrams are similar to one presented in Huston and Krapp (2008; Figure 1C).

During forward self-movement with gaze straight ahead (Figure 17A), owing to geometry, the motion vectors in the far periphery are of a larger magnitude than those nearer the centre of vision which may make it easier to detect self-movement from peripheral flow than on the basis of the shorter motion vectors in central vision. When the observer translates to the left (Figure 17C), the left peripheral field would be exposed to expanding flow with comparable contracting flow in the far right visual field. Yet in central vision, lamellar flow would be present with variations in flow speed due to the distance of different objects in the scene. When gaze is straight ahead, rolling self-movement (Figure 17B) produces a circular flow pattern in central vision and lamellar flow patterns in the far left periphery and far right periphery of the visual field, that move in opposite directions. Yaw flow is generated by both eye and head movements and is distinctive in that it does not produce differences in retinal motion as a function of horizontal eccentricity (Figure 17D). Thus, during yaw rotation, visual flow indicating self-movement is uniform across the visual field and as such one might expect that peripheral flow is equally likely to contribute to flow parsing as central flow. Moreover, if central and peripheral vision are specialised for detecting certain flow structures then the availability of flow in both retinal regions may enhance the ability to flow parse. Thus, peripheral vision may not only contribute to flow parsing but may complement the parsing process which has been previously demonstrated in central vision to improve the identification of self-movement from retinal flow.

The degree to which the flow in central vision and peripheral vision differs depends upon the type of self-movement. As the structure of optic flow is dictated by geometry, then given knowledge of the relationship between gaze and the direction/axis of motion it is possible to make specific predictions about the likely contribution of peripheral flow to flow parsing on the basis of the information that is available on different regions of the retina. Where central and peripheral flow differs (as in Figure 17A, B &C) it is reasonable to assume that peripheral flow will make a greater contribution because additional information about self-movement is available in this retinal region and this could help to improve the ability to identify self-movement in certain circumstances. One such prediction pertains to the utility of peripheral flow in distinguishing between lateral translation and yaw rotation.

During lateral translation and yaw rotation of the observer, the central area of the optic flow field contains lamellar flow, as can be seen in Figure 17C and D. Critically, the flow produced during lateral translation also contains a range of speeds which depend upon the distance of objects in the scene, whereas during rotation the speed of all elements in the scene is the same. Thus, on the basis of central flow, a weak or noisy self-movement signal produced by lateral translation could easily be misinterpreted as yaw, or vice versa. Indeed, it has been demonstrated in the heading literature that flow which simulates forward translation and simultaneous gaze rotations leads to path judgements that are curvilinear (Warren & Hannon, 1990; Royden, Banks & Crowell, 1992; Royden, Crowell & Banks, 1994; see Lappe, Bremmer, van den Berg, 1999 for a review of this work). Thus, flow components which indicate a gaze rotation are misinterpreted as containing a component due to lateral translation suggesting that lamellar flow is difficult to distinguish from a gaze rotation in central vision. In peripheral vision this is not the case. The peripheral flow structure is very different for gaze rotation (Figure 17D) and gaze translation (Figure 17C) and therefore the availability of peripheral flow could be particularly important for distinguishing between these two types of self-movement.

The geometric differences in flow structure observed mean that central and peripheral vision receive different visual information that in conjunction may allow flow parsing mechanisms to operate across a wider range of circumstances or that could potentially be exploited by the visual system to disambiguate the pattern of self-motion on the retina. The next sub-section considers neural sensitivity to optic flow across the retina to establish that the visual system is able to detect these different flow structures.

1.6.2 Sensitivity to optic flow in peripheral vision

A key consideration of this research is whether the visual system can make use of the geometric differences between central and peripheral flow during self-movement. Thus, evidence of neural sensitivity to different patterns of flow in peripheral vision would reinforce the notion that this retinal region provides a useful source of visual self-movement. In turn, if the visual system can readily detect peripheral flow, these signals may input to flow parsing mechanisms.

Albright (1989) recorded from unidirectional cells in macaque area MT whilst visual stimuli were presented on a 60 x 60 degree display. Across all animals in the study, 68% of unidirectional cells with receptive fields in peripheral vision showed a preference for directions in line with a classic radial flow pattern, whereas in the central region (here defined as <12 degrees) only 18% of cells showed such a preference. This pattern of neural sensitivity corresponds to the fact that during forward translation (arguably the most common type of locomotion), the central retina is exposed to radial flow and the peripheral retina is exposed to lamellar flow (Warren & Hannon, 1988).

Research has also explored the receptive field size of optic flow sensitive neurons. This work provides some indication of the neural representation of optic flow from across the retina. Morrone, Burr and Vaina (1995) varied the ratio of coherently moving dots to randomly moving dots in a series of stimuli and asked observers to report the direction of motion in each case. They found that the ability to discriminate the direction of motion improved as the size of the stimulus area increased. This was true for a number of self-movement trajectories; translation, circular and radial motion and suggests that the availability of more eccentric flow provided a stronger motion cue that enhanced the ability to discriminate visual motion. Furthermore, Burr, Morrone and Vaina (1998), demonstrated exceptionally large retinal fields up to 70 degrees in diameter for radial, lamellar and circular (yaw) motion.

1.6.3 Integration of flow from across the retina

Burr, Baldassi, Morrone, and Verghese (2009) cued small patches of visual flow that were presented among patches of random noise and demonstrated that the visual system is able to selectively pool motion signals from across the visual field even when these areas are not spatially linked. For the present work, this past research suggests that a discrete flow stimulus in peripheral vision is likely to activate neurons sensitive to optic flow to drive the flow parsing process. Furthermore, the prior research by Burr et al. (2009) and Burr et al. (1998) indicates that a peripheral flow stimulus that is presented up to 35 degrees from fixation (the near periphery as defined in this thesis) should activate neurons with these large retinal fields. However, it remains to be seen whether the far peripheral stimulus, positioned at a much greater retinal eccentricity, will be readily integrated with flow in the near periphery when they are presented in discrete visual areas.

So far this section has defined what is considered peripheral vision within this thesis and summarised the theoretical background on flow structure and empirical work on neural sensitivity across the visual field. Together, these aspects suggest that peripheral flow might also contribute to the detection of certain forms of self-movement.

1.7 Peripheral self-motion perception

This section considers empirical evidence that indicates peripheral vision is important for the perception and control of self-movement. Firstly, three theories about the role of peripheral vision in the perception and control of self-movement are presented, which indicate some potential findings of this thesis. Three research areas are then discussed in turn: vection, heading perception, and postural control (Sections 1.7.2-1.7.4). This literature suggests that there are underlying differences in functional sensitivity to self-motion between central and peripheral vision. I propose that these differences mean that peripheral and central vision might play complementary roles in the detection of self-movement from retinal flow.

1.7.1 Theories of the contribution of peripheral vision to self-motion perception

Central vision and peripheral vision are often distinguished within the literature on the perception and control of self-movement. Originating in the field of postural control, three prominent theories have been put forward to describe the contribution of central and peripheral vision to self-motion perception (Bardy et al., 1999). These three theories provide a backdrop to the present research but do not form the basis of the empirical approach.

Peripheral vision has traditionally been regarded as the main input to our sense of orientation (Howard, 1982). The Peripheral Dominance Hypothesis (PDH) formalises the claim that the peripheral region of vision is responsible for our perception of self-movement (Held, Dichgans & Bauer, 1975). Under this theory, central vision is prescribed a lesser role and instead is argued to be more concerned with the processing of fine detail such as object features and object movement within the scene. This theory aligns with Trevarthen's two visual system theory of vision. Trevarthen's model (1968) splits vision into ambient and focal vision. The former is concerned with orienting the observer within an environment and the latter with specific features of objects within that environment. Ambient vision, which mostly occupies the peripheral visual field, is characterised by low spatial resolution at the greatest eccentricities and suggestions of a subconscious monitoring of peri-personal space (Previc & Ercoline, 2004). Focal vision and ambient vision are often assumed[3] to map onto the more common terms of central and peripheral vision respectively. PDH and Trevarthen's model both describe a special role for peripheral vision in self-motion perception.

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[3] This assumption ignores the fact that ambient vision includes central regions. This misnomer most likely arises because focal vision sits within the larger ambient visual space. Thus, it is only in the periphery that focal vision does not overlap with ambient vision. In assessing the independent contribution of each visual system, researchers have tended to utilise the notion of central and peripheral regions.

In contrast, the Retinal Invariance Hypothesis (RIH) does not distinguish between central and peripheral retinal regions. Instead this theory argues that self-movement perception is driven by the different flow structures that are typically projected onto the central and peripheral regions of the retina (Gibson 1968; Crowell & Banks, 1993). Central and peripheral retinal regions are assumed to process this information in the same way. Thus, there are no anticipated differences in the ability to detect different types of flow with different portions of the retina. For example, perception of self-motion from radial flow presented in the central visual field and the peripheral visual field would not differ.

The third theory suggests that central and peripheral retinal regions are sensitive to different flow structures. This theory is termed the Functional Sensitivity Hypothesis (FSH) (Andersen & Braunstein, 1985; Stoffregen, 1985; Warren & Kurtz, 1992). This theory differs from RIH because central and peripheral vision are often exposed to different flow structures and FSH suggests that this has resulted in differing neural sensitivity in these regions which in turn produces differences in self-movement perception between central and peripheral vision. The next section considers three research areas under the broad title of self-motion perception that have demonstrated differences between central and peripheral vision in the perception or control of self-movement from visual flow.

1.7.2 Vection

Research on vection has often promoted the idea that peripheral vision is the primary source of self-movement information. Vection is the illusory sense of self-movement that arises when a stationary observer is exposed to visual motion.

PDH gained initial support from vection research. Brandt et al. (1973) compared circular vection (CV) using a 30 degree diameter display presented either centrally or peripherally to full-field viewing. They found that when a display with a width of 30 degrees display was presented 45-75 degrees from fixation it evoked CV equivalent to full-field stimulation. By contrast, the 30 degree display had no effect in central vision. Berthoz, Pavard and Young

(1975) demonstrated similar findings for linear vection and Held et al. (1975) for roll vection.

However, Andersen and Braunstein (1985) found linear vection could be induced with a central stimulus as small as 7.5 degrees. Post (1988) sought to replicate Brandt et al.'s (1973) study and found that the 30 degree display produced approximately equal reports of intensity and velocity of CV regardless of its retinal location. These findings led researchers to consider whether vection was primarily induced by apparent motion of the background rather than by the retinal location of the flow.

Howard and Heckmann (1989) used a central display (54 x 44 degrees) that they varied in disparity to either make it appear in front of or behind a separate peripheral display. They found that when the central display appeared to be behind the peripheral one, vection was induced, but when the same display was in front no vection occurred. This finding brought into question the PDH because it indicated, alongside other work demonstrating vection could be induced by central flow, that peripheral flow was perhaps not specialised for the perception of self-movement. However, whilst the fact that central flow can also give rise to illusory self-movement casts doubt on the PDH, the peripheral contribution to vection still stands. One study that has directly placed central and peripheral optic flow in competition to assess dominance is that of Habak, Casanova and Faubert (2002). In one of their experiments, they simulated forward observer movement using central and peripheral flow (80 degrees diameter). They varied the signal strength in each region by introducing noise dots and measured the effect upon direction discrimination. A no noise condition (100% coherence) provided a baseline measure of performance. When either the central or peripheral region contained noise (0% coherence in either region) observers were less able to discriminate the direction of motion. When the central and peripheral stimuli were congruent (the dots moved in the same direction) but coherence was higher in the peripheral region, they found that performance on the discrimination task was better than when coherence was higher in the central region. This study suggests that both central and peripheral regions provide a cue to self-movement but that when they are placed in competition the peripheral region appears to dominate.

These studies show that visual flow in central and peripheral vision can provide a salient motion cue that results in the illusory percept of self-movement. This suggests that visual flow presented on different parts of the retina can have the same perceptual consequences. Another study, by Lepecq et al. (1993), also considered the effect of a flow stimulus in peripheral vision and demonstrated vection induced by flow in the extreme periphery.

Lepecq et al. (1993) considered how vection affects the perceived location of visual targets. If visual flow indicating self-movement causes observers to update the remembered location of a target then this would suggest that visual cues to self-movement feed in to mechanisms concerned with the spatial representation of objects in the world. Lepecq et al. (1993) placed two monitors either side of the head, facing each other, and presented a translating random dot stimulus on the monitors in far peripheral vision to stationary observers to induce forward linear vection. Lepecq et al. suggested that if a target is located 5 metres in front of an observer and 10 degrees to the right and the observer then moves forwards 2 metres, the target will not only be closer to the observer but will also be more eccentric, that is, further to their right-hand side. Yet a target located straight ahead of the observer, will only change in terms of distance from the observer, whilst eccentricity remains unchanged.

Observers were seated in the dark with a semi-circle of LEDs in front of them that served as visual targets. The targets were either presented straight ahead of the observer (central) or to the left or right of the central target (lateral). Comparing the perceived target location pre and post-vection revealed that lateral targets were judged to be more eccentric after vection but the direction of pointing to central targets remained the same. These results suggest that peripheral visual flow provides a robust cue to self-movement and that this peripheral visual self-motion stimulus was used to update the location of objects relative to the observer. This adds to the studies above because it suggests that peripheral flow in isolation can drive the percept of self-movement, even when the flow stimulus is not contiguous. A peripheral cue to self-movement like that used by Lepecq et al. may also benefit the visual identification and subtraction of self-motion components from retinal flow, as in the FPH.

The phenomenon of vection demonstrates that visual flow alone can provide a cue to self-movement despite the absence of information from the vestibular and proprioceptive systems. The illusory sense of self-movement from peripheral flow in the absence of any extra-retinal signal shows that visual stimulation of the retinal periphery can drive the perceptual experience of self-movement. This sub-section has presented evidence that the presence of visual flow in either central or peripheral vision can produce an illusory sense of self-movement. Importantly for the present work, a number of studies have shown that peripheral visual flow in isolation can drive vection. Taking the evidence together as a whole it appears that central vision and peripheral vision are both equally capable of inducing vection. The next sub-section moves away from an illusory sense of self-movement and instead considers the respective roles of central and peripheral vision in heading perception.

1.7.3 Heading judgements

When presented with radial flow patterns in central vision, observers are able to reliably detect the direction of heading on the basis of visual information alone to within a few degrees (Warren & Hannon, 1988). This ability suggests a high level of sensitivity to optical flow. Researchers have investigated how the ability to detect heading from optic flow might vary as either the eccentricity of the flow or the location of the FOE is increased (Warren & Kurtz, 1992; Crowell & Banks, 1993). Thus, this literature is pertinent to consider because it provides an indication of the sensitivity to flow in different retinal regions. When the FOE is shifted away from the centre of vision the flow field becomes more lamellar in structure and therefore this research has tested sensitivity to both lamellar and radial components in central and peripheral vision.

Research by Warren and Kurtz (1992) and Crowell and Banks (1993) has specifically tested whether there are differences between central and peripheral vision for the detection of heading from optic flow. Warren and Kurtz (1992) measured heading accuracy by asking observers to indicate whether, based on the flow presented in the trial, they would pass to the left or the right of a target that was presented at the end of each trial. They found that with a centrally located FOE, heading judgements were more accurate when the flow stimulus was presented in central vision than when central vision was obscured and a peripheral annulus displayed the flow. However, the FOE was only visible in the central flow condition and the FOE was masked in the peripheral condition. In judging heading one might well expect that heading judgements are better when the FOE is visible than when it is not. In a second experiment, Warren and Kurtz presented flow across the visual field but shifted the eccentricity of the FOE while observers maintained fixation at the centre of the display. The target, which was presented following each trial, was located near to the shifted FOE and observers made their judgements whilst maintaining fixation at the centre of the screen. The results of the second experiment indicated that the ability to accurately judge heading decreased as the retinal eccentricity of the FOE increased, suggesting that peripheral vision is less sensitive to the radial flow structure present near to the FOE.

Crowell and Banks (1993) investigated heading sensitivity using different flow structures placed at different retinal eccentricities. They asked observers to discriminate between two flow fields presented in succession by reporting whether the heading in the second flow field was to the left or the right of the heading in the first sequence. Flow depicted translation through a cloud of dots. Heading eccentricity, i.e. the location of the FOE, was manipulated independently from the retinal eccentricity at which the flow stimulus was presented. For example, for a retinal eccentricity of 0 degrees and a heading eccentricity of 10 degrees, the flow was presented directly ahead of the observer and the FOE was shifted 10 degrees to the right. A large heading eccentricity (i.e. 90 degrees) with 0 degrees retinal eccentricity would have presented lamellar flow in front of the observer. They found that performance was better when radial flow was visible and that performance declined as the flow became more lamellar, regardless of where the flow was positioned on the retina. Thus, these results suggest that peripheral and central vision are both able to detect radial flow patterns but that the ability to judge heading decreases as the visual flow diverges from a radial structure.

1.7.4 Postural control

Researchers have suggested that peripheral vision is the main visual cue that prompts the automatic muscular responses required to maintain balance (Stoffregen, 1985; Lee & Aronson, 1974). The reader can experience the crude difference by standing on one leg while occluding either central or peripheral vision and monitoring the amount of body sway in each case. Typically, greater sway occurs when peripheral vision is occluded than when central vision is occluded. If the availability of peripheral visual flow results in a larger postural response than central flow then this would suggest either that flow on the peripheral retina is more useful for postural adjustments than central flow because the peripheral retina is more sensitive to these patterns of optic flow (functional sensitivity), or, because the peripheral region of the optic flow field is more informative about self-movement.

A number of studies investigating the postural response to visual flow have used a moving room paradigm. In this set-up, the observer stands within a suspended room that can be moved independently of the ground surface (i.e. Lee & Aronson, 1974). This allows the experimenter to generate visual flow despite the observer being stationary. The observer’s postural sway can be measured by means of a tracking system which monitors the position of the head and/or trunk. The typical effect caused by moving the room towards the observer, simulating forward self-movement and expanding radial flow, is a postural response counter to the direction of simulated motion. This is commensurate with the response that would be generated if the observer were falling forwards, and in order to maintain an upright stance they would need to adjust their posture backwards.

Optic flow in central vision produces a postural response. For example, Andersen and Dyre (1989) demonstrated that postural sway is evoked by stimulation of small regions of central vision. There is also evidence that peripheral vision can drive a postural response. Erikson and von Hofsten (2005) used a 150 degree field of view display and occluded central portions. They found that the degree of postural sway was unaffected by occlusions of central vision, indicating that peripheral vision still provides a robust cue to self-movement in the absence of central flow.

Bardy et al. (1999) measured the postural response of observers to patterns of visual flow whilst walking on a treadmill. They presented three types of flow; radial (0 degrees), lamellar (90 degrees), or intermediate conditions (30 & 45 degrees) and varied the eccentricity at which the flow was presented from 0 degrees to 90 degrees from fixation. They found that body sway was along the axis of motion indicated by the visual stimulus, i.e. when viewing radial flow presented at 0 degrees eccentricity observers swayed in the forward/backward direction and when viewing radial flow at 90 degrees eccentricity they swayed from side to side. This suggests that visual flow indicating self-movement in central and peripheral retinal regions provides a cue to self-movement that drives a direction specific postural response.

Stoffregen (1985) presented radial, rotary or lamellar flow to either central or peripheral vision and measured postural sway. The magnitude of body sway provided a measure of the automatic postural response to the visual flow stimulus. If the visual flow stimulus provided an effective indication of self-movement then one would expect body sway to be closely coupled to the visual stimulus. He found that when flow was presented in central vision, compensatory postural sway was evident for radial and lamellar flow structures. Lamellar and radial flow produced equivalent sway when presented in central vision. When presented in the periphery, lamellar flow also produced postural sway. However there was no sway response when radial flow was presented peripherally (FOE at 90 degrees eccentricity). This suggests that peripheral vision is not sensitive to radial flow. Stoffregen argued these findings were evidence of the functional specificity of central and peripheral vision. The finding that radial flow in peripheral vision did not produce a postural response is in accordance with the fact that during forward observer movement the peripheral visual field would predominantly be exposed to lamellar flow rather than radial flow. Peripheral sensitivity to radial flow may therefore be reduced in comparison to lamellar or rotary flow structures that are more frequently experienced by observers as we tend to look in the direction of travel and because gaze rotations produce rotary flow across the visual field.

1.7.5 Peripheral self-motion summary

The three research areas covered above (Sections 1.7.2-1.7.4) indicate that:

1. the presentation of visual flow in peripheral vision leads to the perception of self-movement (even in the absence of a vestibular or proprioceptive input indicating self-movement)

2. the direction of self-movement, or heading can be discriminated on the basis of lamellar or radial flow presented in peripheral vision, but accuracy decreases for more eccentric headings
3. the presentation of lamellar flow in peripheral vision or radial flow or lamellar flow in central vision results in an automatic postural response but when radial flow is presented in peripheral vision the response is minimal.

This prior research clearly demonstrates that peripherally presented visual flow can drive the perception and control of self-movement and this suggests that peripheral flow potentially makes an important contribution to the identification of self-movement which underpins the flow parsing process.

1.8 Summary

In Section 1.5, I presented the key reason to investigate whether peripheral vision contributes to flow parsing: The information available in the optic flow field differs between central vision and peripheral vision (assuming fixation straight ahead). Sections 1.6 and 1.7 reviewed the evidence for neural sensitivity to optic flow and research indicating perceptual and postural responses to optic flow stimuli presented in peripheral vision.

Section 1.7 considered the interrelated research areas that indicate peripheral vision is important for the perception and control of self-movement. Many studies have demonstrated a strong perceptual or postural response to visual flow on the peripheral retina and this confirms that flow in this region is capable of providing a robust cue to self-movement even if it does not dominate our perception (i.e. Post, 1988; Andersen & Dyre, 1989). It appears that peripheral vision contributes to the illusory sense of self-movement (vection), our ability to judge heading from optic flow, and the visual control of stance. As different visual information about self-movement is available in central and peripheral areas of the visual field they may play different, and potentially complementary, roles depending on the type of self-movement. Overall the existing literature suggests that the peripheral flow provides a visual cue to self-movement that, in isolation, can produce changes in the perception of self-movement and the control of self-movement. When visual features indicating self-movement in peripheral vision differ from those available in central vision then peripheral flow is likely to contribute to flow parsing.

There is already compelling evidence for a visual process that subtracts self-motion components from the retinal image; a flow parsing process. However, it is not clear whether self-movement information in peripheral vision also contributes to this process or whether the mechanisms that underpin flow parsing can make optimal use of geometric differences in flow structure between central and peripheral vision. On the basis of previous literature I hypothesised that peripheral flow will contribute to flow parsing, but there may be differences in this contribution between the near and far periphery as well as between different forms of self-movement. In the case of lateral translation and yaw rotation the peripheral and central flow structure, defined relative to the body, shows the greatest divergence and therefore I expect peripheral vision to play an important role in distinguishing between these two types of self-movement. This thesis explores whether peripheral vision feeds into the flow parsing mechanism that has previously been demonstrated in central vision.

1.9 The Experimental Paradigm

The empirical work reported in this thesis employed the same basic experimental paradigm throughout. In order to isolate the visual information, self-movement was simulated using computer-generated stimuli, and the observer remained stationary in all experiments. Self-movement stimuli were presented in peripheral vision and I distinguish between two distinct regions of peripheral vision; near peripheral and far peripheral. These regions are indicated in Figure 15 and the two terms are used throughout. Near peripheral stimuli were displayed on a large projection screen and far peripheral stimuli were presented on monitors that were positioned adjacent to the observer's head and parallel to the line of sight, as in Figure 18 (a plan view of the experimental setup can be found in Figure 19, Page 60). The observer always looked straight ahead and thus peripheral flow was always projected to the peripheral retina. The far peripheral displays were inspired by the work of Lepecq et al. (1993) who also presented flow stimuli adjacent to the observers' head.

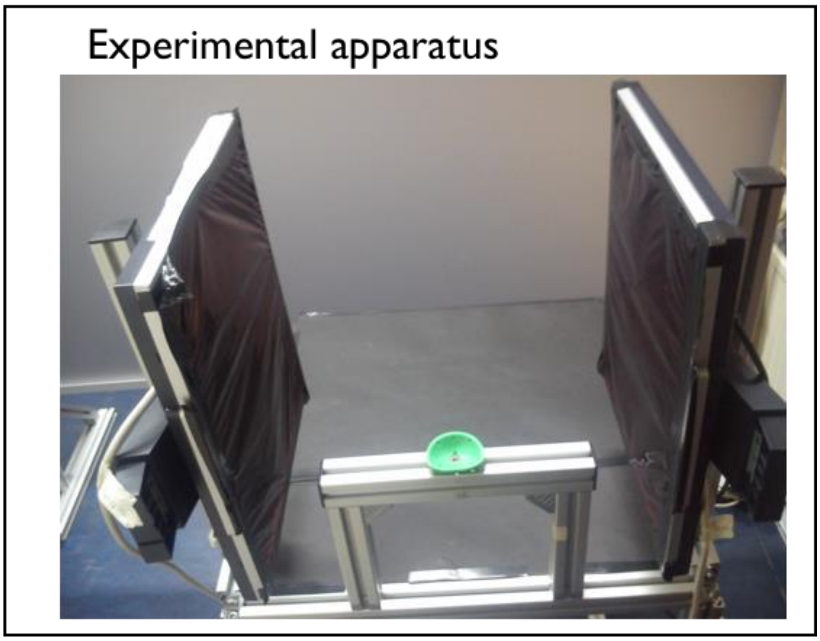


Figure 18 - Photograph of the experimental apparatus used in experiments, the observer placed their head in the green chinrest and looked straight ahead at the projection screen.

Peripheral visual flow was presented at the same time as a visual target in central vision (In Chapter 5, central flow was also presented). The specific attributes of the target differed between experiments. In Chapters 2 and 3 observers reported the perceived trajectory of a small spherical target and in Chapter 4 they reported whether a central disk appeared to expand or contract. In Chapter 5 observers reported the perceived trajectory of a target at three different distances during simulated lateral translation or yaw rotation, either with or without peripheral information and in the presence of stereoscopic or monocular central flow. More detailed information about the stimuli and task for each experiment is contained in the relevant methods section.

1.10 Summary of Empirical Work

Four empirical chapters are presented. These chapters investigate the peripheral contribution to flow parsing for a range of self-movement types and two different tasks (object trajectory assessment and object size change detection).

The first experimental chapter, Chapter 2, presents a series of experiments using radial flow. These experiments provide the first empirical evidence that peripheral flow contributes to flow parsing and examine the relative contributions of near and far periphery to flow parsing. Chapter 3 explores similar questions to Chapter 2 but for simulated rotation about the line of sight. The findings in this chapter were similar to those in Chapter 2 suggesting that the contribution of each peripheral region to flow parsing is consistent across different types of self-movement. Chapter 4 probes a related visual judgement; the perception of size change during self-movement. A radial flow stimulus was used, similar to the one that was employed in Chapter 2. This study demonstrates that judgements of the size of an object can also be detected during simulated self-movement and once again indicates a peripheral contribution to this process. The final experimental chapter (Chapter 5) investigates the peripheral contribution to two further forms of self-movement (yaw rotation and lateral translation) and aims to determine whether the presence of peripheral visual flow might help to disambiguate information about self-movement from central vision. However, surprisingly there was no such benefit of peripheral flow. Appendix B details three additional experiments, two which demonstrate paradigm development and another which serves as a control study. These studies are referred to within the relevant empirical chapter and a short rationale is provided for each experiment within the appendix.

Together, these studies characterise the contribution of peripheral vision to the flow parsing process. Specifically they allow a quantifiable measurement of the contribution of peripheral vision to flow parsing across a number of types of self-movement and employing a variety of flow structures. Furthermore, the use of two peripheral sub-regions (near peripheral and far peripheral) permits an investigation of how self-movement information is integrated from across the peripheral retina. The use of two distinct judgements of object motion during self-movement (trajectory and size change) allows for a comparison of the role peripheral flow plays in each of these tasks. Alongside previous flow parsing research, the findings in this thesis contribute to the understanding of how self-motion information from across the retina is utilised for the detection of object movement during self-movement.

Chapter 2. THE ROLE OF PERIPHERAL VISION IN RADIAL FLOW PARSING

2.1 Chapter summary

This thesis aims to quantify the contribution of peripheral vision to the flow parsing process. This first empirical chapter investigates the case of radial flow, which is generated when an observer moves forward (expanding motion) or backward (contracting motion). A series of studies examined whether visual flow in the peripheral visual field changes the perceived trajectory of a target presented in central vision, indicating a peripheral contribution to flow parsing.

In the first experiment, I systematically manipulated the eccentricity of peripheral flow and found a significant interaction indicating a peripheral input to flow parsing for flow stimuli up to 41 degrees from fixation. The contribution of peripheral flow to flow parsing was found to decrease approximately linearly as a function of retinal eccentricity. The second experiment examined the combination of information across the peripheral retina with designated near and far peripheral displays. Flow was presented to the far periphery using monitors placed to the side of the head, or to the near periphery using a large central projection screen. Flow parsing was measured with near flow, far flow, and a combined near + far flow condition. Regression analysis showed that the relative tilt observed in the Combined condition is primarily accounted for by the flow presented in the near periphery. A third experiment examined the contribution of the horizontal and vertical periphery. A peripheral contribution to parsing was measured with horizontal, vertical, and full peripheral fields. The results showed approximately equal effects in the horizontal and vertical conditions and the magnitude of the effect in the full field condition was predicted by a linear combination of both separate flow regions. The final experiment in this chapter explored whether the smaller contribution of the far periphery in comparison to the near periphery could be accounted for by underlying differences in sensitivity to motion. Speed discrimination thresholds were determined for the near and far peripheral flow stimuli. This study revealed no significant differences in motion perception between the two peripheral regions. In summary, this chapter presents the first empirical evidence that peripheral vision contributes to the flow parsing process for forward and backward self-movement.

2.2 Chapter Introduction

In the General Introduction I made the point that because the structure of the optic flow field differs as a function of retinal eccentricity, central and peripheral vision are often exposed to different visual information about self-movement. For forward or backward movement of the observer, with gaze aligned with the direction of motion, radial flow is produced in central vision and lamellar flow in peripheral vision. As the peripheral information indicating self-movement differs from the central information the peripheral retina may provide additional information for the detection and identification of self-movement for the purposes of flow parsing. If peripheral flow does contribute to flow parsing then it should be possible to demonstrate a signature of flow parsing even in the absence of central visual flow.

Forward translation is arguably the most common form of self-movement, producing an expanding radial flow field. As such, the majority of the empirical work investigating observer translation has only considered forward self-movement rather than both forward and backward self-movement. This imbalance is a cause for concern because research from the vection and heading literature suggests that sensitivity to expanding and contracting optic flow, or forward and backward self-movement information, may not be equivalent.

A number of papers have reported a faster onset and stronger magnitude of vection for contracting (moving backwards) than expanding stimuli (Berthoz et al., 1975; Edwards & Badcock, 1993; Edwards & Ibbotson, 2007, Bubka, Bonato & Palmisano, 2008; although Reinhardt-Rutland, 1982 reports the opposite pattern of results). If this difference indicates a divergence in self-motion perception between forward and backward motion then this would likely lead to differences in flow parsing performance. A stronger self-movement cue from contracting flow would be likely to lead to more robust flow parsing, in the sense that more of the components due to self-movement would be subtracted from the retinal flow. Edwards and Ibbotson (2007) argue that this discrepancy in perception arises due to the necessity of responding to backwards flow more readily because humans are more unstable in this direction as our feet point forwards. However, it may be the case that these reported differences are specific to the phenomenon of vection and have little impact on the initial perception of self-movement which Rushton and Warren see as crucial to the ability to flow parse (Rushton & Warren, 2005). The existing experiments conducted by Rushton and Warren investigating flow parsing with radial flow have only looked at more prevalent case of expanding flow, and the same effects have not yet been demonstrated for contracting flow patterns. Therefore this chapter sought to address this discrepancy in the literature by examining the peripheral contribution to parsing for both forward and backward self-movement.

In this chapter, I report a series of four experiments. A preliminary experiment (Experiment 1.0, Appendix B) showed initial evidence of a peripheral contribution to flow parsing. Experiment 1.1 replicated this finding with a more rigorous methodology and explored how the contribution of visual flow to flow parsing is affected by the eccentricity of the flow stimulus. Experiment 1.2 investigated the peripheral contribution to flow parsing using flow stimuli in the near and far periphery, and considered the relative contributions of each peripheral region to flow parsing. Experiment 1.3 considered whether the configuration of the flow affects the contribution of peripheral flow to flow parsing and Experiment 1.4 was a control study that tested whether there were any differences in motion sensitivity between the peripheral stimuli that were employed. A schematic representation of the stimuli used in these experiments is given in Figure 19 alongside a diagram showing the experimental apparatus.

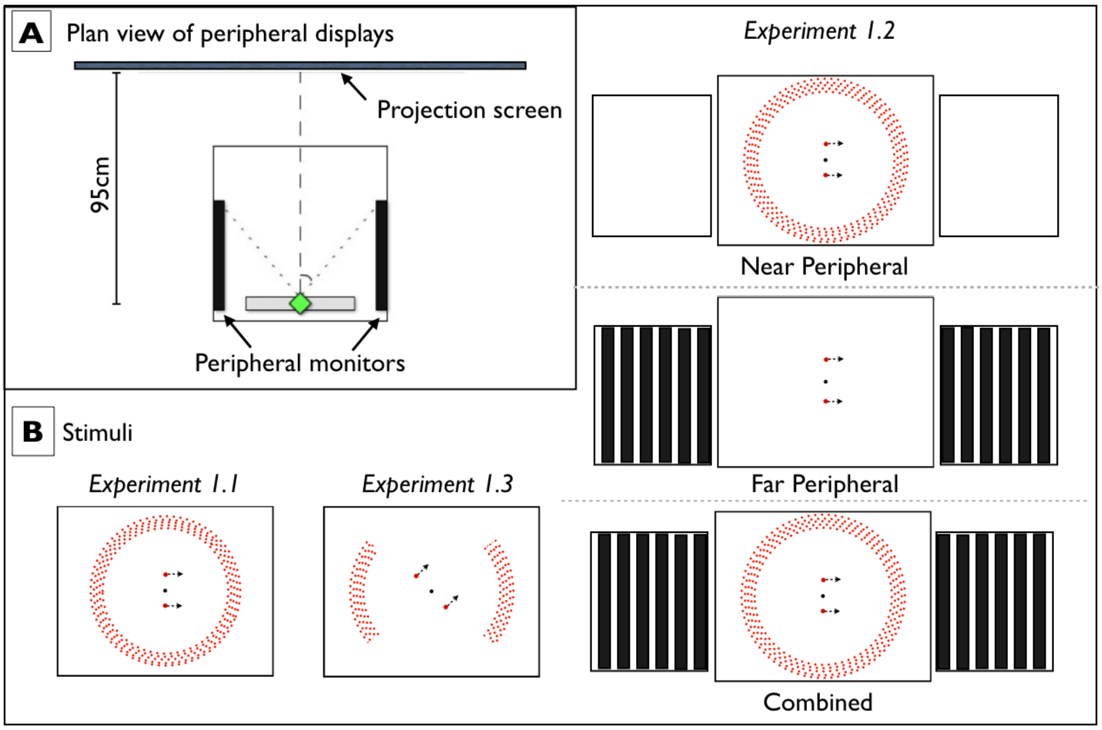


Figure 19 – A) Plan view of display devices for peripheral stimuli. The observer is seated with head in chinrest (green diamond) looking straight ahead. The Near peripheral stimulus is presented on the projection screen and the Far peripheral stimulus is presented on peripheral monitors, each positioned with the nearest edge 45 degrees from the (dashed) line of sight. B) Schematic diagrams of stimuli used in Experiments. Experiments 1.1 and 1.3 used only the central projection screen, while Experiment 1.2 used the central projection screen and peripheral monitors. Experiment 1.4 used the same flow stimuli as Experiment 1.2, but a target was not presented.

2.3 Experiment 1.1: Peripheral contribution to flow parsing with increasing retinal eccentricity

When a moving object is placed away from the FOE of a radial flow field in central vision, the trajectory of the object is perceived to be biased in the opposite direction to the flow at that location (Warren & Rushton, 2009a). In Warren and Rushton's study the flow stimulus was presented within the central 30 degrees of the visual field. Here, peripheral visual flow was used to look for a signature of flow parsing that would indicate that peripheral flow can contribute to this process.

Experiment 1.1 sought to build upon the initial study (Appendix B) to investigate how the relationship between flow direction and perceived target trajectory might change as the eccentricity of the peripheral flow increased. Globally expanding or contracting flow was presented whilst a horizontally moving target appeared either above or below a central fixation point, as depicted in Figure 20A.

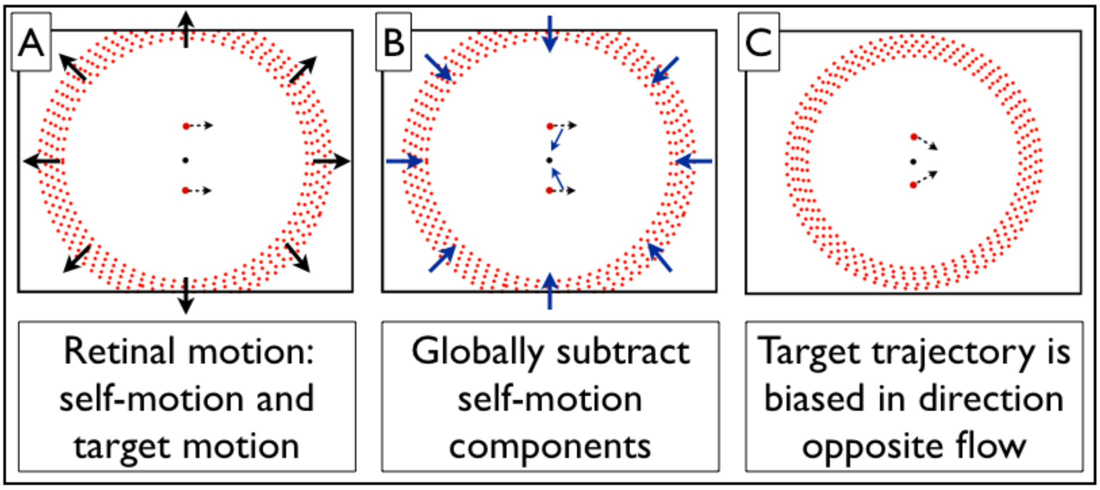


Figure 20 - Predictions of the FPH for Experiment 1.1; Expanding flow condition depicted. Panel A shows the retinal motion associated with forward self-motion, both possible target locations are indicated. The target moves across the screen left to right in a horizontal path. Panel B shows the components that are extracted from the retinal motion under a flow parsing account. Panel C depicts the perceived target trajectory once self-motion components have been parsed from retinal motion. The target trajectory is biased in the direction opposite the flow for both target locations. For contracting flow, target trajectory is predicted to be biased away from fixation, but still in the direction opposite to the flow direction.

Flow parsing predicts that in this case the trajectory bias will be in the opposite direction to flow direction due to the subtraction of self-motion components from the entire retinal image (See Figure 20). If peripheral flow contributes to flow parsing then in the case of expanding peripheral motion, peripheral flow would bias target trajectory towards the FOE (located at fixation) and contracting peripheral motion would instil a trajectory bias away from the FOC. The pattern of results that would indicate a peripheral contribution to flow parsing is shown in Figure 21. As all targets moved across the screen from left to right, these predictions are expressed in terms of a positive or a negative trajectory bias, where positive is anti-clockwise (ACW) (i.e. in Panel C of Figure 20 the target below fixation shows an ACW bias which would be coded as a positive relative tilt, and the target above fixation shows a clockwise (CW) bias, coded as a negative relative tilt). The experiment was designed so that if target eccentricity and the direction of peripheral motion are taken as two independent variables then an interaction is expected.

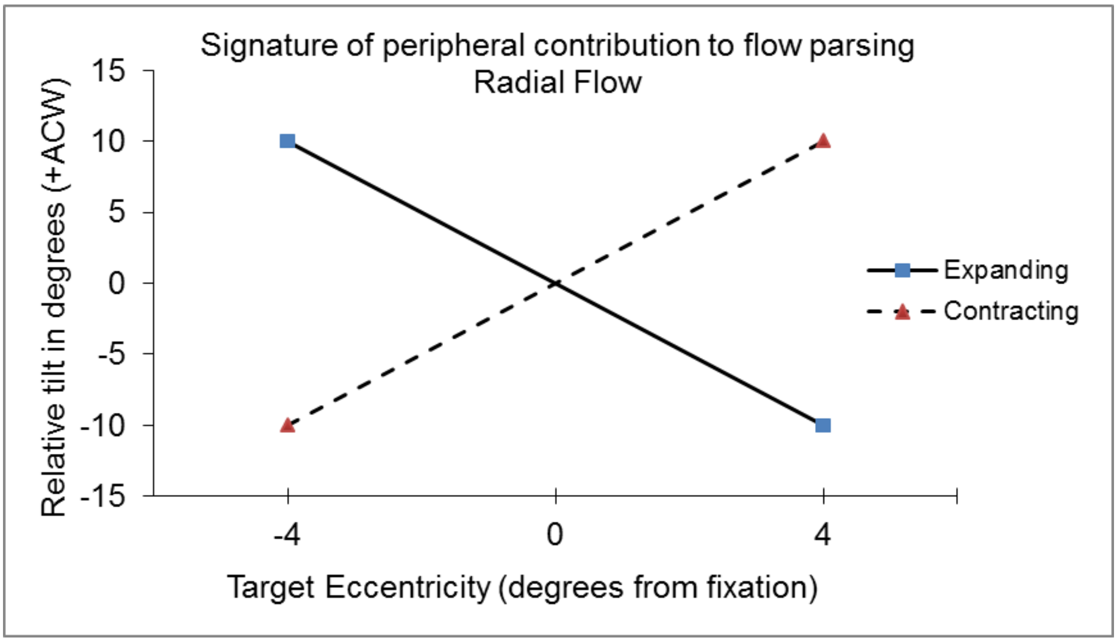


Figure 21 - Predicted interaction between flow type (Expanding = solid line, Contracting = dashed line) and target eccentricity (-4/+4 degrees). Above fixation targets coded as +4 degrees and below fixation targets coded as -4 degrees.

Although an interaction was predicted for each flow eccentricity, indicating a peripheral contribution to flow parsing, no apriori predictions were made about whether the contribution to flow parsing would increase, decrease or stay the same as the eccentricity of the flow stimulus increased.

2.3.1 Methods

2.3.1.1 Participants.

Six postgraduate students (1 male) with an age range of 22 to 26 took part in the study and were naïve as to the experimental hypotheses. Participants for all experiments were recruited from the School of Psychology, Cardiff University and had normal or corrected-to-normal vision. Additional details on the recruitment and payment of participants can be found in Appendix A. Where vision was corrected, participants were asked not to wear glasses during the experiments and instead they were asked to wear contact lenses. This additional restriction was put in place because the frames of a participant's glasses might have obscured (at least partially) the peripheral stimuli used in the experiments.

All recruitment and experimental procedures reported herein adhered to the Declaration of Helsinki and were granted institutional ethics approval.

Although the written consent form stated that participants could leave the study at any time without reason and would not suffer any penalty, an additional verbal reminder was given at the start of each experiment due to a potential risk of nausea. Participants were not explicitly informed that they might feel dizzy or nauseous to avoid priming these expectations prior to the task. Throughout all experiments reported in this thesis there were only a few participants who reported feeling dizzy, whereupon they were asked if they were happy to continue. There were no instances where the participant asked to terminate the experiment.

2.3.1.2 Apparatus.

Computer generated visual stimuli were presented on a large back projection screen using a ChristieT Digital Systems Projector (model DS+26). The projected image size was 127 cm x 96 cm in all experiments. When viewed at a distance of 40 cm, the projected area equated to a 115.58 degrees horizontal visual extent or 12 pixels per degree. The spatial resolution of the display was 1400 x 1050 with a refresh rate of 60 hz.

All experiments were created with an open-source program developer (Lazarus) and stimuli were generated using OpenGL. Stimuli were rendered on a computer running Windows XP with a NVIDIA Quadro NVS 420 Graphics card with four DVI-outputs (2 projectors and 2 peripheral monitors). Except for the experiments in Chapter 5, only one projector was used. All stimuli were drawn in red and presented on a black background unless otherwise stated. A red filter was placed in front of the projector to improve the contrast of the display. Anti-aliasing was set to 4x in order to ensure smooth motion of the stimuli at such a close viewing distance.

For trajectory judgements, participants used a rotating dial, called a jog-wheel (Further details are provided in Appendix A), to orient an onscreen response line and provide angular responses.

2.3.1.3 Stimuli.

The self-motion stimulus was presented on the projection screen and simulated forward or backward translation with the observer kept stationary at all times. The flow stimulus consisted of 3500 red limited lifetime dots (1 second lifetime, 0.4 cm diameter) that were drawn within a volume of 1.6 m x

1.6 m x 3 m that was centred 40 cm from the observer. Dot motion was appropriate for an observer translating either forward or backward at a rate of 30 cm/s. This would be equivalent to an observer moving forwards at a crawling pace. A faster speed of self-movement would be expected to produce larger effects due to global subtraction but this speed was chosen as an approximate average of the forward translation speeds previously used in Warren and Rushton's earlier radial flow studies. However as the dots did not contain cues to depth then the scale of this stimulus is arbitrary as the same dot motion could equally have been produced by dots positioned within a larger volume that moved faster. When a dot moved off-screen or had been present for more than 1 second it was redrawn at a new on-screen location. The central region of flow was obscured by drawing a black circle in front of the dots. This created an annulus, or band of dots, as shown in Figure 19B. Approximately 600 dots were visible at any one time.

The inner radius of the annulus was varied in six conditions: 16.8 cm, 20 cm, 25 cm, 30 cm, 35 cm, 45 cm. Table 1 shows the corresponding visual angle of the inner radius for each flow eccentricity. The width of the annulus had a fixed onscreen size of 10 cm across all conditions, which produced a band of flow with a visual angle between 6 and 11 degrees depending upon flow eccentricity (see Table 1 for exact values).

Table 2 – Screen dimensions and angular equivalents of flow stimulus for each eccentricity condition.

Inner radius of flow annulus (cm)	Visual angle of inner radius (degrees)	Width of flow annulus (cm)	Width of flow annulus (degrees)
16.8	22.78	10	11.04
20	26.57	10	10.30
25	32.00	10	9.18
30	36.87	10	8.13
35	41.19	10	7.18
40	45.00	10	6.34

These eccentricities were used because they provided a broad range from a previously tested flow annulus (22.78 degrees in the initial experiment, see Appendix B) to the largest stimulus, which had a total horizontal extent of 90 degrees (45 degrees either side of fixation).

As well as the flow stimulus, a central fixation dot and target were also presented on the central screen. The target was a small red circle (0.3 degrees), which was placed either above or below fixation at 4 degrees eccentricity. Target motion was predominantly horizontal, from left to right. All targets appeared to the left hand side of the midline and translated rightward along the specified trajectory (see Design section for trajectory details). The target passed through the vertical mid-line of the screen half way along its travelled path.

2.3.1.4 Design.

Three independent variables (IVs) were manipulated: the direction of simulated self-movement (2 levels: Expanding or Contracting flow), the eccentricity of the target (2 levels: -4 degrees/ +4 degrees from fixation) and the eccentricity of the peripheral flow (6 levels: 16.8, 20, 25, 30, 35, 40 cm flow annulus radii).

To avoid potential response biases, rather than repeatedly presenting the same target trajectory, the trajectory of the target was varied within a range about horizontal. This trajectory range was chosen so that participants would be unable to deduce the physical onscreen trajectory of the target on any given trial. In each condition there were 9 physical probe trajectories (±32 degrees either side of horizontal in 8 degree steps), resulting in a total of 216 trials (2 x 2 x 6 x 9), which were all completed in a single experimental session which took approximately 45 minutes. The order of the trials was randomised and all eccentricity conditions were interleaved.

The dependent variable (DV) was relative tilt, which was calculated as the difference between the onscreen trajectory and perceived trajectory reported by the observer. A within-subjects design was used and data collection for each participant was conducted in a single experimental session.

2.3.1.5 Procedure.

Following consent, observers were seated on a static height-adjustable chair, in a dark room with their eyes level with the fixation point and approximately 40 cm viewing distance from the centre of the projection screen. Using the existing equipment it was not feasible to provide participants with a chin rest at this viewing distance but participants (who had all taken part in similar previous experiments) were instructed to keep as still as possible during the experiment. Figure 22 depicts the procedure on each trial: a fixation cross was presented for 0.75 seconds, after which peripheral flow appeared and immediately simulated forward or backward translation at a speed of 30 cm/s. Participants maintained fixation on the central dot throughout each trial and watched for the presentation of the target either above or below fixation. Following a variable 1-1.2 second delay to reduce participant’s ability to anticipate the onset of the target, the target was presented and moved at constant speed of 0.6 degrees/s (1 cm/s) for a 2 second duration. At the end of each trial, a short 2D response line (~ 3 degrees in length) was presented, which rotated about the point at which the target initially appeared. Participants rotated the line using a rotating dial or jog-wheel in order to indicate the perceived trajectory of the target. Participants were told that if they did not perceive the target to move along a straight path then they should set the response line to match the mean linear trajectory of the target. Once the participant had set the onscreen line they clicked a button on the jog-wheel to move on to the next trial. By delaying their click, observers could opt to take a break before continuing.

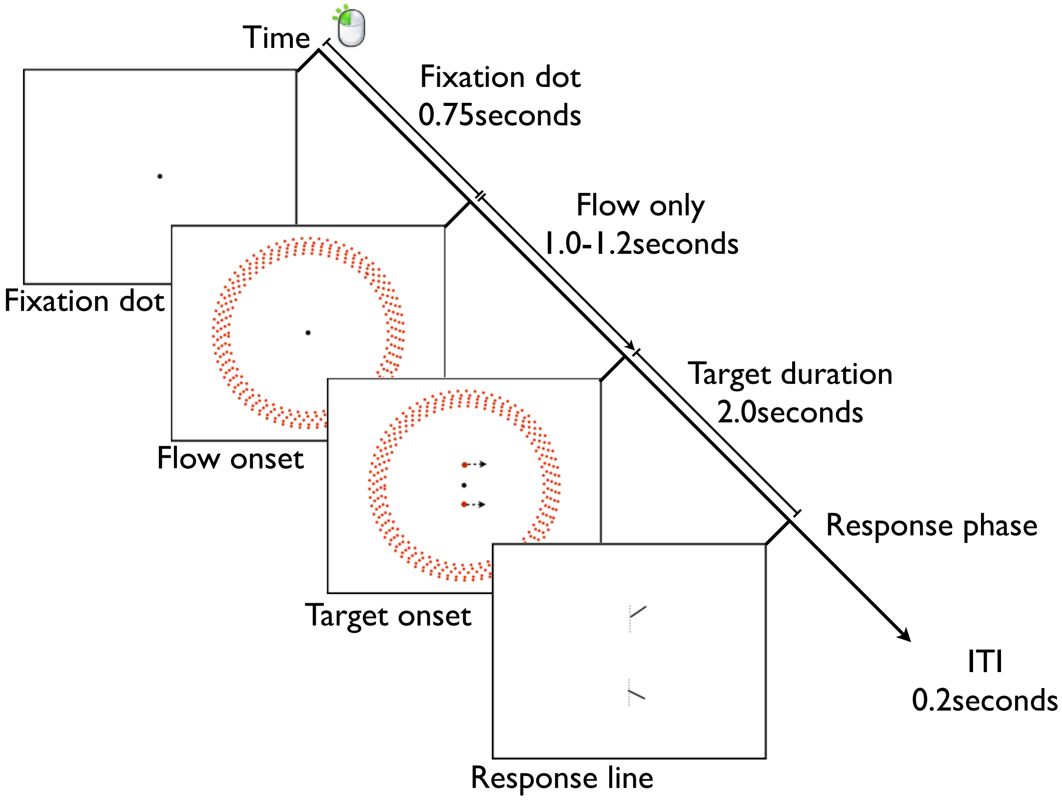


Figure 22 - Procedure timeline for Experiment 1.1. Both possible target locations are indicated but only one target was presented on each trial. The response line appeared in the same location as the target.

Four enforced breaks of 15 seconds duration were provided throughout the experiment at regular intervals. Following the break, participants clicked the response button to continue.

2.3.1.6 Analysis.

In order to equate horizontal target trajectories with non-horizontal trajectories a simple transformation was used for Experiments 1.1-1.3. This method has previously been adopted in flow parsing studies (i.e. Warren & Rushton, 2007). For Experiments 1.1-1.3, observer responses are coded as an angular measure θ_i. This quantity is a measure of the illusory or the “induced” vertical component of target motion perceived by observers, which is converted back to an angular quantity (see Appendix A). In the results that follow, θ_i is referred to as the relative tilt.

To present appropriate within-subject error bars in figures the data was normalised according to the method described in Cousineau (2005). Variance due to individual differences was removed from the dataset by subtracting each participant’s average relative tilt from the same participant’s relative tilt in each experimental condition (for full details and a discussion of the advantage of this procedure see Appendix A). Using the adjusted dataset, the standard error was then calculated for each condition.

Under this experimental design, the signature of a peripheral contribution to flow parsing is an interaction between flow direction (expanding/contracting) and target eccentricity (-4/+4 degrees) variables. A 2 x 2 repeated measures Analysis of Variance (ANOVA) was conducted for each flow eccentricity to test if the data were qualitatively consistent with a peripheral contribution to flow parsing. As a directional interaction was predicted, probability values from the ANOVA interaction term were adjusted (P ÷ 2) (Wuensch, 2006) as the error term for the interaction in an ANOVA does not assume a directional interaction. A significant interaction would therefore indicate that the data supported a peripheral input to flow parsing.

Additionally, to assess the impact of flow eccentricity on this relationship, a 6 x 2 within-subjects ANOVA was carried out. To simplify the results of the second ANOVA the difference in relative tilt between the two target eccentricity conditions was used as the DV (Belowθ_i - Aboveθ_i).

2.3.2 Results and discussion

For each flow eccentricity, a significant interaction was present (Figure 23) and indicated a peripheral contribution to flow parsing up from 23 degrees up to 41 degrees from fixation. In all the radius eccentricity conditions, probability values for the interaction were below 0.01. For the sake of brevity, full statistical results for the interaction between flow direction and target eccentricity can be found in Appendix B.

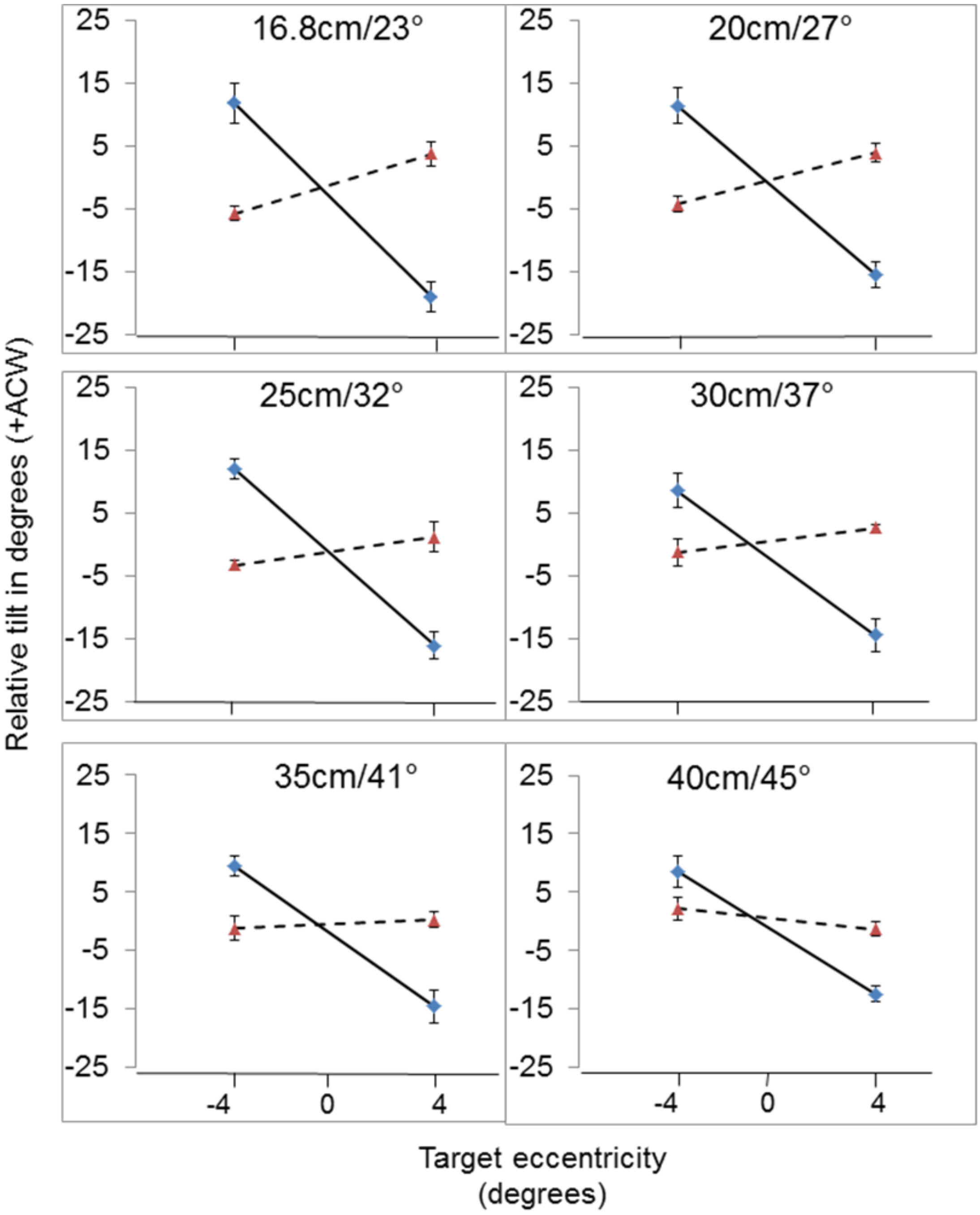


Figure 23 – Line plots for each flow eccentricity condition. Blue circles show expanding flow conditions and red triangles show contracting flow conditions. Error bars show within-subject standard error (*SE*).

In all conditions except the most eccentric flow annulus (40 cm/45 degrees), the pattern was in line with the predictions of a peripheral contribution to flow parsing. For comparison across flow eccentricity conditions, Figure 24 shows the difference in relative tilt between target locations (-4 and +4 degree target eccentricities).

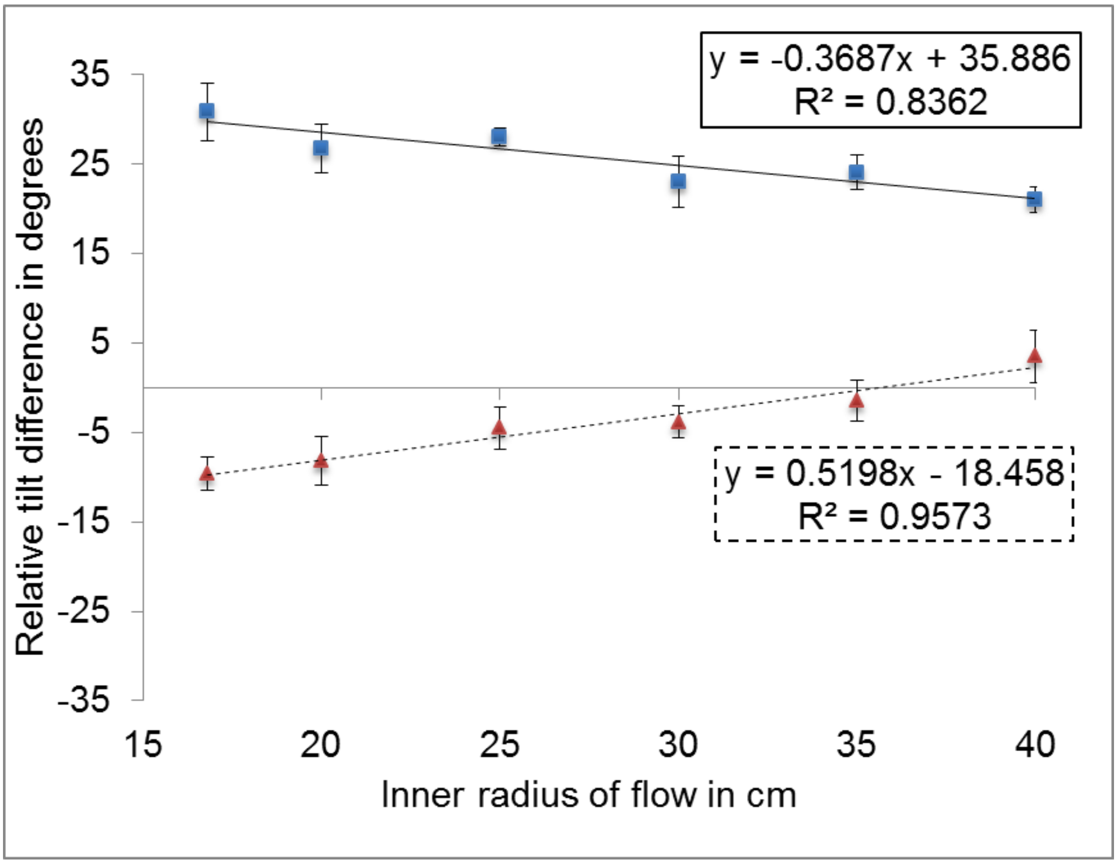


Figure 24 - Difference in relative tilt as a function of flow eccentricity. Square markers = Expanding flow, Triangular markers = Contracting flow. Error bars show within-subjects *SE*. Linear fits of the data and regression coefficients are shown for Expanding flow (Solid line) and Contracting flow (Dashed line).

For both Expanding and Contracting flow, the difference in relative tilt decreased with increasing flow eccentricity. Linear regression analysis revealed that for Expanding flow there was a negative relationship between relative tilt difference and flow eccentricity (β = -0.369, R^2 = 0.836, *F* (1,4) = 20.426, *p* = 0.011). Contracting flow showed a positive relationship between flow eccentricity and the difference in relative tilt (β = 0.520, R^2 = 0.957, *F* (1, 4) = 89.615, *p* =0.001).

A 2 (Expanding/Contracting) x 2 (Eccentricity conditions) within-subjects ANOVA compared of the relative tilt difference (unsigned) between expanding and contracting flow and revealed that the magnitude of relative tilt was significantly larger in the expanding case (*F* (1, 5) = 17.275, *p* = 0.009). Analysis of the unsigned difference in relative tilt at each eccentricity level revealed that in all cases there was a significant difference between the Expanding and Contracting flow conditions with expanding flow resulting in significantly larger relative tilt difference than contracting flow (16.8 cm: *t* (5) =

3.094, *p* = 0.027, 20 cm: *t* (5) = 3.315, *p* = 0.021, 25 cm: *t* (5) = 5.320, *p* = 0.003, 30 cm: *t* (5) = 3.037, *p* = 0.029, 35 cm: *t* (5) = 5.047, *p* = 0.004, 40 cm: *t* (5) = 3.935, *p* = 0.011). This expanding/contracting difference begs the question of whether the flow parsing process is equivalent for forward and backward self-motion. If there are differences in the parsing process between expanding and contracting, with larger relative tilt during expanding than contracting flow then this would be at odds with some of the asymmetry between forward and backward self-movement that have been reported in the vection literature (i.e. Edwards & Ibbotson, 2007) in which contracting flow provoked vection with a larger magnitude and faster onset than expanding flow. Edwards and Ibbotson (2007) argued that a greater sensitivity to contracting flow was beneficial for protecting oneself from falling backwards. Considering the task of detecting moving objects during self-movement, it may be the case that it is more important to detect moving objects when we are moving towards them than when we are moving away from them.

However, the differences observed in this experiment between expanding and contracting flow might be due to broader differences in the neural processing of expanding and contracting motion. As forward self-movement is typically faster than backward self-movement there may well be differences in the speed tuning of neurons in relation to these two directions of motion. In terms of the present experiment, dissimilarity would affect the flow parsing process as different amounts of motion due to self-movement would be parsed from the retinal image, leading to variation in the magnitude of relative tilt. Experiment 1.4 provides some data on the sensitivity to motion between forward and backward self-movement using the present flow stimuli.

The current experiment also provided an opportunity to replicate the preliminary results, which can be found in Appendix B (Experiment 1.0), with a new set of participants and a modified flow stimulus. Furthermore, as the eccentricity of the flow increased, the relationship between flow direction and perceived target trajectory was maintained but there was a decline in the magnitude of relative tilt. Regression analyses showed that the relative tilt difference decreased with increasing flow eccentricity. This reduction in relative tilt is perhaps surprising given the fact that the angular speed of the flow stimulus increases with retinal eccentricity. When the flow stimulus was beyond

41 degrees eccentricity the interaction effect, indicating a peripheral contribution to flow parsing, was no longer evident. This suggests that, the presence of self-movement information at large retinal eccentricities may not be sufficient for flow parsing. One possible reason for the declining contribution of flow with increasing retinal eccentricity is because the cortical area devoted to processing visual stimuli decreases with increasing retinal eccentricity (Mora, Carman, & Allman, 1989). One consequence of this is a reduction in visual acuity towards the periphery. To counteract this reduction, visual stimuli in the periphery need to be larger in order to stimulate the same cortical area as stimuli in the centre of vision. In order to rule out this reduction in acuity as a cause of the reduction in the contribution of peripheral flow to parsing with increasing eccentricity, I conducted a simple control experiment. The same participants (naïve to the hypotheses of Experiment 1.1 and the control study) took part but the width of the flow band and the size of the dots were scaled to account for retinal eccentricity. This experiment is reported in full in Appendix B (Experiment 1.1b). Figure B4 (Page 239) plots the results of both experiments for comparison. A comparison of each participant's regression slopes from Experiment 1.1 and the scaled control study showed there were no differences between the slope for either the Expanding (*t* (5) = 0.138, *p* = 0.896, *n. sig*) or Contracting (*t* (5) = 0.403, *p* = 0.704, *n. sig*) flow conditions and both showed a decline in the contribution of visual flow with increasing retinal eccentricity. Further details of this analysis can be found on Page 230, Appendix B. The results of the control study suggest that the reduction in peripheral contribution to parsing seen with increasing retinal eccentricity of the flow in Experiment 1.1 is not due to the reduction in cortical area activated by the flow stimuli.

Returning to the present study, the lack of the expected interaction at the highest eccentricities may be due to differences between expanding and contracting flow conditions. At the greatest eccentricity tested in this experiment, there was still evidence of a peripheral contribution to flow parsing with Expanding flow, with relative tilts of ~20 degrees. In contrast, the pattern for Contracting flow had reversed, with a positive tilt being observed in place of the negative tilt seen at lower eccentricities. Although these differences disrupt the expected interaction pattern, there is still an indication that visual flow in far peripheral vision contributes to flow parsing processes.

2.4 Experiment 1.2: Contribution of the Near and Far periphery to radial flow parsing

The results of Experiment 1.1 suggest that peripheral flow contributes to flow parsing. However, due to the recurrent suggestion in the broader literature that peripheral vision may be specialised for self-movement perception, it was important to explore whether more eccentric peripheral regions of the visual field might also feed into flow parsing mechanisms. To test this, a more eccentric peripheral flow stimulus was designed, which was presented on monitors either side of the participant’s head. This setup was inspired by the peripheral vection stimulus used by Lepecq et al. (1993) which was reported to create a compelling sense of self-motion and therefore should provide a visual cue to self-movement in this experiment. This more eccentric peripheral stimulus is referred to as the Far peripheral condition hereafter.

Using the results from Experiment 1.1, it is possible to make a prediction about the magnitude of relative tilt that may be observed in this new condition. The most eccentric flow stimulus in the previous experiment had a radius of 45 degrees, which coincides with the nearest extent of the peripheral monitors used in this experiment (45 degrees from line of sight). Thus, although the Far peripheral stimulus extends further into the periphery of vision, similar relative tilts may be observed as in the previous experiment. That is, a larger relative tilt magnitude for Expanding flow than Contracting flow. However, at 45 degrees eccentricity the predicted pattern of results indicating a signature of a peripheral contribution to flow parsing was not borne out in Experiment 1.1 (see Figure 23). Therefore, some uncertainty remains as to whether the predicted direction of the interaction effect will be observed when self-movement is only indicated by flow in the far periphery.

A new set of participants was recruited for this experiment. To draw comparisons between the results of the new Far peripheral condition and the initial pilot experiment (Experiment 1.0, Appendix B) which presented flow in the near periphery, a near peripheral flow condition was also included in the present experiment. Furthermore, to investigate the relative contributions of the Near and Far peripheral flow, a Combined condition was included, in which both stimuli were presented simultaneously. These three conditions aimed to establish whether one peripheral region might dominate over the other, or if the stimuli produce an additive effect when they are presented together.

2.4.1 Methods

2.4.1.1 Participants.

Five undergraduate students (2 male) with an age range of 18 to 21 were recruited using an online participant panel, and received course credit. The same eligibility restrictions and ethical procedures as for Experiment 1.1 were applied. All participants were naïve to the experimental hypotheses.

2.4.1.2 Apparatus.

The central projection screen apparatus was the same as used in Experiment 1.1, but with a viewing distance of 95 cm. At this distance, the projected image size equated to a 67.5 degree horizontal visual extent and 21 pixels/degree. In addition, two 19” (aspect ratio 5:4) BENQ LCD monitors (model number: Q9T4) with a resolution of 1280 x 1050 were placed either side of the observer’s head, in a portrait orientation. The monitors faced each other and were separated by a total distance of 43 cm with the chinrest for observers centred between the two monitors. Thus, each monitor was approximately 15 cm from the observer’s nearest eye. When positioned in a portrait orientation each monitor display had a horizontal visual angle of 90 degrees and a vertical visual angle of 102 degrees. For an observer seated with their head in the chin rest and looking straight ahead, the front edge of each peripheral display (monitor screen) was 45 degrees from the (cyclopean) line of sight (see Figure 19A). Anti-aliasing was set to 2x across all displays. The monitors were covered with a red lighting gel to increase the contrast of the stimuli and reduce ambient light which might have otherwise increased the saliency of the edges of the monitors.

2.4.1.3 Stimuli.

Three peripheral flow conditions (Near, Far, Combined) were employed, which are depicted in Figure 19B. The Near peripheral flow was generated using the same method as reported for Experiment 1.1 and had an inner radius of 40 cm (22.8 degrees) and an outer radius of 50 cm (27.8 degrees).

Far peripheral flow was presented on monitors either side of the head (as in Figure 18, Page 55). Vertical stripes were positioned 50 cm from the observer on two virtual planes, either side of the head that ran parallel to the line of sight. Stripes were used in the periphery on the basis of Lepecq et al.'s (1993) stimuli and because pilot testing demonstrated this stimulus gave a compelling sense of self-movement in comparison to limited lifetime dots that were used in central vision. The Combined flow condition presented the Near and Far peripheral stimuli simultaneously.

As before, the target was a small circular probe (diameter: 0.12 degrees/0.2 cm) positioned either above or below fixation at an eccentricity of 4 degrees (6.64 cm) from fixation and moved in a mostly horizontal trajectory, from left to right. The diameter of the flow dots, target size, fixation size, and target eccentricity were all scaled in accordance with the increased viewing distance (95 cm versus 40 cm).

2.4.1.4 Design.

The IVs were: Target eccentricity (-4/+4 degrees), flow direction (Expanding/Contracting) and Peripheral condition (Near/Far/Combined). For each condition, the nine tilt trajectories were presented twice. Near, Far and Combined conditions were presented in separate blocks consisting of 72 trials each. The DV was relative tilt in degrees. A within-subjects design was used and the order of peripheral conditions was counterbalanced across participants. Each participant completed the three peripheral conditions in a single experimental session.

2.4.1.5 Procedure.

Participants were seated with their head in a chinrest and their eyes approximately 95 cm from the projection screen. The task was explained to participants and they were given a chance to practise and familiarise themselves with the stimuli and response device. As in the previous experiment, participants were instructed to maintain fixation on the dot in the centre of the screen throughout the stimulus presentation.

The trial procedure timings were identical to Experiment 1.1 and the Near, Far, or Combined peripheral flow conditions were presented in separate experimental blocks. An enforced break was included halfway through each of these blocks and lasted for 15 seconds. Between each peripheral condition (Near/Far/Combined) the ceiling lights were turned on and participants had a short (~2 minute) break.

2.4.1.6 Analysis.

A 2 (Expanding/Contracting flow) x 2 (-4/+4 target eccentricity) repeated measures ANOVA was conducted for each peripheral condition to assess whether peripheral flow contributes to flow parsing. Furthermore, to identify any differences in relative tilt between the peripheral conditions a 3 (Near/Far/Combined) x 2 (Expanding/Contracting) ANOVA was conducted using the difference between the -4 and +4 target eccentricity conditions as the DV.

Additional analysis was conducted to investigate whether the magnitude of the data in the Combined condition could be predicted from the Near and Far data. Three linear regression analyses were conducted for each flow condition (Expanding flow and Contracting flow). The first regression analysis entered the linear sum of the Near and Far relative tilt data as a single predictor variable. The second analysis entered only the Near relative tilt data as the predictor variable in a linear regression and the third analysis entered only the Far data as a predictor. Thus, in total three models were assessed for how well they predicted the relative tilt data observed in the Combined condition:

Model 1: Near + Far (linear sum)
Model 2: Near
Model 3: Far

The regression coefficients for each model were assessed as well as the overall model fit to the data. Where both the individual peripheral conditions (Models 2 and 3) and the linear sum (Model 1) both significantly predicted the data, further analysis was undertaken to compare their predictive ability. A chi-squared difference test (Werner & Schermelleh-Engel, 2010) assessed whether the single parameter models (Models 2 and 3) were a better fit to the data than the linear sum (Model 1). This set of regression analyses is also used later in this thesis for Experiments 2.1 and 2.3b.

2.4.2 **Results and Discussion**

Across peripheral conditions (Near, Far, Combined), the degree of relative tilt varied as a function of the direction of peripheral flow and target location. In the Near periphery, the interaction pattern seen in Experiment 1.1 was replicated (Figure 25, left panel; *F* (1, 4) = 185.351, *p* < 0.001).

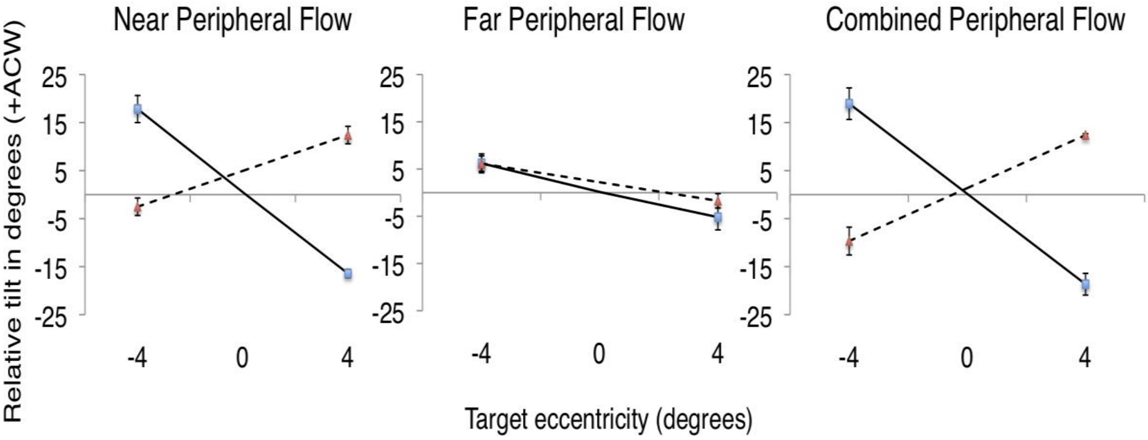


Figure 25 - Relative tilt as a function of target eccentricity for each peripheral condition (solid lines – expanding flow, broken lines – contracting flow). Error bars show within-subjects *SE*.

In the Far peripheral condition, the interaction was less clear (central panel, Figure 25). The magnitude of relative tilt was much lower than in the Near condition. Thus, the effect of Flow direction and target eccentricity upon relative tilt was less pronounced but a significant interaction was still present (Figure 25, central panel, *F* (1, 4) = 6.544, *p* = 0.0315). A one sample t-test using the Above and Below condition data was used to test for a significant difference from zero. For Expanding flow the far data was significantly different (*t* (9) = 2.633, *p* = 0.027) but for Contracting flow the far data was not significantly different from zero (*t* (9) = 1.964, *p* = 0.081, n. sig)

The Combined peripheral condition more closely reflected the predicted interaction between flow direction and target eccentricity and also showed a significant interaction (Figure 25) between flow direction and target eccentricity (Figure 25, right panel, *F* (1, 4) = 68.249, *p* = 0.005).

From Figure 26 it appears that the Near and Combined conditions show the predicted pattern of results but the Far condition does not. A 3 x 2 x 2 repeated measures ANOVA revealed that relative tilt differed between the three peripheral conditions as a function of target eccentricity and Flow direction (*F* (2, 8) = 68.907, *p* < 0.001).

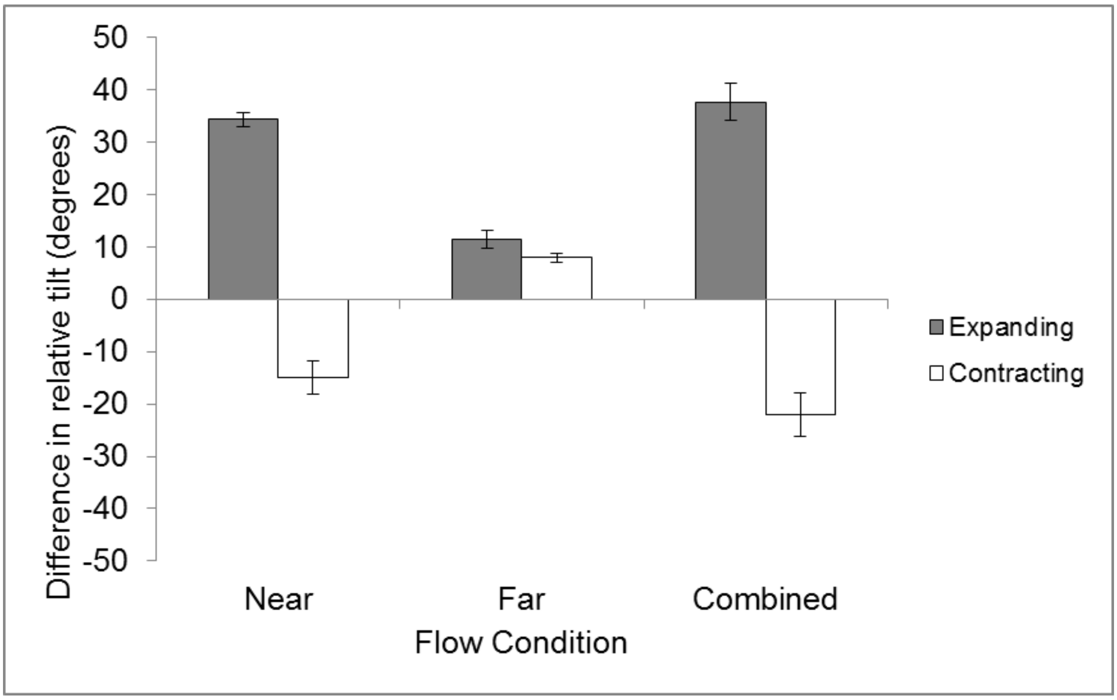


Figure 26 - Difference in relative tilt as a function of peripheral flow condition and flow direction. Error bars show within-subjects *SE*.

For each flow direction (Expanding or Contracting) three linear regressions were conducted to establish whether the relative tilt observed in the Combined condition could be predicted from 1) the linear sum of the Near and Far data 2) the Near data alone 3) the Far data alone.

In the Expanding flow condition, all three models significantly predicted the data in the Combined condition. The sum of the Near and Far data model accounted for 97% of the variance in the Combined data (Figure 27; $\beta = 0.788$, $R^2 = .971$, $F\ (1, 8) = 269.838$, $p < 0.001$), the Near data model also accounted for 97% of the variance in the Combined data (Figure 28; $\beta = 1.111$, $R^2 = .972$, $F\ (1, 8) = 277.554$, $p < 0.001$). The third model, using the Far data only as the predictor variable, accounted for 70% of the variance seen in the combined condition (Figure 29; $\beta = 1.958$, $R^2 = .702$, $F\ (1, 8) = 18.853$, $p = 0.02$).

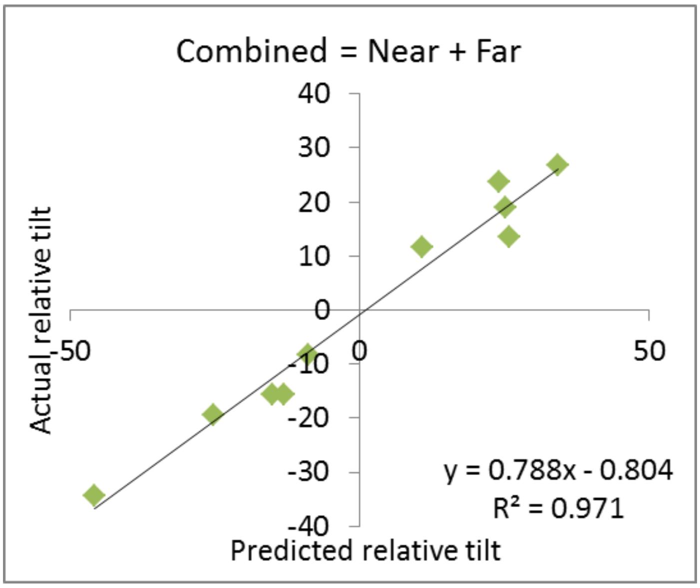


Figure 27 - Actual Combined relative tilt as a function of Predicted relative tilt for Near + Far model for Expanding flow

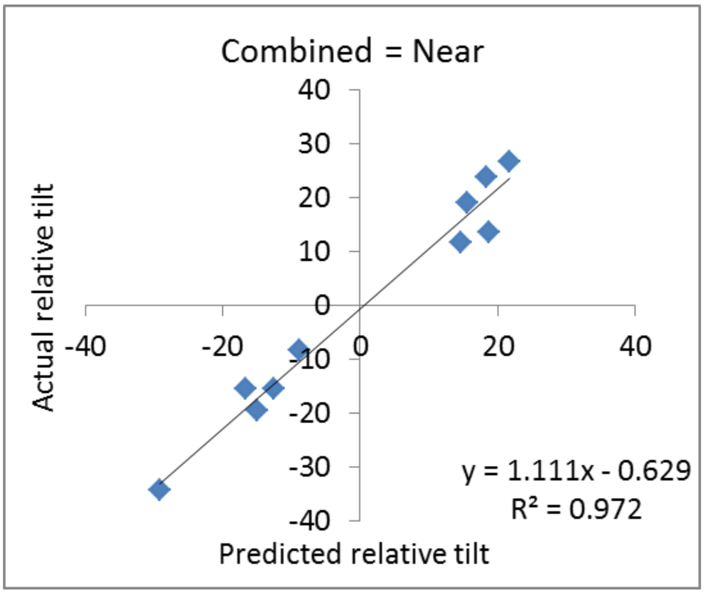


Figure 28 - Actual Combined relative tilt as a function of Predicted relative tilt for Near model for Expanding flow

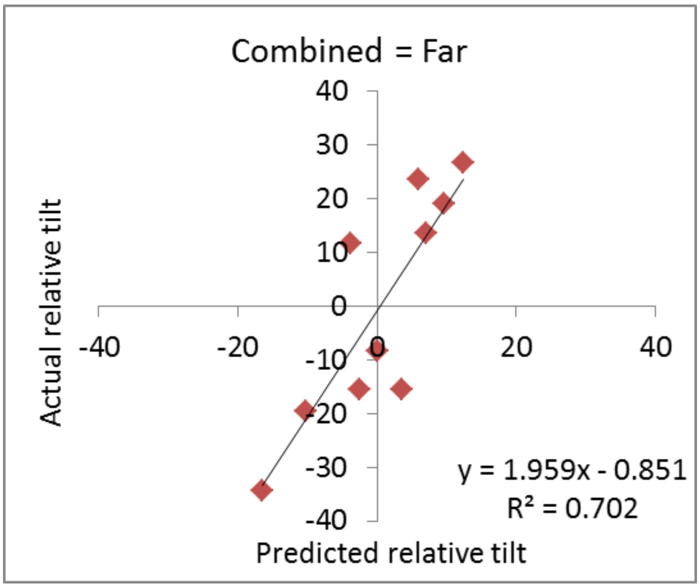


Figure 29 - Actual Combined relative tilt as a function of Predicted relative tilt for Far model for Expanding flow.

A chi-square difference test (Werner & Schermelleh-Engel, 2010) between both the Near and Near+Far model (χ^2 (1) = 0.916, p = 0.339) showed that the fit of the model to the data with only one predictor, the Near only model, was not significantly worse than the fit obtained in the two predictor model. The same test between the Far and Near+Far model (χ^2 (1) = 51.73, $p < 0.01$) indicated that the Far model provided a significantly worse fit to the data than the Near+Far model. In sum, the regression analyses for the Expanding flow condition suggest that the relative tilt in the Combined condition is best predicted by the relative tilt measured in the Near condition.

For Contracting flow, only the Near data model significantly predicted the data in the Combined condition (Figure 30; β = 1.305, R^2 = .823, F (1, 8) = 37.186, $p < 0.001$). The sum of the Near and Far data model accounted for only 34% of the variance in the Combined data (Figure 31; β = 0.817, R^2 = .343, F (1, 8) = 4.170, p = 0.075, *n. sig*). The Far data model was also not a significant predictor for the Combined data, accounting for just 14% of the variance in the Combined data (Figure 32; β = -0.660, R^2 = .139, F (1, 8) = 1.295, p =0.288, *n. sig*). Therefore, as with the Expanding flow condition, the Near data appears to be the best predictor of the relative tilt observed in the Combined condition. This suggests that flow in the near periphery is driving the peripheral contribution to flow parsing observed in the Combined condition.

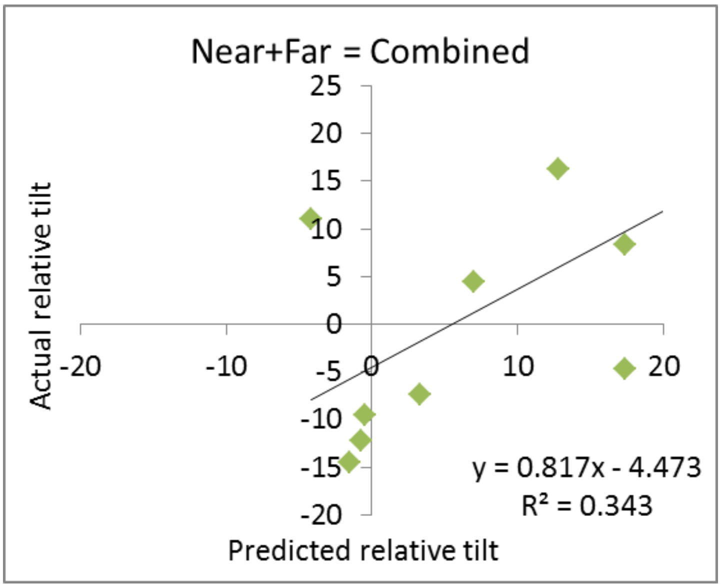


Figure 30 - Actual Combined relative tilt as a function of Predicted relative tilt for Near + Far model for Contracting flow.

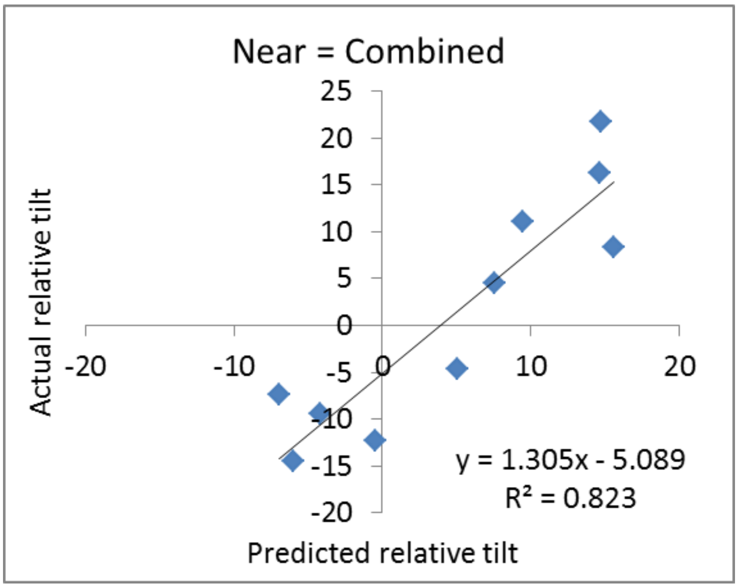


Figure 31 - Actual Combined relative tilt as a function of Predicted relative tilt Near model for Contracting flow.

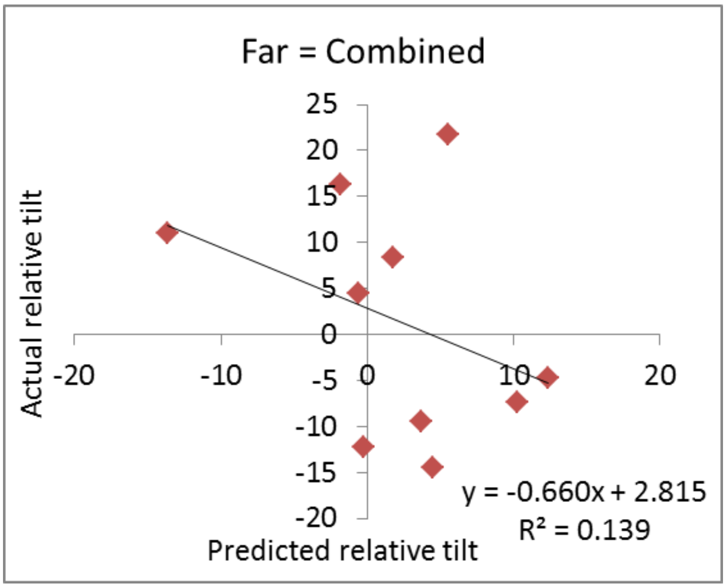


Figure 32 - Actual Combined relative tilt as a function of Predicted relative tilt for Fa model for Contracting flow.

Figure 33 compares the data from the Far peripheral condition with the data from Experiment 1.1. The difference in relative tilt between the Far condition in Experiment 1.2 and the 45 degree condition of Experiment 1.1 was used to compare the effect between the two experiments. An independent samples t-tests confirmed that for both flow directions the difference in relative tilt did not reach statistical significance between the two studies (Expanding: *t* (9) = 1.878, *p* = 0.093, *n. sig*; Contracting: *t* (9) = -1.110, *p* = 0.296, *n. sig*).

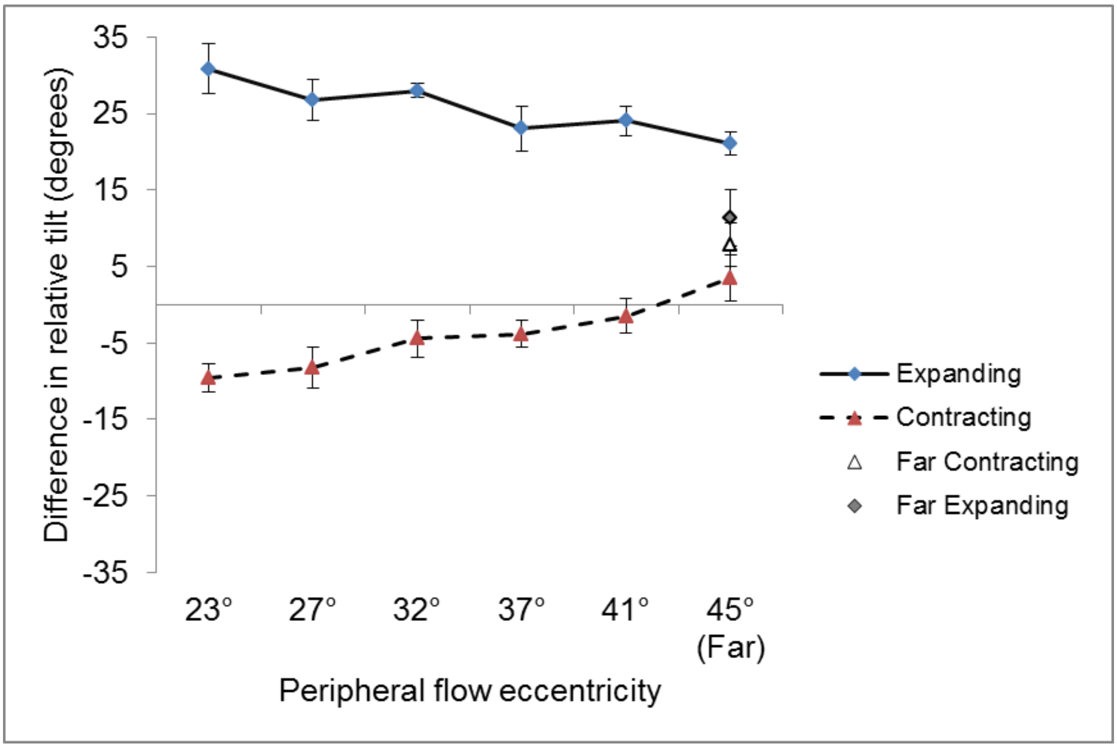


Figure 33 - Difference in relative tilt as a function of flow eccentricity (comparison between Experiment 1.2 & 1.3). Error bars show between-subject *SE* as different participants took part in each experiment.

The results of Experiment 1.2 replicate the peripheral flow parsing effects found in Experiment 1.1 but extend these findings by considering the effect of far peripheral flow. Far peripheral flow produced smaller relative tilts than were predicted by the results of Experiment 1.1, particularly in the case of Expanding flow (See Figure 33). There are two key differences between the stimuli used in this experiment and the radius manipulation performed in Experiment 1.1; the type and location of the flow stimuli.

In Experiment 1.1, the flow stimulus consisted of limited lifetime dots presented in a circumference around fixation whereas in Experiment 1.2 the far peripheral stimuli were large stripes presented only on the left and right of the observer. Larger effects may have been found in Experiment 1.1 because the flow stimulus was present across the visual field, or at critical retinal locations. Thus, the configuration and area of flow in Experiment 1.2 may have not been in the correct location to elicit flow parsing effects of the same magnitude as in Experiment 1.1. Similarly, presenting independent regions of flow on the left and right visual field may not activate neurons sensitive to global flow because of the spatial separation between the sections of flow. Experiment 1.3 investigates whether flow configuration is critical for flow parsing.

2.5 Experiment 1.3: Flow configuration control study

The previous experiment demonstrated that flow presented in the near periphery induces a larger bias in perceived target trajectory in the opposite direction to the flow than a far peripheral stimulus. Furthermore when directly comparing the data from the most eccentric flow eccentricity in Experiment 1.1 (inner radius of 45 degrees) to the Far peripheral stimulus (45 degrees from fixation), the magnitude of relative tilt is reduced in the latter case, especially for expanding flow. Given this difference, it seems unlikely that only the eccentricity of the flow is the root cause of the reduction in relative tilt seen between the Near and Far conditions in the previous experiment.

One key difference between the Near and Far peripheral stimuli was the configuration of flow in the visual field. Although the Near peripheral flow surrounded the fixation point on all sides, the Far peripheral stimulus was only presented as two distinct flow areas on the left and right of the observer. In macaque MT the lower visual field is over represented in comparison to the upper visual field (Maunsell & van Essen, 1987), and this overrepresentation has also been indicated in the peripheral visual field (Naito, Kaneoke, Osaka & Kakigi, 2000). Similar asymmetries have also been demonstrated in humans (see Skarandies, 1987 for a review), suggesting that the lower visual field is especially suited to motion perception. Considering these findings, the smaller effects observed in the far peripheral flow condition may be because the flow was restricted to two spatially separated retinal locations on the left and right of fixation and not present in other potentially important regions, such as the lower or upper visual field.

If the retinal location, visual area or continuity of optic flow is important for a peripheral contribution to flow parsing then different effects on perceived target trajectory may be observed depending on where the flow stimulus, or stimuli, are positioned on the retina. To test this, the Near peripheral display was modified in order to present flow in designated quadrants of the visual field and assess whether magnitude of relative tilt varied as a function of the flow configuration. If a much larger bias in perceived target trajectory is observed when the flow was positioned at the top and bottom of the screen (above/below condition) as opposed to the left/right, then this may help account for the smaller effect seen in the Far peripheral condition in Experiment 1.2. If no differences are observed between left/right and above/below flow locations then flow configuration is unlikely to account for the smaller effect of far peripheral flow.

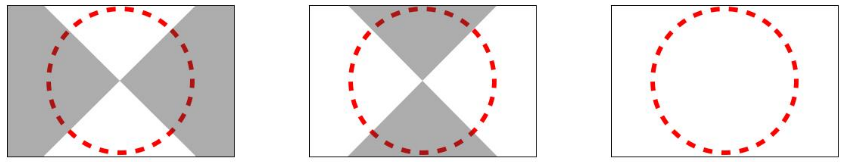
2.5.1 Methods

2.5.1.1 Participants.

Six participants (2 male) took part in all conditions. Individuals were recruited from undergraduate (N = 4) and postgraduate students (N = 2). Postgraduate students received payment at a rate of £10/hour and undergraduates received course credit. The same ethical procedures and eligibility restrictions used in Experiment 1.1 were employed. Aside from the author (CR), all other participants were naïve as to the experimental hypotheses.

2.5.1.2 Apparatus and stimuli.

The Near peripheral stimulus used in the previous experiment was modified; two 90 degree black segments (separated by 90 degrees) obscured two quadrants of the flow field in the Above/Below and Left/Right conditions (Figure 34).



Above/Below flow Left/Right flow Full flow

Figure 34 - Schematic diagrams for each flow configuration. Grey areas indicate the excluded flow regions.

In the Above/Below flow condition the flow field was obscured on the left and right of the screen, with the two black segments centred at +90 degrees and +270 degrees respectively. Similarly, in the Left/Right flow condition, the flow field at the top and bottom of the screen was obscured with segments centred at 0 degrees and +180 degrees. Each obscuring segment had an inner radius of 10 cm and an outer radius of 60 cm to ensure that the fixation point and target were still visible.

In addition to the two partial flow conditions, a full flow field condition was also presented in order to compare the magnitude of the peripheral contribution to flow parsing in the partial conditions to that observed when flow area was not restricted. The stimulus in this condition was identical to the near peripheral stimulus used in the previous experiment (Experiment 1.2).

The target was the same as in the previous experiment (diameter: 0.12 degrees/0.2 cm) and as before was presented 4 degrees from fixation. In a change from the previous experiment, the starting position of the target was shifted away from directly above/below fixation to either -45 degrees or +135 degrees (where 0 degrees is defined as vertically upwards from fixation, +CW). Figure 19B (Page 60) depicts the left/right flow stimulus and both possible target positions. Targets were positioned at these locations so that they were equidistant from the flow stimulus in all conditions.

2.5.1.3 Design.

Three IVs were manipulated: Flow direction (Expanding, Contracting), Target eccentricity (-4/+4 degrees), and Flow configuration (Above/Below, Left/Right, Full Flow). For each condition, 17 different probe trajectories were presented from a range of ±16 degrees in 2 degree steps. Each flow configuration condition was run in a separate experimental block of 68 trials, in which the order of conditions (Flow direction, Target eccentricity and target trajectory) was randomised. The DV was relative tilt in degrees. A within-subjects design was employed and the order in which participants completed the flow configuration blocks was counterbalanced across observers. Each observer completed all blocks within in a single experimental session.

2.5.1.4 Procedure.

Procedure and trial timings were identical to those used in the previous experiment. The flow simulated self-movement equivalent to a forward or backward translation at a rate of 30 cm/s. Alongside the flow stimulus, the target was presented after a delay of 1-1.2 seconds and moved at a speed of 0.6 degrees/s (1 cm/s) for 2 seconds. The response line, as in Experiment 1.1, and was located in the same position as the target, which in this experiment was either -45 or +135 with respect to the fixation cross. Participants made their responses using the jog wheel. There was an inter-trial-interval of 0.2 seconds, but participants were informed that they could opt to take a break by setting the line and withholding their button press until they were ready to continue. One enforced break of 15 seconds occurred in each experimental block.

2.5.2 Results and discussion

The three flow configurations all showed the expected interaction between flow direction and target eccentricity (See Figure 35; *F* (1, 5) = 33.800, *p* = 0.002) indicating a peripheral contribution to flow parsing. A 3 (Flow configuration) x 2 (Flow direction) x 2 (Target eccentricity) repeated measures ANOVA revealed that there were differences in this relationship between the flow configuration conditions in a three-way interaction (*F* (2, 10) = 18.567, *p* < 0.001).

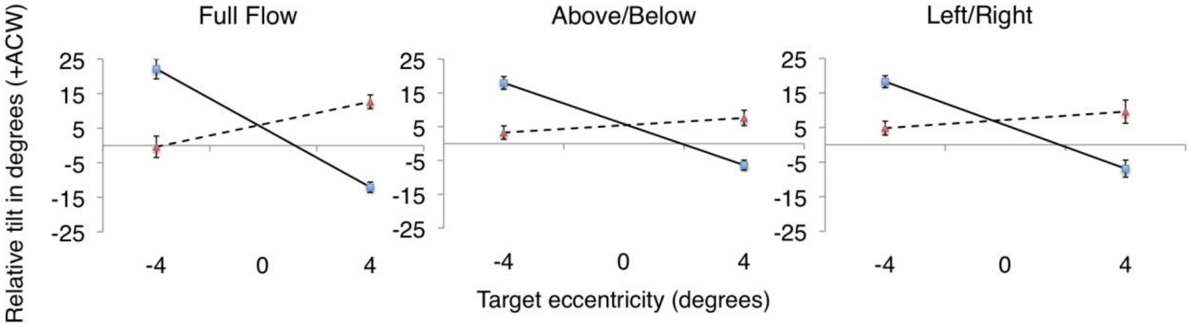


Figure 35 – Relative tilt as a function of target eccentricity and flow direction (solid line – Expanding, dashed line – Contracting) for each flow configuration. Error bars show within-subjects *SE*.

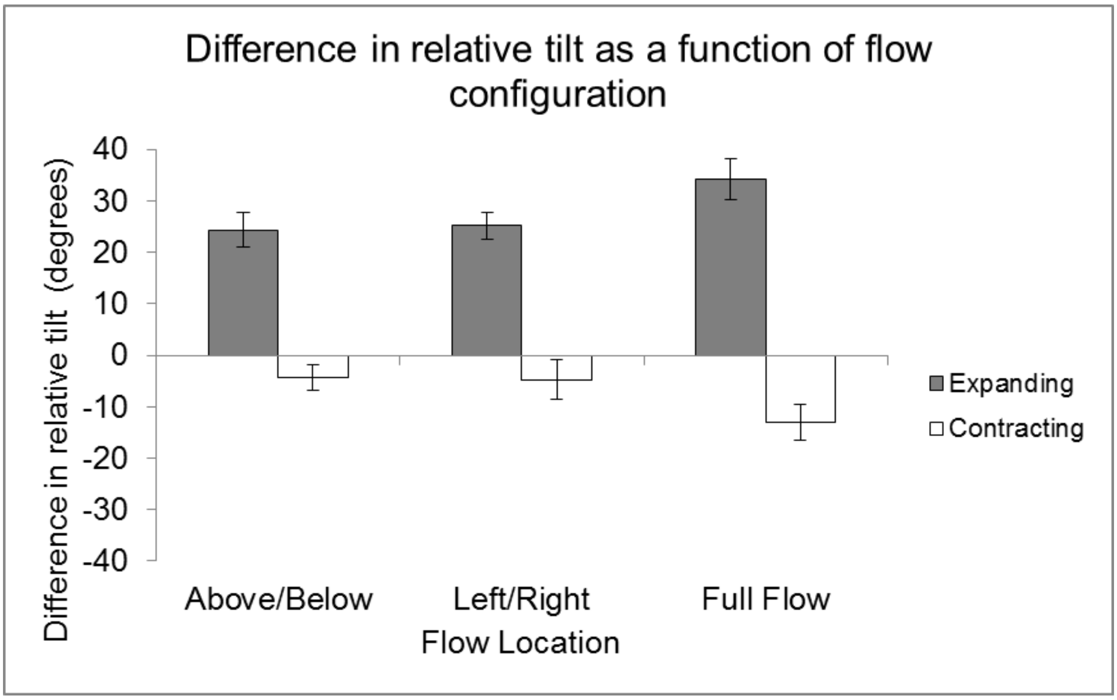


Figure 36 - Difference in relative tilt as a function of flow configuration and flow direction. Error bars show within-subjects *SE*.

In all three conditions the Expanding condition produced a positive tilt difference, and the contracting condition, a negative tilt difference (Figure 36); in line with a peripheral contribution to flow parsing. As before, the unsigned difference in relative tilt was much larger in the Expanding condition compared to the Contracting condition (*F* (1, 5) = 27.884, *p* = 0.003).

In the case of Contracting flow, it appears that the magnitude of relative tilt observed in the two partial flow conditions sums to approximately the same as the Full Flow condition (Figure 36). To further investigate this a linear regression was conducted to assess whether the sum of the tilts left/right and above/below conditions predicted the data in the Full flow condition. The Full Flow relative tilt was predicted by the sum of the Above/Below and Left/Right relative tilts (Figure 37; $\beta = 0.535$) and explained 55% of the variance in the Full Flow data ($R^2 = .546$, *F (*1, 10) = 12.016, *p* = 0.006).

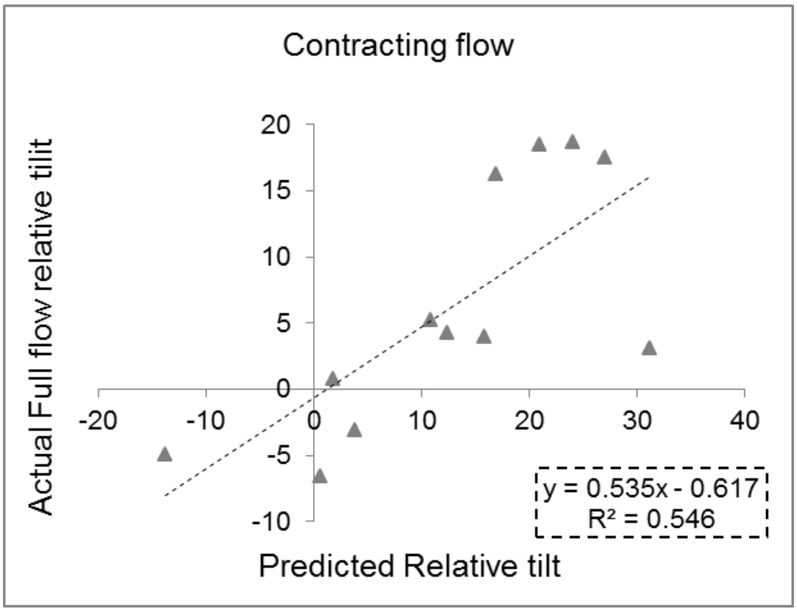


Figure 37 - Actual Full flow relative tilt as a function of Predicted relative tilt (Above/Below + Left/Right) for Contracting flow. Data points from the -4 and +4 target eccentricity locations are shown.

A linear regression was also conducted for the Expanding flow condition to test whether the Full Flow relative tilt was predicted by the sum of the Above/Below and Left/Right relative tilts. This analysis also revealed that the linear sum significantly predicted the Full Flow data (Figure 38; $\beta = 0.652$) and as a predictor explained 93% of the variance in the Full Flow data ($R^2 = .925$, $F(1, 10) = 123.262$, $p < 0.001$).

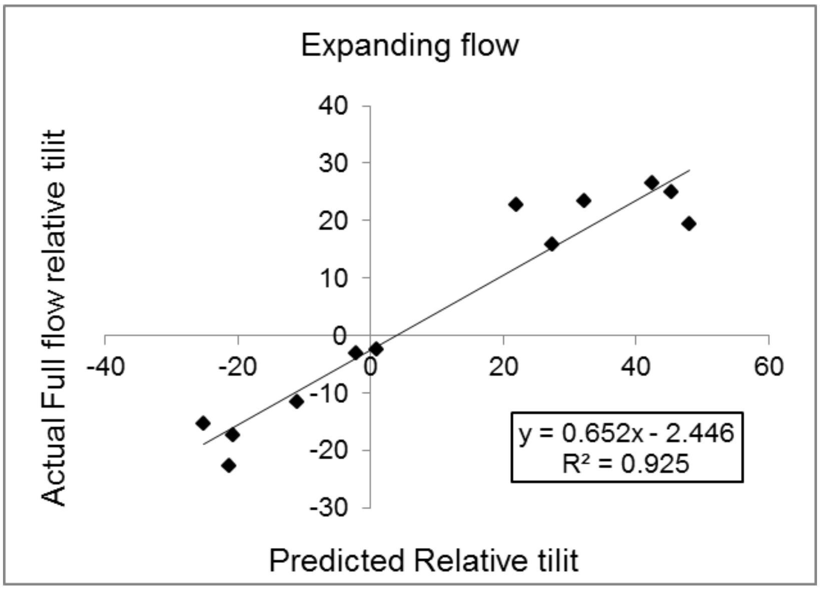


Figure 38 - Actual Full flow relative tilt as a function of Predicted relative tilt (Above/Below + Left/Right) for Expanding flow. Data points from the -4 and +4 target eccentricity locations are shown.

These regression analyses both indicate that for expanding and contracting flow, or forward and backward self-movement, the upper and lower *and* left and right peripheral visual field contribute to the overall peripheral contribution to flow parsing that was observed in the Near condition of Experiment 1.2, akin to the Full Flow condition in the present experiment.

Comparisons were also drawn between the two partial flow configurations, to ascertain whether there were any differences as a function of flow location. Participants reported similar relative tilts for the left/right and above/below conditions and the ANOVA confirmed there was no main effect of flow location (F (2, 10) = 0.261, p = 0.776, *n. sig*) and the interaction between flow location and flow direction was also not significant (F (2, 10) = 1.319, p = 0.310, *n. sig*). The reduction in relative tilt in both partial stimulus conditions is perhaps not surprising given the findings of (Warren & Rushton, 2009a) in which flow presented in one hemi-field produced a smaller magnitude relative tilt than when flow was presented in both hemi-fields. More importantly, the lack of differences between the left/right and above/below conditions indicates that these retinal locations in the periphery equally contribute to flow parsing. In other words, the quadrants of the visual field in which peripheral flow is presented do not appear to be critical for flow parsing. Thus, flow parsing appears to be able to integrate and utilise the visual information about self-movement from both sides of the visual field. Data suggests that flow parsing during forward self-movement is more resistant to a reduction in the size of the flow field than flow parsing during backward self-motion because the magnitude of the relative tilt in the left/right data for expanding flow was 34% reduced from the full flow but for contracting flow the reduction in the left/right data was 49%.

From the results of Experiment 1.1 (eccentricity manipulation) and 1.3 (flow configuration manipulation) a prediction can be generated about the amount of relative tilt that is expected given the parameters of the Far peripheral stimulus employed in Experiment 1.2. The nearest edge of the far peripheral stimulus was 45 degrees from fixation and the flow was presented only on the left and right. To generate a prediction for the eccentricity of the Far peripheral stimulus, I took the magnitude of relative tilt observed in the 45 degree eccentricity condition of the first experiment in this chapter (Experiment 1.1) and reduced the magnitude by the same percentage reduction that I measured between the Full Flow and Left/Right conditions in Experiment 1.3. These predictions are shown in Figure 39. The Far peripheral flow had a minimum eccentricity of 45 degrees from fixation and was only present on the left and right of the visual field.

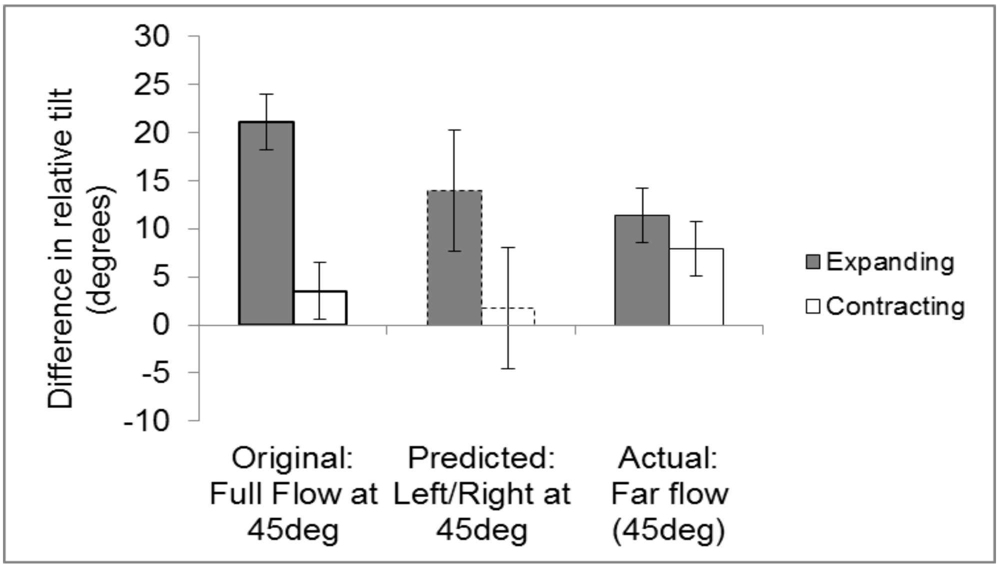


Figure 39 - Comparison of the difference in relative tilt between Far peripheral flow and a flow configuration and eccentricity matched prediction based on the findings of Experiment 1.1 and Experiment 1.3. Original bars show data from the 45 degree radius condition (Experiment 1.1) using the Near peripheral stimulus. Predicted bars show the same data reduced by 34% for Expanding and 49% for Contracting flow in accordance with the findings of Experiment 1.3[4].

For Expanding flow, the amount of relative tilt observed with the Far peripheral stimulus is approximately equal to these predictions. An independent samples t-test revealed there was not a significant difference between the predicted and actual data (*t* (9) = 0.7278, *p* = 0.4852, *n. sig*). For Contracting flow, because the magnitude of the effect was already much smaller in the original full flow condition, the relative tilt is slightly larger than predicted (Figure 39), and in the opposite direction to the flow parsing prediction. Yet, as for Expanding flow, this difference is not significant (*t* (9) = 2.0121, *p* = 0.0751, *n. sig*). Yet there are dangers of placing too heavy a reliance on these non-significant results due to the errors of estimation. However, taken together with

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[4] When calculating the size of the reduction in tilt between Full Flow and Left/Right conditions, one participant's reduction was 2 standard deviations below the group mean in the contracting condition and was therefore removed from the Expanding and Contracting analysis. For expanding flow this did not affect the outcome of the unpaired t-test (*p* = 0.297, *n. sig*), but did for contracting flow (*p* = 0.03) because of the increase in the group mean.

the data reported throughout the chapter, these findings suggest that it is unlikely the smaller relative tilts observed in the Far peripheral condition in Experiment 1.2 were solely due to the use of flow presented only on the left and right of the visual field because the Above/Below condition showed the same pattern of results. Instead, in the case of forward and backward self-motion it seems likely that the near/far difference reported in Experiment 1.2 is accounted for by the extreme eccentricity of the far peripheral stimulus and the fact that the total area of the flow is reduced when it is presented in two distinct areas of the visual field.

Another possible explanation for the near/far difference relates to motion sensitivity in the peripheral retina. If it were the case that neurons with receptive fields in the near periphery are more sensitive to visual motion indicating self-movement than those in the far periphery then this may have produced differences in relative tilt between the two conditions. For example, if sensitivity to self-movement indicated by the far peripheral stimulus was reduced compared to the near peripheral stimulus then this could have resulted in less self-movement being identified in the Far condition. Following on from that, the self-motion component, or amount of flow to be parsed, would therefore be less in the Far condition than the near condition. Under the FPH, and in the present experiments, this would lead to a smaller trajectory bias in the Far condition – as observed in Experiment 1.2. To test whether this was the case, a simple speed discrimination task was conducted using the existing stimuli to test motion sensitivity in the near and far periphery.

2.6 Experiment 1.4: Speed discrimination control study

One potential cause of the smaller far peripheral contribution to flow parsing than near peripheral contribution (Experiment 1.2) is an underlying difference in sensitivity to visual motion indicating self-movement between the near and far periphery. If sensitivity to motion in the far periphery is lower than in the near periphery then this means the ability to detect self-movement information in the far periphery may be reduced compared to the near periphery. This has consequences for flow parsing because the detected self-movement determines the amount of flow to be parsed from the retinal image.

Thus, a reduced sensitivity to far peripheral flow could lead to a less robust parsing of flow from across the retina and reduce the relative tilt effect.

Previous work has suggested that sensitivity to motion does not decline as stimuli move further into the periphery. Orban, Kennedy and Bullier (1986) have shown that thresholds for velocity discrimination thresholds are maintained with increasing retinal eccentricity. However, there are differences in the velocity cut-off (i.e. the maximum speed that can be discriminated), which is higher in peripheral vision than central vision.

Another reason to investigate motion sensitivity for the near and far periphery is due to the different stimuli that were employed in the previous experiments. The use of dots in the Near peripheral stimulus and stripes in the Far stimulus could potentially have caused differences in motion perception between stimulus types. Although the stimuli used in the present experimental work were designed to provide a robust cue to self-movement, it may be that the dots (near periphery) and stripes (far periphery) did not equally stimulate the visual system, with one cue providing a more robust cue to self-movement than the other. Any differences in the perception of self-movement would necessarily have affected perceived target trajectory. Therefore, it is also important to ensure that the choice of stimuli is not responsible for the differences in relative tilt that were observed between the Near and Far peripheral conditions. Thus, in order to compare sensitivity to visual motion indicating self-movement in the near and far periphery, the same stimuli were utilised in the current experiment with dots in the near periphery and stripes in the far periphery.

In this experiment, visual motion sensitivity was assessed through the measurement of speed discrimination thresholds, which provide a measure of the ability to distinguish between different speeds of self-movement. Note that here speed discrimination thresholds are used as an indicator of motion sensitivity rather than perceived speed of self-movement. Sensitivity to visual flow indicating self-movement necessarily impacts upon flow parsing as, at least in a perfect visual parsing process, the self-motion components to be parsed from the retinal image are equal and opposite to the detected flow present on the retina during self-movement. In terms of speed discrimination thresholds, a higher threshold for Far than Near peripheral flow would indicate that in the Far case there is a reduced sensitivity to self-movement. By contrast, a lower speed discrimination threshold would suggest that the visual system is more sensitive to the visual motion indicating self-movement. Therefore, a difference in speed discrimination thresholds between the Near and Far peripheral stimuli could explain the difference in relative tilt magnitude between the near and far peripheral conditions observed in the earlier experiments. Alternatively, if the present experiment reveals no differences in motion sensitivity between the two peripheral conditions then this would indicate that the differences previously observed are unlikely to be driven by a difference in motion perception but are a product of differences in the flow parsing process itself in near versus far periphery.

Alongside identifying if motion perception differs between the peripheral conditions, a secondary aim of this experiment was to assess whether there are differences in sensitivity to motion for expanding and contracting stimuli. In previous experiments, there were differences in the magnitude of the effect for expanding and contracting flow, which may be underpinned by differences in motion sensitivity to these flow stimuli in peripheral vision. One explanation for this difference is that observers are more sensitive to expanding flow than contracting flow. Given that we are more frequently exposed to expanding flow than contracting flow in everyday life it may be the case that the perception of self-movement and the subsequent parsing process is more effective during forward than backward self-motion. This would mean that the self-motion signal would be more precise in the expanding case, and result in a larger trajectory bias following the parsing process. Thus, as for differences between the near and far periphery, finding no differences in motion sensitivity between expanding and contracting flow would suggest that the differences in relative tilt magnitude observed in the earlier experiments reflect differences in the parsing process.

In the present experiment, the Near and Far peripheral stimuli from Experiment 1.2 were used but the target was omitted from the display. To investigate sensitivity to motion in the near and far periphery and to expanding and contracting flow, speed discrimination thresholds were determined. The methodology employed in this experiment was closely based on the speed discrimination task used by Snowden and Kavanagh (Experiment 3; 2006).

2.6.1 Methods

2.6.1.1 Participants.

Six postgraduate students (3 male) with an age range of 24 to 27 were recruited and received payment at a rate of £10/hour for their time. The author (CR) was a participant in this experiment but all other participants were naïve as to the experimental hypotheses. Participant restrictions and ethical procedures from Experiment 1.1 were applied.

2.6.1.2 Apparatus and stimuli.

The near and far peripheral flow stimuli were identical to those used in Experiment 1.2 (see Figure 19C), except that no target was presented. In this experiment, forced choice judgements were required and participants responded using the left and right mouse buttons.

2.6.1.3 Design.

In separate experimental blocks two IVs were manipulated: Flow direction (2 levels: Expanding or Contracting) and Peripheral condition (3 levels: Near/Far/Combined). Expanding and contracting stimuli were presented in alternating blocks to measure speed discrimination thresholds independently for expanding and contracting flow and allow for an independent assessment of speed perception in these two cases. Within each of these conditions, an adaptive staircase method was employed in order to manipulate the difference in speed between the test stimulus and the reference stimulus (see Staircase Design, below). The DV was the speed discrimination threshold. The method for calculating the speed discrimination threshold is given in the Analysis section, below. All participants took part in all conditions in a within-subjects design and the order of the conditions was counterbalanced across observers.

2.6.1.4 Procedure.

As in the previous experiments, participants were seated at a distance of 95 cm from the projection screen and fixated a centrally presented point during stimulus presentation. In each trial, two stimuli were presented which were always in the same peripheral region (i.e. near and near or far and far) and always displayed motion in the same direction (i.e. expanding only or contracting only). One stimulus was always the reference stimulus, which was set to the same forward/backward translation speed used in previous experiments (30 cm/s). On each trial the reference stimulus was randomly presented in either the 1st or the 2nd stimulus interval. Participants responded to the question ‘Which stimulus was faster, 1st or 2nd?’ by clicking the left (1st) or right (2nd) mouse button. They were instructed to guess on any trials for which they were unsure.

The trial procedure closely followed those used in the preceding experiments. Once the participant clicked the mouse to start the trial, a fixation dot was presented for 1.2 seconds prior to the onset of the first stimulus. The first flow stimulus waspresented for 2 seconds, followed by an Inter Stimulus Interval (ISI) of 0.5 seconds during which a black screen was displayed. This was immediately followed by the second stimulus which was presented for 2 seconds(the same duration as the simultaneous flow and target presentation in Experiments 1.1-1.3).. Following the presentation of the two flow stimuli, a black screen was then presented until the observer responded. Following a button press, a white screen was displayed for 1.5 seconds before the start of the next trial. This short break was included to provide a break for participants in order to minimise the build-up of motion after effects across trials and prevent dark adaptation. Introducing this delay between trials stopped the participant from constantly being exposed to the motion stimulus, and therefore hoped to reduce any interaction between the stimuli on adjacent trials.

2.6.1.5 Staircase design.

The data was collected using a staircase procedure that employed two interleaved staircases in each experimental block. One staircase increased the test speed following three consecutive correct answers, using a 3-up, 1-down convergence rule and the other decreased the test speed following the same number of correct responses (1-up, 3-down rule). These rules were chosen because the staircases would converge to the 21% and 79% point on the psychometric function; which would help to establish a test speed that was faster than the reference and a test speed that was slower the reference that participants could discriminate. This data could then be used to reconstruct the psychometric function to derive the speed discrimination threshold; the process for this calculation is described in the Analysis section.

At the start of each experimental block, the 3-up, 1-down staircase began with a test speed of 5 cm/s and the 1-up, 3-down staircase began with a test speed of 55 cm/s. Following a correct response in both cases, the speed of the test stimulus was thereafter selected by the staircase procedure from within a constrained range of approximately ±40% of the reference speed (17.5 cm/s to 42.5 cm/s). Thus, after the initial correct response, the difference between the reference (30 cm/s) and test stimulus, was never more than 12.5 cm/s. Step-size, defined as the change in the test speed triggered by a staircase rule, began at 10 cm/s and following the first reversal reduced to 5 cm/s and then to 2.5 cm/s following the second reversal. Thus, the minimum possible difference between the test speed and the reference speed was 2.5 cm/s. The staircase terminated once 10 reversals of each staircase had been completed.

2.6.1.6 Analysis.

The psychometric function for each participant in each condition was reconstructed using the staircase data. For each test speed, responses were coded as the proportion of trials on which the test stimulus was judged to be faster than the reference stimulus. The data was fitted using a Gaussian cumulative distribution function in Matlab (Żychaluk & Foster, 2009).

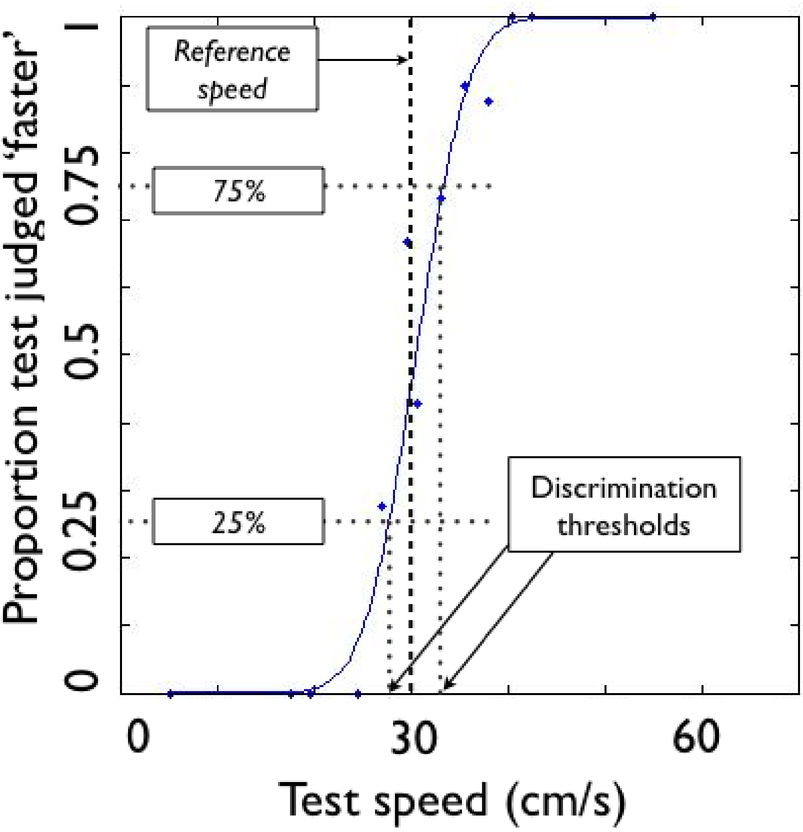

Figure 40 - Example psychometric function fit of staircase data with reference speed (dashed line) and 25% and 75% speed discrimination threshold (dotted lines). The two thresholds were subsequently coded as the absolute difference between test and reference speed and averaged to provide a single measurement of speed discrimination for each of the four conditions (Near-Expanding, Near-Contracting, Far-Expanding, Far-Contracting).

The test speeds on the psychometric function that equated to the respondent judging the test stimulus to be faster than the reference 75% of the time and 25% of the time (See Figure 40) were converted to the difference in speed by subtracting the reference speed (30 cm/s) from each value. The absolute difference in speed was then averaged across these two data points to provide a single measure of the minimum difference in speed that could be discriminated. This speed discrimination threshold was then used for within-subject comparison across conditions.

A 2 (Near/Far) x 2 (Expanding/Contracting) within-subjects ANOVA was conducted to assess whether speed discrimination thresholds differed between the near and far periphery or between expanding and contracting flow conditions.

2.6.2 Results and discussion

There were no significant differences in speed discrimination thresholds between the near and far peripheral flow conditions (Figure 41 & Figure 42; *F* (1, 5) = 2.659, *p* = 0.164, *n. sig*).

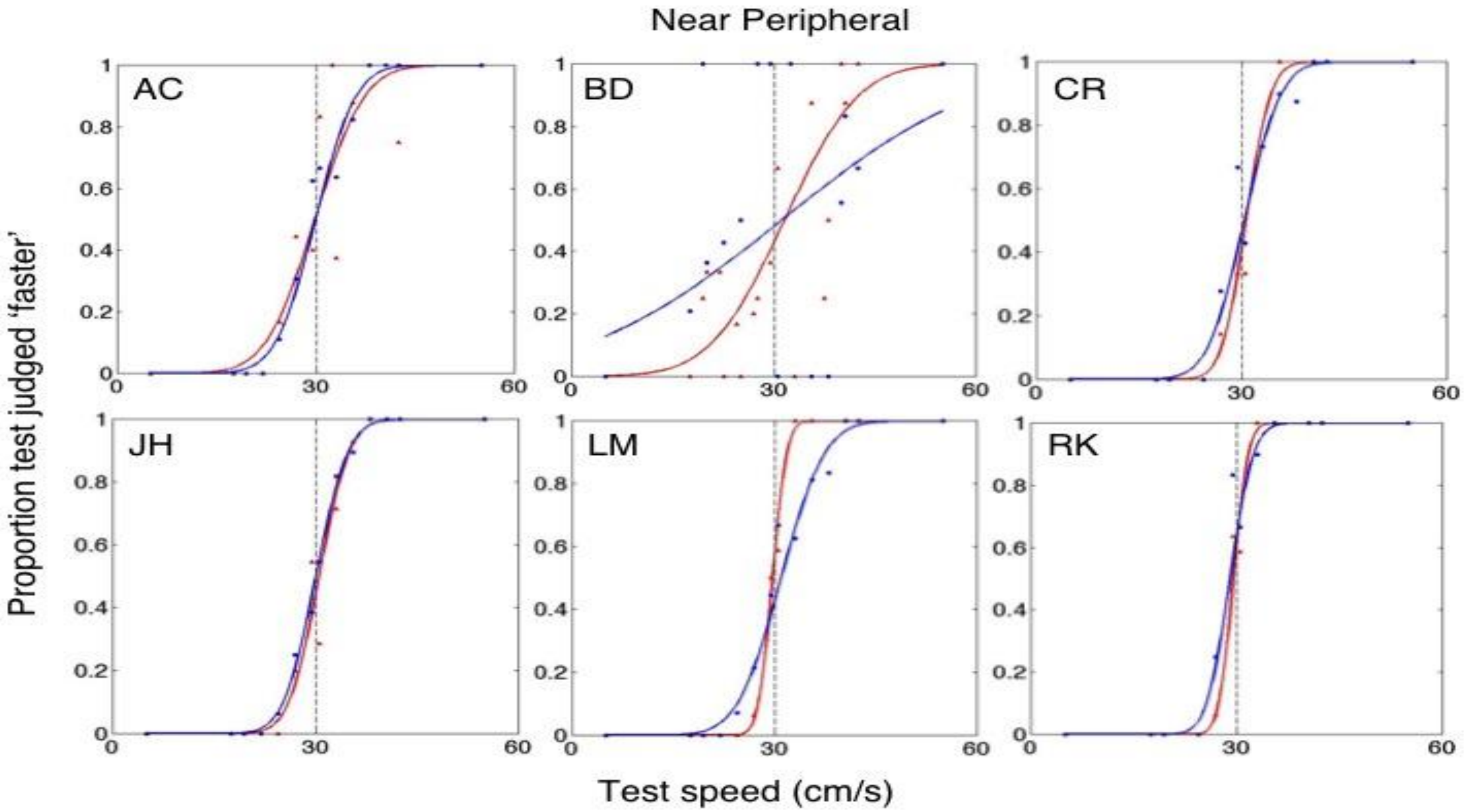

Figure 41 - Psychometric functions showing discrimination thresholds with Near peripheral flow for Expanding (blue line, square markers) and Contracting (red line, triangular markers) flow conditions. Dashed line indicates the reference speed of 30 cm/s.

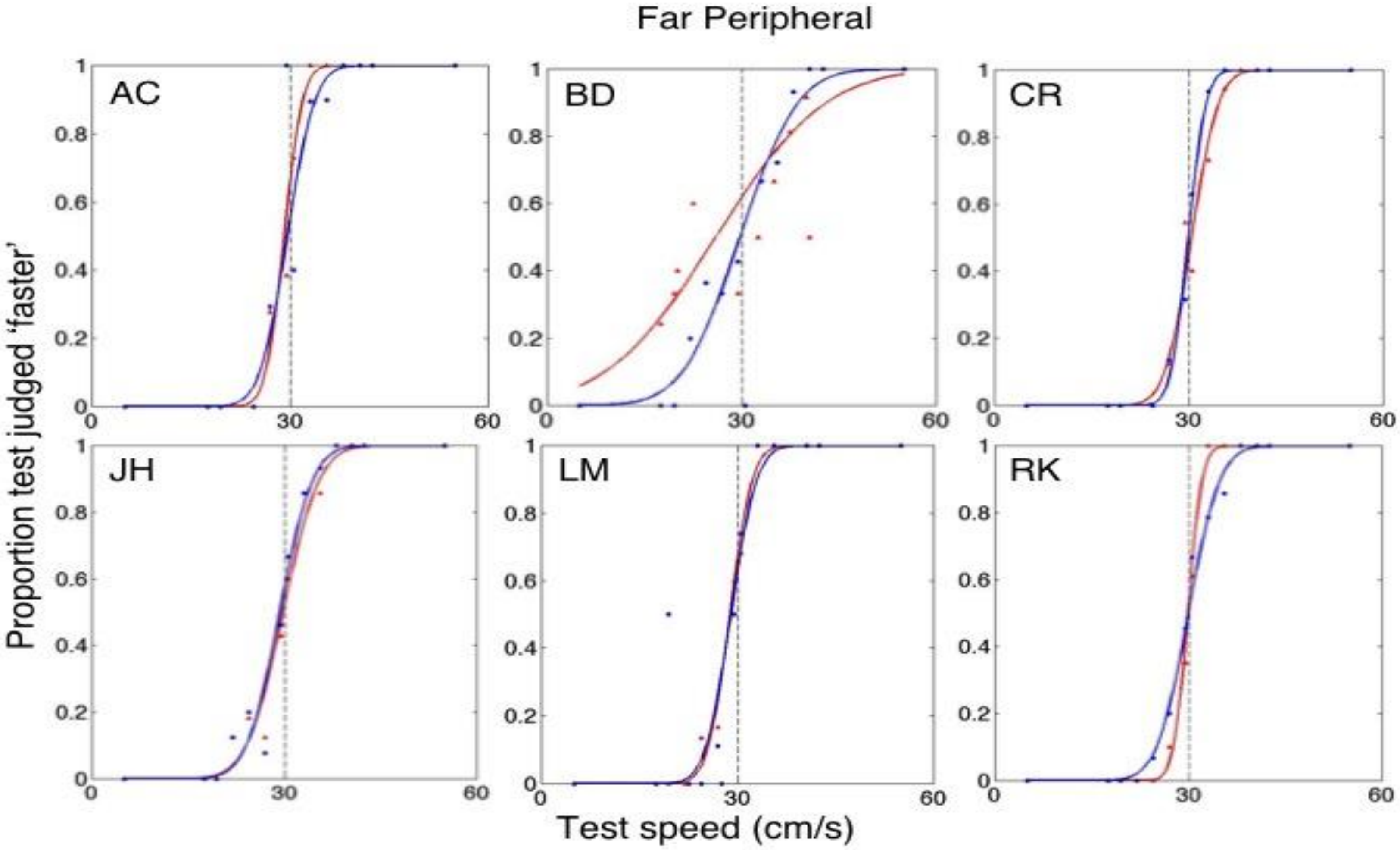

Figure 42 - Psychometric functions showing discrimination thresholds with far peripheral flow for Expanding (blue line, square markers) and Contracting (red line, triangular markers) flow conditions. Dashed line indicates the reference speed of 30 cm/s.

It was also hypothesised that there may be differences between the Expanding and Contracting flow conditions because previous results had found larger relative tilts during simulated forward than backward self-movement. However there were no differences between the speed discrimination thresholds for the two flow directions (*F* (1, 5) = 2.131, *p* = 0.204, *n. sig*) and there was also no interaction between flow direction and peripheral flow condition (near/far) (*F* (1, 5) = 1.407, *p* = 0.289, *n. sig*). The lack of significant differences in speed discrimination between the four experimental conditions suggests that motion perception is equivalent between the two peripheral displays; regardless of the direction of self-motion.

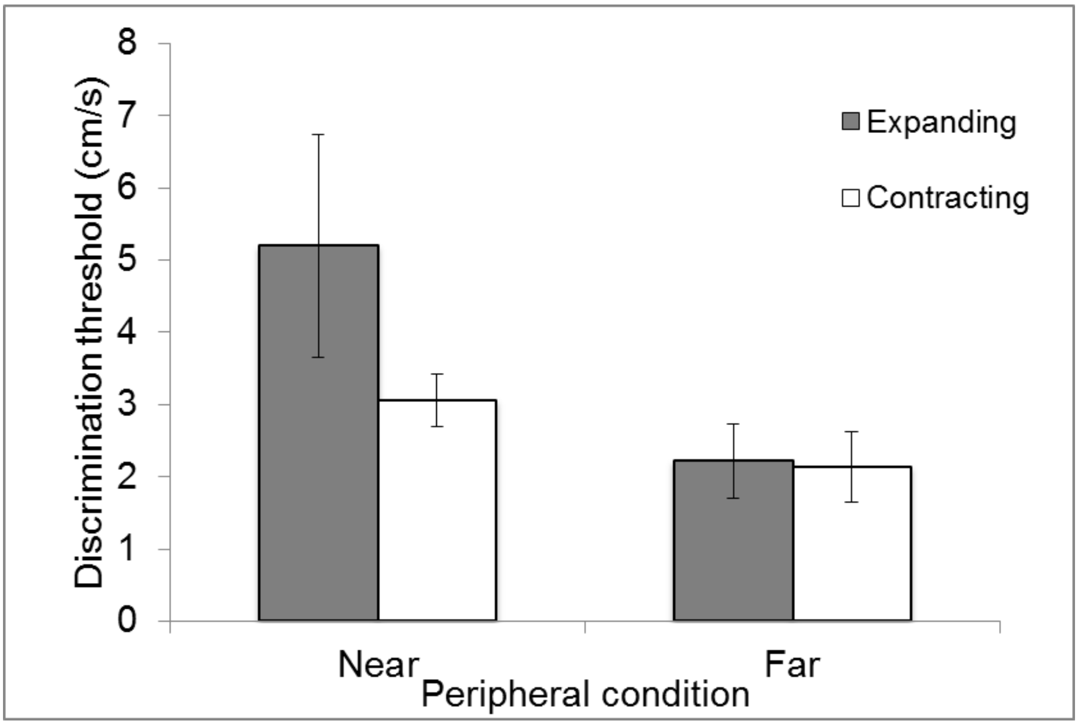

Figure 43 - Speed discrimination threshold (cm/s) as a function of peripheral flow condition and flow direction. Error bars show within-subject *SE*.

As no differences were evident between the conditions (Figure 43), it is important to rule out some potential methodological reasons for this null result. The data was collected using two interleaved staircases so that participants could not track the progress of the staircase. The reference speed was randomly presented in either the 1st or 2nd interval to ensure that participants would not be able to determine which stimulus was the test and which was the standard. The reference speed (30 cm/s) used in this study was chosen because it was the speed employed in Experiments 1.1-1.3. Thus, the majority of the physical flow speeds presented in the present experiment were similar to the stimuli that were used in the earlier experiments in this chapter. There are no strong reasons to suspect that the participants in this study perceived the stimuli any differently than participants in the previous experiments. This is especially true because the majority of observers had taken part in other similar experiments. Furthermore, five of the participants were experienced psychophysical observers (RK was not), who were familiar with making simple visual judgements. Given these methods, it seems unlikely that the results are due to any extraneous differences in stimuli or observers between this study and the preceding experiments.

However, recoding the discrimination thresholds into degrees/s reveals a somewhat different pattern of results, with significantly higher speed discrimination thresholds for the Far periphery than the Near Periphery. This suggests that, given the same rate of motion across the retina, motion sensitivity in the far periphery is lesser than in near periphery (See Appendix B for a figure showing the results in these units). Using these alternative units, it appears that there is a reduced sensitivity to far peripheral flow which might underpin the results obtained earlier in this chapter wherein a smaller relative tilt was found when flow was presented in the far peripheral in comparison to when flow was present in the near periphery. However, as the displays were placed at different distances from the observer, simulation of observer translation produced faster retinal motion in the far periphery than the near periphery. Thus, when converting the discrimination thresholds into degrees/s this difference between the flow stimuli becomes apparent.

In order to determine whether degrees/s or cm/s are the most appropriate units it is important to consider what the measurement of discrimination thresholds reflects. If thresholds represent a constraint in the early stages of motion processing then reporting the results in degrees/s makes most intuitive sense if one assumes that noise increases with each stage of processing. Yet for the present line of research, the ability to discriminate global patterns of motion from different retinal regions is the critical factor under consideration. If, as Warren and Rushton (2008) have suggested, global motion processing underpins flow parsing then it may be the case that it is more appropriate here because motion sensitivity, and therefore relevant discrimination thresholds, might be constrained at a later stage of motion processing.

Thus, while degrees/s thresholds may tell us about the sensitivity to motion from each retinal region, in terms of the present control experiment, the use of degrees/s is somewhat inappropriate because it removes the relative differences in motion across the retina that are present during real self-movement and that observers experienced during the earlier experiments in this chapter for which this study serves as a control.

2.7 Chapter Discussion

This chapter set out to investigate whether peripheral vision contributes to a flow parsing process for forward and backward movements of the observer. The experiments reported in this chapter demonstrate that peripheral visual flow can contribute to flow parsing. When self-movement information is presented in near peripheral vision there is a characteristic bias in perceived object trajectory, indicative of a peripheral contribution to flow parsing. However, the more peripheral the visual flow, the smaller the trajectory bias suggesting that as the eccentricity of the flow increases the contribution of visual flow to the parsing process declines. Far peripheral flow also produced a small but consistent flow parsing effect (Experiment 1.2). The differences in the magnitude of the trajectory bias observed between the near and far peripheral conditions may be due to differences in motion perception between the two stimuli (Experiment 1.4), but not the quadrants of the visual field in which flow was presented (Experiment 1.3). The near/far difference reported in Experiment 1.2 can be accounted for by the eccentricity of the far peripheral stimulus and the fact that in the present experiments the flow in the Far peripheral condition covers a smaller proportion of the visual field than in the Near peripheral condition. In addition, some of the reduction in effect with increasing flow eccentricity might be accounted for by a difference in sensitivity to retinal motion between the near and far periphery (when plotted in degrees/s), but is unlikely to be due to differences in motion sensitivity between the two flow stimuli that were used the experiments in this chapter.

Overall, the induced trajectory bias reported for centrally located targets is perhaps surprising given the spatial separation between the object and flow stimuli employed in these experiments. This serves as further support for the global nature of the flow parsing process outlined by Rushton and Warren (2005). However, considering previous findings from the vection literature have implicated peripheral vision in the perception and control of self-movement, it is notable that peripheral vision does not make a greater contribution to flow parsing. The reasons for this relationship between retinal eccentricity and a reduction in trajectory bias are unclear. Possible reasons for the declining contribution to flow parsing with increasing flow eccentricity are discussed in the General Discussion.

To summarise, this chapter has characterised how peripheral flow contributes to flow parsing during forward and backward translation of the observer. Whilst self-movement information in the near periphery clearly feeds into flow parsing mechanisms, the contribution of more eccentric flow declines with increasing retinal eccentricity. Given that the flow structure during forward and backward self-movement differs between central and peripheral vision I hypothesised that peripheral flow would contribute to flow parsing as the lamellar flow structure in the periphery may provide additional information about self-movement that can be utilised for flow parsing. The near peripheral flow presented in these experiments was more radial in nature and appears to feed in to flow parsing mechanisms that have previously been identified in central vision. However the lamellar flow structure present in the far periphery does not appear to make the same contribution to flow parsing. During contracting flow, specifying backwards self-movement, the same pattern is present, with the far periphery making a smaller contribution to parsing than the near periphery. In addition, in all the experiments reported in this chapter, the contribution of peripheral vision to flow parsing during backward self-movement was markedly less than the contribution during forward self-movement. It is unclear whether the differing peripheral contribution during forward and backward self-movement reflects an underlying difference in the processing of these two types of self-movement or whether this difference only reflects differences in the peripheral input to parsing. Further work might be undertaken to assess whether the same disparity between forward and backward self-movement is present when self-movement information is presented in central vision.

The experiments reported so far provide a foundation for exploring the potential contribution of peripheral vision to flow parsing for other forms of self-movement. Other types of self-movement, such as self-rotation, create a different pattern of retinal flow and by considering how flow structure differs as a function of retinal eccentricity; predictions can also be made about the likely contribution of peripheral flow to the parsing process for these movements. The experimental work in the next chapter explores whether peripheral vision also contributes to flow parsing during roll self-movement.

Chapter 3. PERIPHERAL CONTRIBUTIONS TO ROLL FLOW PARSING

3.1 Chapter summary

The results in the previous chapter show that peripheral visual flow contributes to the extraction of object movement during simulated linear self-movement. The experiments in this chapter examine the contribution of peripheral vision to flow parsing during simulated *rotation* about the line of sight. When gaze direction is aligned with the AOR then the centre of rotation is visible in central vision and flow vectors increase in magnitude with increasing retinal eccentricity, leading to a lamellar flow in opposite directions in the left and right periphery. Thus, the flow structure varies as a function of retinal eccentricity, meaning that central and peripheral regions are exposed to different visual information about self-movement. Preliminary data has shown that rotary flow in central vision gives rise to flow parsing effects (Warren & Balcombe, 2010). This chapter investigates whether peripheral flow also contributes to flow parsing during rotations of the observer about the line of sight.

Patterns of rotary flow were presented in peripheral vision to simulate CW or ACW roll of the observer. The experimental apparatus was the same as in Chapter 2, and the design the same as Experiment 1.2, with flow presented to the near, far, and near + far periphery to assess the integration of flow from across the retina. Observers judged the trajectory of a target located +/-4 degrees from fixation. The signature of a contribution of peripheral flow to a global flow parsing process is a bias in the perceived target trajectory in the opposite direction to the presented motion; negative roll, producing CW flow, would bias perceived trajectory in the opposite direction (an ACW bias), and positive roll (ACW flow) would bias responses CW.

The first experiment showed that both near and far peripheral flow produced perceptual biases in the predicted directions indicating a peripheral contribution to flow parsing. As shown in Chapter 2, a larger effect was found with near peripheral flow than far peripheral flow. Further experiments confirmed effects of target eccentricity and the speed of self-movement upon perceived target trajectory – hallmarks of a flow parsing process. These results are in agreement with those obtained for linear self-movement and extend the findings from the first chapter to show that the peripheral contribution to flow parsing is not limited to forward and backward observer translation.

3.2 Chapter Introduction

In Chapter 2, I explored the role of peripheral vision in flow parsing for forward and backward movements of the observer. The results provided the first evidence that there is a peripheral contribution to flow parsing. However, if peripheral vision is specialised for detecting certain forms of self-movement (Andersen & Braunstein, 1985; Stoffregen, 1985) then this raises the question of whether the peripheral contribution to flow parsing observed in Chapter 2 might only pertain to forward or backward translation and the role of peripheral vision may not be the same across different types of self-movement. The experiments in this chapter explored whether peripheral vision makes a similar contribution to flow parsing during rotations of the observer. As noted below, for this type of optic flow the motion present in peripheral vision is markedly different to that present when translating forwards as the flow present on the left peripheral visual field moves in the opposite direction to flow presented in the right peripheral visual field (Figure 44).

3.2.1 Neural sensitivity to roll flow

As covered in the General Introduction, a number of studies have demonstrated the existence of cells that selectively respond to roll flow in primates (i.e. Duffy & Wurtz, 1991, 1995). Psychophysical experiments have also indicated a similar sensitivity to roll flow in humans that is distinct from sensitivity to radial flow (Freeman & Harris, 1992; Snowden & Milne, 1997; Bex et al., 1998). Functional imaging studies have since revealed some potential neural areas responsible for optic flow processing in humans (Morrone et al., 2000; Smith et al., 2006). In addition, vection research has also suggested that patterns of roll flow provide a cue to self-movement, with observers experiencing illusory self-rotation about the line of sight (Held et al., 1975).

The sensitivity to roll flow is akin to the sensitivity seen for radial flow patterns and this equivalence might mean that visual processes that rely upon the ability to detect self-movement, such as flow parsing, are similar for these two types of self-movement.

3.2.2 Differences in flow structure as a function of retinal eccentricity

Assuming gaze is straight-ahead, central and peripheral vision are exposed to different flow structures during roll self-movement. During an observer rotation the direction and magnitude of the flow vectors vary across the 360 degree optic flow field. Figure 44 depicts the flow structure during CW rotation about the line of sight when gaze and the centre of rotation are congruent.

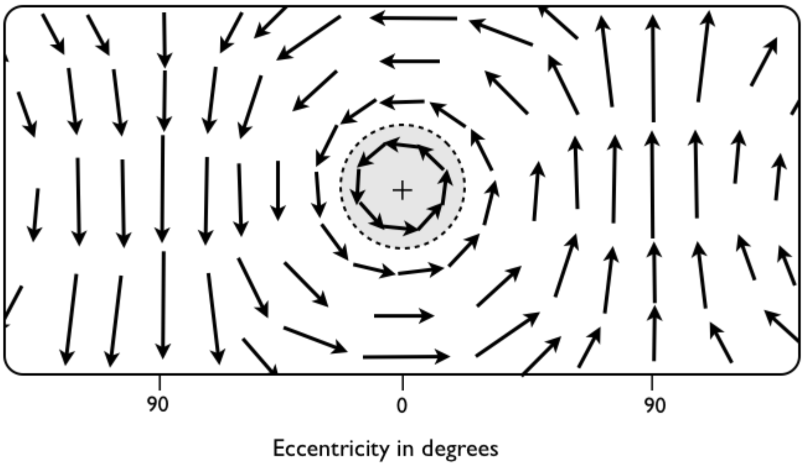

Figure 44 – Flow structure for CW observer rotation about the line of sight. Flow is in the opposite direction to self-rotation (ACW). Up to 90 degrees eccentricity, the magnitude of flow vectors increase with retinal eccentricity.

Roll about the line of sight produces a rotary pattern in central vision and more lamellar-type flow moving in opposite directions in peripheral vision. Instantaneous curvilinear motion vectors near the centre of rotation are small and increase with retinal eccentricity. Thus, retinal speed increases with eccentricity. Central and peripheral retinal regions are exposed to different flow structures and the direction and magnitude of flow vectors varies depending on the location within the visual field, with the direction of flow in opposite directions in the two peripheral extremes. These geometric differences mean that the contribution of peripheral vision to flow parsing may not be equivalent to the central visual component because the visual information received by each retinal region is not the same. In the centre of vision, the AOR is specified, making it a simple task to identify self-movement from central flow. In peripheral vision, it is the combination of peripheral flow which indicates self-movement and in the case of roll flow, the presence of lamellar flow in opposing directions specifies rolling self-movement. Peripheral flow may be particularly important when rotation speed is slow, because motion vectors in central vision will be of a lower magnitude. In this case, the larger motion vectors in peripheral vision would still be likely to provide a more robust cue to self-movement. These geometric differences are in accordance with the speed preferences of motion sensitivity cells in V1 in with cells that receive input from peripheral vision showing a preference for faster velocities than cells with receptive fields in central vision (Orban et al., 1986). The increase in velocity preference with increasing retinal eccentricity suggests that peripheral vision is capable of identifying high velocity peripheral motion and, especially when central information about self-movement is limited, this sensitivity would provide a useful input to flow parsing. This analysis of flow structure across the retina leads to the hypothesis that peripheral flow is likely to contribute the identification and parsing of roll self-motion components from the retinal image as part of a global parsing process.

3.2.3 Roll flow parsing

The FPH suggests optic flow patterns that are characteristic of self-movement can be identified and globally subtracted from retinal motion. This subtraction process is depicted for roll self-motion in Figure 45. Simultaneous CW observer roll rotation and upward object trajectory is depicted in Figure 45A.

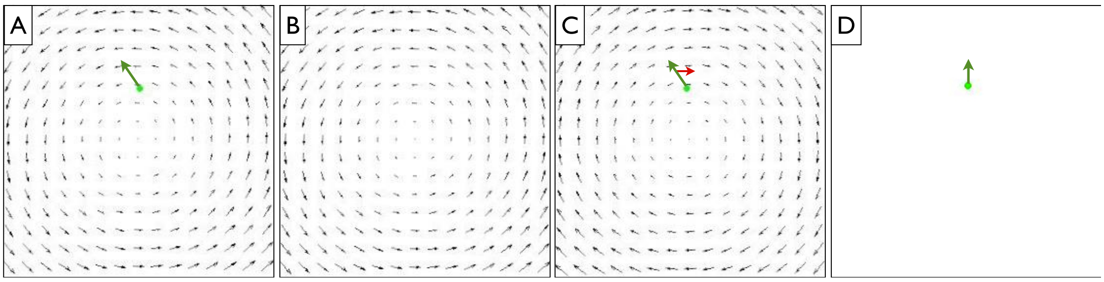

Figure 45 – Flow parsing Hypothesis (Rushton & Warren, 2005). A) Instantaneous retinal motion of a vertically moving probe viewed during CW roll of the observer (ACW flow field). B) Brain identifies self-motion components. C) Self-motion components are subtracted/parsed from the scene (equivalent to adding a CW flow field. D) Any remaining motion is attributed to object movement within the scene.

The global self-motion component is shown in Figure 45B, and in this instance is rotational about the line of sight. A CW rotation of the observer produces a flow field that rotates in the opposite direction; in this case an ACW flow field. The CW flow is identified and then globally subtracted from the retinal image, which is equivalent to adding a CW flow field (Figure 45C). In Figure 45D the resulting percept is shown; any remaining motion is attributed to object movement relative to the scene. Consequently, in this example, the object trajectory differs between Figure 45A and 45D; the latter trajectory is vertical as opposed to the oblique trajectory found in the retinal image. If there is a peripheral contribution to flow parsing during roll self-movement then this process should also occur when flow is presented in peripheral vision.

Previously, an exploratory study reported evidence of parsing rotational flow in central vision (Warren & Balcombe, 2010). Warren and Balcombe simulated rolling self-movement at 60 degrees/s with either a full flow field or two quadrants on the left and right of fixation (see Figure 46).

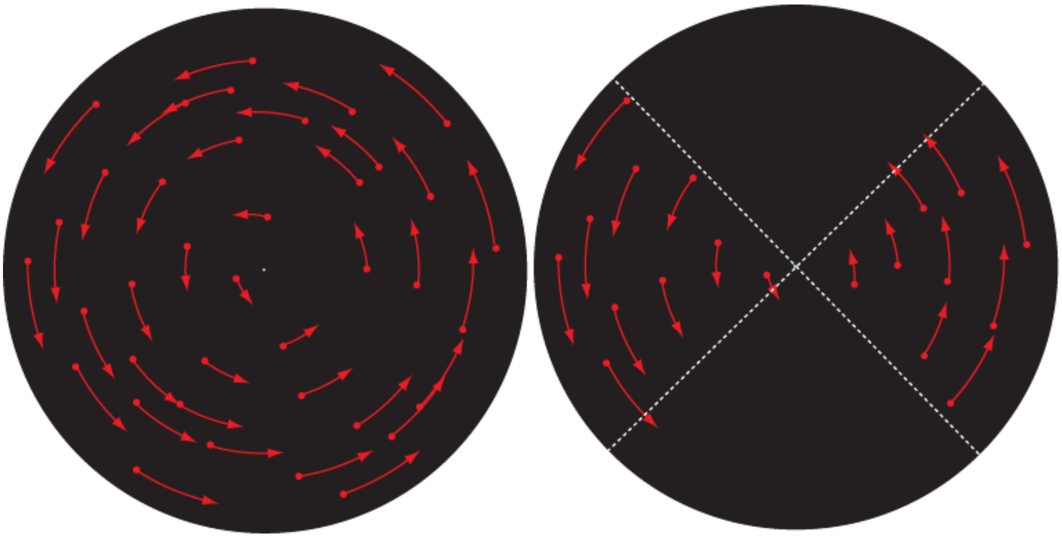

Figure 46 - Flow stimuli used by Warren and Balcombe (2010). Left - Full field. Right - Quadrants.

They asked observers to report the perceived trajectory of a target either ±2 or ±4 degrees above/below a central fixation point. They hypothesised that target trajectory would be biased in the direction opposite the flow such that CW flow (ACW observer rotation) produced an ACW trajectory bias and vice versa. In line with the general expectation that object trajectory depends on the location of the object in the scene, they also expected to find a larger trajectory bias when the target was presented further from fixation (4 degrees) than when it was less eccentric (2 degrees). This is because during roll movement the magnitude of motion vectors increase with retinal eccentricity and therefore targets nearer to the centre will have less flow subtracted from them than targets that are positioned further from fixation. Thus, if flow parsing occurs then the trajectory bias should be larger for more eccentric targets. Warren and Balcombe (2010) found that the presence of rolling flow biased perceived target trajectory between 8-15 degrees, indicative of a global subtraction of self-motion. They also demonstrated a target eccentricity effect, with participants showing a significantly larger trajectory bias when the target was located 4 degrees from fixation rather than 2 degrees from fixation. In addition, a comparison between the full flow field condition and the quadrants condition showed that local motion accounted for approximately 30% of the effect see in the full flow condition. This evidence suggests that it is possible for observers to parse roll flow from the retinal image. Warren and Balcombe's results indicate that this parsing process involves global motion processing because visual flow indicating self-movement in one portion of the visual field leads to a component of motion being subtracted from the target in another part of the visual field. This finding suggests that when flow is presented in peripheral vision this will also drive a global parsing process that can be measured as a bias in perceived target trajectory in central vision.

3.2.4 Radial versus roll flow parsing

Rolling self-movement produces a distinctively different flow structure to linear self-movement, which was considered in the previous chapter (Figure 17A and 17B, Page 41, permits a comparison). The literature on self-motion perception has suggested that peripheral vision may not be equally sensitive to all flow structures. Thus, the results of this chapter may shed some light on whether the peripheral contribution to flow parsing varies depending on the type of self-movement.

In summary, during roll there are clear differences in the flow structure as a function of retinal eccentricity. Peripheral sensitivity to lamellar flow and the global nature of the flow parsing process suggest that roll flow in peripheral vision might provide a useful source of information about self-movement which could feed into flow parsing mechanisms. The results of Chapter 2 and Warren and Balcombe's study have demonstrated in isolation that peripheral vision contributes to flow parsing for translation and that roll flow parsing occurs in central vision. In the present chapter I report the results of a formal test of whether roll flow in peripheral vision contributes to flow parsing and the contribution of different parts of the peripheral retina.

In this chapter, I report a series of four experiments. Experiment 2.1 investigates whether peripheral vision contributes to flow parsing for rolling self-movement. The results suggest peripheral flow does feed into flow parsing mechanisms and as for radial flow the contribution of near peripheral flow is greater than far peripheral flow. A set of control experiments are then described which verify that these findings are the result of a flow parsing mechanism by looking for signature flow parsing effects with the same peripheral stimuli. In these experiments I manipulated flow speed and target eccentricity to probe whether a characteristic pattern of results in line with a peripheral contribution to parsing was observed. Namely, these control studies investigate if there is a peripheral contribution to the target eccentricity effect (Experiment 2.2) that was reported by Warren and Balcombe (2010), and whether the magnitude of relative tilt increases with increasing speed of peripheral flow (Experiment 2.3a and 2.3b). The data provides evidence for both of these effects, corroborating the peripheral contribution to flow parsing that was identified in Experiment 2.1.

3.3 Experiment 2.1: Contribution of the Near and Far periphery to roll flow parsing

The design of this experiment closely follows Experiment 1.2 in the previous chapter. Near and Far peripheral areas (defined in the General Introduction, see Page 39) were used to investigate whether peripheral roll flow influences perceived object trajectory.

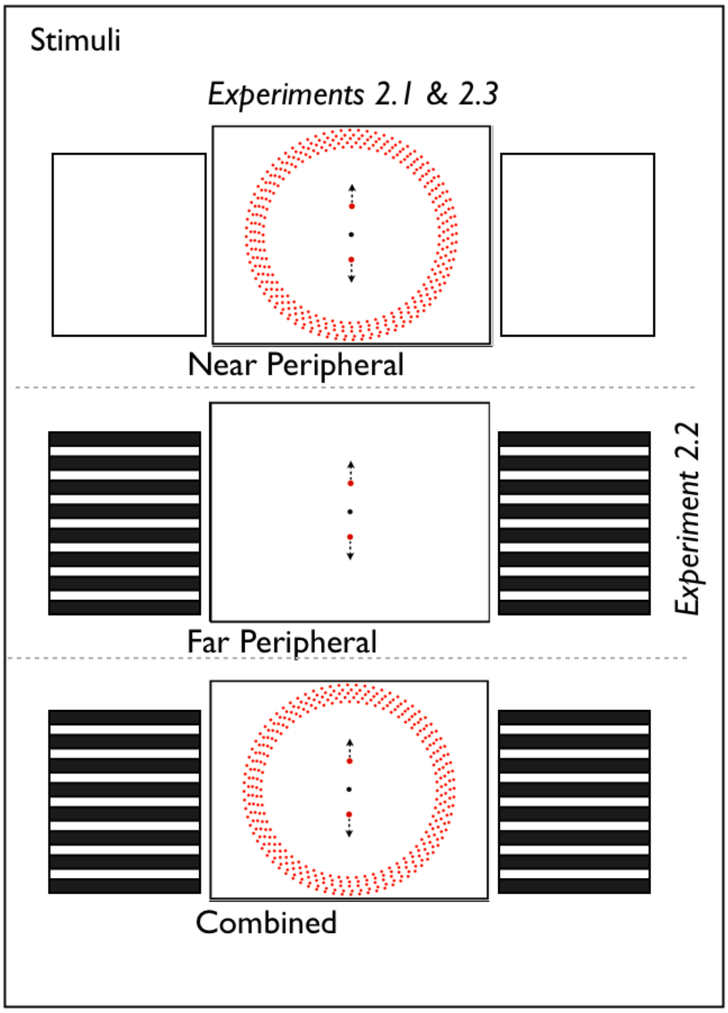

Figure 47 - Stimuli used in roll experiments. All stimuli were coloured red and presented on a black background. Experiments 2.1, 2.3a and 2.3b used the central projection screen and peripheral monitors to display the Near, Far, and Combined stimuli. Experiment 2.2 used only the Far peripheral stimulus and varied the eccentricity of the central target.

Rolling self-motion was simulated about the line of sight by presenting optic flow in the Near periphery, Far periphery, or both (Combined condition). These three peripheral flow conditions were used in the previous chapter but the specific arrangement of the stimuli differed in this experiment. Figure 47 shows the stimuli used in this chapter.

In the present experiment, a peripheral contribution to flow parsing would be evidenced by a bias in perceived target trajectory in the opposite direction to the flow (i.e. target trajectory will have an additional CW component due to global parsing of ACW flow) in all three peripheral conditions. Figure 48 illustrates the predicted flow parsing process, with peripheral flow leading to a bias in perceived target trajectory.

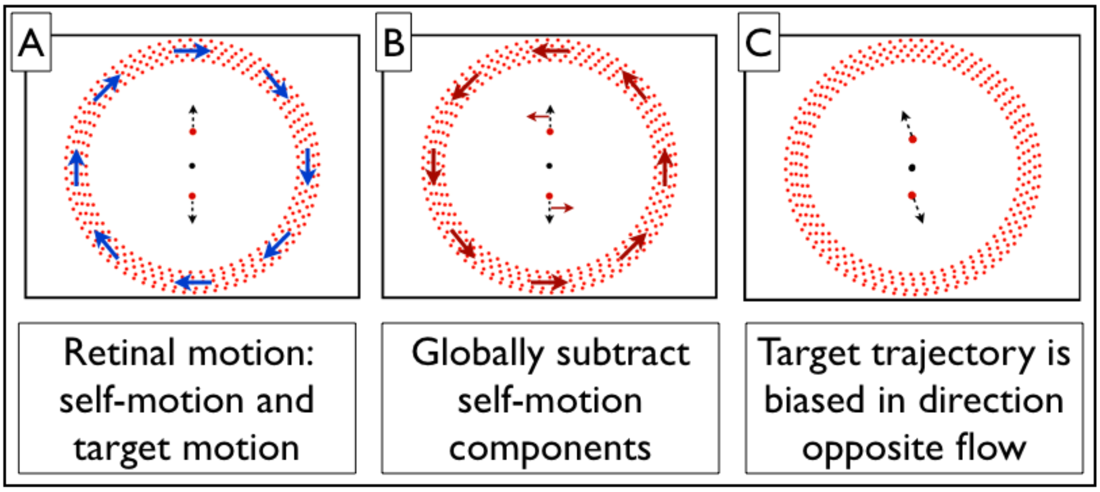

Figure 48 - Predictions for a peripheral contribution to roll flow parsing. A) ACW rotation of the observer is simulated, producing a CW flow field within which a target is presented either above or below fixation and moved vertically. B) In accordance with flow parsing, this flow field is globally subtracted from the scene including the target motion. The instantaneous induced motion of the target is depicted. C) Resultant perceived target trajectories, which are biased away from vertical in the direction opposite the flow; ACW for targets both above and below fixation.

The pattern of results expected if there is a peripheral contribution to flow parsing for roll self-movement is shown in Figure 49.

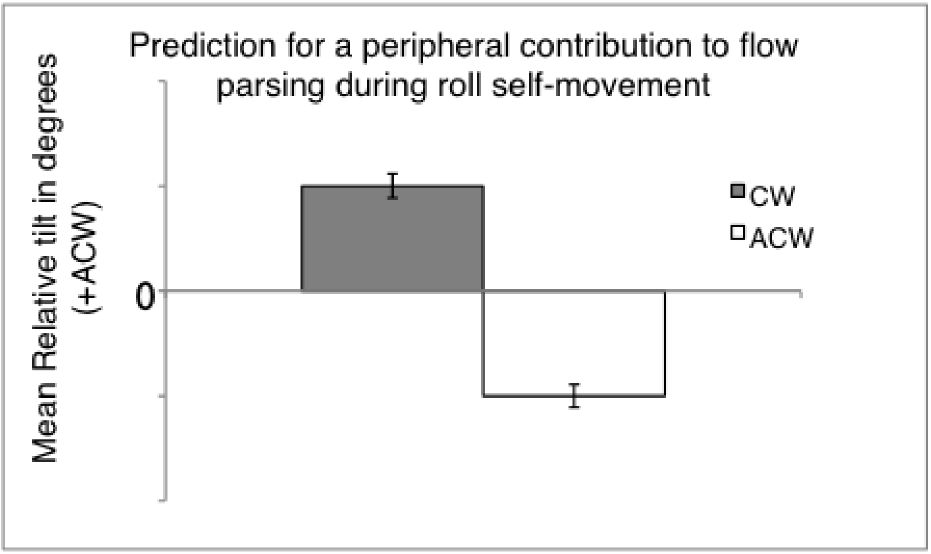

Figure 49 – A) Predictions of the influence of peripheral flow on mean relative tilt for Experiment 2.1 for all peripheral conditions (Near/Far/Combined); perceived target trajectory (as measured by relative tilt) is biased in the opposite direction to the flow. The relative tilt in degrees for -4 and +4 target eccentricities are compiled to present a single value for each flow condition (CW and ACW).

If peripheral vision makes a similar contribution during rotation as it does during translation then rolling flow in the near periphery would generate a larger trajectory bias than far peripheral flow. As in Chapter 2, regression analyses were performed to assess the contribution of near and far peripheral flow to the flow parsing effect observed in the Combined condition.

3.3.1 Methods

3.3.1.1 Participants.

Ten female undergraduate students from the School of Psychology, Cardiff University took part and received course credit. All participants were naïve as to the experimental hypotheses and had normal or corrected-to-normal vision. Eligibility criteria and ethical procedures were identical to those reported in Experiment 1.1.

3.3.1.2 Apparatus.

The apparatus was identical to Experiment 1.2, reported in Chapter 2.

3.3.1.3 Stimuli.

The large central projection screen presented the near peripheral flow, fixation point and target, and two portrait-orientated monitors to the side of the head presented the far peripheral flow. These stimuli were both used in isolation (Near and Far conditions) as well as together in a third Combined condition (See Figure 47).

The Near flow stimulus was generated in the same way as in Experiment 1.2. The Far peripheral stimulus consisted of 36 solid red cylinders positioned horizontally and parallel to the line of sight arranged on a cylinder surrounding the observer's head (Figure 50). The cylinders were placed at a distance of 50 cm[5] at 10 degree intervals around the zenith.

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[5] The virtual distance of the Far stimulus was inconsequential, because no depth cues were present in the stimulus and the visual consequences of observer rotation are independent of depth. The same stimulus at a different distance would have moved at the same rate with respect to the eye.

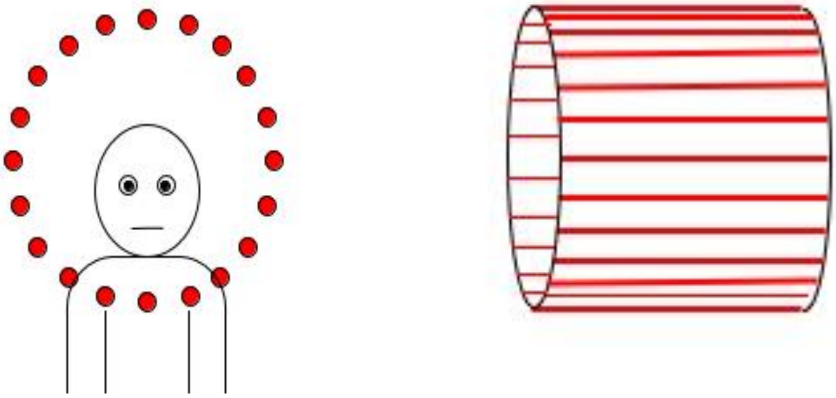

Figure 50 - Depiction of the far peripheral stimuli used in Experiments 2.1-2.3 - a series of cylinders surrounded the observer at a fixed distance. The centre of rotation was approximately at eye level.

Each cylinder had a diameter of 2 cm and a length of 60 cm (twice the width of the monitor in a portrait orientation). When displayed on the monitors, the cylinders appeared as horizontal bars with a width of 0.6 cm in the centre of the display, with a length that subtended the width of the monitor. Due to perspective projection, the bars towards the upper and lower edges of both monitors were slightly wider.

In all conditions the rotation speed of the peripheral flow was 60 degrees/s following the precedent of Warren and Balcombe (2010) who had reported consistent relative tilts in central vision, suggesting that this was an appropriate speed at which to investigate roll flow parsing and would allow the magnitude of relative tilt with peripheral flow to be compared against Warren and Balcombe’s results with central flow. Pretesting revealed that this speed did not cause observers to experience persistent vection (such that would cause them to feel nauseous and potentially withdraw from the study) and that it was still possible to visually distinguish the individual peripheral bars as they rotated.

The target was a small circular dot presented at ±4 degrees from fixation (above or below) and moved away from fixation in a mostly vertical trajectory at a rate of 1 cm/s (0.6 degrees/s).

3.3.1.4 Design.

The independent variables manipulated in this experiment were Target location (2 levels: Above/Below fixation), flow direction (2 levels: CW/ACW) and Peripheral condition (3 levels: Near/Far/Combined).

As in the previous chapter, to avoid potential response biases, rather than repeatedly presenting the same target trajectory, the trajectory of the target was varied within a range about vertical. The trajectory range was chosen so that participants would be unable to deduce the onscreen trajectory of the target on any given trial. In this experiment, the trajectory of the target was selected from a range of 9 possible trajectories that was each used once (± 32 degrees relative to vertical in 8 degree steps). For each of the four experimental conditions, each of the nine tilt trajectories was repeated twice. The three peripheral conditions (Near/Far/Combined) were conducted in separate experimental blocks of 72 randomly ordered trials.

The dependent measure was the mean relative tilt for the above and below target locations: the difference between the onscreen target trajectory and the angle reported by the observer, measured in degrees. A within-subjects design was used and the order of the peripheral conditions was counterbalanced across observers. Each participant completed the data collection in a single experimental session.

3.3.1.5 Procedure.

The procedure was identical to Experiment 1.2, with the observer seated in a dark room with the head in a chin rest, 95 cm from the centre of the projection screen.

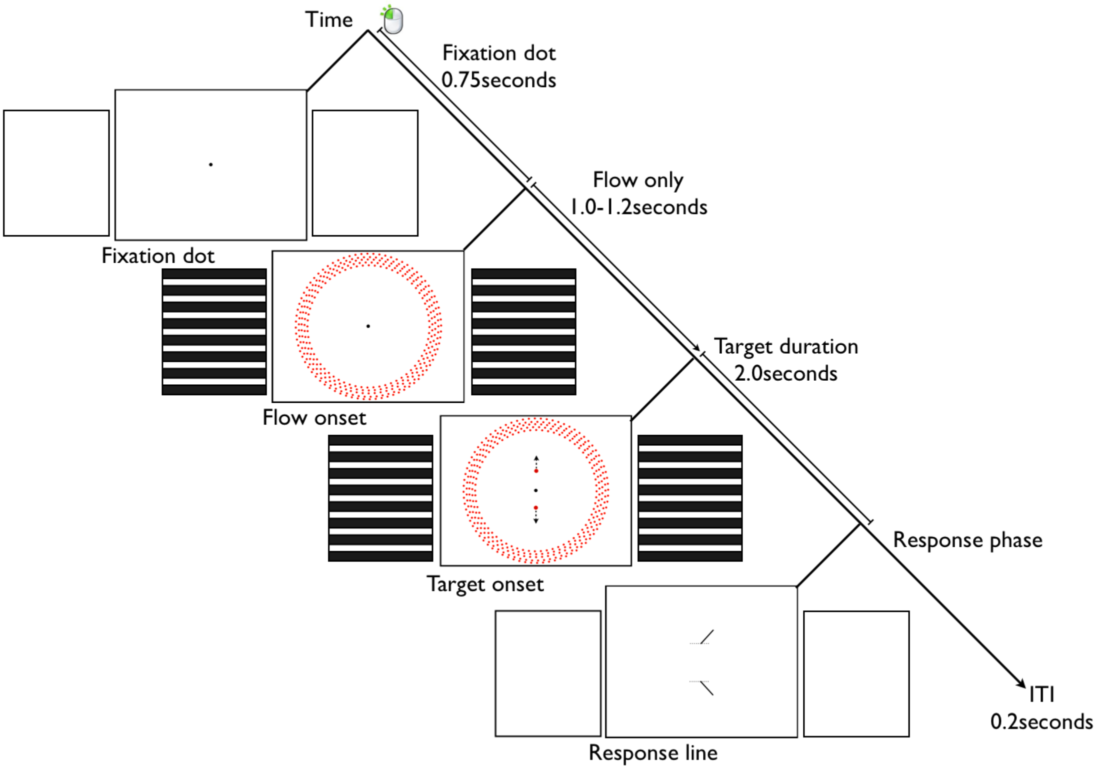

Figure 51 - Procedure timeline for Experiment 2.1, showing Combined peripheral condition.

Participants were instructed to maintain fixation on a small dot located at the centre of the screen throughout each trial and to watch for the presentation of the target either above or below fixation. Figure 51 depicts the trial procedure. Participants received a short break between each peripheral condition.

3.3.1.6 Analysis.

In order to equate vertical target trajectories with non-vertical trajectories a simple transformation was employed for Experiments 2.1, 2.2, 2.3a and 2.3b. This method has previously been adopted in flow parsing studies (i.e. Warren & Rushton, 2007) and is principally the same as the transformation used in Chapter 2 except that targets moved vertically in the roll studies rather than horizontally as they did in the radial studies. For all the experiments in this chapter, observer responses are coded as an angular measure θ_i. This quantity is a measure of the illusory or the "induced" horizontal component of target motion perceived by observers, which is converted back to an angular quantity (see Appendix A). In the results that follow, θ_i is referred to as the relative tilt. As no differences were expected, or found, between the Above and Below target locations the responses were recoded as if all targets were presented above fixation.

As in the previous chapter, to present appropriate within-subject error bars in figures the data was normalised according to the method described in Cousineau (2005; for full details see Appendix A). Using the adjusted dataset, the standard error was calculated for each condition.

If peripheral flow contributes to parsing during roll then the presence of CW flow would lead to a global subtraction, equivalent to adding an ACW flow field, and ACW flow would lead to a global subtraction of ACW flow, equivalent to adding a CW flow field. In terms of perceived target trajectory this would result in a CW bias in the presence of ACW flow and an ACW bias when CW flow was present. Thus, the perceived trajectory of the target would be biased in opposite directions during the two flow conditions. For the DV, this would be evidenced by a difference in relative tilt between the CW and ACW flow directions, with CW flow generating ACW relative tilt and ACW flow producing CW tilt.

As well as the predicted difference in relative tilt as a function of flow direction, the magnitude of relative tilt was predicted to vary between the three peripheral flow conditions (Near/Far/Combined). The radial flow findings (Chapter 2) showed that the far peripheral made a smaller contribution to parsing than the near periphery. If the same holds true for roll self-movement then the magnitude of relative tilt observed in the Far Peripheral condition would be less than in the Near and Combined flow conditions.

To test whether these two differences were present in the data, a 3 (Near/Far/Combined) x 2 (CW/ACW flow direction) within-subjects ANOVA was conducted. An interaction was predicted between peripheral flow condition and flow direction. Posthoc analyses were employed to investigate any significant interaction.

As for Experiment 1.2, additional analysis was conducted to investigate whether the magnitude of the data in the Combined condition could be predicted from the Near and Far data. Three linear regression analyses were conducted to assess for how well three models predicted the relative tilt data observed in the Combined condition. The three models, as in Chapter 2, were:

Model 1: Near + Far (linear sum)

Model 2: Near

Model 3: Far

Where both the individual peripheral conditions (Models 2 and 3) and the linear sum (Model 1) both significantly predicted the data, a chi-squared difference test was employed to compare their predictive ability.

3.3.2 Results and discussion

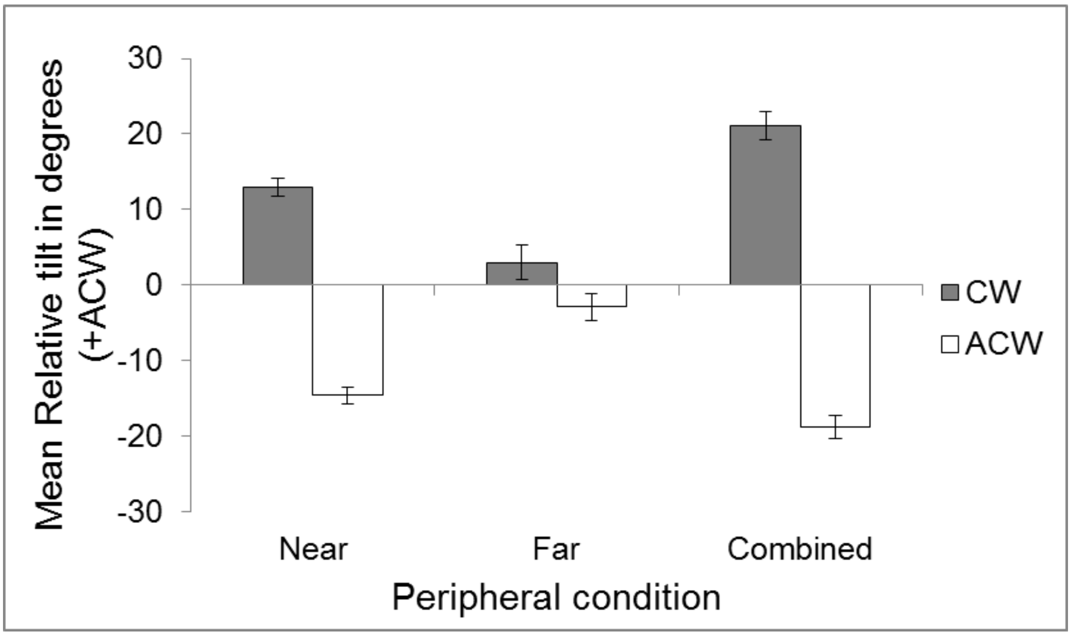

Figure 52 - Mean relative tilt as a function of peripheral condition and flow direction. Error bars show within subject standard error (SE).

Figure 52 shows that for all three peripheral conditions the expected pattern of results was observed; relative tilt is observed in the direction opposite the flow; ACW tilts for CW flow direction, and CW tilts for ACW flow. The magnitude of relative tilt also varied between the peripheral conditions, with larger relative tilts reported in the Near and Combined peripheral conditions than in the Far peripheral condition. A one sample t-test confirmed that the Far data was significantly different from zero in both the CW (t (9) = 3.805, p = 0.004) and ACW conditions (t (9) = -4.086, *p* = 0.003). A 3 x 2 within-subjects ANOVA confirmed that there was an interaction between peripheral flow condition (Near/Far/Combined) and flow direction (CW/CCW) (*F* (2, 18) = 18.579, *p* <0.001). There were also main effects of flow direction (*F* (1, 9) = 30.574, *p* < 0.001) and peripheral flow condition (*F* (1.205, 10.845) = 4.831, *p* = 0.045, *Greenhouse-Geisser adjusted*). As flow direction significantly affected perceived target trajectory in all conditions, a pattern of results that are a signature of flow parsing, this indicates that visual flow in the near and far periphery both contribute to flow parsing.

Figure 52 indicates that the difference in relative tilt between the CW and CCW conditions is greatest for the Combined condition and smallest for the Far condition. Posthoc analysis using the difference in relative tilt as the DV, confirmed that there were differences between the Near and Far conditions (*t* (9) = 3.966, *p* = 0.010), the Near and Combined conditions (*t* (9) = -3.007, *p* = 0.044) and the Far and Combined conditions (*t* (9) = -4.856, *p* = 0.003). Thus, perceived target trajectory varied as both a function of peripheral flow direction (or the direction of simulated self-movement) and the eccentricity of the peripheral flow.

The different perceived trajectory directions observed for the CW and ACW conditions are in accordance with a peripheral contribution to flow parsing and suggest that near and far peripheral regions both feed into flow parsing mechanisms alongside the processes already identified in central vision. The pattern of results for the Near, Far and Combined peripheral conditions are remarkably similar to those observed with peripheral radial flow (Chapter 2). As for radial flow, the near periphery makes a larger contribution to flow parsing than the far periphery.

Linear regression analyses were conducted to assess the ability of three models (Near, Far, or Near+Far) to predict the data in the Combined condition. The linear sum of the Near and Far conditions (Model 1) significantly predicted the Combined data (β = 1.118) and accounted for 91% of the variance in the Combined peripheral condition (Figure 53; R^2 = .905, *F* (1, 18) = 172.299, *p* < 0.001). The Near model also significantly predicted the data (Figure 54; β = 1.341, R^2 = .911, *F* (1, 18) = 185.347, *p* < 0.001) and so did the Far model (Figure 55; β = 3.814, R^2 = .497, *F* (1, 18) = 17.751, *p* = 0.001). Comparing the R^2 values of these three models, it is clear that the Near and Near+Far models account for a greater proportion of the variance than the Far model. Consideration of Figure 55 suggests that the far peripheral flow is making a limited contribution to the relative tilt observed in the Combined condition. Furthermore, the high gain does not make sense as it would suggest the visual system is adding to the effect in the far periphery to arrive at a larger relative tilt in the Combined condition.

A chi-square difference test between both the Near and Near+Far model (χ^2 (1) = 1.48, $p = 0.224$) showed that the fit of the Near model to the data was not significantly worse than the fit obtained with the Near+Far model. The same test between the Far and Near+Far model (χ^2 (1) = 73.30, $p < 0.01$) confirmed that the Far model was a significantly worse fit to the data than the Near+Far model, as suggested by the R^2 values. Thus, the Near model, with only one predictor variable provides a more parsimonious account of the data in the Combined condition than the Near+Far model, and the Near model is also a better fit to the data than the Far model. Overall, the results of the regression analyses suggest that the relative tilt in the Combined condition is best predicted by the relative tilt measured in the Near condition.

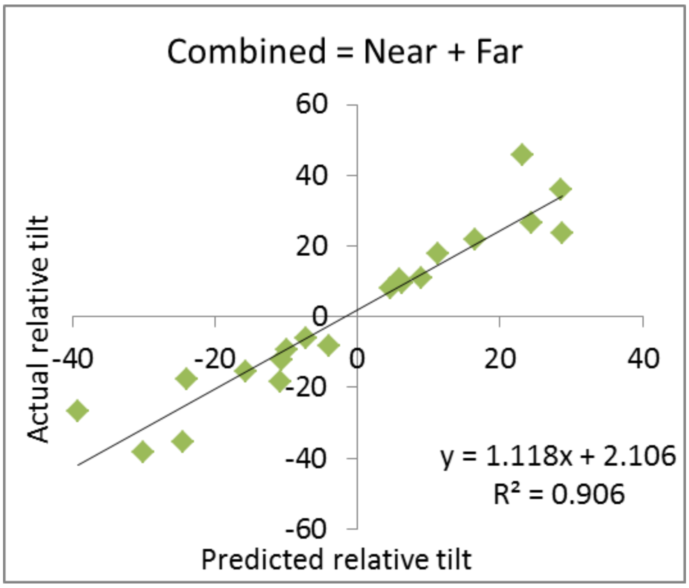

Figure 53 - Actual Combined relative tilt as a function of Predicted relative tilt Near + Far model.

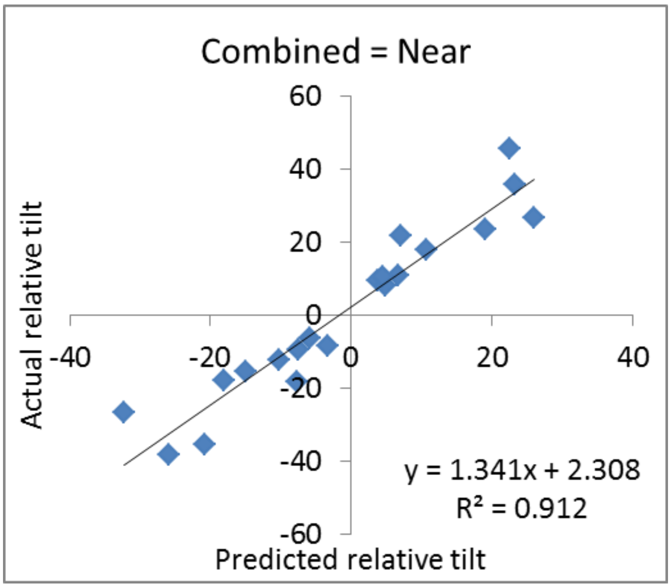

Figure 54 - Actual Combined relative tilt as a function of Predicted relative tilt Near model.

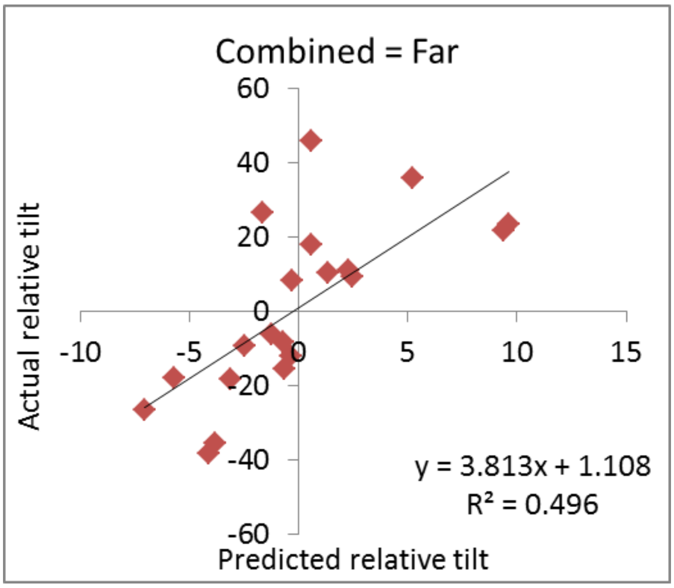

Figure 55 - Actual Combined relative tilt as a function of Predicted relative tilt for Far model.

Overall these results illustrate that peripheral vision makes a contribution to flow parsing during observer roll. However, in line with the results for linear self-movement, the near periphery makes a greater contribution than the far periphery. In order to establish whether these findings are the product of a flow parsing process, I conducted a series of control experiments to further probe the relationship between peripheral flow and relative tilt. The control experiments that follow all sought to provide evidence that the results of this experiment were the product of a peripheral contribution to flow parsing. To this end, I investigated whether other signature flow parsing effects could also be produced by peripheral flow specifying rolling self-movement. In the following experiments, I manipulated the object and flow parameters to test for a characteristic pattern of effects predicted by the FPH and to help confirm that these results are due to flow parsing.

3.4 Experiment 2.2: Effect of Target Eccentricity

The previous experiment reported evidence that peripheral vision contributes to flow parsing during roll self-movement. However, to further verify that these results demonstrate a peripheral contribution to flow parsing this experiment looked for another signature of a peripheral contribution to flow parsing; an effect of target eccentricity. Recall from the General Introduction a key principle of the FPH: the perceived trajectory depends upon the optic flow components and the location of the object. Thus, if the results of Experiment 2.1 are due to flow parsing then modifying either the flow components or the target location should produce predictable changes in relative tilt. This experiment manipulates target location and the later experiments in this chapter manipulate the flow itself.

During rolling self-movement, the FPH predicts that the magnitude of relative tilt will increase with increasing target eccentricity because the components to be parsed from the retinal image are greater further from fixation. Therefore, global subtraction should result in a larger trajectory bias in the opposite direction when targets are more eccentric. The target eccentricity effect has been demonstrated in central vision with radial flow (Warren & Rushton, 2008) and using roll flow in the preliminary study by Warren and Balcombe (2010).

If the findings of Experiment 2.1 are the result of this process then it should also be possible able to demonstrate that trajectory bias increases in line with increasing target eccentricity (as in Figure 56). In all the earlier experiments of this thesis, smaller effects have been observed in the Far peripheral flow conditions than the Near peripheral flow conditions. Thus, in this study, only the far peripheral condition is used as this provides a more stringent test of the target eccentricity effect. Presenting flow in the far periphery also reduces any potential influence of local motion contrast due to the spatial separation between the central target and far peripheral displays. Finding an effect of target location with a Far peripheral stimulus would suggest that the results of the previous experiment represent a peripheral contribution to a flow parsing effect.

Rolling flow was presented in the far periphery and a target was simultaneously presented at either 2 degrees or 4 degrees eccentricity from fixation. It was anticipated that the magnitude of relative tilt would be greater for more eccentric targets (4 degrees) than those closer to fixation (2 degrees).

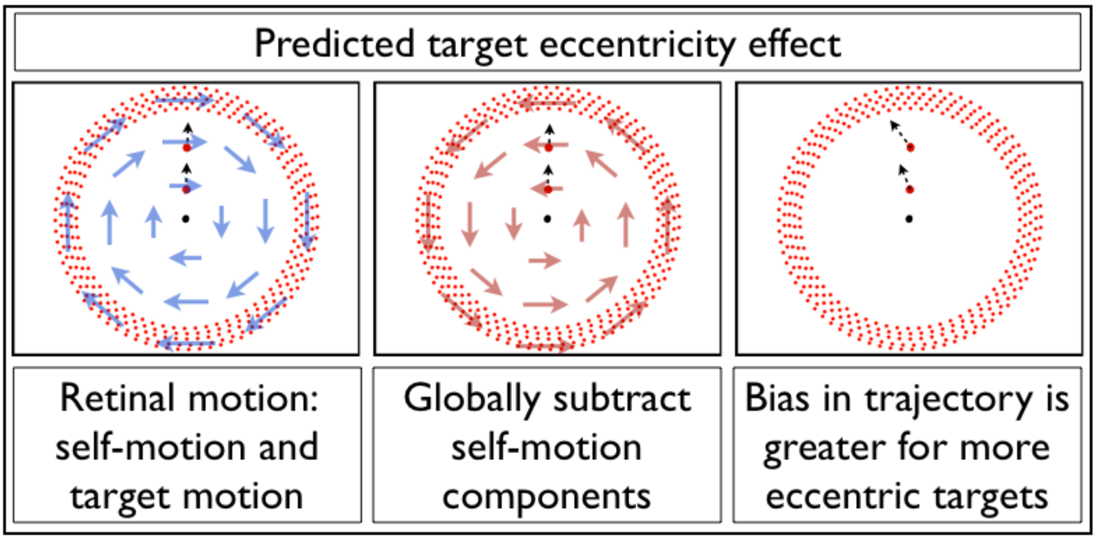

Figure 56 – Predicted target eccentricity effect for Experiment 2.2. As the magnitude of self-motion vectors increases with retinal eccentricity, targets that are presented further from fixation are subject to a greater subtraction during flow parsing than those closer to fixation. The right hand panel shows how this process affects perceived target trajectory. Only above fixation targets are shown in this figure, but the same pattern was predicted for targets below fixation.

3.4.1 Methods

3.4.1.1 Participants.

Ten postgraduate students (7 male) took part in the study. The age range of the sample was 24 to 46 years. All participants except the author (CR) were naïve as to the experimental hypotheses and were subject to the same restrictions and ethical procedures as Experiment 1.1. Participants received payment at a rate of £10/hour.

3.4.1.2 Apparatus and stimuli.

The apparatus was identical to Experiment 1.2 and the Near peripheral flow stimulus was identical to Experiment 2.1.

Far peripheral stimuli:

Computer generated stimuli were presented in far periphery vision and consisted of Long horizontal cylinders with a diameter of 1 cm and length of 60 cm were positioned 51 cm from the observer on the circumference of a drum orientated along the line of sight (Figure 50). The cylinders were spaced 1.2 degrees apart, were long enough to fill the height of the monitor so that the ends of the cylinders were not visible, and had an onscreen width of 1 cm.

The target was a red circle with an onscreen diameter of approximately 0.5 cm was positioned at an eccentricity of either 2 degrees (3.32 cm) or 4 degrees (6.64 cm) above or below fixation. The target moved at a rate of 0.72 degrees/s (1.2 cm/s), which was slightly faster than the previous experiment, as pretesting showed that at the slower speed the movement of the target was less salient and participants found it hard to judge the trajectory. Target trajectory was manipulated as in Experiment 2.1.

3.4.1.3 Design.

Three IVs were manipulated: Target location (Above/Below), flow direction (CW/ACW) and target eccentricity (2 degrees/4 degrees). For each of these conditions there were 9 target trajectories resulting in a total of 72 trials per run. The dependent measure was mean relative tilt in degrees, averaged across above and below target locations. As before, a within-subjects design was employed. Participants completed one set of data each and all data collection was completed in a single experimental session.

3.4.1.4 Procedure.

The procedure was identical to Experiment 2.1.

3.4.1.5 Analysis.

As in Experiment 2.1, the raw data was transformed to equate vertical and non-vertical target trajectories and responses were recoded as if all targets were presented above fixation. To ascertain whether relative tilt increased as a function of target eccentricity a t-test was conducted using the difference between the CW and ACW relative tilt as the DV. This test sought to confirm a significant difference in relative tilt between the 2 degree and 4 degree target eccentricities, with relative tilt being larger in the latter condition. A t-test was also conducted to confirm there was a significant difference between CW and ACW flow locations, averaging across target eccentricity, with more positive relative tilt in the CW condition and negative tilt in the ACW condition. As a directional effect was predicted for target eccentricity and flow direction, probability values from the t-tests were adjusted (P ÷ 2) in line with a one-tailed hypothesis (Wuensch, 2006). A larger relative tilt for targets positioned at 2 degrees than 4 degrees would indicate a far peripheral contribution to flow parsing, as demonstrated in Experiment 2.1. Furthermore, an increase in relative tilt as a function of target eccentricity would support the assertion that these results are due to flow parsing.

3.4.2 Results and discussion

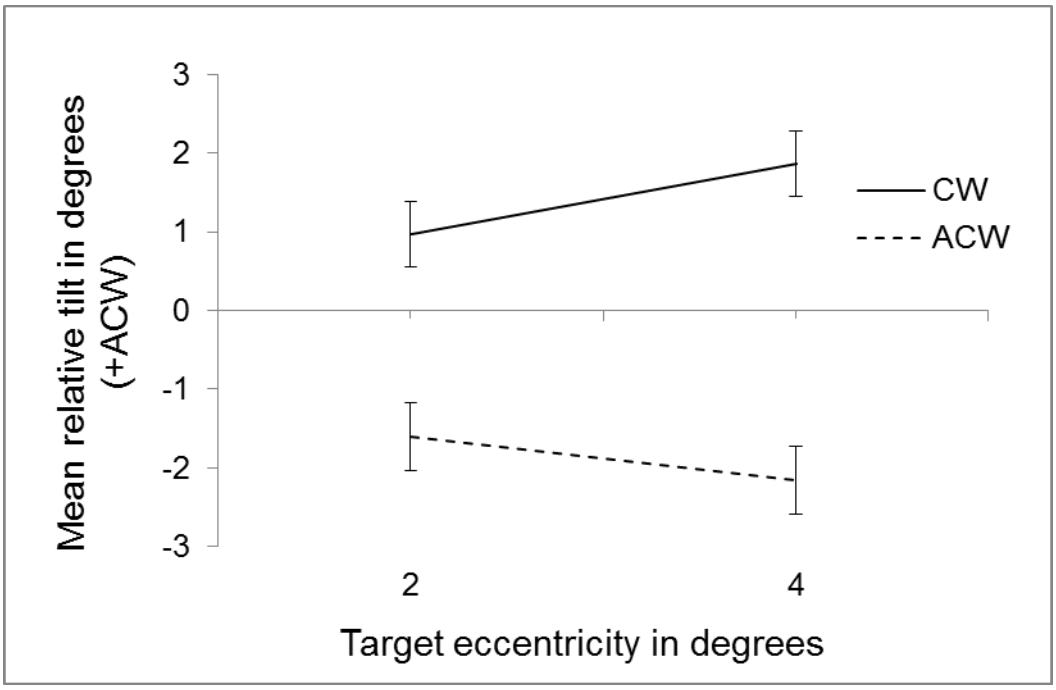

Figure 57 - Mean relative tilt as a function of target eccentricity. Error bars show within subject SE.

Relative tilt differed between CW and ACW flow direction, with mean relative tilt being positive when CW flow was presented and negative when ACW flow was presented (Figure 57). This difference was in the expected direction and a paired t-test confirmed that relative tilt was statistically different between the CW and ACW conditions for targets located at 2 degrees (*t* (9) = 2.804, *p* = 0.021) and 4 degrees (*t* (9) = 2.933, *p* = 0.017).

Figure 57 also suggests a difference in relative tilt as a function of target eccentricity, with the magnitude of relative tilt being larger for targets located 4 degrees from fixation than 2 degrees. A one-tailed paired t-test on the difference between the CW and ACW data at each eccentricity confirmed that this difference was statistically significant (*t* (9) = 1.950, *p* = 0.042). This data implies a peripheral contribution to the target eccentricity effect that has been shown in previous research (Warren & Balcombe, 2010 and Warren & Rushton, 2009a). Additionally, the key finding from the Far flow condition from Experiment 2.1 was replicated, as visual flow in the far periphery produced a signature flow parsing effect in both conditions in the present experiment.

The target eccentricity effect seen in this experiment was slightly smaller than the effect reported by Warren and Balcombe (2010) but due to differences in the stimuli between these studies a direct comparison is not appropriate. However, this difference may in part be due to the larger spatial separation between the flow and the target in the present study. Furthermore, from Experiment 2.1 it was clear that the Far peripheral flow produced weaker flow parsing effects than the Near flow. Therefore demonstrating the effect with only far peripheral flow suggests that it exists regardless of where flow is located in the visual field and is therefore a robust feature of flow parsing.

This experiment supports the results of the previous experiment in two ways. Firstly, the existence of a target eccentricity effect corroborates the results of Experiment 2.1 which showed a peripheral contribution to roll flow parsing and suggests that these results are the product of a peripheral input to a flow parsing mechanism. Secondly, the contribution of the far periphery to flow parsing for roll self-movement was replicated in a new group of participants. Experiment 2.3 aims to further substantiate the findings of Experiment 2.1 using roll flow by varying the speed of the simulated self-rotation.

3.5 Experiment 2.3a: Effect of peripheral flow speed

In this study, I investigated whether peripheral flow produced another key flow parsing signature; a dependence on flow speed. The near and far peripheral stimuli from Experiment 2.1 were employed to investigate whether different flow speeds give rise to any differences in perceived target trajectory. The target location was held constant and roll speed was manipulated. If peripheral vision contributes to flow parsing (as in Experiment 2.1) then in the present study faster self-motion will lead to a greater self-motion component that must be parsed from the scene. In terms of simulated self-motion, this would be evidenced by a larger bias in target trajectory in the opposite direction to the flow (as in Figure 58).

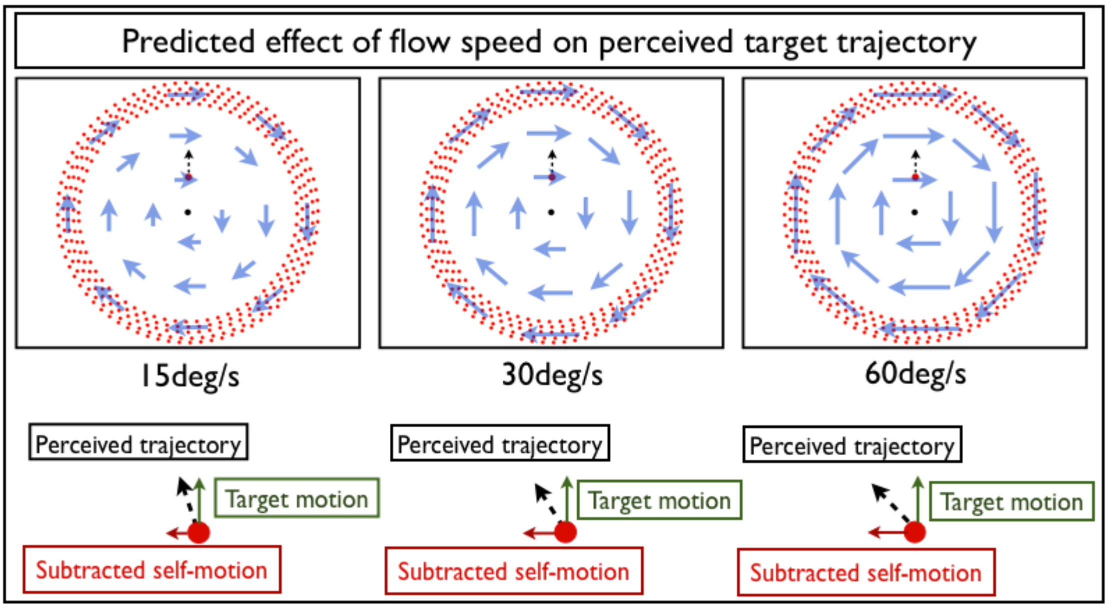

Figure 58- Predicted speed effect in Experiment 2.3a. As flow speed the magnitude of the self-motion vectors in the retinal image increase. When these self-motion components are parsed from the retinal image the amount to be subtracted from the target motion is proportional to the flow speed. If the target itself moves by the same amount in the three speed conditions then the trajectory bias will be greater for the faster speeds because perceived trajectory is a combination of target motion and subtracted self-motion.

Thus, a flow parsing account predicts that relative tilt, the measure of bias in object trajectory, will increase with increasing roll speed.

3.5.1 Methods

3.5.1.1 Participants.

Eight undergraduate students (2 male) were recruited at Cardiff University. All participants were naïve to the experimental hypotheses and were subject to the same restrictions and ethical procedures as Experiment 1.1.

3.5.1.2 Apparatus and stimuli.

The apparatus was identical to Experiment 1.2 and the peripheral flow stimuli were identical to those reported in Experiment 2.1, except that speed of the simulated roll was varied. As before the target was a small red circle with a diameter of 0.18 degrees, positioned at ± 4 degrees eccentricity. The target translated away from fixation at a rate of 1 cm/s.

3.5.1.3 Design.

Four IVs were manipulated: Target location (Above/Below), flow direction (CW/ACW), Roll Speed (15, 30, 60 degrees/s) and Peripheral condition (Near/Far). A within-subjects design was adopted and there were 9 tilt trajectories per condition. The DV was defined as the mean relative tilt across the two target locations. The Near and Far conditions were run in separate experimental blocks with half of the participants completing the Near block first, and the other half completing the Far block first. Within each block roll directions and speeds were randomly intermixed.

3.5.1.4 Procedure.

A fixation dot (0.3 cm diameter) was presented throughout each trial. Following a button press, flow onset occurred after a 0.75 second delay and simulated rotation at one of three speeds: 15 cm/s, 30 cm/s, or 60 cm/s. After a random delay from the range of 1-1.2 second the target was presented.

Participants set the angle of a short response line to indicate perceived trajectory using the jog wheel. Two 15 second breaks were included in each experimental block.

3.5.1.5 Analysis.

Participant’s angular responses were converted to relative tilt (see Appendix A). As before, responses were coded as if all targets were presented above fixation. An overall 2 x 4 x 2 repeated measures ANOVA (Flow direction x Roll Speed x Peripheral Condition) was used to assess if there were any differences in relative tilt as a function of roll speed between the three peripheral conditions. The DV was mean relative tilt.

A main effect of flow direction was anticipated with CW roll inducing greater trajectory bias than ACW roll, as seen in the previous two experiments. A main effect of Peripheral condition was also predicted with Near flow producing larger relative tilts than Far peripheral flow. If relative tilt increased as a function of roll speed then this would be confirmed by an interaction between roll speed and flow direction. As in Experiment 2.2, the *p*-value for this interaction term was divided by two, because a directional interaction was predicted (Wuensch, 2006). Posthoc tests with bonferroni correction would be used to further investigate any such interaction.

3.5.2 Results and discussion

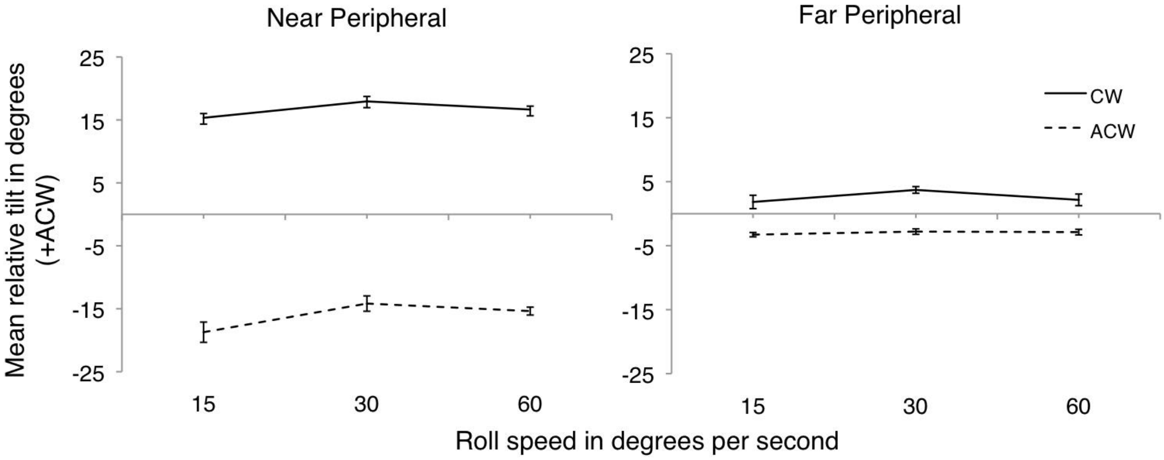

Figure 59 - Mean relative tilt as a function of roll speed and roll direction. Error bars show within-subject SE.

As in Experiment 2.1, a significant difference in relative tilt as a function of roll direction (Figure 59; *F* (1, 7) = 39.46, *p* < 0.001) was observed. Comparison of the absolute relative tilt values for the CW and ACW conditions, significantly larger tilts were reported in the Near than Far peripheral condition across all speeds and roll directions (*F* (1, 7) = 30.41, *p* = 0.001), corroborating the previous findings. However there were no differences in relative tilt as a function of roll speed in either the Near (CW: *F* (2, 14) = 2.50, *p* = 0.118; ACW: *F* (2, 14) = 2.49, *p* = 0.119, *n. sig*) or the Far peripheral condition (CW: *F* (2, 14) = 0.93, *p* = 0.420, *n. sig*; ACW: *F* (2, 14) = 0.26, *p* = 0.772, *n. sig*).

The speed of the peripheral flow stimulus may not impact upon relative tilt. This may be due to the spatial separation of the peripheral flow and central target, especially in the Far peripheral condition. It is possible that an increase in the speed of peripheral flow does not equate to any change in perceived target trajectory in central vision. If speed detection in peripheral vision is not integrated with flow parsing processes then any change in peripheral flow speed would not convert to a change in the amount of flow that was 'parsed' from the global scene and therefore would not lead to any change in relative tilt. However it would be surprising if the speed of peripheral flow did not impact upon relative tilt merely due to spatial separation as all results have so far indicated that flow parsing effects can be driven by peripheral self-movement information.

One other reason for not finding any change in relative tilt with increasing speed is that the range of speeds that were tested may have been too high given that peripheral vision is more sensitive to higher velocities than central vision (Orban et al., 1986; McKee & Nakayama, 1984). Repeating the experiment with slower speeds may still reveal differences in perceived target trajectory as a function of roll speed. In the following experiment a range of slower speeds were tested.

3.6 Experiment 2.3b: Effect of slower peripheral flow speeds

In the previous experiment, there were no changes in relative tilt with increasing roll speed. One reason for the lack of roll speed effect may be because the speeds chosen in Experiment 2.3a were too fast or too slow to reveal any noticeable differences in relative tilt. This experiment investigated a broader range of speeds, ranging from 3.25 degrees/s to 30 degrees/s. Slower speeds were used rather than faster speeds, as these were considered more likely to be within the preferred speed range of cells responding to peripheral motion. Furthermore, faster speeds may have unnecessarily induced nausea in observers. This range meant that slower speeds could be tested alongside those previously used in Experiment 2.3a.

3.6.1 Methods

3.6.1.1 Participants.

Three male and three female (N = 6; age range = 24-27) postgraduate students (including the author) took part. Aside from the author, all participants were naïve to the experimental hypotheses being investigated in the study. Eligibility criteria and ethical procedures were the same as in Experiment 1.1.

3.6.1.2 Apparatus and stimuli.

Near and far peripheral stimuli were all identical to those used in the previous experiment. This experiment also included a Combined peripheral flow condition.

3.6.1.3 Design.

The IVs were the same as in the previous experiment (Above/Below x CW/ACW x Speeds x Peripheral condition), but a slower range of speeds was used: 3.25 degrees/s, 7.5 degrees/s, 15 degrees/s, 30 degrees/s and added a

Combined level to the Peripheral condition variable. Aside from these two differences, all design parameters were the same as in the previous experiment. The order of peripheral conditions was counterbalanced across observers.

3.6.1.4 Procedure.

Trial procedure was identical to the previous experiment except that there was an additional 15 second break because an additional speed condition was included and this resulted in more trials in this experiment.

3.6.1.5 Analysis.

Predictions and analyses were the same as in the previous experiment. As a Combined peripheral condition is also being tested on a new set of participants and with an increased number of trials, a set of linear regression analyses, as in Experiment 2.1, were conducted to assess whether the relative tilts observed in the Combined condition are best accounted for by the Near, Far or a linear sum of the Near+Far data.

3.6.2 Results and discussion

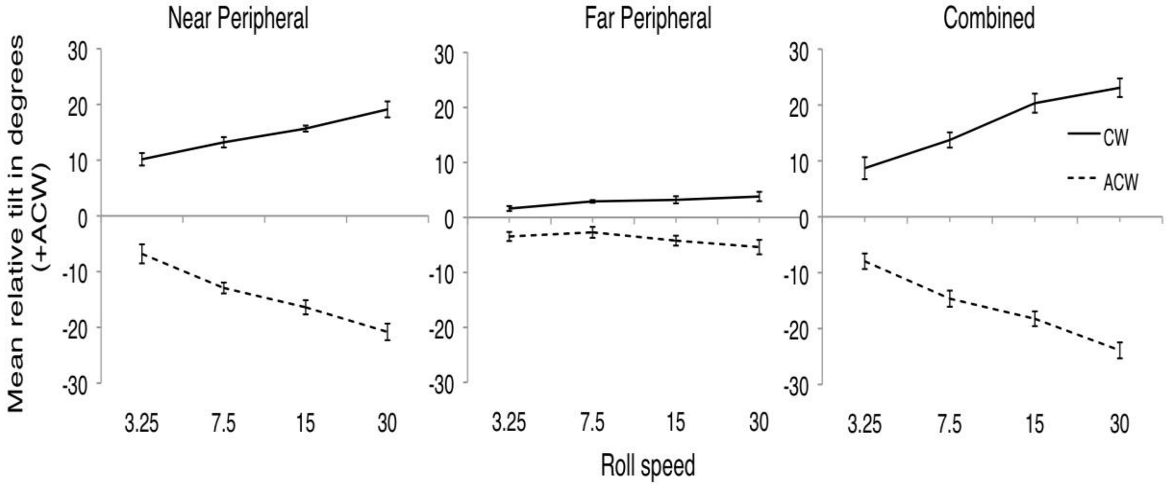

Figure 60 - Mean difference in relative tilt as a function of roll speed and peripheral condition. Error bars show within-subject SE.

As in Experiment 2.1 there was a basic effect of flow direction (*F* (1, 5) = 38.43, *p* = 0.002). As reported in earlier experiments, a comparison of absolute relative tilt reveals that the magnitude of relative tilt is significantly larger in the Near condition compared to the Far condition (*F* (1, 5) = 16.05, *p* = 0.01).

Figure 60 shows that there is an increase in relative tilt with increasing roll speed for Near (conducted using absolute values, F (3, 15) = 14.09, $p <$ 0.001) and Combined flow conditions (F (3, 15) = 15.02, $p < 0.001$) but not for Far peripheral flow (F (3, 15) = 2.48, $p = 0.101$, *n. sig*). These results indicate that perceived target trajectory is dependent upon the speed of the flow and is in line with a peripheral contribution to flow parsing during rolling self-movement.

As in Experiment 2.1, three linear regressions were conducted to assess whether the sum of the tilts in the Near and Far conditions predicted the data in the Combined condition, or whether the Near or Far peripheral data predicted the Combined data. The Near+Far model (Figure 61; $\beta = 0.845$, $R^2 = .762$, F (1, 22) = 70.516, $p < 0.001$) and the Near model (Figure 62; β = 0.1.007, $R^2 = .816$, F (1, 22) = 97.643, $p < 0.001$) significantly predicted the Combined data. However the Far data did not significantly predict the Combined data (Figure 63; $\beta = 0.966$, $R^2 = .089$, F (1, 22) = 2.140, $p = 0.158$).

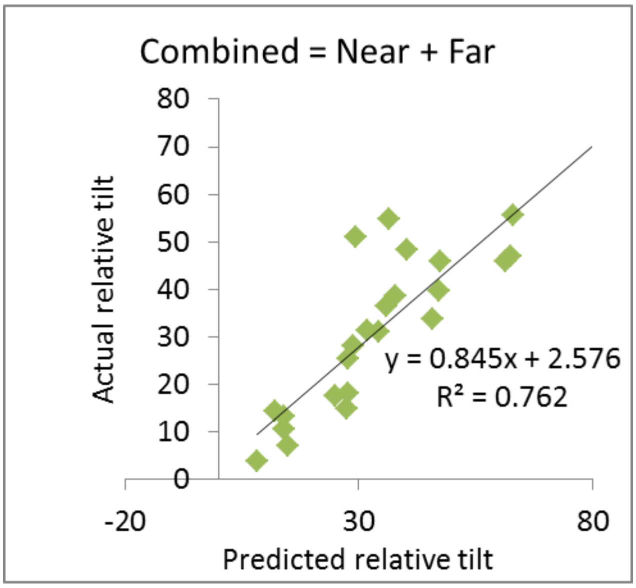

Figure 61 - Actual Combined relative tilt as a function of Predicted relative tilt Near + Far model.

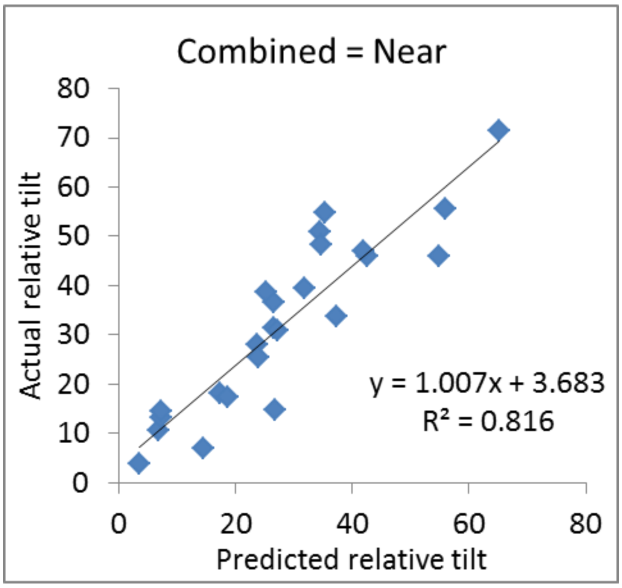

Figure 62 - Actual Combined relative tilt as a function of Predicted relative tilt Near model.

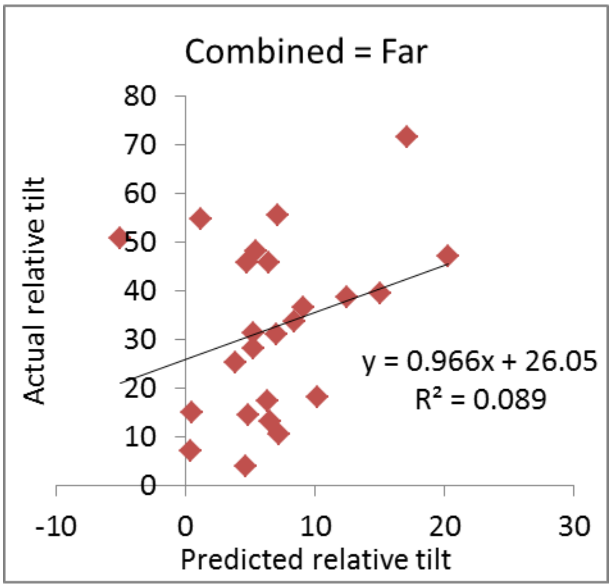

Figure 63 - Actual Combined relative tilt as a function of Predicted relative tilt for Far model.

The chi squared value for the Near model (χ^2 = 60.71) was comparable to the value obtained for the Near+Far model (χ^2 = 60.91), suggesting both models equally predict the Combined data. However, as the Near model has only one predictor variable, the model provides the more parsimonious account of the data.

3.7 Chapter Discussion

The experiments in this chapter have found evidence that peripheral vision contributes to flow parsing during self-rotation about the line of sight.

Specifically, in Experiment 2.1 the results showed a consistent bias in perceived object trajectory in the direction opposite that of the flow stimulus, in line with a peripheral contribution to parsing of self-motion components from the retinal image.

In order to confirm that the results of Experiment 2.1 were due to a peripheral input to flow parsing two further experiments were conducted. These experiments manipulated the location of the target and the speed of simulated self-movement to look for signatures of a flow parsing mechanism. These two factors were tested because the FPH states that perceived object trajectory is a function of the optic flow components and the location of the object. Thus, changes in relative tilt as the peripheral flow components (flow speed) and object location (target eccentricity) are manipulated would suggest that the results of the first study in this chapter are due to a peripheral contribution to flow parsing. As predicted, Experiment 2.2 demonstrated an effect of target eccentricity on relative tilt. However, Experiment 2.3a did not show an effect of flow speed on relative tilt. When the study was repeated with a slower range of speeds, relative tilt increased with flow speed as predicted (Experiment 2.3b).

Taken together, the findings in this chapter strongly suggest that peripheral self-motion indicating observer rotation can be parsed from the retinal image and this allows for a scene-relative judgement of object trajectory. Furthermore, perceived object trajectory during presentation of peripheral roll motion appears to exhibit the characteristic signatures of the flow parsing mechanism; being dependent on flow speed and target location. These effects provide additional confidence that the results of Experiment 2.1 reflect the output of a flow parsing mechanisms that is driven by peripheral information about self-movement.

As was observed for radial flow, there is a marked difference in the magnitude of mean relative tilt between the near and far peripheral flow conditions in Experiments 2.1, 2.3a and 2.3b, with the former showing a much smaller trajectory bias than the latter. This presents further evidence for a decreasing influence of peripheral flow on perceived target trajectory with increasing retinal eccentricity, which was also indicated in Chapter 2. As the far peripheral stimulus contributed less to flow parsing than the near periphery in the experiments of the last two chapters, this could indicate that visual flow from these two peripheral regions is not treated equivalently by the visual system. Although a functional sensitivity account (FSH) would suggests that different retinal regions play different roles in self-motion perception depending upon the flow available in these regions but I have not found any evidence that the respective roles of the near and far periphery differ between radial and roll flow. However, the results of this chapter and the previous chapter do suggest that the near periphery is seemingly more important for flow parsing than the far periphery. One reason the far peripheral flow may make a much smaller contribution to flow parsing is because the visual information available in this retinal region might not provide a very robust cue to self-movement and so, in isolation, does not appear to allow self-movement to be identified from retinal flow. Furthermore, it may be the case that the receptive field size of cells sensitive to global patterns of flow is not large enough to incorporate the far peripheral retina that was stimulated in this study. Although Burr et al. (1998) report summation of motion signals up to 70 degrees eccentricity, suggesting very large receptive fields for optic flow, monkey neurophysiology has suggested neurons in MST have smaller receptive field sizes in the region of 40 degrees (Tanaka, Hikosaka, Saito, Yukie, Fukada & Iwai, 1986). Alternatively, the declining influence of visual flow within increasing retinal eccentricity could simply be due to the use of distinct areas of flow which make a reduced contribution to parsing, as demonstrated in Experiment 1.3. Comparing Near peripheral parsing to flow parsing in central vision, there do not appear to be any differences in the magnitude of the effect and this suggests that these two retinal regions are equally adept at providing information about self-movement in order to drive the flow parsing process.

This thesis has so far considered the effect of peripheral flow upon judgements of object trajectory in order to assess the contribution of peripheral vision to flow parsing. The findings of the first two empirical chapters show that self-movement information in peripheral vision produces flow parsing signatures that have previously only been reported using central visual flow. However, if peripheral vision does play a role in flow parsing then it should also be possible to find evidence of a peripheral contribution to flow parsing for other visual judgements. The next chapter considers whether peripheral flow also allows observers to make scene-relative judgements of objects which change in size.

Chapter 4. PERIPHERAL CONTRIBUTION TO THE DETECTION OF SIZE CHANGE BY MOVING OBSERVERS

4.1 Chapter Summary

Chapters 2 and 3 demonstrate that peripheral visual flow contributes to a process that allows observers to make scene-relative judgements of object *trajectory*. This chapter investigates whether peripheral vision is also important for judgements of object size change during self-movement.

A change in the retinal size of an object might arise from a change in the physical size of the object or from a change in relative distance between the object and the observer. Rushton and Warren suggested that flow parsing would disambiguate changes in an object's retinal size because any changes in retinal size that were due to self-movement would be parsed from the scene. Thus, a parsing process would reveal any changes in an object's physical size. Preliminary data (Rushton & Warren, 2011) indicates that flow parsing can facilitate the perception of size change during self-movement. In this chapter I explore whether peripheral flow contributes to flow parsing for the detection of size change.

Peripheral flow stimuli similar to those used in Chapter 2 were employed, with near, far, and near + far conditions to assess the contribution of these two retinal regions and the integration of flow across the peripheral retina. The flow stimuli simulated either forward or backward self-movement. During the presentation of the peripheral flow, a circular probe disk appeared in the centre of the projection screen and changed in diameter. Observers reported whether they perceived the disk to expand or contract in size. If peripheral flow contributes to the ability to judge object size change during self-movement then, due to the parsing of self-motion from the retinal image, globally expanding flow should bias the disk to be seen as contracting and contracting flow should bias the disk to be seen as expanding.

When flow was presented in the near periphery, expanding flow resulted in a tendency to judge the object as decreasing in size, and contracting flow biased perception towards an object that was increasing in size. This pattern of bias is compatible with the subtraction of self-motion from the retinal image and indicative of a role for near peripheral vision in perception of size change during self-movement. However, in the far peripheral condition no significant difference between expanding and contracting flow conditions was present. The magnitude of the flow parsing effect in the combined condition was comparable to that obtained with the near flow alone, suggesting that visual flow on the near peripheral retina drives the effect seen in the combined condition. In summary, peripheral flow appears to contribute to the perception of size change during linear self-movement and, similar to judgements of object trajectory, the near periphery seems to play a greater role in this process.

4.2 Chapter Introduction

In order to interact with or react to objects in our environment, it is important that we can accurately detect changes in their size. For visual judgements of size change one must rely on the information contained within the retinal image. When the observer and object are stationary this is an easy task as changes in size are uniquely identified by local retinal motion, a change in retinal size, and the visual system is highly sensitive to these changes (Regan & Hamstra, 1993). When the observer is moving this task becomes more complex because objects that are stationary in the scene will also change in retinal size as the distance between them and the observer increases or decreases. Specifically, objects will increase in retinal size as the observer approaches and decrease in retinal size as the observer moves further away. Changes in an object's retinal size during self-movement therefore complicate the task of detecting any changes in physical size of an object because a change in retinal size could be due to a change in physical size *or* retinal size.

Previously, Rushton and Warren (2011) have extended the predictions of the FPH and suggested that the parsing of visual self-motion from the retinal image allows observers to detect size change during self-movement. In this chapter, I propose that peripheral visual flow contributes to a flow parsing process that enables the visual system to discriminate changes in an object's retinal size due to self-movement from changes in physical size. Thus, in relation to the previous experimental chapters, which considered ambiguity in retinal motion in relation to object trajectory, the present chapter considers the ambiguity of objects that change in retinal size during self-movement.

4.2.1 Flow parsing and size change

To explain how the parsing of self-motion components from the retinal image may help to disambiguate changes in the retinal size of an object, compare the retinal motion of an object that uniformly (isotropically) increases in physical size in all directions (e.g. a ball being inflated) viewed by a stationary observer with that of a moving observer approaching a stationary object of a fixed size (a ball not being inflated). The retinal motion of the object in both instances is the same - the object expands in retinal size. However, there is a critical difference between the visual information in these two scenarios. When the observer moves, a pattern of global retinal motion is also produced by forward movement in the world. Rushton and Warren (2011) have suggested that the ability to parse self-motion from the retinal image may facilitate an assessment of object size whilst the observer is moving. This is because, when the object is not changing in size, the retinal motion associated with the object (the ball) would also be parsed from the retinal image which would cancel out the change in the retinal size of the object and reveal that the object was of a fixed size. The same parsing process could also reveal any changes in physical size during self-movement (an inflating ball) because any remaining retinal motion which is not accounted for by self-movement could be attributed to a physical change in the size of the object. Figure 64 illustrates this process and shows how self-movement information can help to determine whether an object is changing in size during self-movement. The top row shows the process for an object of a fixed size and the bottom row shows the process for an object increasing in size (such as the inflating ball).

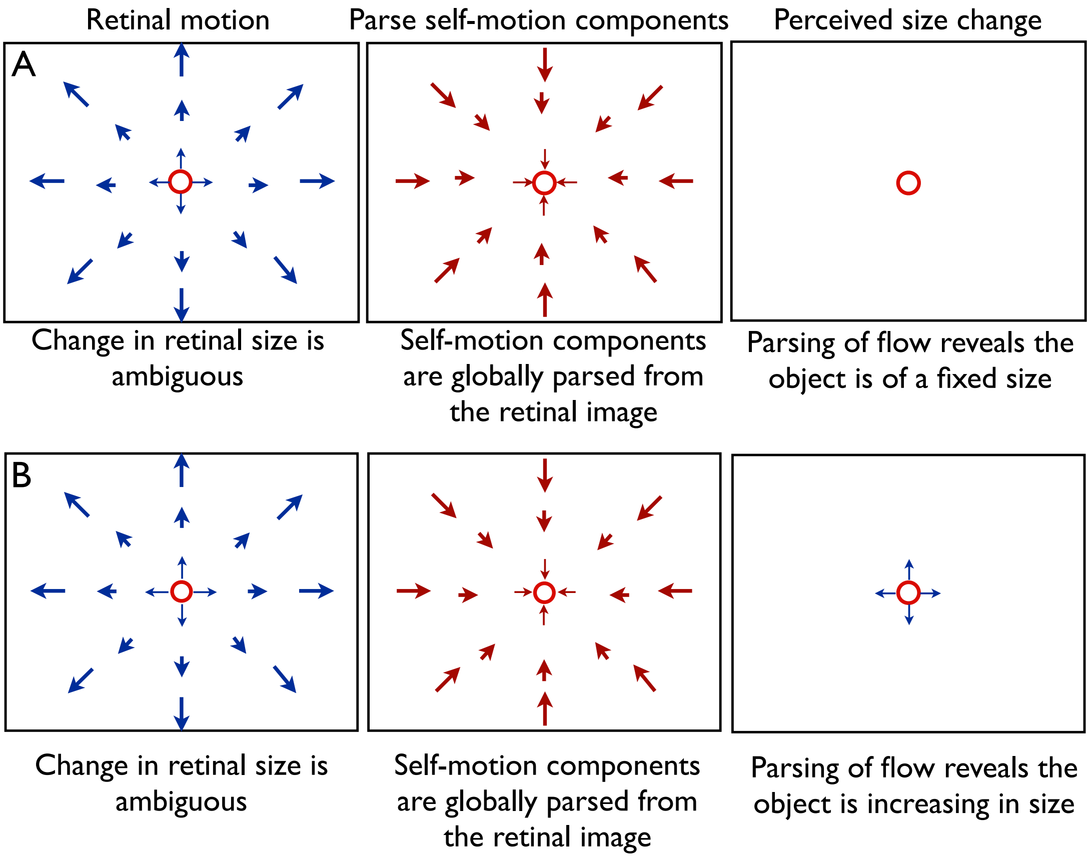

Figure 64 – Predictions of the FPH for an observer moving towards an object of a fixed size (A) or an object that is increasing in size (B). The parsing of self-movement reveals whether the object that changes in retinal size during self-movement is also changing in physical size.

The FPH allows for a clear set of predictions about the perceived change in size during self-movement. During forward self-movement towards a stationary object, the parsing of self-motion from the retinal image would mean that a contraction is applied to all elements in the retinal image. If flow parsing occurs then despite a change in the retinal size of the object, the perceived size of the object should remain unchanged because the change in the retinal size of the object is attributed to self-movement. The same parsing process should also enable observers to detect changes in the physical size of an object during self-movement (as in Figure 64B).

When the observer is not moving and self-movement is simulated, the FPH predicts a systematic pattern of results with expanding flow biasing the perception of an object of a fixed size towards that of an object which is contracting in size and with contracting flow biasing the perception of the same object to appear as expanding in size. Similarly, if flow parsing is operating then it should be possible to demonstrate that observers can also detect changes in the physical size of an object during simulated self-movement.

It is important to note that the visual solution to the detection of size change during self-movement set out by Rushton and Warren does not exclude the contribution of extra-retinal self-movement signals which have been investigated by other researchers. Indeed, Wexler and colleagues have studied the influence of both visual and non-visual cues to self-movement on judgements of object motion (van Boxtel et al., 2003; Wexler, Panerai, Lamouret & Droulez, 2000; Wexler & van Boxtel, 2005), and size constancy (Combe & Wexler, 2010) but not size change.

Rushton and Warren (2011) tested whether flow parsing facilitates scene-relative judgements of object size during self-movement. They compared the ability of observers to detect changes in an object's size in two conditions: 1) when the object moved in depth 2) when the object was stationary but was set within a pattern of visual flow indicating forward self-movement. They hypothesised that in the self-movement condition the availability of visual flow indicating self-movement would result a better ability to detect changes in the size of the object because the parsing of retinal motion components due to self-movement would reveal any changes in the physical size of the object. By contrast, when the object moves in depth and visual flow indicating self-movement is not available, the ability to detect whether the object changes in size should be reduced because the retinal motion due to the change in depth cannot be distinguished from a change in size.

To test their predictions, in two experiments, Rushton and Warren (2011) asked observers to report whether a sphere that moved in depth was also changing in physical size. On half of the trials the object did not change in size and on the rest of the trials the object either increased or decreased in size. In the first experiment the moving object was placed within a stationary scene of wireframe shapes. Observers only correctly identified an object which was changing in size about 50% of the time; performance was not significantly better than chance. In the second experiment the same scene moved with the object. This stimulus created a pattern of optic flow appropriate for an observer moving towards a stationary object. When the whole scene moved, observers were much better at detecting whether the object had changed in size and correctly identified these instances more than 90% of the time. These results indicate that observers are able to successfully detect size change within a pattern of visual motion consistent with self-movement. Yet performance was at chance levels when observers were presented with the same local object motion in the absence of optic flow. It appears that the flow parsing process allows observers to determine whether an object is changing in size during self-movement.

In their work, Rushton and Warren (2011) presented self-movement information within the central visual field. In the next section, I consider whether peripheral flow contributes to the process that enables observers to detect size change during self-movement.

4.2.2 Peripheral contribution to size change during self-movement

In Chapter 2 I investigated the peripheral contribution to flow parsing for judgements of object trajectory during forward or backward translation of the observer. The present chapter investigates the same two forms of self-movement but during judgements of size change. Linear translation is particularly applicable to the detection of size change because, as discussed earlier in this introduction, movement towards or away from an object produces the same change in retinal size as a physical expansion or contraction of the object itself. The similarity of these two events in terms of the pattern of retinal motion that is produced provides a strong test of whether self-movement information can help to disambiguate retinal motion into self-movement and object size change components.

The use of translational self-movement in this chapter means that the differences in flow structure between central and peripheral vision that were discussed in Chapter 2 also apply here. To recap, translation of the observer either forwards or backwards produces a pattern of radial flow in central vision and lamellar flow in peripheral vision. These differences the geometry of the optic flow field mean that, when gaze is straight ahead, different information about self-movement is available in central and peripheral vision. In Chapter 1 I reviewed evidence that central and peripheral flow can both give rise to an illusory sense of self-movement indicating the importance of visual flow in both retinal regions for the perception of self-movement. Furthermore, cells with receptive fields in central vision show different preferences for motion direction, with cells receiving input from peripheral vision preferring directions in line with a lamellar flow structure (Albright, 1989). The work of Stoffregen (1985) demonstrated that lamellar flow presented in central or peripheral vision produces equivalent postural sway, indicating that both retinal regions are sensitive to this flow structure. Thus, this prior work indicates that peripheral flow provides a robust cue to self-movement during forward motion and should therefore contribute to flow parsing for the detection of size change as already identified in central vision.

In seeking to characterise the role of peripheral vision in size change judgements during self-movement, the findings of this study could potentially reveal important differences in how visual flow from across the retina is utilised for this task, which may differ from judgements of object trajectory. Although the visual information indicating self-movement is of course identical in both cases, it is possible that the mechanisms which support judgements of object trajectory differ from those responsible for extracting changes in object size during self-movement. If judgements of size change are more reliant on the relative motion between the object and the background (whether that be optic flow arising from self-movement or a stationary background with the object moving in depth) then it may be the case that local motion is comparatively more important when judging size change than when judging trajectory. Rushton and Warren have previously investigated the global and local motion contribution to their flow parsing effects (i.e. Warren and Rushton, 2008), but these findings were in relation to judgements of object trajectory rather than size change. Therefore, it may be the case that local motion contrast plays a more critical role in judgements of size change during self-movement. The present results may provide an indirect indication of the local motion contribution because the peripheral flow stimuli are spatially separated from the object and therefore local motion contrast is likely to be excluded from the stimuli in this study. A limited contribution of peripheral flow in the present study might therefore indicate that the relative importance of global and local motion signals differ for judgements of trajectory compared to size change.

In summary, changes in the retinal size of an object can arise from a number of events in the world. Rushton and Warren have suggested that visual self-movement information enables observers to disentangle changes in retinal size that are due to self-movement from those that are the result of a change in the physical size of the object. Peripheral flow is a potential source of information about linear self-movement that may contribute to this process. In Chapter 2 I demonstrated that peripheral vision contributes to flow parsing for judgements of object trajectory during forward and backward self-movement. The experiment that follows investigates whether peripheral vision also plays a role in the perception of size change during the same type of self-movement.

4.3 Experiment 3.0: Contribution of the Near and Far periphery to size change detection during self-movement

This experiment probed whether peripheral vision plays a role in resolving the ambiguity of an object that changes in retinal size during self-movement. As in previous experiments in this thesis, self-movement was simulated and observers remained stationary throughout the experiment. In contrast to the other experiments in this thesis, which used a matching paradigm, the present experiment utilised a nulling paradigm. A forced choice task was used in which participants judged whether a centrally presented object expanded or contracted in size. Participants' responses were used to determine whether there was a characteristic perceptual bias in responses that indicated flow parsing.

Expanding or contracting flow, which simulated forward or backward self-movement respectively, was presented in the Near periphery, Far periphery, or both (Combined condition). These self-movement stimuli were similar those employed in Experiment 1.2. A circular probe disk was simultaneously presented in central vision. The disk changed size at the same time as the flow moved in the periphery.

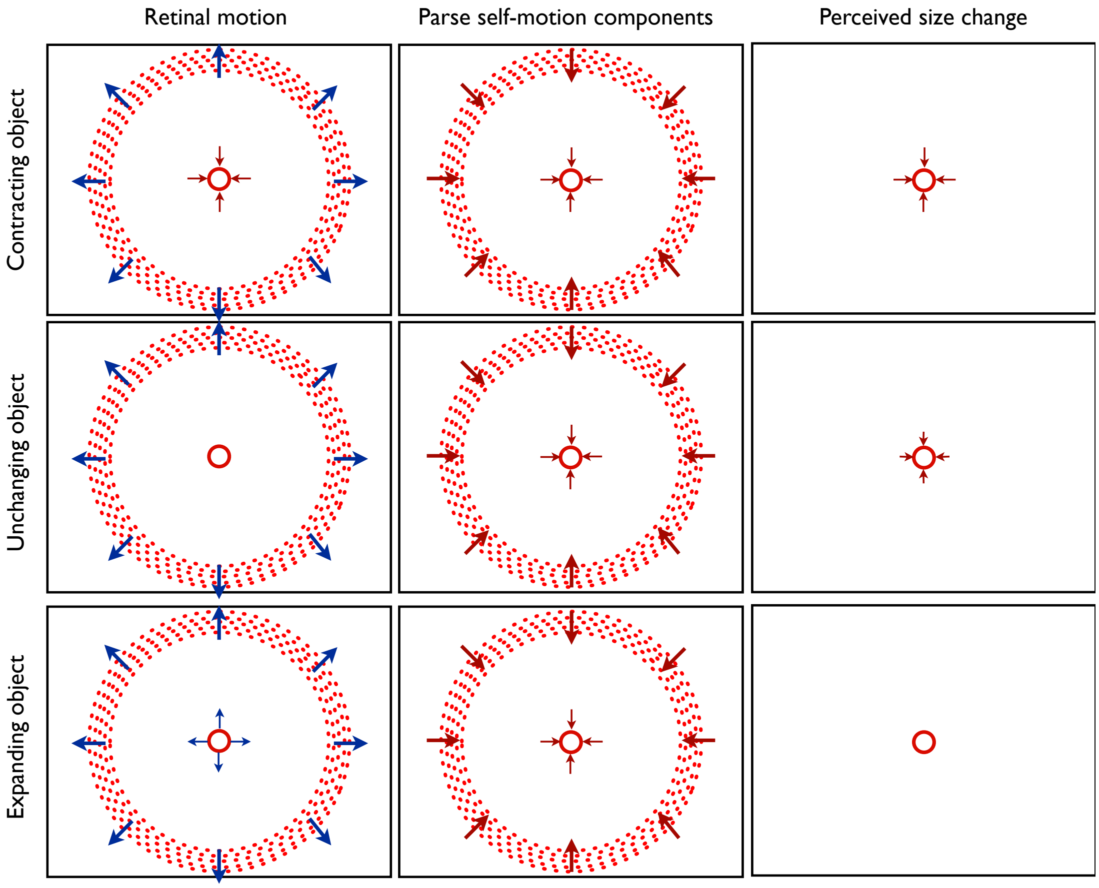

Figure 65 -- Flow parsing predictions for expanding flow, simulating forwards self-movement. Three instances of object size change: Contracting (top row), unchanging (middle row) and Expanding (lower row). Note that in the experiment the object always changed size and the middle row is purely provided to illustrate the hypotheses. Arrows indicate motion of the stimulus and were not shown in displays.

Figure 65 and 66 each provide three examples to illustrate the predictions for a peripheral contribution to flow parsing in this experiment. To clarify these predictions, consider the case where the object does not change in size: in this instance, the object has a fixed onscreen size and therefore has no associated retinal motion (middle row, Figure 65 & 66). Expanding peripheral flow (simulating forward observer movement) would bias the perception of the object such that it is perceived to contract, due to the subtraction of global motion from the retinal image. However, when the same object is presented during contracting peripheral flow, the object would be perceived to expand (increase in size).

Observers judged whether the central disk increased or decreased in size and subsequent analysis was used to estimate the onscreen change in size of the probe that corresponded to the perception of a stationary object.

The Point of Subjective Equality (PSE) was the point at which neither expansion nor contraction of the probe disk was perceived by the observer. This point provides a measure of the amount of physical expansion or contraction necessary to null the induced change in the object's size. Thus, a peripheral contribution to flow parsing predicts that during expanding flow, the object will need to be physically expanding in order to be perceived as a fixed size owing to the global subtraction across the retina. Similarly, for contracting flow, the object will need to be physically contracting in order to be perceived as a fixed size. Given the findings of Chapters 2 and 3, it is appropriate to expect that Near and Combined peripheral flow will result in a greater difference between Expanding and Contracting conditions than Far peripheral flow.

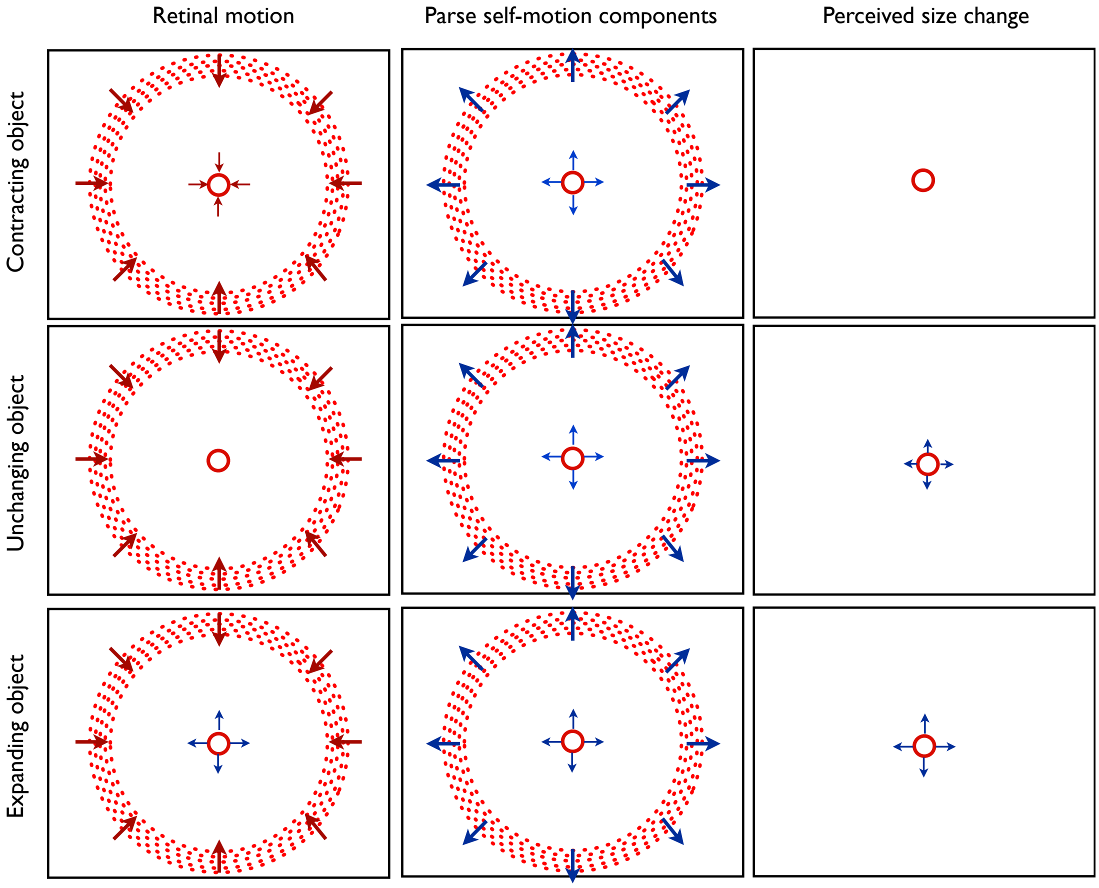

Figure 66 - Flow parsing predictions for contracting flow, simulating backwards self-movement. Three instances of object size change: Contracting (top row), unchanging (middle row) and Expanding (lower row). Note that in the experiment the object always changed size and the middle row is purely provided to illustrate the hypotheses. Arrows indicate motion of the stimulus and were not shown in displays.

4.3.1 Methods

4.3.1.1 Participants.

Six participants (3 male) took part in all experimental conditions. The age range of participants was 24 to 27 years (M = 25.00, *SD* = 1.26). Eligibility criteria and ethical precautions were identical to Experiment 1.1.

4.3.1.2 Stimuli.

The near peripheral stimulus was similar to the one used in Experiment 1.2. All size and drawing parameters remained the same. The velocity of the peripheral flow was equivalent to forward or backward self-movement at 5 m/s, or 8 cm/frame.

The Far peripheral stimulus consisted of bars that were positioned on a plane that was parallel to the line of sight and set at a distance of 2 0cm from the observer’s nearest eye on each side. Each stripe was 2 cm wide and they were equally spaced 4 cm apart. As the distance of the peripheral monitors was only 15 cm from each eye, each bar equated to an onscreen width of 1.8 cm (6 degrees) and there was a gap of 3.5 cm (12 degrees) between each bar (see Figure 67).

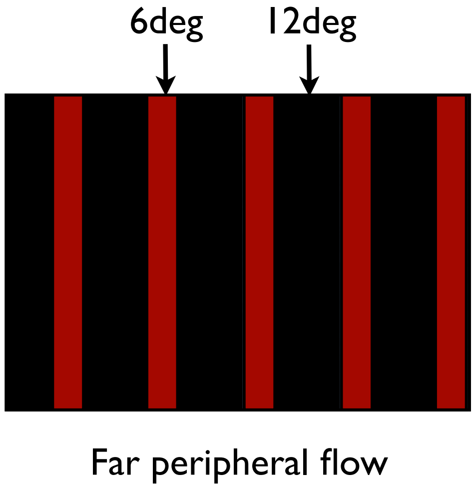

Figure 67 – Stimulus spacing for Far Peripheral flow.

This stimulus was the same as used in Experiment 1.2 except that the bars were positioned slightly closer to the observer (they were 50 cm away in Experiment 1.2). This increased the width of each individual bar to produce a lower spatial frequency. Pilot testing suggested that modifying the stimulus in this way provided a more effective percept of peripheral motion given the slightly faster speed of simulated self-movement that was employed in this experiment.

The probe disk was a solid ring presented in the centre of the screen. The size of the disk (defined by the outer radius) was randomly varied on each trial within the range 1-1.3 degrees (1.7-2.2 cm), with a constant ring width of 0.09 degrees (0.015 cm). On each trial, the disk changed size by expanding or contracting at one of four possible rates, as in Figure 68. The size change had a minimum rate of 0.08 degrees/s to a maximum rate of 0.53 degrees/s (0.125, 0.375, 0.625, or 0.875 cm/s onscreen dimensions).

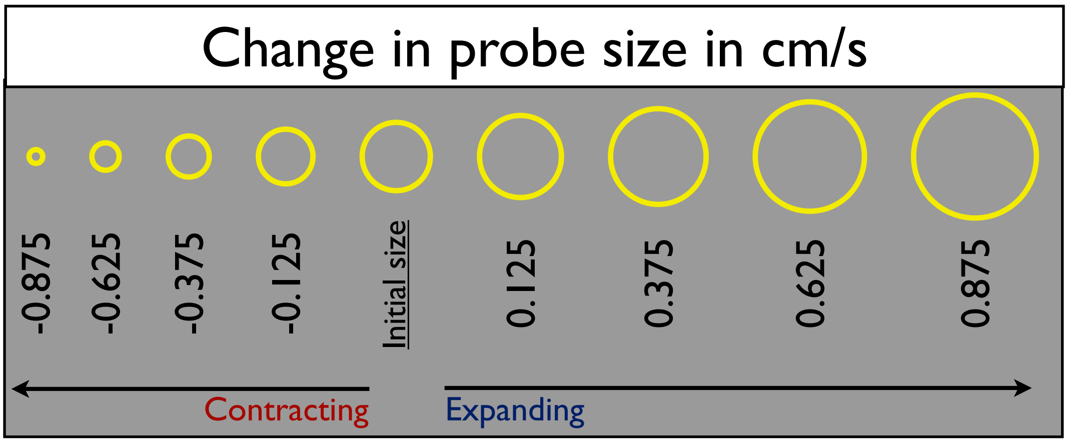

Figure 68 - Change in probe size in cm/s. Not to scale. The initial size of the probe disk was variable.

4.3.1.3 Design.

Two key IVs were manipulated: flow direction (expanding/contracting), peripheral condition (Near/Far/Combined). The change in probe size (-0.875, -0.625, -0.375, -0.125, 0.125, 0.375, 0.625, 0.875 cm/s) was also manipulated in order to derive the PSE in each experimental condition. The DV was the PSE, the change in probe size for which observers were equally likely to report expanding or contracting. As before, a within-subjects design was employed. Each peripheral condition (Near/Far/Combined) was presented in a separate experimental block. Within each block there were four repetitions of each trial type (32 trials/probe speed) and trials were presented in a random order. Each participant completed four blocks per peripheral condition and the order of these blocks was counterbalanced across observers. Participants completed the data collection across two separate ~40 minute experimental sessions.

4.3.1.4 Procedure.

Observers were seated with their head in the chin rest 95 cm from the projection screen. After the task had been explained to participants they were given the chance to practise before the main experiment began. They were instructed to look at the central disk during the task and to be as accurate as possible with their responses and were explicitly told to guess on any trials for which they were unsure of the answer. Participants were also informed that there was no time limit for their response, but that they should not take too long to make each judgement.

On each trial, the flow and probe disk appeared simultaneously and remained stationary for 450 ms. The probe then expanded or contracted and flow moved for 4 frames (approximately 66 ms) before disappearing. The stimulus durations in this experiment are much shorter than in the preceding experiments, owing to the fact that a longer duration would result in a probe that dramatically increased in size. Following stimulus presentation, observers viewed a blank screen (black) and used the mouse buttons to indicate if they perceived the probe as contracting (left button) or expanding (right button). There was a 1.5 second interval between their response and the start of the next trial.

4.3.1.5 Analysis.

Two psychometric functions were generated for each peripheral condition, one for expanding flow and one for contracting flow (predicted results are indicated in Figure 69). Data points for each stimulus level were obtained by calculating the proportion of trials where the observer judged the probe to be contracting (i.e. responded using the left mouse button). All psychometric functions were fitted using a Gaussian cumulative distribution function (Żychaluk & Foster, 2009).

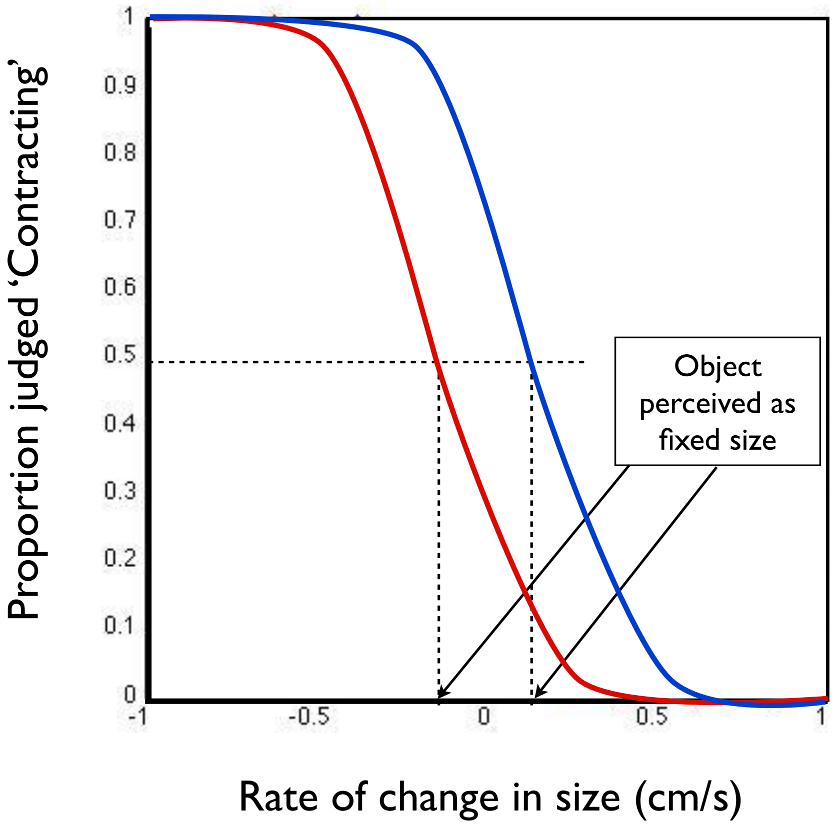

Figure 69 – Hypothetical psychometric functions. The 50% PSE is indicated for expanding (blue) and contracting (red) flow conditions. The bias is symmetrical about 0; a stimulus which is not changing in retinal size.

This method was employed to obtain the PSE. The PSE was averaged across subjects and within-subjects error bars were generated using Cousineau's method (2005; see Appendix A). A 3 x 2 repeated measures ANOVA was used to identify if there was a significant difference in PSE between expanding and contracting flow conditions for each peripheral condition. In light of the results in previous chapters, differences were anticipated between the three peripheral conditions (Near/Far/Combined), which would be revealed as a main effect of Peripheral condition in the ANOVA output.

In addition to the PSE (which indicates the bias in the perceptual judgement of size change), the slope of the psychometric function will provides a measure of the precision of this judgement. A steep slope would indicate a sharp perceptual distinction between objects which expand in size and objects which contract in size indicating that the visual system is highly sensitivity to the rate of change in size. However, a shallower slope would indicate a more gradual change from one percept to the other. Therefore, to ascertain if there were any differences in the precision of the visual judgement between the conditions, the slope of each psychometric function was measured and then averaged across observers. A further 3 x 2 repeated measures ANOVA was conducted to establish if there were any significant differences in slope.

One participant, LM, showed different pattern of responses and therefore the results are presented both with and without this participant to allow for comparison.

4.3.2 Results

The data showed that the presence of self-movement information in the Near periphery biased the perception of an object changing in size.

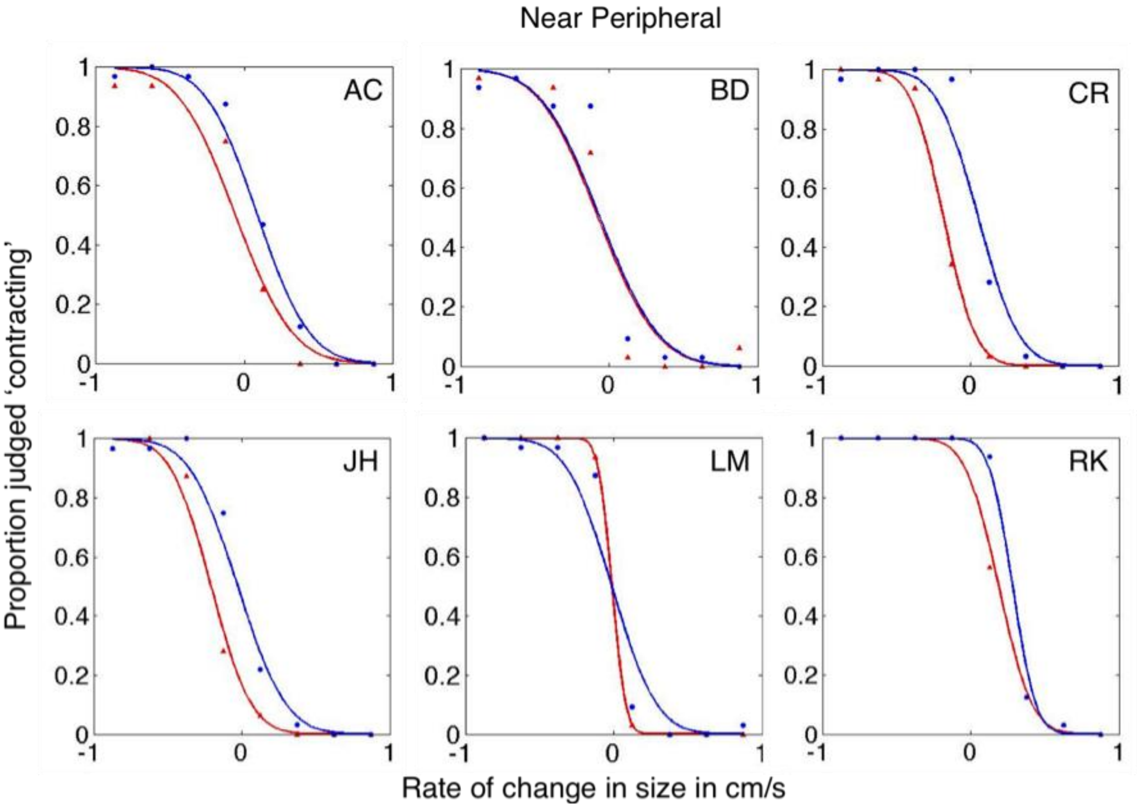

Figure 70 - Psychometric functions for individual participants in Near peripheral condition for Expanding (blue) and Contracting (red) flow conditions.

In line with a peripheral contribution to flow parsing, during expanding flow, a probe which did not physically change in size was perceived as decreasing in size (see Figure 70). During contracting flow, the same probe was perceived to increase in size. Statistical comparison of the PSE for expanding and contracting flow conditions revealed that this was a significant difference (*t*

(5) = 2.968, *p* = 0.031). There were no differences in the gradient of the fits between conditions (*t* (5) = -0.863, *p* =0.427, *n. sig*) suggesting participants found it equally easy to judge whether the object expanded or contracted in size regardless of the direction of the peripheral flow.

In the Far peripheral condition (Figure 71), there was no clear pattern observed in the data and as such there was no statistical difference between the expanding and contracting flow conditions (*t* (5) = 1.208, *p* = 0.281, *n. sig*).

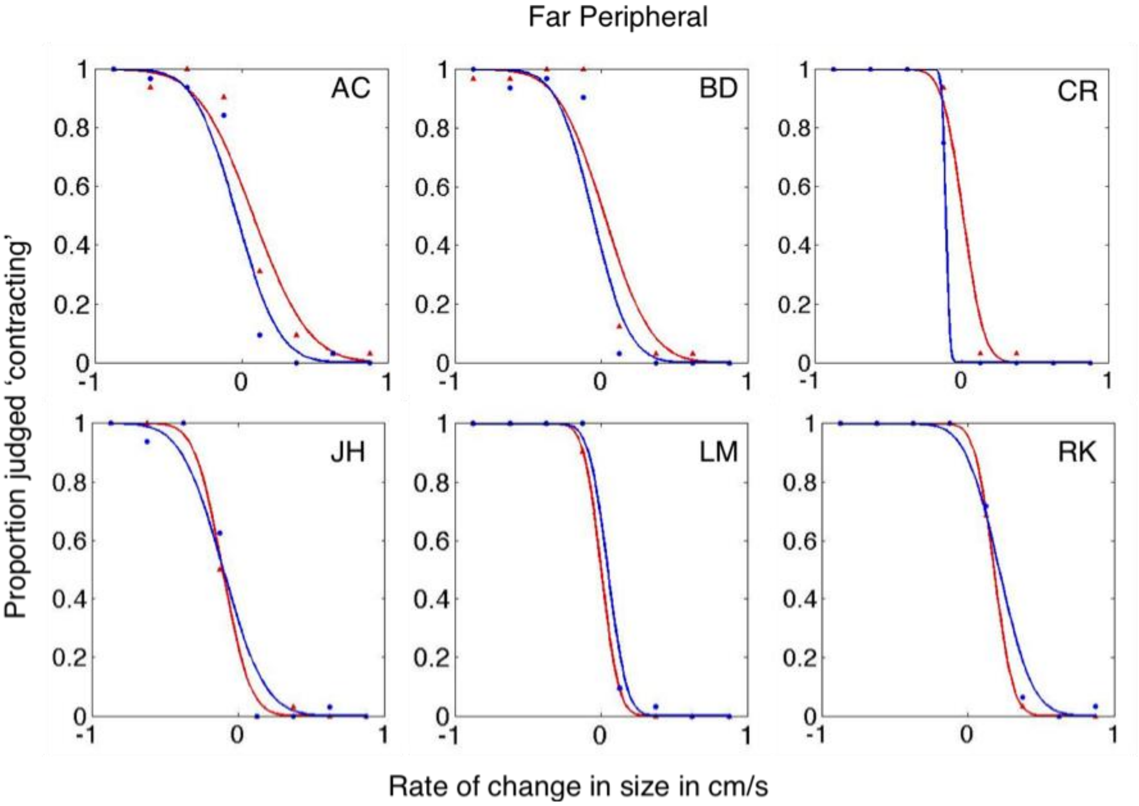

Figure 71 – Psychometric functions for individual participants in Far peripheral condition for Expanding (blue) and Contracting (red) flow conditions.

As before, the gradient of the psychometric functions did not differ between conditions (*t* (5) = 0.828, *p* = 0.445, *n. sig*). In the Combined condition, the expected pattern of results was demonstrated (expanding PSE > contracting PSE, Figure 72), with expanding flow biasing a fixed size target to appear to be contracting in size and vice versa, but this result was not significant (*t* (5) = 1.946, *p* = 0.109, *n. sig*). As in the Near and Far conditions, no differences were observed in the gradient of the psychometric functions between the Expanding and Contracting conditions (*t* (5) = -0.925, p = 0.397, *n. sig*).

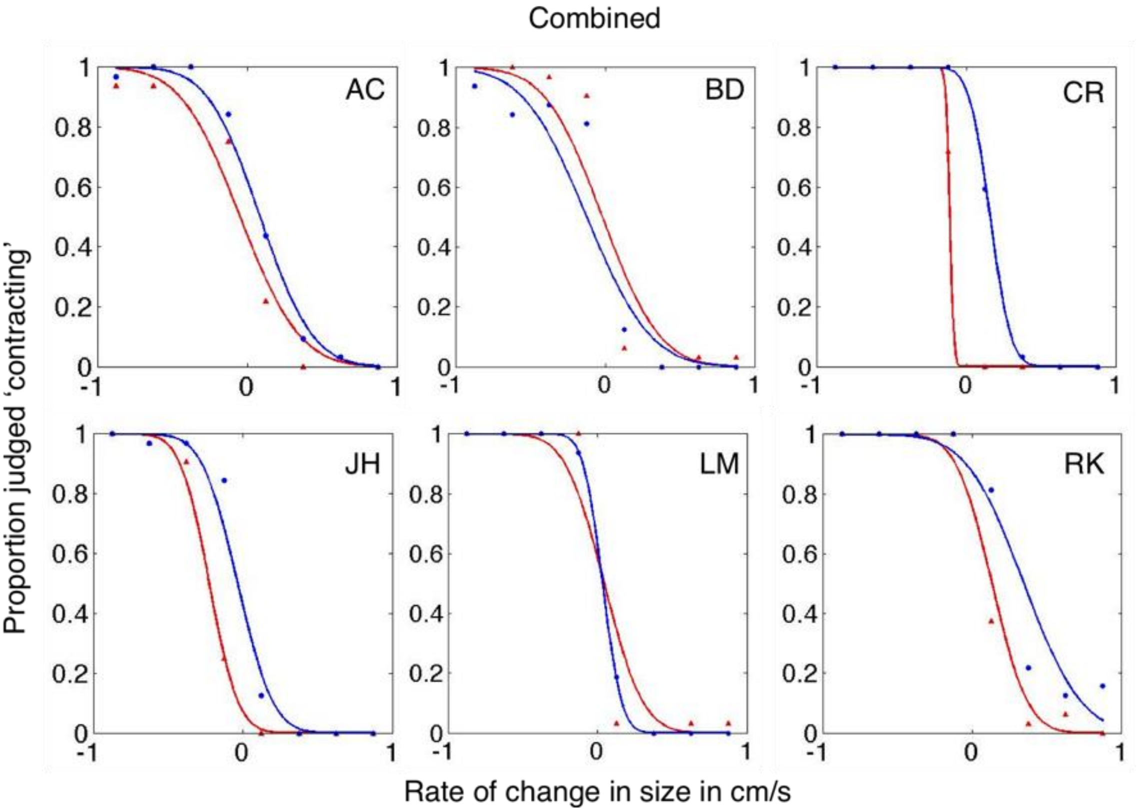

Figure 72 - Psychometric functions for individual participants in Combined peripheral condition for Expanding (blue) and Contracting (red) flow conditions.

Figure 73 shows the average psychometric function across observers and the difference in size change judgements for expanding and contracting flow is evident for the Near and Combined conditions but not the Far peripheral condition. Figure 74 plots the PSE for each condition with error bars.

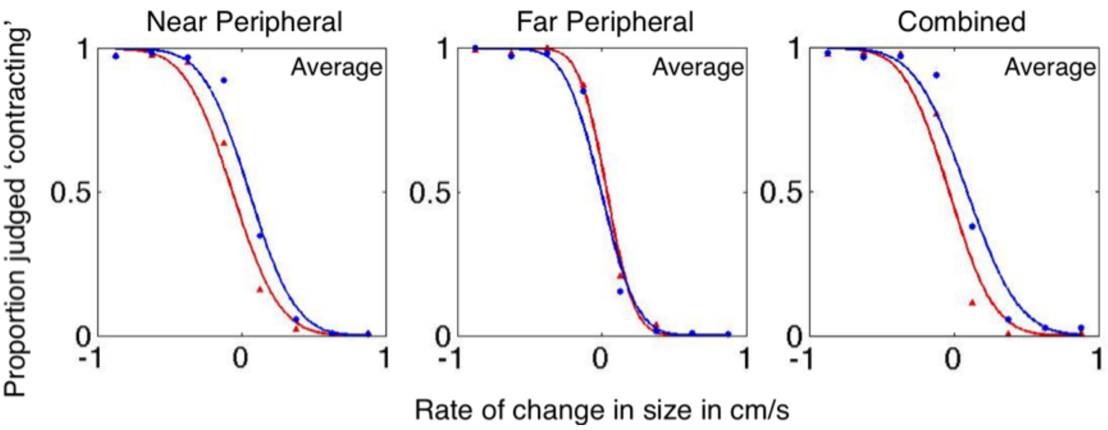

Figure 73 – Average psychometric functions for each peripheral condition for Expanding (blue) and Contracting (red) flow conditions.

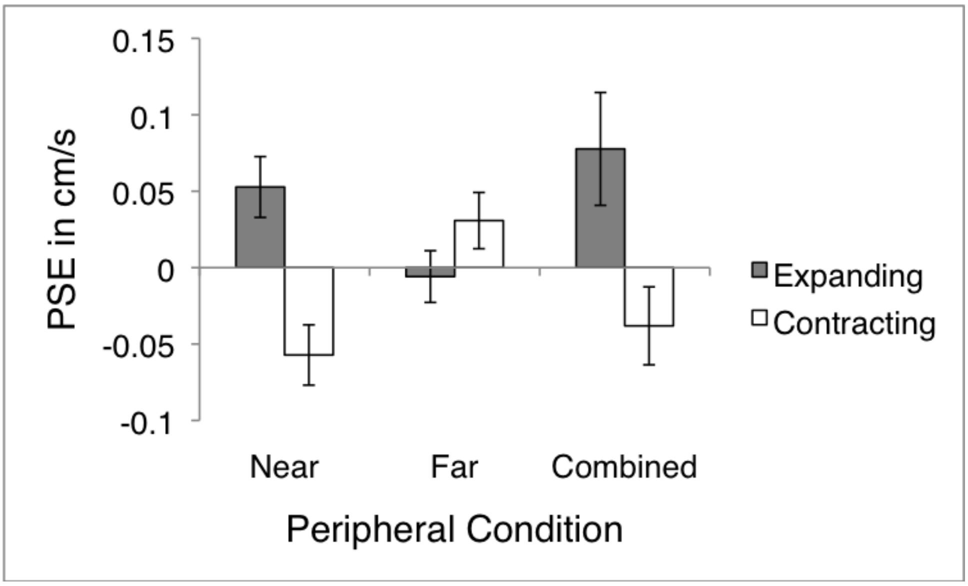

Figure 74 – PSE for each Peripheral condition and flow direction. Error bars show within-subject SE.

These results were also compared across the peripheral conditions by performing a 3 x 2 repeated measures ANOVA. This confirmed that there was a significant interaction between the location of the peripheral flow (Near, Far, Combined) and the direction of the flow (Expanding/Contracting) upon the perceived size change of the target (*F* (2, 10) = 4.865, *p* = 0.033). This interaction is likely driven by the opposing pattern of results observed in the Far condition in comparison to the other two peripheral conditions, as shown in Figure 74. Post hoc analysis showed that there was not a significant difference in the PSE between the three peripheral conditions for Expanding flow (*F* (2, 10) = 2.717, *p* = 0.144, *n. sig*) but that there was for Contracting flow (*F* (2, 10) = 6.230, *p* = 0.017), supporting the suggestion that the Far results are responsible for the significant interaction between peripheral condition and flow direction.

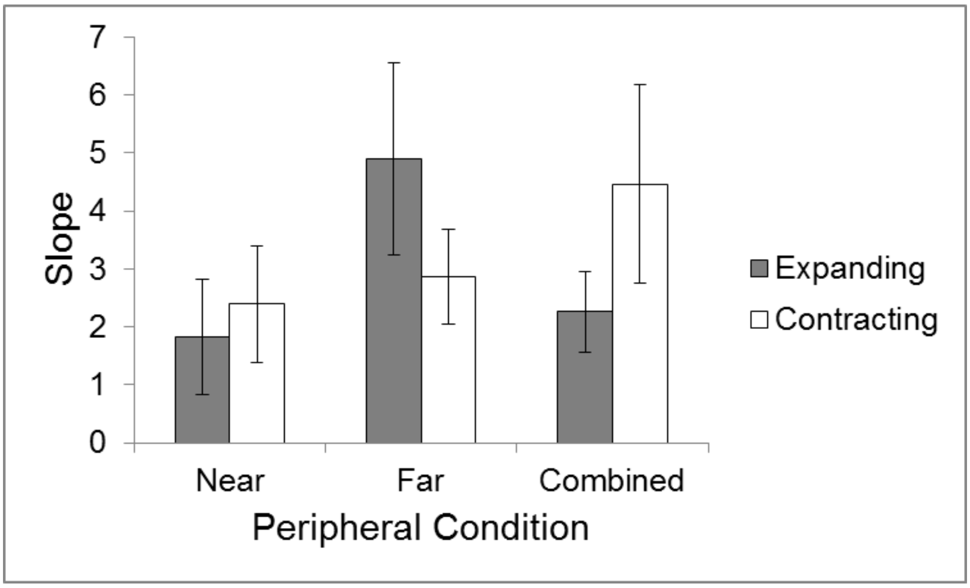

Figure 75 – Slope of psychometric function for each Peripheral condition and flow direction. Error bars show within-subject SE.

There were no apparent differences in slope between conditions (Figure 75). A 2 x 3 ANOVA confirmed there were no significant differences in slope as a function of peripheral condition (*F* (2, 10) = 1.209, *p* = 0.399, *n. sig*) or flow direction (*F* (2, 10) = 2.431, *p* = 0.180, *n. sig*). However, there was a trend indicating a steeper slope for Contracting flow than Expanding flow in the Near and Combined condition. These differences potentially indicate that observers responded with greater precision when flow depicted backwards self-movement.

4.3.2.1 Participant LM.

Participant LM is an experienced psychophysical observer with self-reported normal vision who did not report any difficulty with the task, and had sufficient time to practise before beginning the experiment. However, his results differed markedly from the other participants. In a related study (Rushton, unpublished data), the same participant showed the same ‘reversed’ pattern of responding in comparison to the other participants in the sample. This pattern cannot be explained by the participant confusing the response buttons during the task or from incorrectly reporting the global flow direction rather than the object motion. Instead, it appears that the participant’s responses were based upon another perceived aspect of the stimulus. After data collection, the participant revealed that he had suffered an unexplained period of total visual loss during childhood. Normal vision was subsequently restored. The participant's results, both in the present study and in related experiments not reported here, indicate an atypical processing of object size during self-movement. If LM is excluded from the analysis the same general pattern of results is obtained (Figure 76): For PSE values, the interaction between peripheral flow condition and flow direction remains significant (*F* (2, 8) = 8.185, *p* = 0.012).

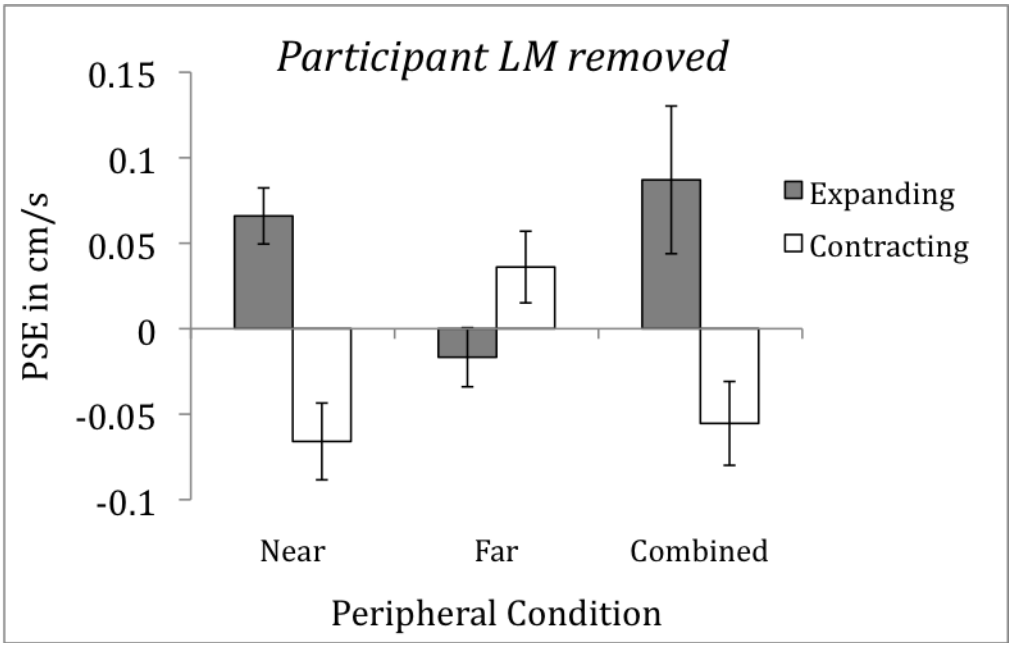

Figure 76 – PSE for each peripheral condition and flow direction when participant LM is removed from the dataset. Error bars show within-subjects *SE*.

As before, 2 x 3 ANOVA confirmed there were no significant differences in slope as a function of peripheral condition (without participant LM: *F* (2, 8) = 1.183, *p* = 0.355, *n. sig*) or flow direction (without LM: *F* (2, 8) = 0.963, *p* = 0.382, *n. sig*).

Although LM does not alter the group results it would be interesting to further investigate this atypical pattern of results as exploration of such individual differences may help to elucidate important aspects of the underlying flow parsing mechanism.

4.4 Chapter Discussion

This chapter investigated a different perceptual task to the previous chapters; the detection of an object's change in size during simulated self-movement. The results revealed that peripheral self-motion produces a perceptual bias in object size change, indicative of a parsing process. The findings suggest that for this task near peripheral flow contributes to flow parsing but that there is no apparent role of the far periphery. This reiterates a key finding of Chapters 2 and 3; that the near periphery makes a greater contribution to flow parsing for judgements of object trajectory than the far periphery. The current study also extends Rushton and Warren's (2011) work, which previously demonstrated that central visual flow allows observers to disambiguate retinal size change. However it is worth noting that the bias in perceived size change reported in this Chapter are 5-10 times smaller than the presented rates of expansion or contraction of the target disk and is therefore a very minor effect. Nevertheless, the change in the PSE does appear consistent across participants, as Figure 73 attests. Together with the present work, these findings demonstrate an effect of visual flow on judgements of size change and suggest that both central flow and near peripheral flow contribute to the ability to distinguish between changes in an object's retinal size due to self-movement and changes in retinal size due to changes in physical size.

The availability of peripheral visual flow appears to not only be important for judgements of object trajectory during self-movement but also for judgements of an object's size. This parsing process, which appears to be able to utilise information about self-movement from either central vision or the near periphery, means that stationary objects of a fixed size that change in retinal size due to self-movement are not mistakenly perceived to change in physical size. Therefore, the parsing of self-movement components from the retinal image might be thought of as a specific example of a size constancy mechanism. Such a mechanism would allow dynamic changes in an object's retinal size to be attributed to changes in the relative distance between the object and the observer because they arise from self-movement. Thus, visual flow enables the perceived size of an object to remain unchanged despite changes in retinal size arising from self-movement. This process is akin to the manner in which static cues to depth mean that the same object viewed at different distances is not perceived as different physical sizes in each case but instead maintains a constant perceived size because the retinal size of the object is scaled for distance (Holway & Boring, 1941). Recently, Mruczek, Blair and Caplovitz (2014) reported a new dynamic size-contrast illusion. In this illusion, a visual bar appears to shrink if an expanding box surrounds it and if other dynamic motion cues are present. This illusion reveals that a variety of visual motion cues, alongside the previously identified static cues, also play a part in allowing us to maintain a constant percept of size across a range of situations and suggests that visual self-movement information is not the only dynamic cue that can be utilised in this way. Mruczek et al.'s findings are distinct from flow parsing in that they considered how changes in the visual context in which an object is placed affects the perceived size of that object. Herein, I have considered how the visual context of self-movement in peripheral vision affects the perceived size of an object. The role of far peripheral flow is less clear in this study than in previous chapters, which have demonstrated that far peripheral flow contributes to flow parsing for judgements of object trajectory. The present study did not find evidence that far peripheral flow had any impact upon judgements of size change during either forward or backward self-movement. This initially suggests that far peripheral vision does not contribute to flow parsing for judgements of an object's size. However, there are a number of alternative explanations for these results.

The lack of a far peripheral contribution to flow parsing in this study may stem from a difference in the parsing process for judgements of object size during self-movement compared to object trajectory. Given that the results in this experiment suggest no contribution of far peripheral flow to parsing, the neural mechanisms for detecting size change may be different from those responsible for assessing object trajectory. This argument is supported by the fact that the far peripheral stimulus used in this study was very similar to the one employed in Experiment 1.2, in which forward and backward self-movement was also simulated. However, there were three key differences between the far peripheral flow stimuli used in these separate studies which should be noted: the speed of simulated self-movement (5 m/s in this study and 30 cm/s in Experiment 1.2), the size of the peripheral stripes (6 degrees here and 4.6 degrees in Experiment 1.2), and the duration of the flow presentation (~66 ms here and 3000-3200 ms in Experiment 1.2). Thus, in comparison to Experiment 1.2, the flow stimulus moved considerably faster and the peripheral bars were slightly wider. It is possible that the resolution of far peripheral vision might not have been sufficient to reliably identify self-movement from this stimulus. Yet the results of the speed discrimination experiment presented in Chapter 2 (Experiment 1.4, Page 100) argue against this explanation because there were no apparent differences in motion sensitivity between the near and far periphery when tested with the same stimuli. In addition, Orban et al. (1986) have shown that although velocity discrimination in peripheral vision is equivalent to central vision, higher velocities can be discriminated in the periphery. This would suggest that the presence of faster speeds in far periphery in the present experiment is unlikely to result in a reduction in the perception of self-movement from this stimulus.

Alternatively, the processes which underpin judgements of size during self-movement may be more sensitive to the spatial separation between the flow and the target. Looking at related judgements of angular expansion, there is a suggestion that the spatial separation between peripheral flow and a centrally presented object affects perceived object motion. Motion in depth (MID) and time-to-contact (TTC) are both judgements related to the dynamic change in an object's retinal size over time. TTC is a specific case of MID where the object is approaching the observer. For objects that are far away, these judgements mainly rely on the availability of monocular cues in the 2D retinal image as binocular cues are of limited use at distances beyond ~6 metres (Gregory, 1966, but this has been challenged more recently, see Gillam, Palmisano, Govan, Allison & Harris, 2009). The principle monocular cue to MID and TTC is a change in angular size, which is the same cue to size change in the present experiment and therefore results pertaining to TTC or MID are relevant to judgements of size change during self-movement.

Gray and Regan (2000) investigated TTC judgements during simulated self-movement and their findings are of particular relevance to the findings in the Far peripheral condition in the present study. In Gray and Regan's (2000) study they found that the influence of peripheral flow upon TTC judgements decreased as the distance between the central object and the surrounding flow was increased. The spatial separation between the visual flow and expanding object clearly affected the ability of observers to accurately assess TTC. Whilst judgements of TTC are not equivalent to judgements of size change, they do share the common monocular component of angular expansion. It therefore seems reasonable that Gray and Regan's results, showing a reduction in the influence of peripheral flow on TTC judgements, and the present results, showing a reduction in the contribution of peripheral flow to parsing for judgements of size change, may stem from the same underlying mechanism. This raises the question of whether there might be a greater role for local motion contrast when judging the angular expansion of an object than when judging object trajectory. As I mentioned in the introduction to this chapter, Warren and Rushton (2008) have investigated the global nature of flow parsing and sought to isolate the contribution of local and global motion to the effects they have reported. However all of the relevant studies have tested the influence of local and global motion on the perception of object trajectory rather than object size change. An interesting avenue for future work, which would draw together the present findings with Rushton and Warren's work utilising central visual flow, might investigate the contribution of local and global motion for other visual judgements during self-movement.

Another possible explanation for the results of the Far condition rests on the attentional demands of the task. The short stimulus presentation time (~66 ms) could have made this task more demanding than the trajectory judgements that participants made in the experiments of Chapters 2 and 3. No effort was made to equate the difficulty of these two tasks because there was no intention to directly compare the data across studies. If the central task was more demanding in the current experiment than in Experiment 1.2 then it is possible that there may be an attentional modulation of flow parsing. This idea is considered more fully in the General Discussion in relation to avenues for future research.

To summarise, near peripheral vision appears to contribute to the parsing process during judgements of object size. However the role of the far periphery in this process remains unclear. It may be the case that local motion contrast plays a more critical role in flow parsing for judgements of size change than it does for object trajectory. It is possible that the minor differences between the far peripheral stimuli in this study and those reported in Chapter 2 reduced the contribution of peripheral flow to parsing in this task, but this seems unlikely given the flow stimuli were still on the whole the same and because faster self-movement in the periphery would be more likely to improve the detection of self-movement rather than reduce it. Additionally, there may be an attentional aspect which underpins the different contribution of the far periphery for object trajectory and size change judgements, and this could potentially be explored in future research.

This chapter has helped to establish that the contribution of peripheral flow to the parsing process is not limited to judgements of object trajectory but that near peripheral vision also plays a role in judgements of size change during self-movement. Thus far, I have investigated the role of peripheral visual flow in flow parsing, and experimental findings suggest that this retinal region does contribute to this process. In Chapters 2-4 I tested the independent contribution of peripheral flow and found compelling evidence of flow parsing on the basis of peripheral self-motion for both linear and rotary self-movement and judgements of object trajectory and object size change. Building upon these findings, the final chapter explores whether peripheral flow might help to disambiguate central visual information associated with two forms of self-movement; yaw rotation and sideways linear translation. This provides a critical test of whether peripheral flow, and the different flow structures present in this retinal region, contributes to flow parsing in the presence of ambiguous central flow for these two types of self-movements.

Chapter 5. THE CONTRIBUTION OF PERIPHERAL VISION TO FLOW PARSING DURING YAW ROTATION AND LATERAL TRANSLATION

5.1 Chapter Summary

Chapters 2 to 4 tested the contribution of peripheral vision to flow parsing in the absence of central flow. In this final experimental chapter two further types of self-movement, lateral observer translation and yaw rotation, are examined. These two types of self-movement produce very different patterns of optic flow in peripheral vision. However, in central vision the same observer movements produce very similar patterns of flow. Therefore peripheral flow may have a particularly important function in this context as it could potentially disambiguate these two types of self-movement. The aim of the two experiments in this chapter was to determine whether the presence of peripheral flow improved the ability to distinguish between lateral translation and yaw rotation for flow parsing. In the first experiment each type of self-movement was simulated either with central information only, or with both central and peripheral information to investigate the influence of peripheral flow. To probe whether peripheral flow showed a greater contribution when central flow structure was ambiguous, the depth information differed between two central flow conditions in which the stimuli were either stereoscopic (unambiguous depth) or monocular (ambiguous depth). Observers fixated a central, upward moving, target at a stereoscopically defined distance of 65, 95, or 125 cm and then reported its perceived trajectory. During movement of the target, peripheral and central flow indicated either lateral translation or yaw rotation.

The addition of peripheral flow did not produce a systematic change in performance, suggesting that the contribution of peripheral flow to the flow parsing process is limited during lateral translation and yaw rotation. A second experiment using the same observers investigated whether the lack of effect might be due to the incongruence of the central and peripheral flow (motion of wireframe objects and motion of vertical bars respectively). This experiment presented wireframe objects in central and peripheral displays to produce a congruent motion stimulus. Performance in this study was compared to performance in the absence of peripheral flow in the first experiment. No difference was found. This supports the conclusion that peripheral flow makes a minimal contribution to flow parsing during lateral translation and rotation. This result stands in contrast to the results of the other experimental chapters and is somewhat surprising given the potential usefulness of peripheral flow structure in disambiguating lateral translation and yaw rotation.

5.2 Chapter Introduction

The FPH (Rushton & Warren, 2005) predicts that perceived object movement will differ as a function of the flow components in the retinal image and the location of the target in the scene. To perceive scene relative object movement, Rushton and Warren (2005) have suggested that the visual system identifies self-movement on the basis of retinal flow and subtracts retinal motion due to self-movement from the retinal image. Logically, if self-movement is misidentified then the subtraction of self-motion components from the retinal image will be not be appropriate and this will lead to incorrect parsing of self-motion. Yaw rotation and lateral translation produce very similar patterns of optical flow in central vision, but the differences between the two flow patterns is markedly different in peripheral vision. If yaw rotation is misinterpreted as lateral translation (or vice versa) then, as a result of the flow parsing process, objects which are stationary in the scene may be perceived to move, or objects which are moving in the scene may be perceived as stationary.

Research on the use of optic flow for judgements of heading direction has investigated this problem with respect to gaze rotations during forward translation and found that on the basis of retinal flow, gaze rotations during forward translation are misidentified as a component of lateral translation (Warren & Hannon, 1990). For the present research, this implies that visual information about self-movement in central vision may not always be appropriately separated into components of yaw rotation and translation. An analysis of the flow structure between central and peripheral vision leads to the prediction that peripheral flow provides additional visual information that might aid the ability to distinguish between yaw rotation and lateral translation and enhance flow parsing during these two types of self-movement.

5.2.1 Flow structure as a function of retinal eccentricity

Figure 77 shows the 2D pattern of flow that is produced when an observer makes a lateral translation to the left with eyes straight ahead (panel A), and during observer yaw rotation (about the y-axis; panel B).

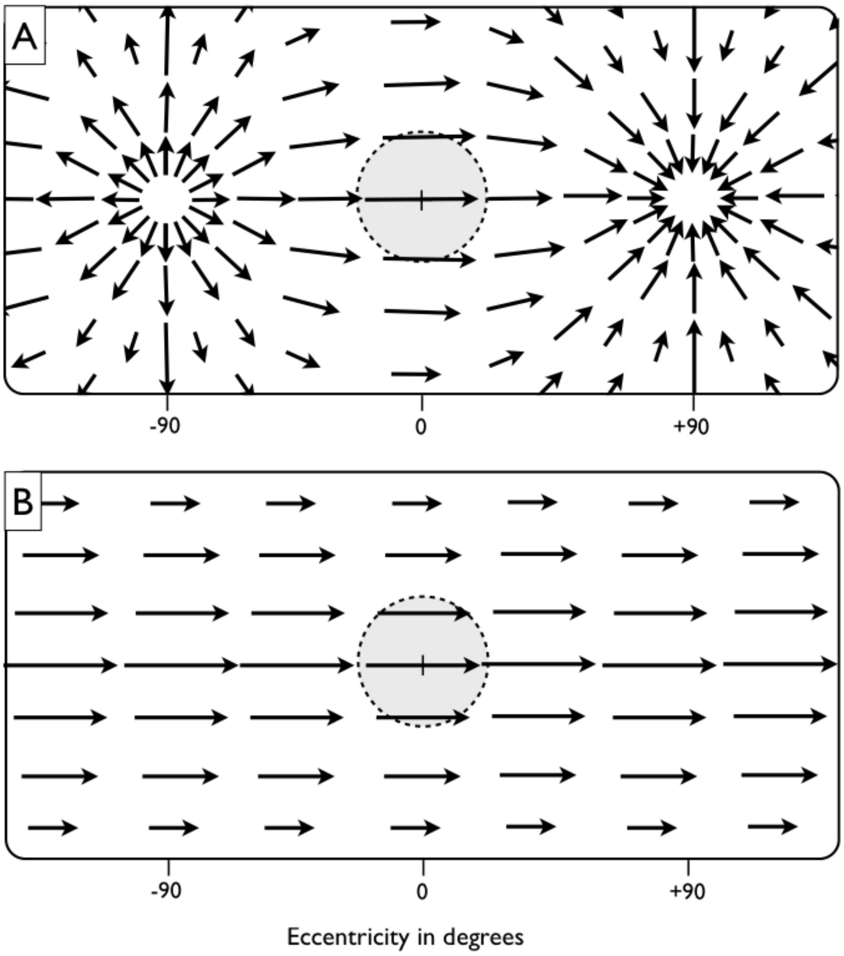

Figure 77 –A) Flow structure for translation to the left with observer looking straight ahead. Flow vectors vary with retinal eccentricity and a pattern of radial expansion is seen in the left peripheral visual field and contraction is present in the right peripheral visual field. B) Flow structure for rotation about the y-axis (yaw). Flow vectors do not vary with retinal eccentricity along the x-axis.

During observer translation the 2D flow structure differs as a function of retinal eccentricity along the x-axis but during yaw rotation the flow structure is the same regardless of retinal eccentricity. Assuming the observer is looking straight ahead, lateral translation generates lamellar flow in central vision (directly ahead of the observer) and in the far periphery the flow structure is radial in nature (Figure 77A). If the observer translates to the left, then in the left periphery an expanding pattern is present and on the right-side a contracting flow pattern is produced. Thus, peripheral vision and central vision are exposed to different patterns of flow during sideways movement of the observer. Observer rotation, unlike lateral translation, produces the same flow structure across the visual field (Figure 77B). If the reader compares the flow patterns for these two types of self-movement, it should be clear that they produce almost indistinguishable 2D flow fields in central vision, a potentially ambiguous cue to self-movement, but the flow patterns are markedly different in peripheral vision. If the visual system is sensitive to this peripheral flow then these differences in the periphery may improve the ability to detect and extract self-motion from the retinal image. In other words, peripheral information about self-movement may improve the ability to flow parse.

5.2.2 Flow structure as a function of depth

To test for a peripheral contribution to flow parsing during yaw rotation and lateral translation, I made use of the difference in depth dependence between these two forms of self-movement (as in Warren & Rushton, 2007). The relationship between the 2D flow field and the 3D structure of the environment differs between yaw rotation and lateral translation (see Figure 78). During translation the retinal motion of stationary objects in the scene is a function of their distance from the observer, whereas during rotation the retinal motion of objects in the scene is independent of their distance.

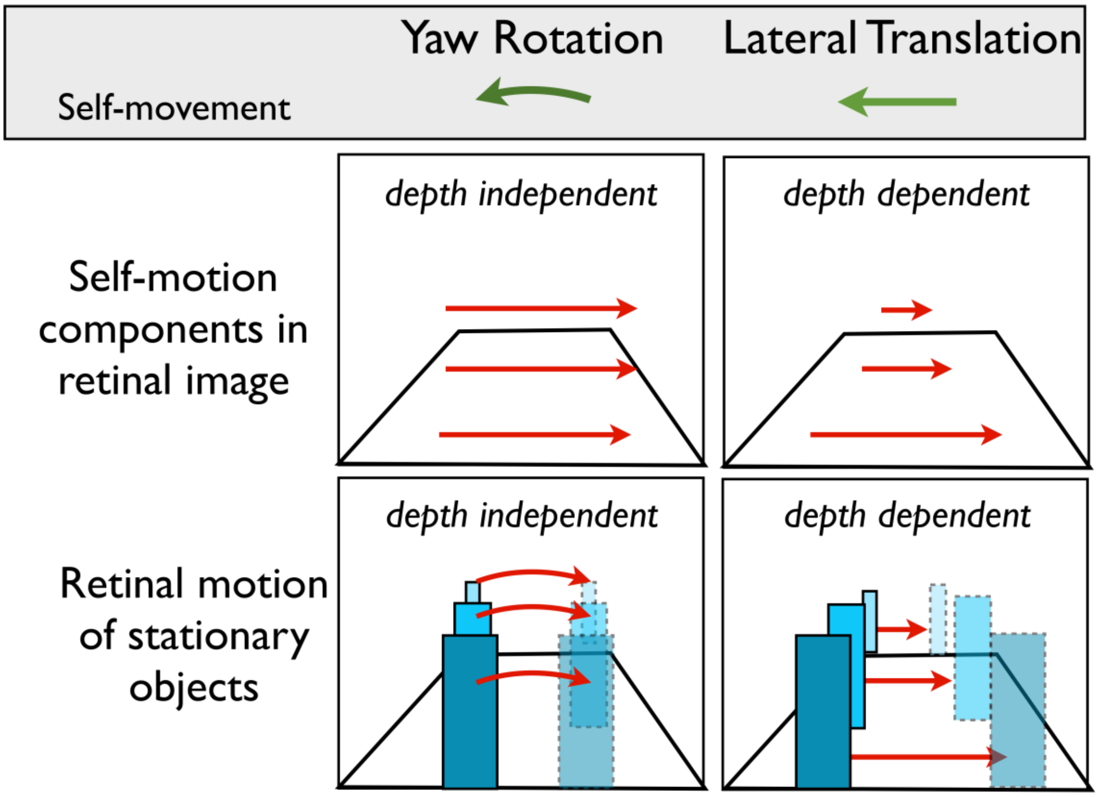

Figure 78 – Differences in flow structure and retinal motion of stationary objects during yaw rotation (left column) and lateral translation (right column). During rotation, objects in the scene all move by the same visual angle on the retina, which is equal and opposite the direction and degree of motion. During translation, objects at different distances move by different amounts, with closer objects being displaces across the retina more than objects which are further away.

During lateral translation (right column, Figure 78), stationary objects in the world which are closer than the point at which the observer is fixating will move in the retinal image in the opposite direction to self-movement and their retinal motion is a function of their distance from the observer and the velocity of self-movement. The projected image of an object on the retina will be displaced more by self-movement if the object is close to the observer than if the object is further away. In contrast, during self-rotation about the y-axis (yaw; left column, Figure 78), objects move on the retina by the same visual angle regardless of their distance.

5.2.3 Distinguishing yaw rotation from lateral translation for flow parsing

The availability of peripheral flow may make it much easier for the visual system to distinguish between lateral translation and yaw rotation. For flow parsing, it is important that the type of self-movement is identified so that the subtraction of self-motion from objects in the retinal image is appropriate. When retinal motion is not correctly identified as the product of self-movement then perception may be compromised; indeed the heading literature has shown that judgements of heading become less accurate when gaze rotations are attributed to a curved path rather than eye movements (Warren & Hannon, 1990). For lateral translation the subtracted component of self-motion should depend upon the distance of the object in the scene but for yaw rotation the subtraction of self-motion should be equivalent regardless of the distance of objects in the scene. Thus, if the visual system cannot distinguish between these two movements the ability to detect object movement during self-movement is likely to be compromised.

Warren and Rushton (2007) previously exploited the contrast between flow structure with respect to the geometry of the scene during yaw rotation and lateral translation to further examine whether perceived object trajectory is influenced by the flow components in the retinal image and the location of the object in the scene. They simulated lateral translation or observer rotation using a stereoscopic display in central vision. A target was positioned in the centre of the display and sat within an array of textured cubes (see Figure 6, Page 17). The target was presented in stereo and placed at a disparity-defined distance either in front of the plane of the screen (-20 cm), on the plane of the screen (0 cm) or beyond the plane of the screen (+20 cm). The textured cubes moved either to simulate an eye/head rotation or a lateral translation (i.e. a side step with gaze straight ahead) and the target moved upwards from fixation and, most importantly, its motion was scaled for distance. Observers were asked to fixate the target and report its perceived trajectory at the end of each trial using an onscreen response line.

The geometry of the scene allowed Warren and Rushton to make predictions about how perceived target trajectory would differ for rotation and translation when the target object was placed at each distance. They hypothesised that the perceived trajectory of the target would vary as a function of the self-movement type and the depth of the target in the scene. Figure 79 indicates these predictions. In this experiment, because the vertical component of target motion was scaled for distance (as in Figure 79, black arrows) the predictions for translation and rotation become counterintuitive. For lateral translation, the perceived trajectory (green arrows) is constant regardless of the distance of the target. This is because the upward motion of the target (black arrows) and the flow components to be parsed from the scene (red arrows) are *both* dependent on depth and therefore cancel each other out. In the rotation condition, *only* target motion is dependent on depth and therefore when self-motion is parsed from the scene the perceived trajectory of the target becomes depth dependent.

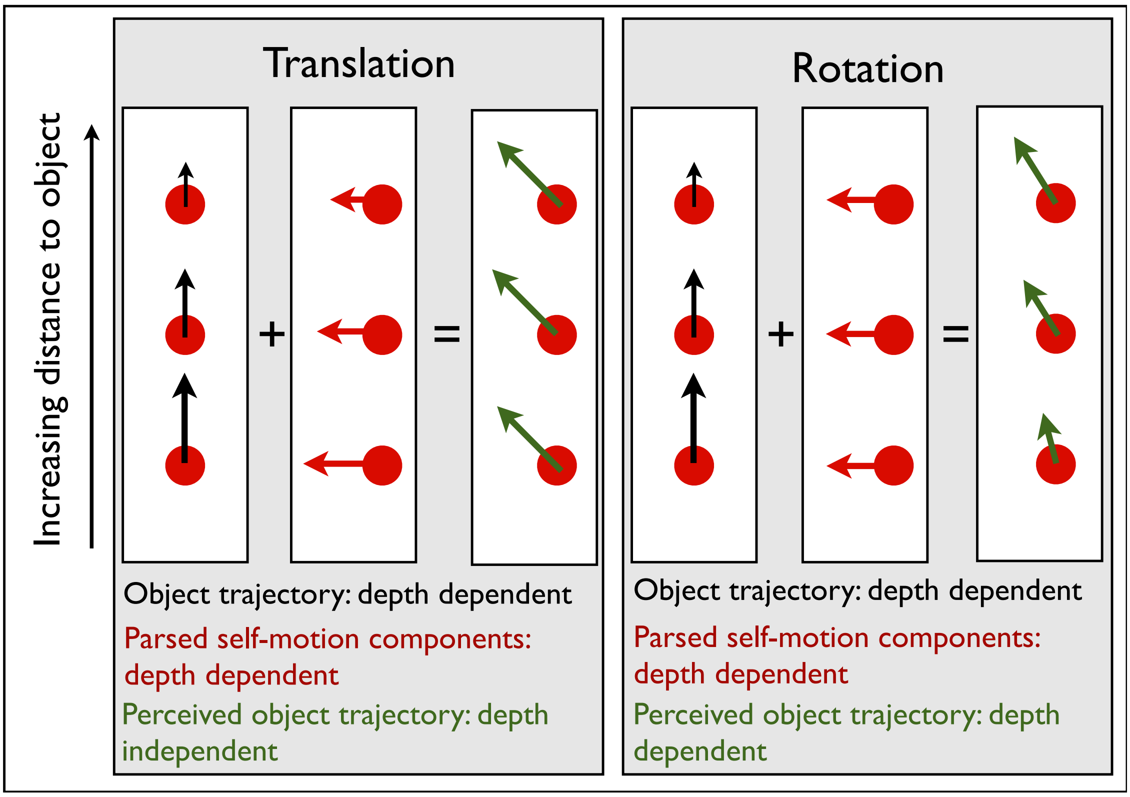

Figure 79 – Flow parsing predictions for an object at three different distances viewed during translation (left) or rotation (right). The object's motion (black arrows) is scaled with distance, equivalent to the object moving at a constant speed in the world. The self-motion components to be parsed from the retinal image (red arrows) are dependent on depth during translation and independent of depth during rotation. For someone familiar with the optic flow literature, this results in a perhaps counterintuitive prediction in which perceived object trajectory (green arrows) is *dependent* on depth during rotation but *independent* of depth during translation.

Figure 80 shows the results obtained by Warren and Rushton (2007). As predicted, perceived trajectory was dependent on target depth for rotation (red lines) with relative tilt increasing with the distance of the target. In the case of translation (blue lines) perceived target trajectory was independent of target depth. Thus, observers responded in line with the predictions of the FPH. The experiments in this chapter extend this study to investigate whether the availability of peripheral information influences this effect. Specifically, I test whether peripheral presented information indicating yaw rotation or lateral translation can strengthen this effect because the flow structure permits a more robust identification of lateral translation.

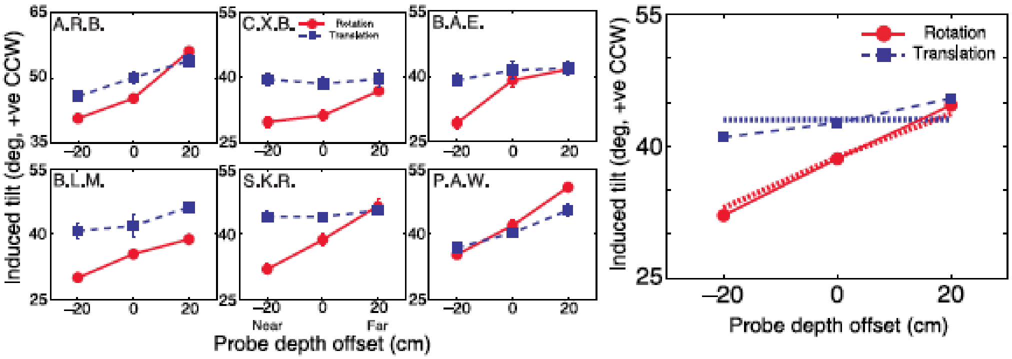

Figure 80 – Results of Warren and Rushton (Experiments 1& 2; 2007) for each observer (left) and a composite observer (right). Target trajectory judgements differed between the type of simulated self-movement and the depth of the target.

5.2.4 The utility of peripheral flow for flow parsing during yaw rotation and lateral translation

Peripheral vision provides visual information (Figure 77A) that specifies lateral translation. By comparison, the flow structure during yaw rotation is the same across central and peripheral vision (Figure 77B). As the flow structure for these two movements is markedly different in peripheral vision this leads to the hypothesis that peripheral vision will be particularly important for distinguishing between yaw rotation and lateral translation. If this self-movement information available on the peripheral retina can be detected, then it is reasonable to expect that the visual system will utilise peripheral flow when necessary, such as when central information is unreliable.

Support for peripheral sensitivity to patterns of radial flow is provided by research on the ability to discriminate the direction of motion across the retina, up to 40 degrees retinal eccentricity (Crowell & Banks, 1993). This prior work independently manipulated heading direction and retinal eccentricity to test whether visual judgements of heading direction were affected by the information available in the stimulus (i.e. whether the FOE was visible) or by the retinal location of the stimulus (whether flow was presented centrally or peripherally). They found that performance was more affected by the structure of the flow than the retinal location of the flow. The ability to discriminate motion direction was better when heading eccentricity was lower (more radial flow structure) than for larger heading eccentricities (more lamellar flow structure) irrespective of whether the stimulus was presented in central or peripheral vision. This suggests that the visual system is able to detect radial flow patterns when the FOE is presented in peripheral vision, as would be the case for lateral translation. Performance was marginally better when a radial flow stimulus was presented to the fovea than to the periphery, but this effect was not consistently observed. As a whole, these results suggest that central and peripheral vision are equally sensitive to radial and lamellar flow and it is the information contained in the flow stimulus that dictates the ability to judge heading. Specifically, when flow is more lamellar, direction discrimination is impaired compared to when the heading specified by the flow is less eccentric and the flow structure is more radial in nature.

Further support for a peripheral sensitivity to radial flow, specifically expansion, is provided by Regan and Vincent’s study of the ability to discriminate the rate of expansion for looming objects across the retina (Regan & Vincent, 1995). A looming object produces localised radial expansion of the same form as radial flow generated by linear translation. Thus, if observers can detect and discriminate the rate of expansion of an object in peripheral vision this would suggest that there are neurons with receptive fields in peripheral vision that are sensitive to this type of flow, which may also be utilised to detect components of self-movement consistent with lateral translation for flow parsing. Regan and Vincent found that the discrimination threshold for looming objects was relatively preserved with increasing retinal eccentricity up to the 32 degrees they measured in their study (thresholds increased by only 1.5-3.1 times from 0 degrees to 32 degrees eccentricity). It appears that the visual system can readily detect and discriminate locally expanding flow in the periphery. Although this study only investigated the detection of radial expansion up to 32 degrees retinal eccentricity, this provides some evidence that the ability to detect radial flow is not limited to the very centre of the visual field. Alongside Crowell and Banks’ (1993) findings, although also tested at lesser retinal eccentricities, this previous research indicates that in the present work, the presence of radial flow in peripheral vision (simulating lateral translation) will be detected by the visual system and contribute to flow parsing.

In contrast to Crowell and Bank's findings, one study that investigated a different aspect of self-motion perception, the influence of visual flow in central and peripheral vision on the regulation of stance, has claimed that peripheral vision is less sensitive to patterns of radial flow, such as would be present in peripheral vision during lateral translation (Stoffregen, 1985). This prior work reported that radial flow patterns presented in peripheral vision up to 90 degrees eccentricity, indicating lateral translation of the observer, did not produce large changes in postural sway. This was in contrast to sway responses to lamellar flow in central vision and lamellar flow in peripheral vision that produced large postural responses. The researchers suggested these results were evidence that peripheral vision is not especially well attuned for the detection of a radial flow structure. Stoffregen's results showed that lamellar flow in central or peripheral regions (as would be present during yaw translation) produced equivalent postural sway. The findings for lamellar flow are more in accordance with a consideration of the flow structure during yaw rotation (Figure 77), which is the same across central and peripheral regions of the retina. However the results for lateral translation do not tally with a consideration of flow structure in which radial flow in peripheral vision potentially provides a robust cue to self-movement.

At first glance, Stoffregen's work appears to suggest that the availability of peripheral flow during lateral translation might not contribute to flow parsing. Yet Stoffregen's study was concerned with postural response to optic flow rather than the pure detection of self-movement and this crucial difference means that the findings do not necessarily indicate that expanding or contracting flow in peripheral vision cannot be detected and utilised by the mechanisms that underpin flow parsing. One reason why Stoffregen's results may not marry with the potential utility of peripheral vision for detecting lateral translation is because the need for observers to make a postural response to lateral translation is not necessarily equivalent to the need for a postural response to forward or backward translation. This point seems particularly important to emphasise here as it draws a necessary distinction between the detection of self-movement from peripheral flow and the subsequent response to that self-movement. When an observer is stood with their feet parallel but apart, lateral movement is inherently more stable than movement along the fore-aft axis because the position of the feet means weight is more evenly distributed sideways than forwards or backwards. It is possible that Stoffregen's results reflect differences in the need to respond to visual flow indicating self-movement rather than the ability of peripheral vision to *detect* self-movement. If this were the case then in the present work peripheral flow might still provide a robust cue to lateral translation and feed into flow parsing mechanisms. On the other hand, if the results of the present study reveal that radial flow in the periphery does not contribute to flow parsing then this might suggest that postural responses to visual flow and judgements of object movement during self-movement both share some of the same underlying mechanisms.

In order to effectively test whether peripheral vision does contributes to flow parsing during lateral translation and yaw rotation it is also important to consider the reliability of flow in central vision. If central visual flow provides sufficient information about self-movement then it may be difficult to measure any impact of peripheral flow upon the flow parsing process. Therefore, in order to explore whether the parsing process can utilise information from across the visual field I changed the reliability of the central visual information. As detection of the 3D flow structure is an important cue by which yaw rotation and lateral translation can be distinguished in central vision, reducing the visual cues to depth may force a reliance on peripheral vision for disambiguating central flow. The depth information in the central flow cue was degraded by removing stereoscopic cues to depth, to create a monocular central flow condition that was presented either with or without peripheral flow. By removing stereoscopic depth information from central vision it becomes harder to assess whether the pattern of motion is commensurate with a rotation or translation (Warren & Rushton, 2009b). This is because when depth information is monocular the variation in speed in the retinal image could be either due to objects placed at different distances from the observer, or might arise due to noisy detection of rotation (Royden et al., 1994). Note that Warren and Rushton (2009b) showed that when a number of monocular depth cues are available, the ability to object trajectory during simulated self-movement is almost equivalent to when stereoscopic depth information is available. However, in the present experiment, only motion parallax specified the depth of objects in the scene. The monocular conditions were contrasted with those in which central flow was presented stereoscopically, either with or without peripheral information, to determine whether the peripheral cue to self-movement was more critical when 3D flow structure in central vision was ambiguous due to the lack of stereoscopic depth information.

The empirical findings presented thus far in this thesis have indicated that self-movement information in the far periphery makes a much smaller contribution to flow parsing than flow in the near periphery. In the previous chapters, peripheral flow was presented in isolation, but the studies in this chapter present central flow and far peripheral flow. Given that the previous results showed a minimal contribution of the far periphery to flow parsing, if there is similarly a small far peripheral contribution to flow parsing during yaw rotation and lateral translation then such an effect may not be evident in the presence of central flow. To guard against this outcome, two central flow conditions were used; one in which stereoscopic cues to depth were present and provided a rich cue to depth, and a second condition in which only monocular cues to depth were present. The use of the monocular condition aimed to maximise any potential contribution of the periphery by limiting the information that is available centrally.

5.3 Experiment 4.1: Effect of peripheral flow on flow parsing during yaw rotation and lateral translation

This study investigated whether the presence of peripheral flow enhances the ability to distinguish self-motion associated with yaw rotation from self-motion indicating lateral translation. The central flow stimulus was similar to Warren and Rushton’s but wireframe polygons (hereafter referred to as objects) were used in the central display instead of cubes and a peripheral stimulus was included in the present study. It was anticipated that peripheral information might be weighted more heavily by the visual system when central visual information was more ambiguous. To manipulate the reliability of the central self-movement information, the central flow stimulus was presented either monocularly or stereoscopically. The central information was presented either alone or with the addition of far peripheral flow to produce four viewing conditions: 1) Central stereoscopic flow without peripheral flow 2) Central stereoscopic flow with peripheral flow 3) Central monocular flow without peripheral flow 4) Central monocular flow with peripheral flow. Figure 81 depicts the viewing conditions. It was hypothesised that peripheral flow would make the greatest contribution to flow parsing when central information was ambiguous (monocular condition). When central information provided a strong cue to self-movement (stereoscopic condition) there was not expected to be much benefit of peripheral information. Thus, an interaction was anticipated between the central flow condition (stereo/mono) and the presence or absence of peripheral flow; with a benefit of peripheral flow in the monocular conditions but not in the stereoscopic conditions.

5.3.1 Methods

5.3.1.1 Participants.

Fourteen observers (7 male; age range = 22-31, M = 25.43, *SD* = 2.59) were recruited from postgraduates and undergraduates who had taken part in previous studies. Eligibility criteria and ethical considerations were the same as in Experiment 1.1 with the additional constraint that all observers reported good stereovision.

5.3.1.2 Apparatus.

The laboratory set up was the same as outlined in Chapter 2 (i.e. Experiment 1.2) except that an additional ChristieT Digital Systems Projector (model DS+26) projector was used. One projector displayed the image for the left eye and the other projected the right eye. Each projector was fitted with a linear polarising filter (SilverFabric SF-POLAR linear polarisers: 45 degrees and 135 degrees). Participants viewed all conditions wearing similarly polarised glasses. The frames of the glasses were made of thin black plastic and the arms were approximately 1 cm thick at their widest point. The frames did not excessively obscure the monitors positioned to the side of the head and the flow stimuli were still clearly visible. All responses were made using a Logitech Attack 3 Joystick.

5.3.1.3 Stimuli.

The stimulus on the central projection screen consisted of 24 wireframe polygons with a radius of 7.5 cm which were drawn on a 2D grid measuring 75 cm (x) x 50 cm (y). Wireframe objects were chosen because they provide more structure to the 3D objects as the rear face is not occluded. In addition there was a restriction on the level of anti-aliasing that could be employed in the current study due to the use of four displays (2 x projectors and 2 x peripheral monitors) and rendering these objects required a lower level of anti-aliasing than the textured cubes used by Warren and Rushton (2007). Each shape was randomly orientated in pitch, yaw and roll and randomly repositioned within a range of ±5 cm on the x and y axis. The position of each shape was also allowed to vary randomly in the z-direction within -25 cm to +25 cm of the plane of the screen.

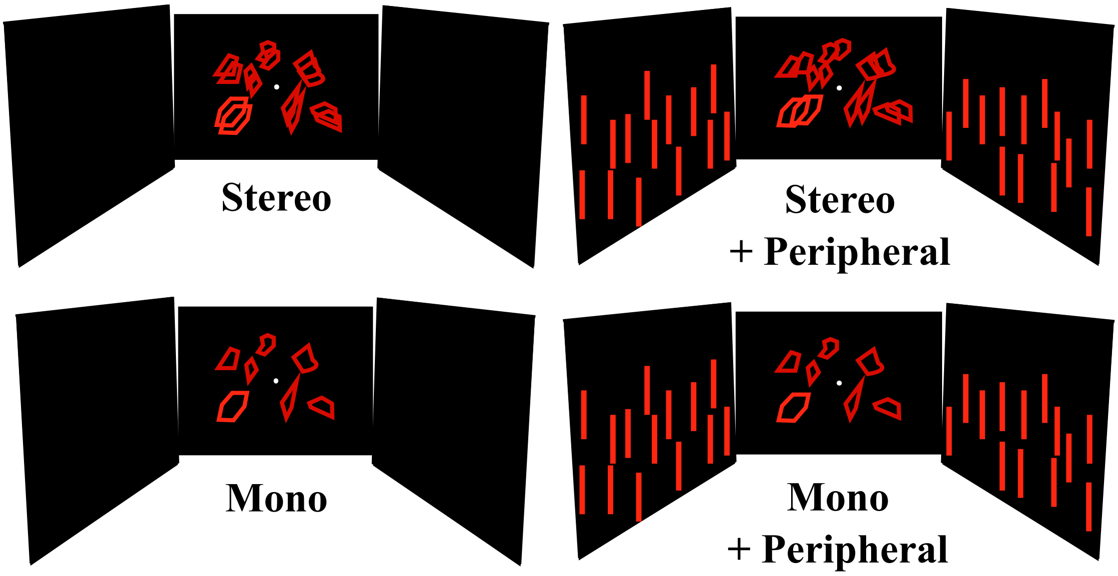

Figure 81 – Four viewing conditions used in Experiment 4.1. The left column shows the Stereo and Mono conditions where no peripheral stimulus is present. The right column shows the Stereo + Peripheral and Mono + Peripheral conditions in which flow stimuli are also present in the far periphery on the monitors to the side of the head.

To produce the stereoscopic stimuli on the central screen, the left and right eye images were presented using different projectors (see *Apparatus*). The inter-pupillary distance was set to 6.4 cm. In the stereo condition the wireframe objects were drawn in red at half the maximum intensity (128 in 255 RGB colour space) to reduce the cross talk between the left and right eye images.

In order to probe whether peripheral flow was more important for flow parsing when central information was more ambiguous, a second central flow condition was used in which depth information was reduced by removing stereoscopic cues to depth. If flow parsing mechanisms can utilise information from across the retina then peripheral information should be most informative when central information is less reliable. In the monocular condition, each projector displayed 12 wireframe objects. Whether a given object appeared in the left or right eye was randomly determined on each trial. This procedure was chosen over just presenting all the objects in one eye because it reduced the difference in luminance between the two projected images and pre-testing had suggested this led to reduced binocular rivalry and an improved percept of the scene.

It was important that observers could determine the depth of the target because the predictions of a peripheral contribution to flow parsing differ with target depth for the rotation condition. The predictions for a peripheral contribution are in accordance with the basic predictions of a flow parsing mechanism where perceived trajectory is dependent upon the 3D position of the object in the scene. To assist with the percept of the target's depth in the scene by providing relative depth information, the monocular stimulus was supplemented by eight small, limited lifetime dots drawn in the central scene and arranged using the same method as for the wireframe objects. During the stationary phase of the trial, each dot lasted 20 frames before it was repositioned. During the motion phase of the trial the dots were then repositioned every frame (60hz refresh rate) for the remainder of the trial and produced high-speed flickering dots.

In the two peripheral conditions, the monitors to the side of the head presented flow stimuli in the far periphery. The stimulus consisted of 200 short wireframe cylinders (1.5 cm diameter x 18.5 cm height) that were drawn on a receding ground plane around the observer and varied in distance from 27-112 cm (a schematic version of the stimuli can be seen in Figure 81).

A centrally positioned target (0.6 cm diameter) was placed within the scene, at a depth of 65 cm, 95 cm or 125 cm (-30 cm, 0 cm, or +30 cm with respect to the plane of the screen). Target depth was defined stereoscopically in all conditions and the target was always drawn at half the maximum intensity

(128 in 255 RGB colour space) to reduce unwanted crosstalk between the left and right eye images. In all conditions the target translated upwards.

5.3.1.4 Design.

Two IVs were manipulated to produce four experimental conditions; Central viewing condition (2 levels: Stereo/Mono) and the presence of far peripheral stimuli (2 levels: with peripheral/without peripheral). Each of these conditions was run as a separate experimental block and the order in which participants completed the different conditions was counterbalanced across observers. Within each viewing condition, the depth of the target in the scene was manipulated (-30 cm, 0 cm, 30 cm) and the type of self-motion (Rotation/Translation). For each type of self-motion both left-ward and right-ward motion was simulated in different trials and the target was presented at nine different tilt trajectories within a ±32 degree range in 8-degree steps. This resulted in a total of 108 trials per experimental condition. The DV was relative tilt, which provided a measure of the difference between the onscreen target trajectory and perceived target trajectory in order to assess whether the results showed evidence of a peripheral contribution to flow parsing. To generate a measure of the difference in relative tilt between the rotation and translation conditions and to compare the effect across viewing conditions (mono/stereo and with peripheral/without peripheral), I plotted the data for the rotation and translation condition separately and fitted a line of best fit for each flow condition. The difference in gradient between the lines of best fit for the rotation and translation conditions was then used to assess whether there were any differences between the viewing conditions.

5.3.1.5 Procedure.

On each trial, all stimuli initially remained stationary for 2 seconds to aid fusion of the left and right eye images, and then the scene and target began to move. The central objects and peripheral stimuli simulated either a leftward or rightward rotation at a rate of 1.5 degrees/s or a leftward or rightward lateral translation at a speed of 2 cm/s for 2 seconds in both cases. For comparison, the speeds used in Warren and Rushton (2007) were: rotation: 0.75 degrees/s and translation: 2 cm/s. The speed of simulated self-movement was slightly faster for the rotation condition in the present study compared to Warren and

Rushton's study because pretesting showed that, due to the slower refresh rate in the present work, the original rotation speed made it difficult to determine the movement of the scene within the duration of the trial. The target used in the current experiment translated upwards at a constant speed of 0.6 cm/s (Warren & Rushton's target moved at 0.9 cm/s). The target speed was reduced slightly from the speed used by Warren and Rushton because the frame rate in this study was slower (60hz versus 100hz) and this change ensured the target motion remained smooth. At the end of each trial a response line was presented and participants set the angle of the line to match the perceived target trajectory using the joystick.

Each condition took approximately 20 minutes to complete and was run in a separate block to provide participants with a short break in-between. Participants typically completed the data collection across two experimental sessions of approximately 45 minutes each.

5.3.1.6 Analysis.

The raw data was coded as if all rotations and translations were leftward by reversing the sign of the relative tilt measure for rightward trials, i.e. as if the scene always moved to the right. As in previous experiments, relative tilt was coded so that a bias in the ACW direction was positive, i.e. a 10 degree bias to the left of vertical would be +10 degrees and a 10 degree bias to the right of vertical would be -10 degrees. For each of the four viewing conditions, two-way within-subjects ANOVA was used to test for a difference in relative tilt as a function of target depth and self-motion type. This tested that the pattern of results predicted by the FPH was evident. An interaction was expected with the magnitude of relative tilt increasing more as a function of target depth during yaw rotation than during lateral translation (see Figure 80 for the predicted pattern of results which have previously been reported by Warren & Rushton, 2007).

The main aim of the present experiment is to ascertain whether the presence of peripheral flow influenced this effect. Lines of best fit were fitted to the plotted rotation and translation data and then the difference in gradient of the lines (rotation - translation) was calculated in order to draw comparisons between the different viewing conditions. A larger difference in gradient between rotation and translation conditions would suggest that participants found it easier to distinguish between the two types of self-movement. It was predicted that peripheral information would increase this difference, i.e. the flow parsing effect, more in the monocular condition than in the stereoscopic condition, as in Figure 82.

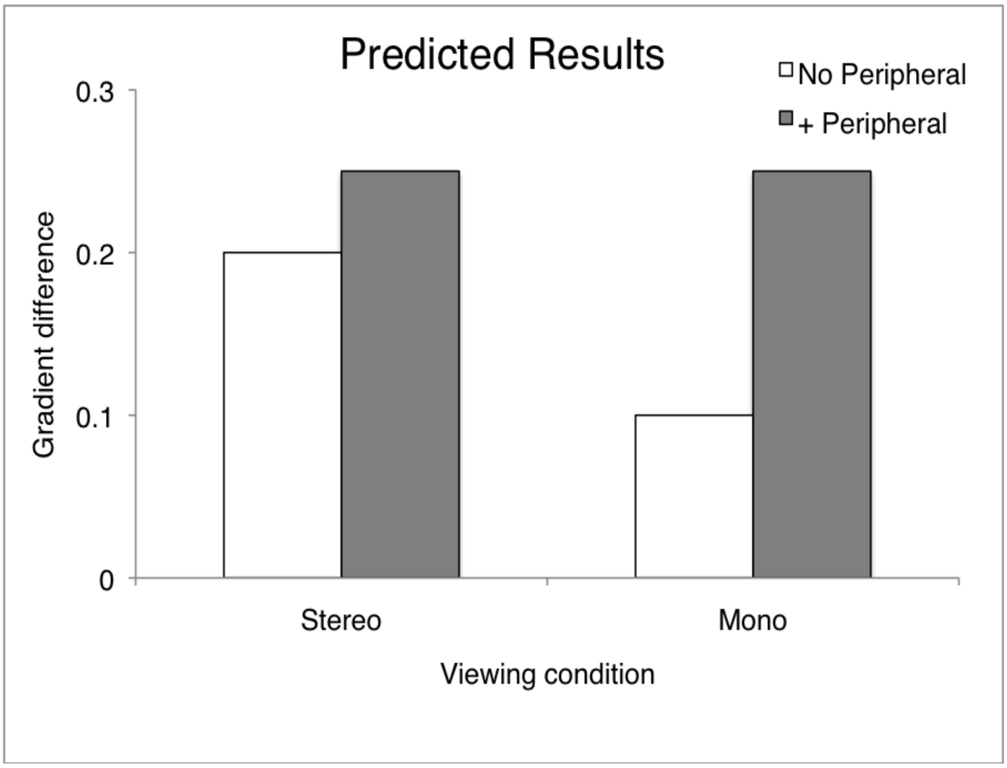

Figure 82 – Predicted results showing a peripheral contribution to distinguishing between rotation and translation, with a greater benefit of peripheral information when central information is monocular than when central information is stereoscopic.

A two-way within-subjects ANOVA (Stereo/Mono x no peripheral/+peripheral) was conducted to identify whether the difference in gradient was greater when peripheral information was available than when it was absent. A significant interaction would indicate that peripheral information had a different effect during the stereoscopic than monocular conditions.

5.3.2 Results and discussion

The results are presented in two sections. The first section considers the effect of self-movement type and target depth on perceived object trajectory (as measured by relative tilt) and confirms that the results demonstrate a signature flow parsing effect. The second section utilises the difference between the rotation and translation conditions to examine this effect across the four viewing conditions and assess the critical question of whether the presence of peripheral flow had any impact upon this effect. Thus, relative tilt results indicate the influence of visual flow upon perceived target trajectory in each viewing condition and the gradient difference between rotation and translation then provides a measure of how the influence differs between the viewing conditions.

5.3.2.1 Rotation versus translation

In the two stereoscopic conditions (top row, Figure 83), the results show that perceived target trajectory differed depending on the type of self-movement (rotation or translation) and the depth of the target in the scene. Specifically, relative tilt in the rotation condition increased as the distance of the target increased, and the translation condition showed less variation in relative tilt with increasing target distance. In the two monocular conditions this pattern is less distinct (bottom row, Figure 83) as relative tilt in the translation condition appears to vary more with target distance than in the equivalent stereo conditions. In the Mono + Peripheral condition, relative tilt appears to vary with target depth for both the rotation and the translation conditions indicating that observers may not have been able to distinguish between the two forms of self-movement in this condition.

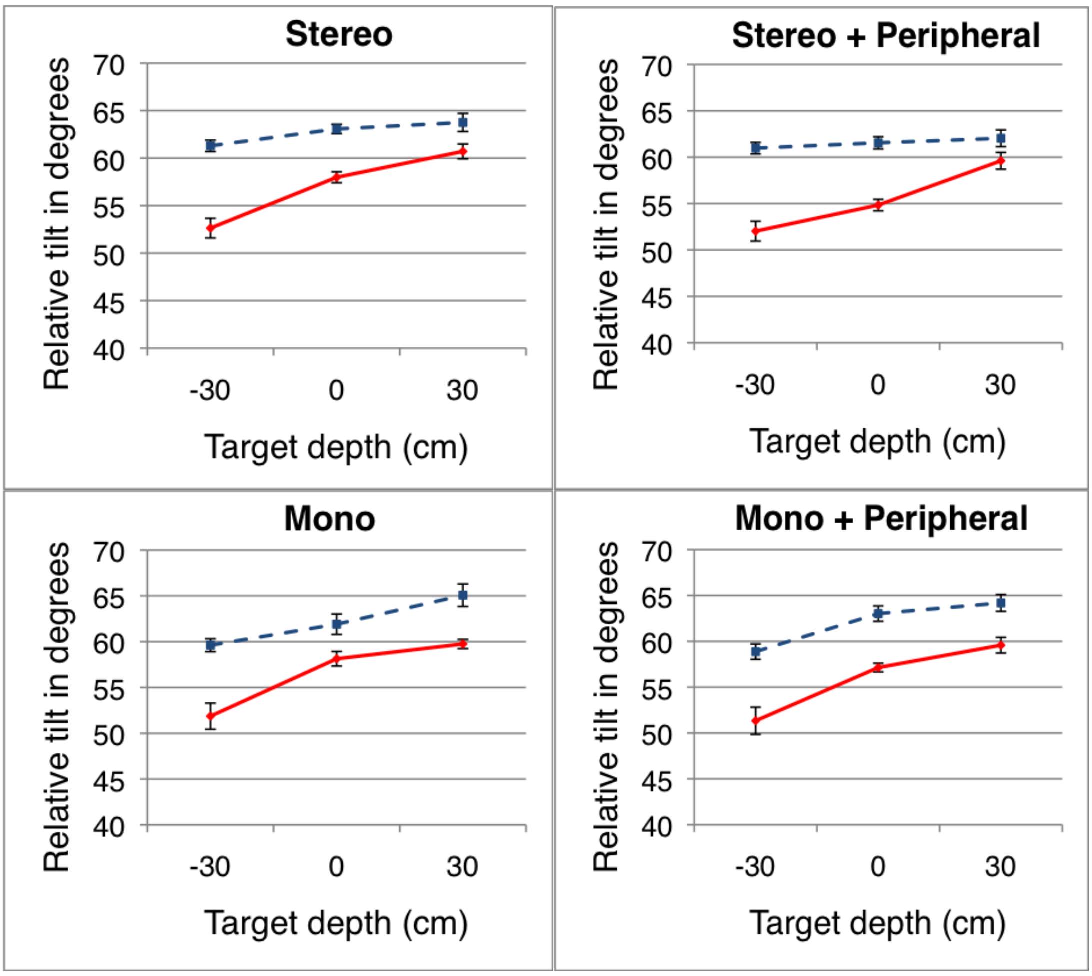

Figure 83 – Mean relative tilt in degrees as a function of self-movement type (blue, dashed line = translation, red, solid line = rotation) and target depth for each viewing condition. Error bars show within-subjects SE.

A two-way ANOVA was performed for each viewing condition and confirmed the predicted interaction between self-motion type and target depth was present in all conditions except the Mono + Peripheral condition (Stereo: *F* (2, 26) = 8.028, *p* = 0.002; Mono: *F* (2, 26) = 4.703, *p* = 0.018; Stereo + Peripheral: *F* (2, 26) = 8.347, *p* = 0.002; *F* (1.352, 17.573) = 1.776, *p* = 0.202, *n. sig*; Greenhouse-Geisser corrected).

5.3.2.2 Presence of Peripheral flow

Comparing the difference in gradient between the four conditions (Figure 84) it can be seen that the difference is much larger in both of the stereoscopic conditions than the two monocular conditions. However, there does not appear to be any influence of peripheral flow on the size of this difference regardless of whether the central information was stereoscopic or monocular.

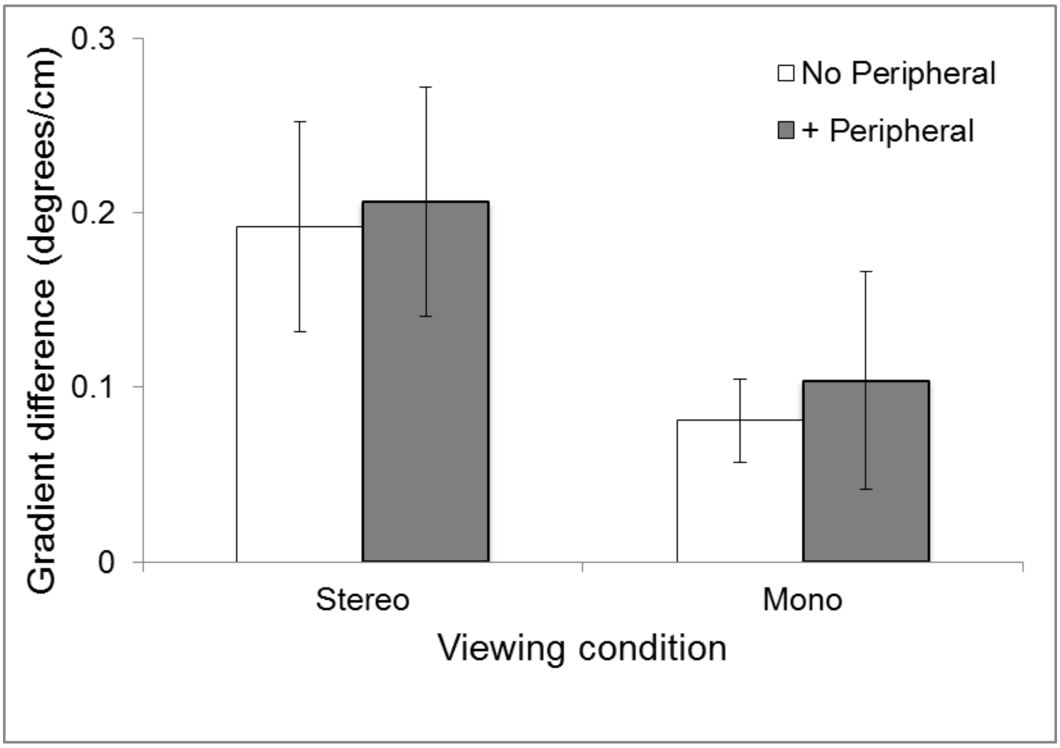

Figure 84 – Mean gradient difference as a function of central viewing condition and peripheral condition. Error bars show SE.

A two-way ANOVA confirmed that the gradient difference was significantly higher for the stereoscopic than the monocular conditions (*F* (1, 13) = 5.134, *p* = 0.041), but that there was no difference between the no peripheral and the + Peripheral conditions (*F* (1, 13) = 0.119, *p* = 0.735, *n. sig*) indicating that the presence of peripheral information did not affect the gradient difference. Counter to the hypotheses, the interaction term was also not significant (*F* (1, 13) = 0.006, *p* = 0.938, *n. sig*) indicating that peripheral information did not increase the gradient difference significantly more in the mono condition relative to the stereo condition.

The results of this study replicate the findings of Warren and Rushton (2007) and showed that perceived target trajectory differed as a function of the type of self-movement and target depth. The difference between the two self-motion conditions was greater during stereoscopic than monocular viewing and, as expected based upon a consideration of flow structure, this difference appears to be driven by changes in the translation condition. The line plots in Figure 83 show that the rotation data does not vary much between the different viewing conditions with all plots showing a clear increase in relative tilt with increasing target distance. Yet in the translation condition, the gradient of the fitted line differs between the stereo and mono viewing conditions, with less change in perceived relative tilt with target depth during stereoscopic viewing than during monocular viewing. Thus, it is the changes in perceived target trajectory during lateral translation which give rise to the changes in gradient difference between the monocular and stereoscopic conditions. This suggests that when central information is less reliable, as in the monocular condition, the ability to correctly perceive scene-relative object movement is reduced during lateral translation but not during yaw rotation. These findings are in line with an analysis of the information that is available in central vision during these two movements. In contrast to the monocular conditions, when central information provides robust depth cues then the pattern of self-motion seems to be readily identified as translation or rotation and the parsing process enables observers to detect any object movement relative to the scene. The results are in line with those reported by Warren and Rushton (2009b), demonstrating the importance of stereoscopic depth cues for assessing object movement during self-movement.

The results of this experiment did not reveal any benefit of peripheral flow in distinguishing between lateral translation and yaw rotation. If there was any benefit of the peripheral information then it is reasonable to assume that it would have come to the fore in the monocular condition where, in the absence of peripheral information, the pattern of relative tilts was less in line with the predictions of the FPH. It is possible that the lack of peripheral effect is due to the type of stimuli that were presented in peripheral vision. It may be the case that far peripheral flow stimuli did not provide a sufficient cue to self-movement. The vertically orientated cylinders that were used to indicate self-movement in the periphery are limited in their ability to signal expansion or contraction because an increase in their size is only really noticeable in the horizontal direction (i.e. the bars appear to get wider as they move closer or narrower as they recede). The use of an alternative peripheral stimulus might reveal a benefit of peripheral flow that was not observed with the stimuli used in this experiment.

Another reason to consider modifying the peripheral stimuli is because it is possible that the use of different stimuli in central displays and peripheral monitors compromised the integration of the self-movement information. As the self-motion stimuli differed, with wireframe objects in central vision and solid bars in the periphery, observers may not be able to successfully combine these two cues to self-movement as they do not superficially appear to be the same. Although this has not proved to be an issue in the earlier experiments, given the surprising null result of this experiment it is important to rule out this explanation. Therefore, the next experiment used wireframe objects in central *and* peripheral vision to provide uniform self-motion information across the two displays.

5.4 Experiment 4.2: Stimulus congruence control study

In this study the wireframe objects that were employed as the central flow stimulus in Experiment 4.1 were also used for the far peripheral stimulus. Thus, the flow stimuli were congruent across the two displays.

The stimulus conditions in this experiment were run alongside the conditions in Experiment 4.1 in a counterbalanced design following the first phase of data collection, but the data is presented here as a separate experiment. The participants in this experiment were the same as in the previous experiment and the congruent stimuli conditions were included as part of a counterbalanced design following the first phase of data collection for the previous experiment. As such, the results of this study are compared with the data from the conditions in Experiment 4.1 in which no peripheral information was presented. This should help to determine whether there is any benefit of peripheral information when the peripheral and central flow stimuli are congruent.

In comparing the data from the no peripheral Stereo and Mono conditions of Experiment 4.1 and the new peripheral conditions in the present experiment there are two possible outcomes: 1) If the results of Experiment 4.1 are due to the incongruence of the stimuli then the results of this experiment should show that when the stimuli in the central display and the far peripheral display are congruent there is a benefit of the peripheral information. 2) However, if the results of the previous experiment represent a lack of peripheral input to flow parsing for distinguishing between these two types of self-movement then the results of this study will mirror those of Experiment 4.1. Namely, there will be no marked difference in the pattern of the results when peripheral flow supplements the central self-movement information. Within the new data presented in this study it was expected that the stereoscopic condition would show a larger gradient difference than the monocular condition, as in Experiment 4.1.

5.4.1 Methods

5.4.1.1 Participants.

Participants were the same as those who took part in Experiment 4.1.

5.4.1.2 Apparatus.

The apparatus was identical to the previous experiment.

5.4.1.3 Stimuli.

The stereoscopic and monocular central stimuli and the target were all the same as in the previous experiment. The far peripheral objects were identical to the wireframe polygons used in central vision. There were two viewing conditions which can be seen in Figure 85.

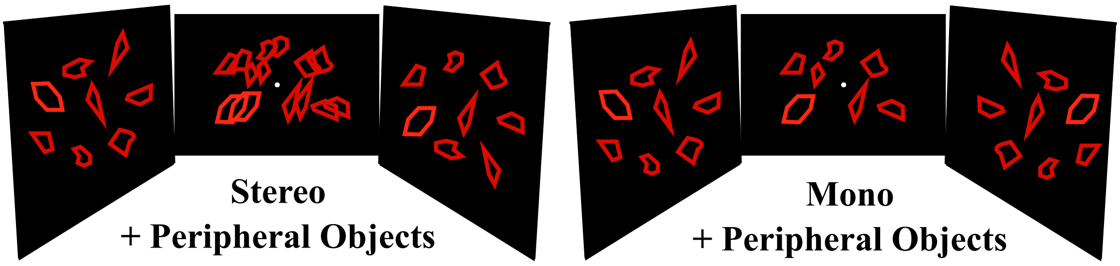

Figure 85 - Viewing conditions used in Experiment 4.2. Central stimuli were either stereoscopic (left) or monocular (right) and wireframe objects were presented in the far peripheral in both conditions.

The method for positioning of the peripheral objects horizontally (across the monitor) and in depth (perpendicular to the participant's line of sight) was identical to the arrangement of the peripheral bars in Experiment 4.1. Each shape was initially positioned on a fronto-parallel plane (y-axis) within a grid formation. From these initial positions, the specific location of each shape was then shuffled within a range of ±5 cm on the x, y, and z axis. As in Experiment 4.1 the roll, yaw, and pitch of each shape was free to vary.

5.4.1.4 Design.

One IV was manipulated (central viewing condition) to produce a stereoscopic and a monocular condition. Peripheral information was present in both conditions. As before, within each condition, the depth of the target in the scene (-30 cm, 0 cm, 30 cm) and the type of self-motion (Rotation/Translation) was manipulated. For each type of self-movement both left- and right-ward movement were simulated and the target was presented at nine different tilt trajectories within a ±32 degree range. This resulted in a total of 108 trials per experimental condition. The DV was relative tilt, measured in degrees. A within-subjects design was employed and most participants completed data collection in a single experimental sessions of ~60 minutes duration each. The same participants as in the previous experiment took part in this study. The data collection for the two experiments in this chapter was conducted concurrently. This allowed the conditions in Experiment 4.1 and 4.2 to be counterbalanced across observers so it was *not* the case that all participants completed the conditions in Experiment 4.2 after Experiment 4.1. This enabled within-subject analysis to be conducted across the two studies.

5.4.1.5 Procedure.

Trial procedure was identical to Experiment 4.1.

5.4.1.6 Analysis.

As in Experiment 4.1, the relative tilt data was analysed using a two-way within-subjects ANOVA was used to test for a difference in relative tilt as a function of target depth and self-motion type. An interaction was anticipated for both the monocular and stereoscopic conditions. Linear gradients were fitted to the Rotation and Translation data as in the previous experiment and the gradient difference was calculated (Rotation – Translation).

In addition to the analysis of the new data in this experiment, the data was compared with the Stereo and Mono conditions from the previous experiment to provide a baseline with which to assess the influence of the peripheral display. A two-way within-subjects ANOVA (Stereo/Mono x with/without Peripheral) was conducted on the gradient difference data. As in Experiment 4.1, it was predicted that peripheral flow would benefit the flow parsing process more in the monocular condition than in the stereoscopic condition (Figure 86 shows predicted interaction). In addition, a main effect of viewing condition was anticipated, with significantly larger gradient differences in the stereoscopic conditions than the monocular conditions.

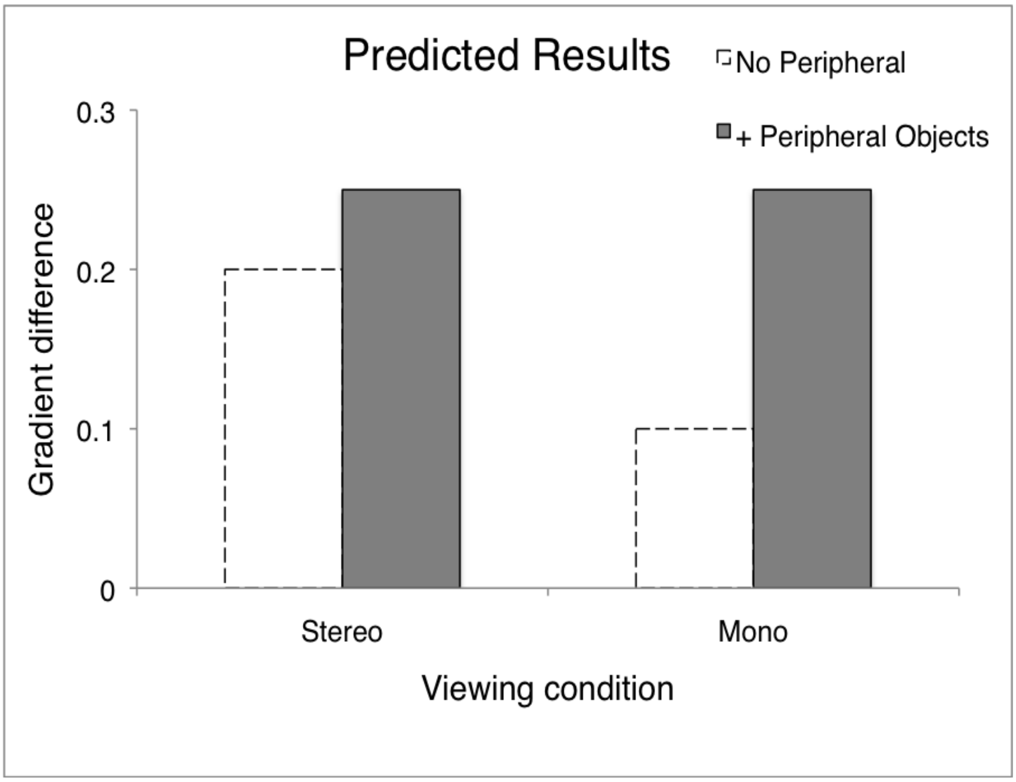

Figure 86 – Predicted pattern of results for the comparison of Experiment 4.1 No peripheral conditions (Stereo and Mono) and the peripheral objects conditions of the present experiment. An interaction was expected, indicating a greater peripheral benefit during monocular central viewing than during stereoscopic viewing.

5.4.2 Results

5.4.2.1 Rotation v Translation

In Figure 87 the pattern of relative tilt for the translation and rotation conditions are notably similar and counter to the hypotheses. It does not appear that perceived trajectory varied as a function of target depth and self-movement type as it did in Experiment 4.1. A two-way within-subjects ANOVA revealed that there was a significant interaction between self-motion type and target depth in the monocular condition (*F* (2, 26) = 4.178, *p* = 0.027) but not in the stereo condition (*F* (2, 26) = 2.261, *p* = 0.124, *n. sig*). This suggests that, unlike in the previous experiment and contrary to expectations, in the stereoscopic condition participants were unable to differentiate between the two types of self-movement. It is clear from Figure 87 that the magnitude of the effect was similar to the previous experiment but the depth independence that would indicate a peripheral contribution to flow parsing was absent in the translation condition. Some potential reasons for this result are presented in the Chapter Discussion.

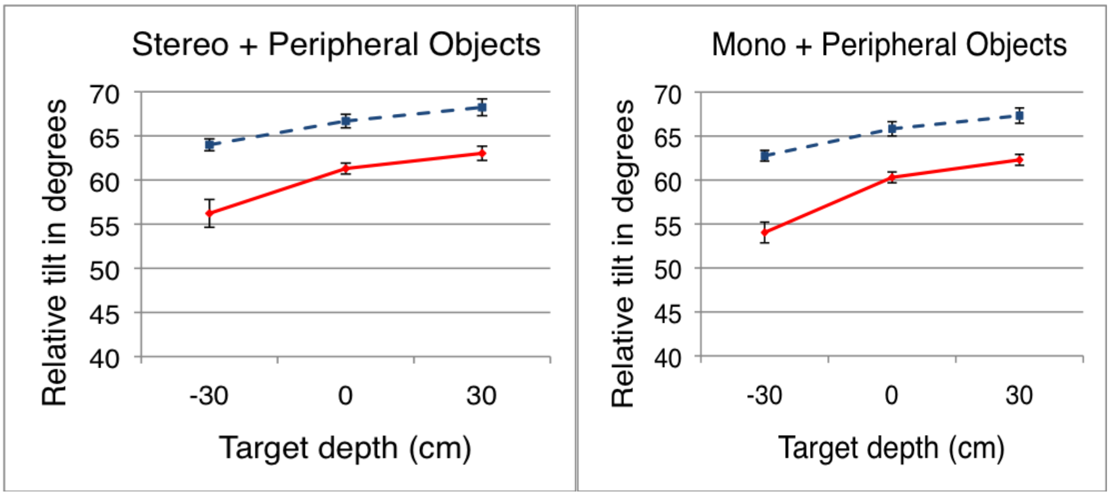

Figure 87 – Mean relative tilt as a function of self-movement type (blue, dashed line = translation, red, solid line = rotation) and target depth for Stereo + Peripheral objects and Mono + Peripheral objects viewing conditions. Error bars show within-subject SE.

5.4.2.2 Comparison to results of Experiment 4.1

Comparing the gradient difference for the Stereo + Peripheral Objects, Mono + Peripheral Objects and the two conditions with no peripheral flow from Experiment 4.1 (Figure 88) reveals an unexpected pattern of results.

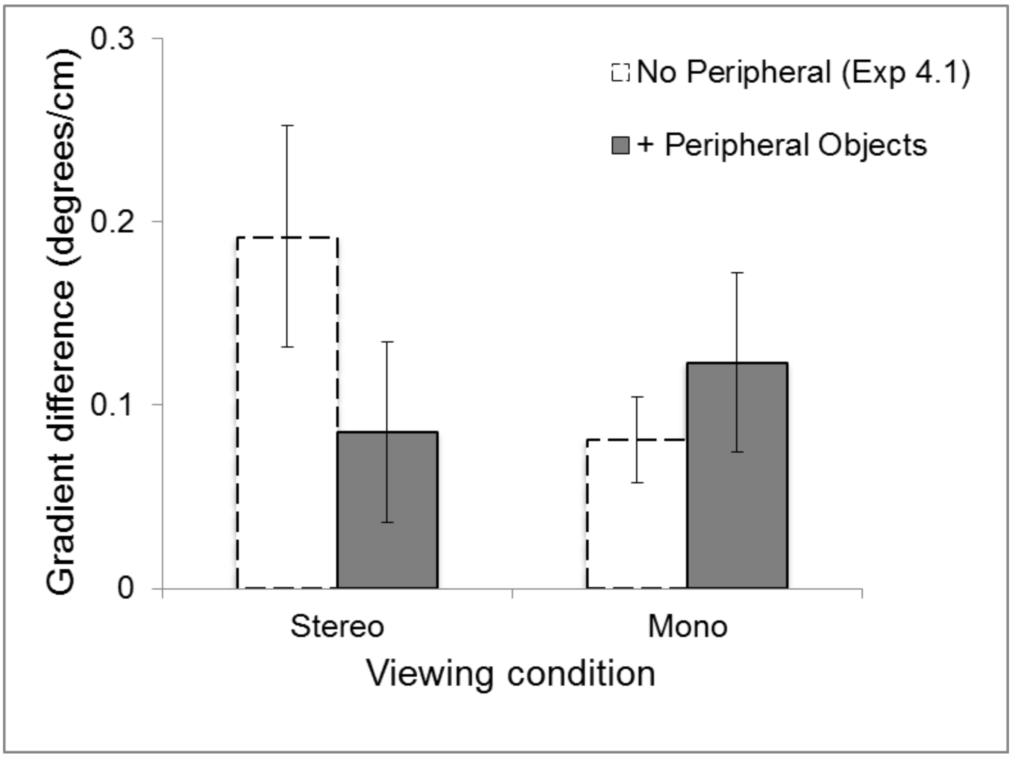

Figure 88 – Mean gradient difference for Stereo and Mono + Peripheral objects conditions (shaded bars). Stereo and Mono data from Experiment 4.1 (dashed bars) provide a baseline for any peripheral effect. Error bars show within-subject SE.

When central information is presented stereoscopically, the addition of peripheral wireframe objects depicting self-movement appears to have reduced the ability to discriminate between rotation and translation (a decrease in the gradient difference). When central information is presented monocularly, and depth cues are reduced, the additional of peripheral objects slightly improves the ability to distinguish between the two types of self-movement. A two-way within-subjects ANOVA revealed that there were no differences in gradient difference between the stereo and mono conditions (*F* (1, 13) = 0.910, *p* = 0.357, *n. sig*) or between the no peripheral and peripheral objects conditions (*F* (1, 13) = 0.251, *p* = 0.625, *n. sig*). The latter implies that peripheral information did not improve the ability to differentiate yaw rotation from lateral translation, and therefore replicates the findings of Experiment 4.1. In addition, the interaction term was also not significant (*F* (1, 13) = 2.238, *p* = 0.159, *n. sig*).

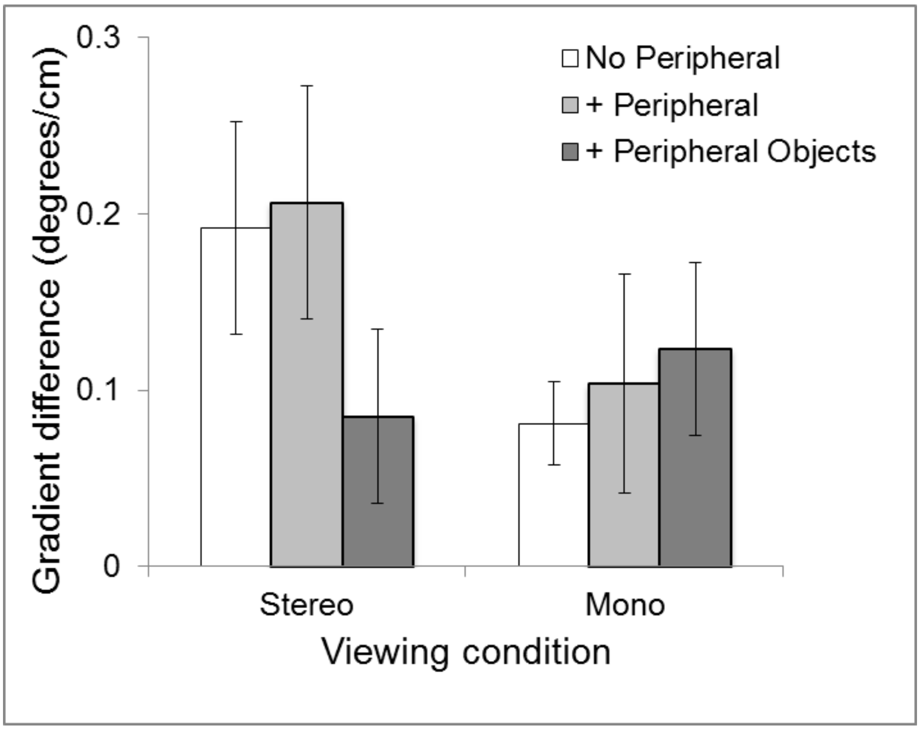

Figure 89 - Comparison of the gradient difference between rotation and translation conditions across viewing conditions in Experiments 4.1 and 4.2. Error bars show within-subject SE.

Comparing the gradient difference across viewing conditions from both Experiment 4.1 and 4.2 (Figure 89), it becomes clear that the results for the Stereo + Peripheral Objects condition are markedly different than the two other Stereo conditions. Plotting the data for each participant across the three Stereo conditions did not reveal any systematic pattern of results, with some participants showing a decrease in gradient difference between the + peripheral and +Peripheral Objects conditions and others showing a slight increase or no difference. It appears that the addition of bars indicating self-movement in peripheral vision (+ Peripheral condition) did not impact upon the ability to distinguish between rotation and translation but the addition of objects in peripheral vision negatively affected the ability to detect translation when central information was stereoscopic. The monocular data did not show the same decline in performance, and does hint towards an improved ability to detect translation with the addition of peripheral flow (Figure 89).

The next section discusses some possible reasons why the Stereo + Peripheral Objects condition produced a smaller gradient difference than the two other stereo conditions, before considering the broader question of why peripheral flow does not appear to improve the ability to distinguish between lateral translation and yaw rotation.

5.5 Chapter Discussion

This chapter set out to investigate whether the additional self-movement cues in peripheral vision help differentiate lateral translation and yaw rotation for flow parsing. It was hypothesised that peripheral flow would improve the ability to distinguish between these two types of self-movement when the depth information in central vision was reduced, but not when the central flow stimulus was stereoscopic. The results of Experiment 4.1 revealed that regardless of the depth cues present in the central flow stimulus, peripheral flow did not appear to impact upon flow parsing performance.

A control study (Experiment 4.2) was conducted to ascertain whether these findings might be due to incongruence between the central and peripheral flow stimuli, but once again there did not appear to be any influence of peripheral flow even when the same flow stimuli were used in both displays. Although the critical condition in Experiment 4.2 was the monocular condition, the stereo condition unexpectedly produced a much smaller gradient difference than was observed in Experiment 4.1. The reduced gradient difference stems from the lateral translation condition, which shows some unexpected depth dependency (see line plots, Figure 83, Page 179). One potential explanation of this finding is that the detection of a flow structure commensurate with lateral translation was compromised in this condition, leading to parsing of self-motion components from the retinal image that were more in line with observer rotation. It is important to note that the stereoscopic central flow stimulus was identical in the No Peripheral and the + Peripheral conditions, which indicates that there is some aspect of the peripheral objects stimulus which disrupted performance when paired with stereoscopic central flow. It may be the case that the presence of objects in the periphery somehow detracted from or interfered with the central information specifying self-movement, perhaps because the peripheral information was more salient in Experiment 4.2 when central and peripheral stimuli were congruent than when the stimuli differed in Experiment 4.1 and the peripheral information might have had less of an impact because it was not perceptually grouped with the central information. Note that in the Monocular condition this saliency may not have had any negative impact because the central information was already ambiguous.

It is worth mentioning that the notable decline with the addition of a congruent peripheral stimulus in the stereo condition but not the monocular condition cannot be explained by any differences in the apparatus used in these conditions. In all conditions both projectors displayed images to each eye meaning that the time taken to render the stimuli would be equivalent across the conditions. Participants also wore stereo glasses to view the stimuli in all viewing conditions because the target was defined stereoscopically. Given that these details did not differ between the conditions, future work might investigate the interaction between self-movement information in central and peripheral vision to determine whether there are specific properties of peripheral flow that negatively impact upon flow parsing in the presence of central flow.

Despite the unusual result for the Stereo + Peripheral Objects condition, the critical condition for evaluating the contribution of peripheral flow was in the monocular condition. Considering the monocular data across the three conditions (No peripheral, +Peripheral and +Peripheral Objects) it seems that in the presence of ambiguous central self-movement information, peripheral flow does not contribute any additional information to flow parsing mechanisms during observer translation or yaw rotation.

It is somewhat unexpected that there was no effect of peripheral flow upon the flow parsing effect in either of the experiments in this chapter, especially given the potential utility of the peripheral flow structure for disambiguating translation and rotation. However, given that the far periphery made a minimal contribution to flow parsing in Chapters 2 and 3 and no discernible contribution in Chapter 4, it may simply be the case that in the experiments in this chapter, central flow primarily drove the identification of self-movement, and that this outweighed any potential contribution of peripheral flow which potentially would have enabled translation and rotation to be disambiguated. Thus, even in cases where central information about self-movement was ambiguous (monocular conditions) the availability of peripheral flow may not have led to lateral translation being identified because information in central vision dominated the percept of self-movement.

In Experiments 4.1 and 4.2 yaw rotation and lateral translation conditions were randomly intermixed, which may have exacerbated a reliance on central flow because the visual information during rotation gave a reliable indication of self-movement but the same was not true in the translation condition. In the monocular conditions where an effect of peripheral flow was anticipated, this procedure may have contributed to the lack of any evidence of a peripheral contribution to flow parsing for these two types of self-movement. In the rotation condition, central and peripheral vision provide equivalent information about self-movement, and even in the monocular condition, yaw rotation can still be identified on the basis of central flow alone. Thus, for yaw rotation, peripheral visual information does not provide any additional information about self-movement. Given the invariant nature of flow structure across the retina during yaw rotation the visual system may have relied on central flow as this provides a reliable cue to the type of self-movement for flow parsing. During lateral translation, the central flow structure appears much the same in the monocular condition meaning that this stimulus alone does not necessarily alert the visual system that the type of self-movement is any different from a rotation condition. Therefore, when yaw rotation and lateral translation conditions are intermixed the central flow information switches between being informative (rotation) and uninformative (translation) and unless peripheral flow is continually monitored by the visual system the information is this retinal region may not be integrated with central flow in determining the type of self-movement. One way to exclude this possibility would be to run a further control experiment in which rotation and translation conditions were run in separate experimental blocks. Such an experiment may reveal a peripheral contribution to flow parsing during lateral translation when central information is ambiguous and that the only reason it does not appear to contribute in the present study is due to the changing reliability of the information in central flow.

On the other hand, if the results herein truly reflect a lack of peripheral input to flow parsing during lateral translation then this would be in-keeping with the findings of Stoffregen (1985) in which the presence of radial flow in peripheral vision did not result in any change in postural sway. In Experiment 4.1, the reduction in flow parsing performance in the monocular conditions compared to the stereoscopic conditions was primarily driven by changes in the translation condition. Namely, that target trajectory became more dependent on depth and closer to the pattern of results predicted for observer rotation. As the translation condition presented radial flow in the far periphery it may be the case that (at least for the +peripheral conditions) observers were unable to utilise this flow structure to detect visual self-motion consistent with lateral translation. A reduced sensitivity to radial flow in the periphery would explain why there was not an advantage of peripheral flow in the translation condition. Stoffregen’s results on postural control indicated a lack of automatic postural response to radial flow in peripheral vision and similarly the present findings indicate that radial flow in peripheral vision does not contribute to flow parsing. Together these findings suggest that the underlying detection of radial flow in peripheral vision may be reduced in comparison to lamellar flow. This is in keeping a functional distinction between central and peripheral vision (Andersen & Braunstein, 1985; Stoffregen, 1985; Warren & Kurtz, 1992). A functional sensitivity account (FSH), argues that central vision is sensitive to radial, rotary and lamellar flow and that peripheral vision is predominantly sensitive to lamellar flow. This pattern of sensitivity mirrors the statistical frequency with which each retinal region is exposed to these flow structures (Warren & Hannon, 1988; Warren & Kurtz, 1992). As we tend to look in the direction of motion, peripheral vision is less frequently exposed to radial flow than to lamellar flow and consequently there is a difference in neural sensitivity to radial flow in the periphery. Albright (1989) showed that cells in MT with receptive fields in peripheral vision showed a preference for lamellar flow directed away from the fovea in macaque. However, Crowell and Banks (1993) presented compelling evidence that the peripheral retina is equally sensitive to radial flow as the central retina in relation to discriminating the direction of self-movement.

Reconciling Crowell and Bank's findings with those of Stoffregen and the present results is challenging. While the former makes a strong case for retinal invariance of self-motion between central and peripheral vision, the results of the present chapter and Stoffregen's results in relation to postural control suggest differences in sensitivity to different flow structures between these retinal regions. Yet it should be noted that these three studies have investigated three different aspects of self-motion perception; heading, postural control, and flow parsing and it is possible that even though the visual input to these three tasks is identical the mechanisms that support each task diverge at a later stage of processing. Indeed, as I argued in the introduction to this chapter, Stoffregen's results only pertain to the automatic postural response and do not necessarily reflect the ability to detect self-movement from peripheral flow. It could be that postural adjustment is less often required in response to this pattern of visual stimulation. In the same vein, judging heading from radial flow in the periphery, or identifying self-movement on the basis of the same stimulus, is not an everyday task. Although Crowell and Banks provided evidence that peripheral vision is sensitive to radial flow, it does not automatically follow that this information is utilised by the visual system. The results herein support this argument by demonstrating that when radial flow is presented to the peripheral retina the visual information specifying self-movement in this region does not appear to be utilised, implying that peripheral vision does not contribute to flow parsing during lateral translation.

An additional reason why patterns of radial flow in peripheral vision did not lead to an improved ability to flow parse during lateral translation is because extra-retinal signals to self-movement may be more reliable than visual information under such circumstances (MacNeilage et al., 2012). Previous research by MacNeilage et al. (2012) has indicated that vestibular information about self-movement makes a greater contribution to flow parsing when heading direction is more eccentric (up to 90 degrees) than when heading direction is aligned with the line of sight. The researchers suggested that this was because central vision is particularly sensitive to radial expansion and can readily detect the FOE, whereas with more peripheral heading directions (which are more comparable to the lateral translation condition here) central visual flow does not uniquely specify heading. It would be interesting to investigate whether the combination of peripheral visual flow and vestibular information provided a more robust cue to self-movement during lateral translation in comparison to either central flow and vestibular information or central and peripheral flow.

To summarise, Chapters 2 and 3 indicated a clear peripheral contribution to flow parsing for radial and roll flow respectively, with a small effect of far peripheral flow on perceived object trajectory. However, Chapter 4 and the results of the current chapter suggest that the far periphery does not contribute to flow parsing for either size change judgements or in order to enhance the discrimination of yaw rotation and lateral translation. The experiments presented in this chapter are the only experiments in this thesis in which central flow was available in conjunction with peripheral flow. It may be the case that central information dominates the identification and parsing of self-motion components from the retinal image during these types of self-movement. A reliance on central flow may have been compounded in these experiments by randomly intermixing the rotation and translation trials, meaning that central information was not consistently ambiguous in the monocular conditions. Alternatively, although peripheral flow structure contains information about self-movement to distinguish between yaw rotation and translation it may not be the case that the visual system can effectively detect or make use of this information for flow parsing. The results in this chapter appear to indicate that peripheral flow does not contribute to flow parsing during lateral translation, a result which is contrary to the present predictions on the basis of flow structure but is in accordance with the FSH of self-movement perception. To probe the reasons for the present findings, future work might explore the relative contribution of central and peripheral flow during lateral translation as well as the potential enhancement of the peripheral contribution to parsing in the presence of extra-retinal sources of self-movement. The General Discussion draws on the key findings of Chapters 2 to 5 to explore how peripheral flow contributes to flow parsing for the types of self-movement and visual judgements that were examined in this thesis.

Chapter 6. GENERAL DISCUSSION

6.1 Summary of findings

The aim of this thesis was to characterise the contribution of peripheral vision to flow parsing. During self-movement the flow structure often differs as a function of retinal eccentricity meaning that peripheral vision contains different visual information about self-movement than central vision. Thus, the availability of peripheral flow can provide additional information specifying self-movement that could help to resolve ambiguities in retinal flow. Existing research on illusory self-movement, the perception of self-movement from optic flow, and the visual control of posture has indicated that visual flow in peripheral vision provides a strong cue to self-movement and the present findings suggest that peripheral flow is also important for flow parsing.

This thesis has reported the first evidence that peripheral vision contributes to the flow parsing process. Across a series of studies, I presented stationary observers with optic flow patterns that were consistent with observer movement. Peripheral flow produced a perceptual bias in judgements of perceived object trajectory and object size change in central vision. This bias is commensurate with a scene-relative percept of object movement during self-movement and indicative of a peripheral contribution to a global parsing process.

On the basis of differences in flow structure as a function of retinal eccentricity, I predicted that peripheral vision would contribute to flow parsing for radial and roll self-movement. In addition, I expected that the far periphery would contribute to flow parsing during lateral translation, but not during yaw rotation where flow structure is uniform across the retina. In the present experiments, simulated forward or backward self-movement and rolling self-movement presented lamellar flow in peripheral vision and the results indicated that this flow structure in peripheral vision contributes to flow parsing, in line with the predictions on the basis of flow structure. In the presence of globally expanding or contracting radial flow patterns, observers were able to utilise visual flow from the retinal periphery to perceive object movement relative to the scene (Chapter 2). Equally, during rotary self-movement observers can make use of peripheral flow to identify and globally parse self-motion components from the retinal image (Chapter 3). For judgements of object size change, flow in the near periphery contributed to the perception of size change during self-movement (Chapter 4) in line with predictions, but flow in the far peripheral flow did not, contrary to predictions. Lastly, the results of Chapter 5 went against the predictions on the basis of flow structure, which had led to the hypothesis that peripheral flow would be useful in disambiguating between lateral translation and yaw rotation. Instead, peripheral flow does not appear to be beneficial in distinguishing between these two types of self-movement despite the potential utility of the peripheral flow structure for detecting lateral translation.

Figure 90 shows that across experiments there was a decline in the contribution of flow with increasing retinal eccentricity of the flow stimulus. This decline is most clearly evidenced by the data from Experiment 1.1, but was also evident as a difference in relative tilt magnitude between the Near and Far peripheral conditions for rolling self-movement (Experiment 2.1) and the ability to detect size change in the presence of radial flow (Experiment 4.0) and was also present in other experiments (Experiment 1.2, 2.3a & 2.3b).

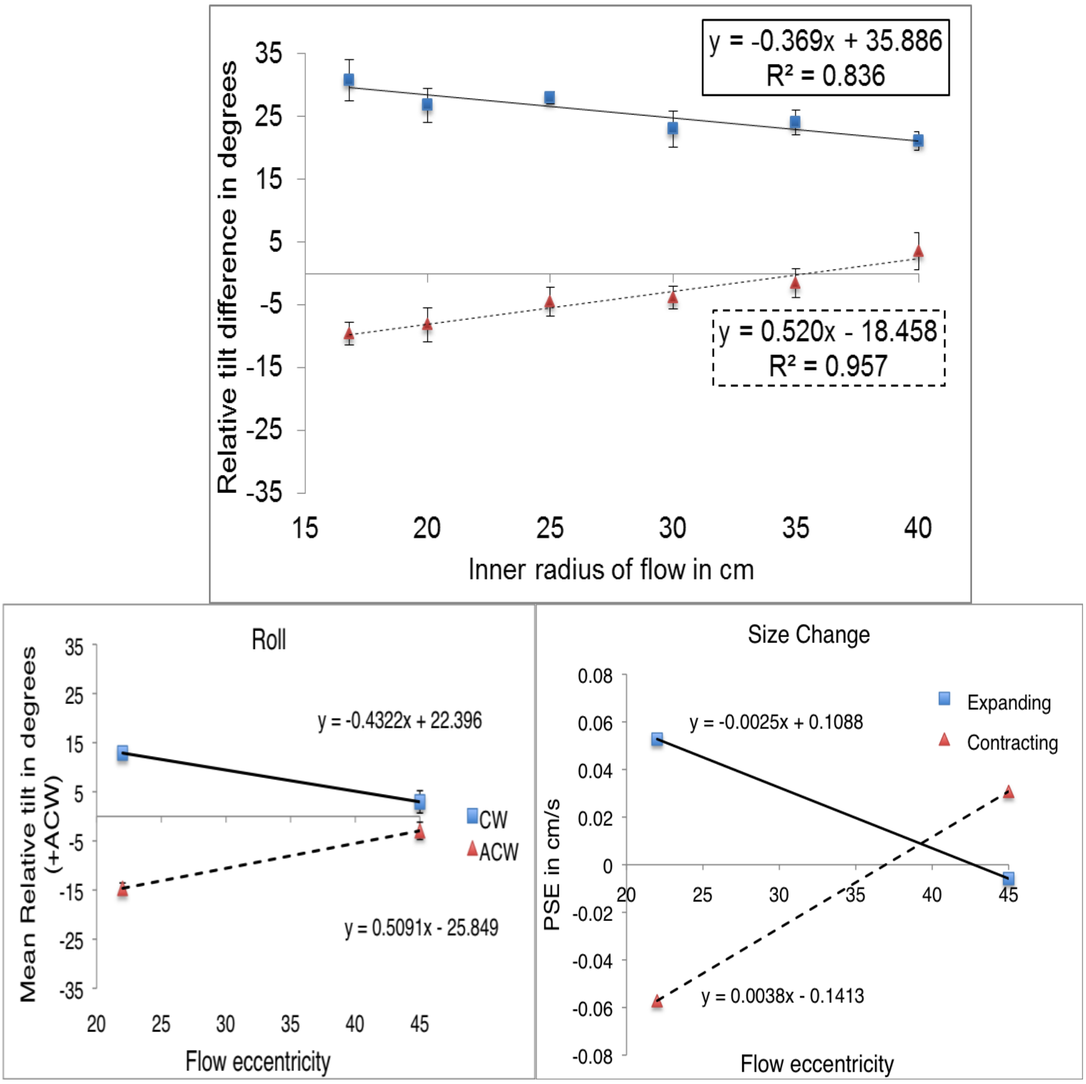

Figure 90 – Declining contribution of peripheral flow to flow parsing with increasing retinal eccentricity for 1) Radial flow, data from Experiment 1.1; 2) Roll flow, data from Experiment 2.1; 3) Size change judgements with radial flow, data from Experiment 4.0.

Overall, the findings reported in this thesis demonstrate a peripheral input to the flow parsing mechanisms that have previously been identified in central vision. Together with previous work by Rushton and Warren, this indicates that the mechanisms that support flow parsing can utilise self-movement information from the peripheral retina. This chapter brings these findings together to characterise the role of peripheral vision in flow parsing. The results are discussed in relation to the FPH and theories of central and peripheral self-movement perception. Subsequently, applications of this research are considered before outlining avenues for future work.

6.2 Characterising the role of peripheral vision in flow parsing

In the General Introduction I outlined the geometric differences in the flow field between central and peripheral vision and reasoned that these differences might result in different flow parsing characteristics between the two retinal regions. This section examines the key findings from the empirical studies in Chapters 2 to 5 and aims to describe the role of peripheral vision in flow parsing.

6.2.1 Differing contributions of the near and far periphery

A recurrent finding in this thesis was that flow in the near peripheral induced a significantly larger relative tilt than far peripheral flow. This was true for all of the experiments which included a near and far condition, indicating a robust effect.

In Chapter 2 I explored some potential reasons for this difference. Aside from the increased retinal eccentricity of the flow in the far condition, there are three key reasons why the far periphery may have contributed less to flow parsing than the near periphery because:

1) the far peripheral stimuli were presented on two monitors whereas the near stimuli was presented on a large projection screen. This means the visual area of the flow in the far peripheral condition was approximately half that of the near flow.
2) the flow stimuli used in the near and far displays were different (bars/stripes in the far periphery but dots in the near periphery) which could have impacted upon the ability to detect self-movement information.
3) sensitivity to visual flow indicating self-movement in the far peripheral visual field may differ from sensitivity in the near periphery

To address these points in order, the control experiments in Chapter 2 indicated that:

1) the smaller display size in the far peripheral condition could account for some of the reduction in relative tilt between the near and far peripheral conditions (Experiment 1.3).
2) the reduced effect seen with far peripheral flow was not due to the choice of stimuli as when the participant viewed peripheral dots at the same eccentricity as the far peripheral stimulus the same decline in relative tilt was observed (Experiment 1.1 vs 1.2).
3) when the ability to discriminate speed was tested for the two peripheral stimuli there did not appear to be any differences in motion sensitivity (Experiment 1.4).

Furthermore, when the peripheral stimuli were scaled for retinal eccentricity (Experiment 1.1b, Appendix B), there was still a reduction in relative tilt with increasing flow eccentricity, suggesting that the decline in relative tilt was not due to a reduction in the neural area activated by the stimulus. Together, these results indicate that the reduced effect seen in the Far peripheral condition is driven by the increasing spatial separation between the flow and the target *and* the reduction in the total area of visible flow (left and right of the head only). This is most clearly revealed by the comparison between the Far peripheral flow results of Experiment 1.2 and the prediction based upon the left/right condition of Experiment 1.3 and the same retinal eccentricity of flow in Experiment 1.1 (See Figure 33, Page 81). Comparing the prediction with the data reveals that the reduced magnitude of relative tilt observed in the Far peripheral condition is in line with what would be expected given the reduction in flow area and eccentricity of the flow stimulus and was not due to the use of different stimuli in the far periphery. Figure 90 presented earlier in this chapter provides equations for the contribution of flow as a function of eccentricity for radial and roll flow. The contribution of visual flow to parsing during self-movement, as measured by a bias in perceived object trajectory, appears to decreases roughly half a degree for each degree of increasing retinal eccentricity (although for expanding radial flow the decline is slightly less (0.4 of a degree per 1 degree of flow eccentricity).

Section 6.2.4 discusses potential reasons for the reduction in the efficacy of the visual flow with increasing spatial separation between the visual flow and the target in relation to the present findings and in comparison to flow parsing with central visual flow.

6.2.2 The contribution of peripheral flow as a function of self-movement type

The ability to detect self-motion components from peripheral flow and then globally parse self-motion seems to be the same for linear and rotary self-movement, when lamellar flow is present in peripheral vision. Studies of optic flow sensitivity have repeatedly found selective responding for radial flow and roll flow (i.e. Duffy & Wurtz (1991;1995) in primates and Freeman & Harris (1992) psychophysically, in humans) and perhaps it is not surprising that these two flow patterns produce very similar flow parsing effects as the visual system seems attuned to detect both, either in isolation or a combination of both as with spiral motion detection (Snowden & Milne, 1997). The current findings show that even when the central portion of the flow field is removed, the visual system is able to detect the structure of the flow field and utilise this information to globally subtract self-motion across the retina, producing a signature pattern of bias which is commensurate with a peripheral contribution to flow parsing. Particularly in the case of far peripheral flow, the bias in perceived trajectory despite the large spatial separation between the flow and the target demonstrates the flow parsing process achieves robustness by using information across the visual field.

The theories of self-motion perception presented in the General Introduction suggested that this research might find that peripheral vision made a different contribution to flow parsing depending upon the type of self-movement. For example, if peripheral vision is specialised for the detection of lamellar flow then the results might have revealed a large relative tilt effect with far peripheral flow during forward translation but during lateral translation there would be no effect of flow in the far periphery. To some extent, the results indicate that peripheral flow does make a different contribution to parsing depending upon the type of self-movement, or the flow structure that is present in peripheral vision.

From the results of Chapter 2 and 3, it is possible to quantify the size of the effect from peripheral flow, and compare this to the same task in central vision. However, there are limitations to this comparison. As this thesis never set out to compare central and peripheral flow parsing, there are minor methodological differences in the speed of simulated self-movement and the target motion between the experiments reported here and the prior studies of Warren and Rushton. Using the previous findings with central flow as a baseline, Figure 91 plots the relative tilt data for expanding radial and roll flow as a function of retinal eccentricity. Note that the radial data plots all the peripheral eccentricities that were tested in Experiment 1.1 whereas the roll data is restricted to the central, near and far peripheral data points. No data exists for contracting radial flow in central vision and therefore the data from this condition is not plotted.

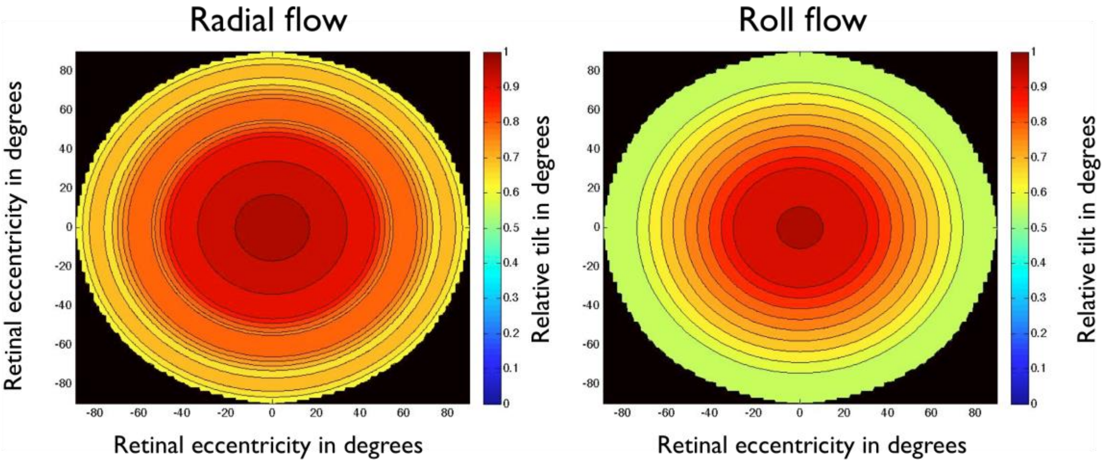

Figure 91 – Relative tilt as a function of retinal eccentricity as a ratio of relative tilt in central flow (1). A) Expanding radial flow, central data: Warren and Rushton (2009a), peripheral data: Experiment 1.1. B) Roll flow, central data: Warren and Balcombe (2010), peripheral data: Experiment 2.1 (Near and Far peripheral conditions. Far peripheral tilt is increased by 42%, the average of the reduction in relative tilt observed between partial flow and full flow conditions in Experiment 1.3).

In both figures, there is clear decrease in relative tilt with eccentricity indicating that towards the extreme periphery there is a decline in the contribution of this region to flow parsing. The presence of near peripheral flow (23 degrees) produces relative tilts that are approximately equivalent to those reported in central vision and the far peripheral flow produces much smaller relative tilts in comparison to both. This suggests that the contribution of visual flow to flow parsing is not uniform across the retina and instead that central regions are preferred. However, in all these studies the location of the target was also in central vision and it may be the case that peripheral flow would make a greater contribution if the target were also peripherally located.

For lateral translation, when central visual flow is available, either with or without stereoscopic depth information (Chapter 5), there is no discernible contribution from peripheral flow, even in situations where there are potentially useful geometric differences. I did not find evidence that peripheral vision can help to resolve ambiguity between lateral translation and yaw rotation in central visual information and there did not appear to be any measurable contribution of peripheral flow. This finding is in accordance with Stoffregen's work (1985) that investigated the postural response to radial flow presented in peripheral vision. Stoffregen found that radial flow in the periphery did not produce a postural response, whereas lamellar flow in the periphery did. A number of reasons could explain the lack of postural response to a radial flow structure in the periphery. For example, radial flow in the periphery would indicate sideways motion and when the observer is face forwards (head aligned with the trunk) the observer is physically more stable in the sideways direction than front to back. This possibility was controlled for in Stoffregen's study as observers always swayed in the fore-aft direction and merely turned their head 90 degrees to the side to experience radial flow in peripheral vision. However, during everyday locomotion, experiencing radial flow in peripheral vision might not require a postural response given our stability in this direction. Therefore, finding no postural sway in response to a radial pattern of motion in the periphery could simply reflect the frequency with which we are required to make a postural response to this pattern of visual motion. Thus, a lack of postural response to radial flow does not necessarily indicate a lack of sensitivity to radial flow in the periphery. Nevertheless, Stoffregen's findings laid the foundation for the idea that peripheral vision is not sensitive to radial flow.

However, as mentioned in Chapter 5, other researchers have presented findings that do indicate a peripheral sensitivity to radial flow. Regan and Vincent (1995) found that ability to detect looming objects (indicated by expanding flow) did not show a decline with increasing retinal eccentricity. Although they only measured thresholds for locations up to 32 degrees from fixation this does at least suggest that the ability to detect radial flow is not limited to the centre of vision. The heading literature has also suggested that observers can utilise radial flow patterns to determine heading across the retina, with the results of Crowell and Banks (1993) suggesting that the ability to discriminate between heading direction is preserved up to 40 degrees from fixation. These findings are not necessarily at odds with those of Stoffregen though, because Stoffregen tested the effect of peripheral flow at much greater eccentricities (90 degrees from fixation), which are more akin to the methods I adopted when testing for a peripheral contribution to parsing during lateral translation in Chapter 5.

The results of Chapter 5 support Stoffregen's claims and indicate that there is reduced sensitivity to radial flow in peripheral vision and in terms of flow parsing, suggest that the availability of peripheral flow is of little benefit during lateral translation. In considering why peripheral vision may not contribute to parsing during this type of self-movement it is important to remember that flow parsing presents a purely visual solution to the problem of detecting object movement during self-movement, but that this does not exclude the contribution of extra-retinal cues. In the discussion of Chapter 5, I suggested that the lack of peripheral contribution to during lateral translation might be explained by the availability of extra-retinal cues during such movements. MacNeilage et al. (2012) presented observers with visual flow indicating different heading eccentricities, from 0 degrees up to 90 degrees, and found a benefit of vestibular information when heading was more eccentric – i.e. radial flow was presented towards the periphery. It may be the case that peripheral vision does not contribute in these circumstances simply because extra-retinal information is typically able to help resolve the ambiguities of central visual flow. Indeed, when observers make their own eye-movements (rather than simulating retinal flow from eye-movements) they have no difficulty in attributing flow components to gaze rotations rather than a curvilinear heading trajectory (Royden et al., 1992; Royden et al., 1994), suggesting that extra-retinal information is a reliable source with which to resolve ambiguity in retinal flow. Thus, the lack of a peripheral contribution to flow parsing observed in Chapter 5 may underlie a re-weighting of visual and non-visual cues to self-movement in the presence of ambiguous visual information.

The contrast between the results of Chapters 2 and 3, and Chapter 5 provides some evidence in support of the idea that the contribution of peripheral vision to flow parsing is not equivalent across all types of self-movement. This discrepancy between experiments in the peripheral contribution to parsing supports Stoffregen’s (1985) assertion that different retinal regions are specialised to detect certain flow structures, with peripheral specialisation for lamellar flow. When considering the different flow structures that were present in the displays in each experiment in this thesis, there is consistency between the results of the radial and roll chapters, when lamellar flow is present in the periphery, suggesting that it may just be during lateral translation that peripheral flow fails to make a contribution. This would be in accordance with a functional sensitivity account of self-movement perception (Andersen & Braunstein, 1985; Stoffregen, 1985; Warren & Kurtz, 1992). An alternative explanation is that because the studies in Chapter 5 also included a central stimulus, that this outweighed any potential peripheral benefit. This idea was explored in more detail in the discussion of that chapter.

6.2.3 The contribution of peripheral flow for different visual judgements

In Chapter 4 I reported evidence suggesting that peripheral flow also contributes to flow parsing for judgements of objects changing in size. This study was important because it employed an alternative visual task and methodology to the earlier experimental chapters. On the basis of peripheral self-movement information, the parsing process does not appear to be specific to judgements of object trajectory. However, near peripheral flow appears to be critical for this task. The data for the Far peripheral flow did not show any significant differences between the expanding and contracting flow conditions, contrary to predictions on the basis of flow structure and suggesting that the far periphery does not contribute to flow parsing for judgements of size change. These findings stand in contrast to the results of Chapter 2, which also utilised radial flow, and found a small contribution of the far periphery to judgements of object trajectory. Some potential caveats of the size change study, which may explain these results, were explored in greater detail in the Discussion of Chapter 4.

Superficially, it appears that the contribution of peripheral vision to flow parsing is not the same for judgements of object trajectory (i.e. Figure 26, Page

77 & Figure 52, Page 118) as it is for object size change (Figure 74, Page 153). The presence of flow in the far periphery did not produce any bias in size judgements as was predicted if there was a peripheral contribution to flow parsing. The eccentricity of the target (Experiment 1.2) and probe disk (Experiment 4.0) did differ across the studies, with the target never more than 4 degrees from fixation and the probe disk never expanding to a size greater than 2 degrees. However it is worth noting that when roll flow was presented in the far periphery, a target located 2 degrees from fixation did show a bias in perceived trajectory (Experiment 2.2). It is nonetheless possible that the eccentricity of the probe disk could explain why the far periphery did not appear to contribute to flow parsing during size change judgements. Considering the demands of each task in more detail, this may be because observers found it difficult to accurately assess the size of the central object when the flow stimulus was at such an extreme eccentricity. It may be the case that local motion plays a more important role in judgements of size than it does for object trajectory.

Warren and Rushton (2008; 2009a) have previously investigated the contribution of local and global motion to flow parsing with radial flow. However, these studies all pertained to judgements of object trajectory and not size change. It would be interesting to investigate how the contribution of local motion might differ between these two tasks.

6.2.4 Comparison of peripheral and central contributions to flow parsing

The findings of this research add an important element to our understanding of the mechanisms that support the flow parsing process. The results have indicated that the peripheral retina seems to be able to utilise peripheral flow for flow parsing in a similar way to the central retina and this information can be utilised for flow parsing. In contrast to the Peripheral Dominance Hypothesis (PDH;Held et al., 1975), there does not appear to be a dominant role for peripheral vision in flow parsing. However, peripheral flow still produces characteristic flow parsing effects. These effects reveal that this region provides an input to the global mechanisms that subtract self-motion components from the retinal image during self-movement.

An important difference between the studies reported here and prior work investigating flow parsing in central vision is the presence of local motion surrounding the target. In present experiments, flow was presented some distance from the central target (with the exception of C5). This spatial separation is likely to have eliminated the contribution of a local motion component from the observed effect. In previous studies, Warren and Rushton (2009a) have separated the local and global contribution by placing an aperture around the target or probe and typically found a reduction in relative tilt when local motion is removed. As local motion was unlikely to be present in the experiments of Chapters 2, 3 or 4 then it is not surprising that the relative tilt is somewhat reduced from the effects see in central vision. If one compares the relative tilt size seen in central vision with local motion removed (as in Figure 10, Page 25) to that of the near peripheral stimulus, the size of the relative tilt is approximately equal (~27 degrees in Warren & Rushton (57 cm/s self-movement speed, 3 degree aperture, Experiment 1, 2009a) compared with 34 degrees in the Near peripheral condition of Experiment 1.2 for self-movement at a rate of 30 cm/s and a 23 degree aperture). This helps to confirm that at least some of the reduction in relative tilt in the peripheral flow results is due to the removal of local motion from the stimulus.

However, the exclusion of local motion alone cannot explain the difference in relative tilt seen between the near and far flow conditions (Experiment 1.2 and Experiment 2.1), or the decline in relative tilt shown most clearly in Experiment 1.1, as local motion between the flow and the target would not have been present in either the near or far conditions. One way to reconcile the differences between the central and peripheral and between the near and far peripheral rests on the division between local and global motion. Warren and Rushton placed an aperture surrounding the probe in their experiments to exclude local motion, but it may be the case that rather than two classes of neurons; one with small receptive fields and one with large receptive fields spanning large areas of the retina (local and global respectively), that there exist neurons with a variety of receptive field sizes. If this were the case then Warren and Rushton’s manipulation may have only prevented the activation of neurons with very small receptive fields rather than neurons with larger, or much larger receptive fields. This would mean that although close proximity local motion contrast was removed from their displays, motion nearby may still have contributed to the effects they reported. In contrast, in the work reported here, the effects are only likely to be driven by neurons with very large receptive fields that would be activated by the peripheral flow stimuli. Furthermore, if there are neurons sensitive to self-motion with a range of different receptive field sizes then it may well be the case that the far peripheral stimulus only activated neurons with the largest receptive field size and not those with slightly smaller receptive fields, which would be activated by the near peripheral stimulus. This difference in activation could further explain why the far peripheral stimulus contributed less to flow parsing than the near peripheral stimulus.

However, it is worth noting that motion contrast alone might still explain the larger relative tilt observed when flow was presented in the near peripheral as opposed to the far periphery. For example, the motion contrast would be greater when the target and flow were in closer proximity (near periphery) than when they were further away (far periphery). Although the previous results of Warren and Rushton suggest that the effects reported herein are due to a flow parsing mechanism, it would be worthwhile to conduct an additional control study which dissociates the predictions of motion contrast and flow parsing.

6.3 The Flow Parsing Hypothesis

The present research extends the understanding of the FPH as it demonstrates that observers can utilise self-movement information from across the retina. This suggests that flow parsing is a process which operates globally to identify and then subtract self-motion components from the retinal image. Even though it is possible that Warren and Rushton (2008) did not exclude enough local motion from their displays, in the current work a peripheral only self-movement stimulus excludes the possibility that the present results are driven by local motion. The presence of flow in near peripheral vision (23 degrees flow eccentricity & ±4 degrees target eccentricity) affords the ability to parse self-motion from the retinal image in order to judge object movement during self-movement. The far periphery appears to make a limited contribution to the parsing of self-movement components from targets located in central vision.

Leading on from this research, the next aspect of the FPH that warrants investigation is how self-movement information from across the central and peripheral retina is integrated for flow parsing or weighted during different types of self-movement and also whether this relationship is modified by attention. The section below on future directions explores these two topics.

6.4 Implications

6.4.1 Visual field loss

The contribution of the peripheral visual field to flow parsing could have had important implications for individuals with visual field loss. The absence of central (Central scotoma) or peripheral (Bitemporal hemianopia) vision may affect the ability of observers to visually identify self-movement and consequently disrupt the flow parsing process, especially in situations where extra-retinal cues to self-movement are limited. A transient example of the same issue is clothing which reduces the field of view. Hooded jackets and headgear can also restrict peripheral vision, and therefore the availability of self-movement information from this region. Although the present findings indicate that peripheral vision contributes to flow parsing, they do not suggest that individuals who suffer from tunnel vision are likely to be disadvantaged when undertaking visual judgements during self-movement as the effects were either comparable (near periphery) or reduced (far periphery) in comparison to parsing from central visual flow. Thus, for those who suffer from peripheral visual field loss the current findings are potentially informative. The ability to identify (and parse) self-motion components from retinal motion appears to be possible across a large proportion of the visual field. The current findings imply that individuals with peripheral visual loss would still be capable of making scene-relative judgements of object motion despite their own movement. Yet a fuller comparison of the relative contribution of central and peripheral flow to flow parsing would be required in order to determine whether the absence of peripheral flow has any detrimental effect upon flow parsing.

6.4.2 Spatial disorientation in flight

Another potential implication of the current work is in relation to the prevention of spatial disorientation in pilots. The focus of research in this area has been on providing visual information about self-movement in order to combat a series of illusions that lead to a misperception of self-orientation and self-movement. Such illusions arise when unreliable information from the vestibular system dominates the perception of self-movement; typically resulting in a mismatch between the way the pilot believes he/she is orientated with respect to the earth and their veridical orientation. The use of a visual display therefore has advantages in this setting because extra-retinal cues often provide inaccurate or unreliable information about self-movement. Researchers in this field have favoured the idea that peripheral vision provides an observer with an automatic and largely sub-conscious awareness of their orientation and self-movement (Previc & Ercoline, 2004). In this thesis I have considered whether peripheral visual flow provides a source of information about self-movement that can be utilised for flow parsing. Thus, the current findings are relevant to the use of visual information about self-movement in flight because the same type of visual information is used to provide an indication of self-movement and, by extension, provides a basis for judgements of object trajectory during self-movement.

As well as preventing spatial disorientation, peripheral flow has been implicated in aviation in circumstances where there is reduced visual flow, such as when flying at night or over sparse landscapes. In these conditions, the use of artificial peripheral flow might provide an alternative visual source of information about self-movement. The results of prior work in this area have been encouraging (i.e. Erikson & von Hofsten, 2005), suggesting that peripherally located displays of visual flow provide a robust cue to self-movement to help pilots maintain an awareness of their orientation and movement. However, it is dangerous to assume that the presence of the same visual flow in the periphery will be an adequate substitute for central or full-field flow for a range of visual tasks. Although peripheral flow may provide a strong cue to self-movement, the present results indicate that it does not automatically follow that this visual cue is sufficient for flow parsing to occur. If the peripheral cue to self-movement does not feed in to flow parsing mechanisms then judging the motion of other objects in central vision, such as other aircraft, would be reliant on retinal motion that is confounded by self-motion components.

The findings reported in this thesis suggest that when detecting or making judgements about centrally located moving objects the presence of visual flow in the far periphery does not lead to the same percept of object movement as with a central flow stimulus. This highlights the need for research in this area to ensure that peripheral displays do not only provide a strong cue to self-movement but that this cue can be utilised for judgements of object movement during self-movement.

6.5 Future directions

Following on from the findings of this thesis, I propose two potential avenues for future research: 1) the relative contributions of central and peripheral vision and the integration of information from across the visual field 2) the role of attention on flow parsing from central and peripheral self-movement information.

The first of these avenues would focus on the integration of visual flow across the retina and seek to determine the relative contributions of central and peripheral vision. For radial and roll flow (Chapters 2 and 3) the results for a combined peripheral stimulus, extending from the near periphery to the extreme periphery on both sides of the visual field, appear to be mostly accounted for by flow presented in the near periphery. The presence of flow in the far periphery does not seem to add to the effect on object trajectory in central vision, suggesting that this area of the visual field provides a limited input to flow parsing. However, as both the near and far periphery always moved in the same direction (congruent motion) it is possible that ceiling effects prevented any additional benefit of the far periphery from being revealed. Further work, building upon these findings, might explore the integration of flow across the retina, in the periphery and also between central and peripheral areas. One potential means of assessing the contribution of each region is to place them in competition, by varying motion coherence as a function of retinal eccentricity. For each level of motion coherence and each eccentricity manipulation, the effect on object trajectory can then be measured. When motion coherence is low the quality of the flow, or the self-movement signal, would be degraded in that retinal area. If the visual system combines flow from across the retina in an optimal fashion then the retinal area with the most reliable signal should drive the effect, regardless of the retinal locus of the flow. If, on the other hand, flow is not integrated this manner then placing the information from these two areas in competition should reveal which areas of the visual field are most critical for flow parsing. If the central region is most important then when motion coherence in this area was very low (a noisy flow stimulus) then there would be little effect upon object trajectory, even if more peripheral regions provided a strong indication of self-movement.

The second avenue of investigation concerns the effect of attention on flow parsing. Using dual task paradigms, it has been demonstrated that visuo-motor tasks in central vision are disrupted by increased attentional load (Wickens, 2008). However, when the same visuo-motor tasks rely on peripheral visual information there is no cost of increased attentional or cognitive load. The majority of the prior research investigating attentional modulation of visuo-motor tasks has utilised the visual control of stance or gait. Such tasks are often considered to be subconscious or automatic processes but their disruption by attention when they rely on central visual information means this cannot be the full story.

These findings are supported by research that has indicated that the perception of self-movement can be affected by attention. For example, Seno, Ito and Sunaga (2011) presented a rapid serial visual display of letters over a moving upward or downward vection stimulus. Participants were asked to press a button if the same letter was repeated in succession and also to hold down a button indicating they were experiencing vection. They measured the latency and duration of vection both when participants were told to attend to the letter stimulus and when they were told to passively view the stimulus. They found that when participants were attending to the letters there was a reduction in the onset and duration of reported vection but the same was not true when participants passively viewed the stimulus.

Other research has shown that there is a re-weighting of cues to self-movement when attention is allocated to another task, but suggests that extra-retinal rather than peripheral visual information comes to the fore when attentional demands are high. Wann, Swapp and Rushton (1998) investigated how performing an attentionally demanding task during simulated forward motion affected heading perception. They found that when the visual flow indicated linear translation with a simulated gaze rotation, heading accuracy was impaired by the attentional tasks. Yet when observers made their own gaze rotations (providing extra-retinal information) whilst completing the same attentional tasks, the ability to detect heading significantly improved. They suggested that during high cognitive load, there was a reduction in the area of the visual field to which observers were actively attending, which meant that the visual system did not take into consideration peripheral flow and instead reweighted the importance of extra-retinal cues to determine heading. They argued that this reweighting improved the ability to segregate visual flow into components due to linear translation and those due to gaze rotation.

Wann et al.'s results indicate that peripheral vision might actually play a lesser role when attentional load is high in central vision, contrary to the benefit of peripheral vision shown in visuo-motor tasks. The role of attention in the perception of self-movement from peripheral flow certainly warrants further investigation, particularly into whether the perception of self-movement information in central and peripheral visual areas is differentially affected by concurrent cognitive tasks.

The key research question I would seek to explore in this second line of research would be whether flow parsing performance also suffers under dual task conditions. If it is the case that the processing of central flow indicating self-movement suffers under dual task conditions then the availability of peripheral flow could provide an alternative source of self-movement information when the processing of central flow was impaired. To test this it would be important to first establish that the identification of self-movement from central visual flow for flow parsing is disrupted by when an additional task is performed, but that when visual flow is provided only in the periphery performance on both tasks is unaffected. Central and peripheral flow could then be presented together to establish whether the reliance on visual flow switches from central flow to peripheral flow in the presence of the secondary task. This line of research could have important implications, especially if visual information about self-movement from different retinal regions made differing contributions to flow parsing during high cognitive load as this would imply that the ability to identify object movement during self-movement might be compromised in certain situations.

6.6 Conclusions

Across a series of experiments in this thesis, I found evidence that peripheral visual flow contributes to flow parsing. Peripheral motion consistent with self-movement provides an independent input to the parsing process. Chapters 2 and 3 demonstrated that peripheral information about linear or rotary self-movement contributes to a scene-relative percept of object trajectory in central vision. The results do not indicate any differences in the parsing process for observer translation and observer roll, when lamellar flow is present in peripheral vision, suggesting that peripheral flow contributes to parsing in a similar manner for these two types of self-movement. Alongside these judgements of object trajectory, evidence of a near peripheral contribution to flow parsing was also revealed for judgements of object size change (Chapter 4). Finally, Chapter 5 showed that when both central and peripheral flow are available during lateral translation and yaw rotation the additional information in the periphery does not appear to be utilised by the visual system for flow parsing. In collaboration with previous findings, the flow parsing process appears to be able to utilise self-movement information from across the retina.

This work confirms that peripheral vision does contribute to flow parsing and establishes a foundation for future work. The results inspire a set of follow on questions about the relative contribution of central and peripheral regions of flow to the parsing process when both are readily available, and the potential influence of attention on the contribution of peripheral flow to flow parsing.

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Appendix A - Additional Methodological Details

Additional Participant Information

Postgraduate participants were obtained via opportunistic sampling and undergraduate participants were recruited using an online participant sign-up system (EMS), both from within the School of Psychology at Cardiff University. Undergraduate participants had an estimated age range of 18-21 and postgraduate participants had an age range of 22-46. Postgraduate students received payment at a rate of £10/hour and undergraduates received course credit.

Additional Ethical Information

The School of Psychology Ethics Committee, Cardiff University, approved all experiments. Participants gave informed consent prior to the commencement of each experiment. Observers that participated in more than one condition and/or experiment were debriefed once all data collection had been completed.

Response devices

For trajectory judgements, participants used either a Logitech Attack 3 Joystick (Model: J-UJ18) or a jog-wheel (See Figure A1, Contour Design, ShuttleXpress S-XPRS) to orient an onscreen response line and provide angular responses. A jog-wheel is a standard video-editing tool, which has two central wheels that both rotate and are typically used to progress through video media by either jogging (slowly; inner wheel) or shuttling (fast; outer ring). In this research, participants could choose which wheel they used to make their response. In

Figure A1 - Jog wheel used by participants to provide angular responses

Experiments 1.4 and 3.0, where forced choice judgements were required, participants responded using the buttons on an optical computer mouse.

Radial - Relative tilt analysis details

The coordinate system and sign conventions used in Chapter 2 and Chapter 5 are shown in Figure A2. Angles describing “real” physical target trajectory, θ_R, and perceived trajectory, θ_P, are defined relative to the Y-axis (anticlockwise +ve)

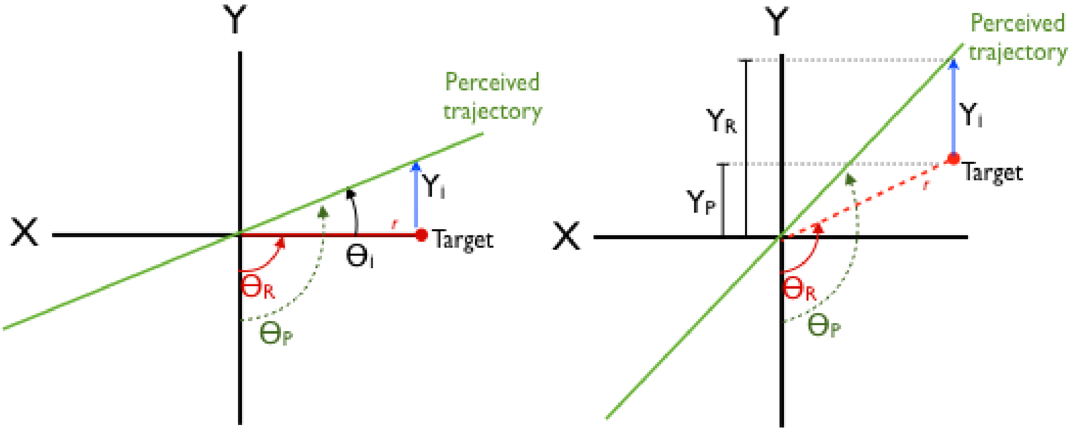

Figure A2 - Schematic diagram of the response line adjusted by observers. For illustration only, axes, coordinate system and key parameters are also shown. Absolute angles are measured relative to the Y-axis in an anticlockwise direction. Quantities Y_i and θ_i characterize the perceived change in trajectory. Left panel shows the special case in which the target moves horizontally (i.e., $\theta_R = \pi/2$). Right panel shows case when target does not travel horizontally.

It was assumed that the simulated horizontal observer movement did not interfere with the perceived vertical motion of the target (i.e., the perceived and the physical horizontal motion were identical). Consequently, any difference between the perceived and the physical angles was due to an additional perceived vertical component of target motion Y_i. Using simple trigonometry, given the distance travelled by the target, r, this quantity can be calculated as

$$Y_i = Y_R - Y_P = r\sin(\theta_P - \theta_R) / \sin(\theta_P). \qquad [A-1]$$

For the sake of consistency with angular measures (which increase in an anticlockwise direction), Y_i is defined as positive upwards. To make the measurement commensurate across the different target trajectory conditions, it was calculated as follows. The component Y_i was transformed back to an angular quantity θ_i, as if it had been induced relative to a physical target motion that was purely horizontal:

$$\theta_i = \tan^{-1}(Y_i/r). \qquad [A-2]$$

This quantity also increases in an anticlockwise direction but is now measured relative to the X-axis. In the results of Chapter 2 and Chapter 5, θ_i is referred to as the relative tilt.

Roll- Relative tilt analysis details

The coordinate system and sign conventions used in Chapter 3 are shown in Figure A3. Angles describing "real" physical target trajectory, θ_R, and perceived trajectory, θ_P, are defined relative to the X-axis (anticlockwise +ve)

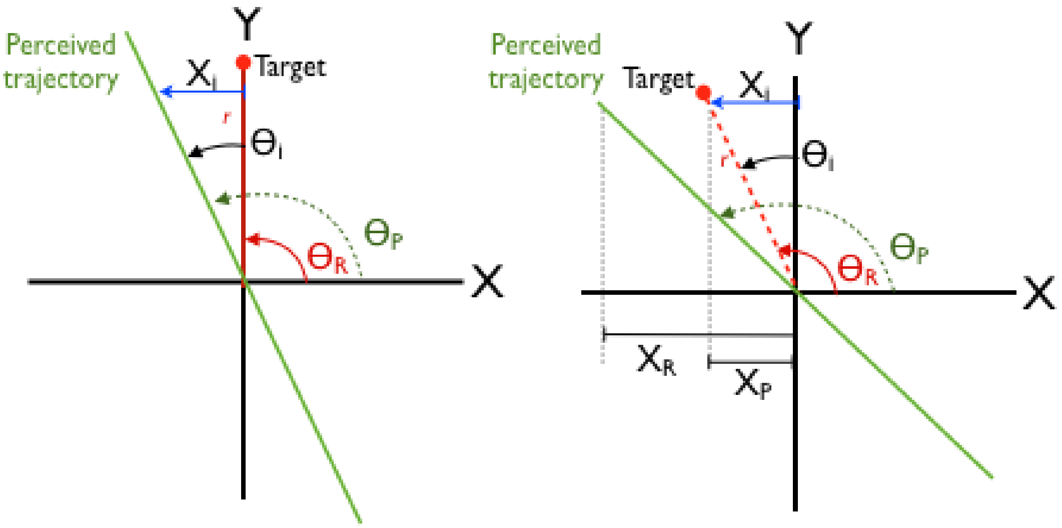

Figure A3- Schematic diagram of the response line adjusted by observers. For illustration only, axes, coordinate system and key parameters are also shown. Absolute angles are measured relative to the X-axis in an anticlockwise direction. Quantities X_i and θ_i characterize the perceived change in trajectory. Left panel shows the special case in which the target moves vertically (i.e., $\theta_R = \pi/2$). Right panel shows case when target does not travel vertically.

It was assumed that the simulated rotational observer movement did not interfere with the perceived vertical motion of the target (i.e., the perceived and the physical vertical motion were identical). Consequently, any difference between the perceived and the physical angles was due to an additional perceived horizontal component of target motion X_i. Using simple trigonometry, given the distance travelled by the target, ***r*****,** this quantity can be calculated as

$$X_i = X_R - X_P = r\sin(\theta_P - \theta_R) / \sin(\theta_P). \qquad [A\text{-}3]$$

For the sake of consistency with angular measures (which increase in an anticlockwise direction), X_i is defined as positive leftwards. To make the measurement commensurate across the different target trajectory conditions, it was calculated as follows. The component X_i was transformed back to an angular quantity θ_i, as if it had been induced relative to a physical target motion that was purely vertical:

$$\theta_i = \tan^{-1}(X_i/r). \qquad [A\text{-}4]$$

This quantity also increases in an anticlockwise direction but is now measured relative to the Y-axis. In the results of Chapter 3, θ_i is referred to as the relative tilt.

Within-subject error bar calculation

This method, proposed by Cousineau (2005), involved calculating a series of means prior to the data being transformed. In the equations that follow the following notations are used: k= number of participants, m = number of conditions, i = 1 to k, j = 1 to m, n = number of trials, P = participant and C = experimental condition.

1. Calculate the mean relative tilt for each participant in each condition:

$$\bar{x}_{PiCj} = \Sigma\,(x_1 \ldots x_n)/n. \qquad [A\text{-}5]$$

2. Calculate the mean relative tilt for each condition across participants:

$$\bar{x}_{Cj} = \Sigma\,(\bar{x}_{P1Cj} \ldots \bar{x}_{PkCj})/k. \qquad [A\text{-}6]$$

3. Calculate the mean relative tilt for each participant across conditions:

$$\bar{x}_{Pi} = \Sigma\,(\bar{x}_{PiiC1} \ldots \bar{x}_{PiCm})/m. \qquad [A\text{-}7]$$

4. Calculate the grand mean across participants and conditions:

$$\bar{x}_{grand} = \Sigma\,(\bar{x}_{PiCj})/(k*m). \qquad [A\text{-}8]$$

5. Finally, to normalise the data, for each participant's original condition mean ($\bar{x}_{PiCj}$), subtract the associated participant mean ($\bar{x}_{Pi}$) and then add the grand mean:

$$T\bar{x}_{PiCj} = (\bar{x}_{PiCj} - \bar{\bar{x}}_{Pi}) + \bar{x}_{grand.} \text{ [A-9]}$$

Advantage of Cousineau's procedure

Error bars present a visual indication of the variance between experimental conditions. When error bars represent variance that also includes between participant differences then small differences between conditions can easily be masked. Within-subject designs permit the removal of variance due to individual differences from the dataset.

Cousineau (2005) proposed that the data from such designs be transformed to subtract the participant's mean from their data in each condition. In Cousineau's method, determining the average value of the DV for each participant provides a measure of each individual's response level across conditions. Subtracting each participant's own average from their data removes this individual element from the data but retains the differences between conditions thought to be driven by the manipulation of the IV. The grand mean is then added to all values so that the mean value of each condition is restored (Baguley, 2012). In the transformed dataset, between subjects variability has been removed. When error bars are generated from the transformed dataset they now represent only the variance within subjects and therefore any clear differences between conditions should be visible from the figure.

Figures A4 and A5 demonstrate the impact of the transformation for a subset of the data in Experiment 1.1. In Figure A4, the unadjusted data shows how the magnitude of mean relative tilt differs between participants but the pattern across participants is consistent. The transformed data shows the same data with between-subject variability removed using Cousineau's method (2005) and as a consequence the data points are less dispersed.

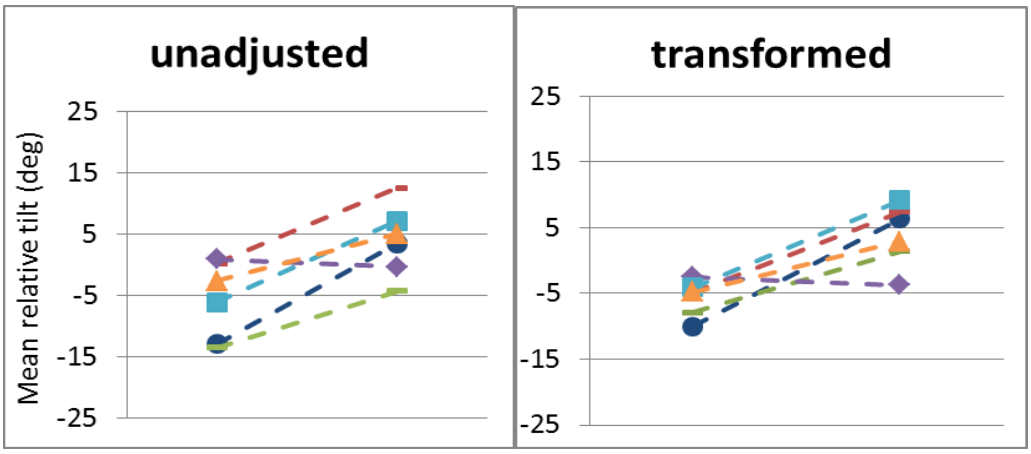

Figure A4 – Unadjusted (left) and transformed (right) data from Experiment 1.1, Contracting condition at 16.8 cm eccentricity.

Figure A5 shows the consequence of the transformation upon the error bars. Note that the means remain the same in both figures but that the error bars are reduced, due to the removal of individual differences, in the transformed figure. This change is most noticeable in the left hand data point.

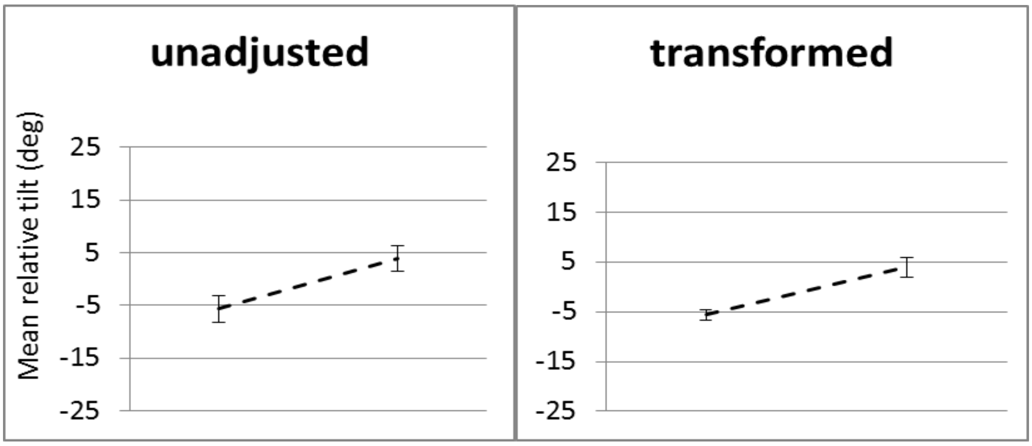

Figure A5 – unadjusted (left) and transformed (right) data from the same experiment.

Although Cousineau's method was adopted in this thesis, there are other alternatives. Loftus and Masson (1994) have previously proposed a method for generating within-subject error bars. Their method derives a measure of pooled variance from the within-subject error term, which excludes between-subject variability. Error bars depicting this pooled variance are therefore based upon the same error term that is used for statistical analysis providing a graphical equivalent to confidence intervals for between-subject designs. However Loftus and Masson's method assumes homogeneity of variance between conditions and as a result the error bars produced are the same size across all conditions (Baguley, 2012). This means that information about the variance within a condition is not represented in the figure. Therefore, in order to preserve information about variance within conditions in the figures presented in this thesis, and in case of violations of homogeneity of variance, Cousineau’s method was selected.

Appendix B - Additional Experiments and Analysis

Experiment 1.0 - Near peripheral flow: Paradigm development

Experiment rationale

This initial experiment tested whether peripheral flow resulted in flow parsing type effects, akin to those previously reported in central vision. However, the stimulus used in the Near peripheral display was not optimal. Subsequent experiments replicated these results with a new set of participants and improved the flow stimulus (Experiment 1.2). Thus, this experiment is not included in the main body but demonstrates the methodological progression that led to the experiments reported in Chapter 2. As such, the hypothesis was the same as for the Near peripheral condition in Experiment 1.2 and the same interaction pattern was anticipated between flow direction and target eccentricity, indicating a peripheral contribution to flow parsing.

Methods

Participants.

Eight postgraduate participants (5 male) with an age range of 24 to 31 (M = 26.25, *SD* = 2.71) took part.

Apparatus and Stimuli.

The apparatus was the same as in Experiment 1.2 except that the monitors to the side of the head were switched off as they were not used in this study.

Near Peripheral Flow:

On the large projection screen a peripheral flow stimulus was presented in the near peripheral region. The flow stimulus was almost identical to the one reported in Experiment 1.2, except that the inner radius was larger in this experiment and there was no restriction on the maximum radius of the flow.

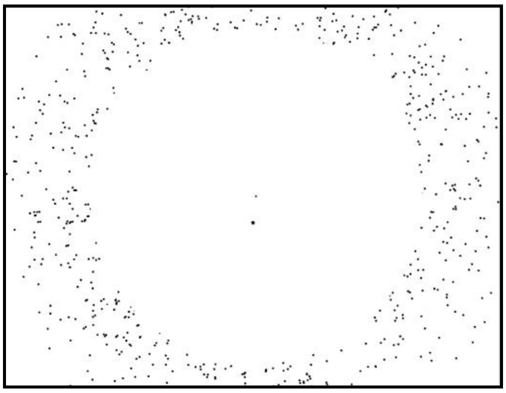

Figure B1 - Flow stimulus for Experiment 1.0. The colours were reversed in the stimulus.

The central portion of the flow stimulus was obscured by drawing a black circle with a radius of 22.83 degrees in front of the dots (see Figure B1). This created a circular ‘ring’ of dots with a diameter of 45 degrees and a fixed width of 15.30 degrees (26 cm). At the top and bottom edge of the display the flow band slightly exceed the edges of the projected image (as can be seen in Figure B1). Dot motion was appropriate for an observer translating either forward or backward at a rate of 30 cm/s.

The target was a small red circle (0.3 degrees), which was presented at 4 degrees eccentricity above or below fixation on the central projection screen. The trajectory of the target was selected without replacement from a range of 17 possible trajectories (±16 degrees either side of horizontal in 2 degree steps). Targets always appeared to the left hand side of the midline and translated rightward along the given trajectory at a constant speed of 6.9 degrees/s (12 cm/s) for 300 ms. Therefore, the target passed through the vertical mid-line of the screen half way through its trajectory.

Design.

Across trials the direction of simulated self-movement (expanding or contracting peripheral motion) was manipulated as well as the target eccentricity (-4/+4 degrees) to give four conditions. For each condition there were 17 physical probe trajectories, resulting in a total of 68 trials, which were presented in a random order. The dependant measure was relative tilt: the difference in target trajectory between the onscreen target trajectory and the angle reported by the observer, measured in degrees.

Procedure.

Following briefing and consent, observers were seated in a dark room with their head in a chin rest, 95 cm from the centre of the projection screen. Before the experiment began, each participant was given the opportunity to practice the task for a few trials to familiarise themselves with the stimuli and response buttons.

Participants were instructed to maintain fixation on a small point located at the centre of the screen throughout each trial and to watch for the presentation of the target either above or below fixation. At the start of each trial, the flow stimulus was presented and simulated an observer moving either forwards or backwards at a rate of 30 cm/s. This translation speed was an approximate average of the two speeds used in each experiment of Warren and Rushton (2009a). After a delay of 1.3 seconds the target was presented.

At the end of each trial, a 2D response line was presented in the centre of the screen. Participants rotated the line using the joystick in order to indicate the perceived trajectory of the target. Participants were told that if they did not perceive the target to move along a straight path then they should set the response line to match the mean linear trajectory of the target. Once the participant had set the onscreen line they clicked any joystick button to move on to the next trial. By delaying their click, observers could opt to take a break before continuing. Following the participant's response, there was an interval of 1.2 seconds before the start of the next trial.

Analysis.

For each trial, the onscreen trajectory angle was subtracted from the participant's response angle to provide a measure of relative tilt, with positive numbers indicating an ACW direction. A significant interaction was predicted, as in Figure 21 (Page 62), and would indicate a peripheral contribution to flow parsing. A two-way within-subjects ANOVA was then conducted to ascertain whether there was a significant interaction effect within the data. Probability values from the ANOVA interaction term were adjusted (P÷2) because a directional interaction was predicted (Wuensch, 2006). Appropriate within-subject error bars were generated using the procedure described in the Appendix A.

Results

The data showed the expected interaction between flow direction and target location (*F* (1, 7) = 5.779, *p* = 0.047). The difference in relative tilt as a function of target eccentricity was significantly stronger when the target was accompanied by expanding flow than contracting flow (*F* (1, 7) = 12.592, *p* = 0.009). Commensurately, in Figure B2 it is evident that contracting flow induced a much smaller bias in the perceived trajectory of the target than expanding flow.

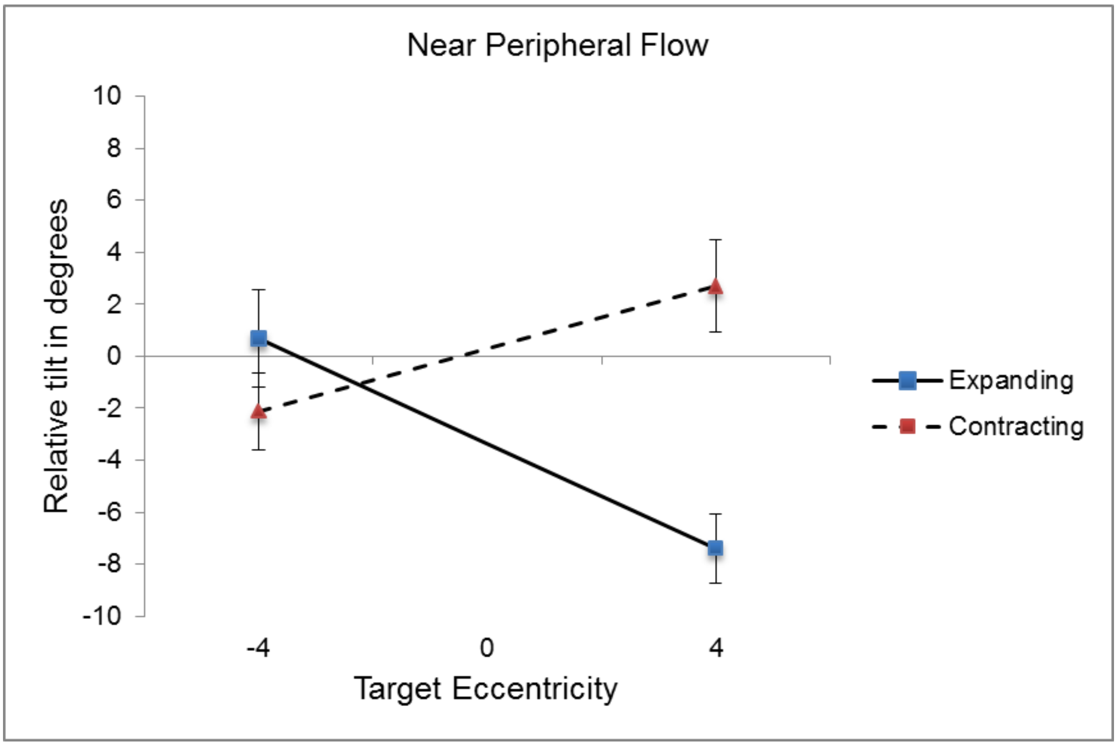

Figure B2 - Relative tilt in degrees as a function of flow direction and target eccentricity. Error bars show within-subject *SE*.

Critique

The results demonstrated the predicted interaction effect, commensurate with a flow parsing account. However, the interaction pattern is not particularly striking. Relative tilt is greatly reduced in the -4 target eccentricity condition compared to the +4 target eccentricity. This critique highlights some elements of the experiment that may explain these results. Ultimately, this evaluation process led to the paradigm being developed for subsequent experiments, many of which are included in the main body of this thesis.

A key methodological flaw in this experiment relates to the flow stimulus. In an attempt to make the flow stimulus as large as possible on the projection screen, visible edges were present in the display. To clarify, because the outer radius of the flow annulus was greater than the vertical extent of the screen, the edges of the stimulus were cut off at the top and bottom of the projected display (the reader can refer to Figure B1 to visualise this). As observers were making angular judgements this presents an issue because they could have utilised the edges of the display as a reference to horizontal or vertical when making their judgements. Instead, it was desirable that observers made their trajectory judgements in relation to the other visual elements of the stimulus. Thus, a clear visual reference may have led observers to report the perceived object trajectory in relation to this marker.

To clarify, under the simulated self-motion paradigm, the display on the screen presents observers with a pattern of visual motion that is appropriate for object motion during self-motion – the pattern of motion on the projection screen should be identical to the pattern of motion on the retina (assuming as the participant maintains fixation). Relative tilt can then be used to measure how much the participant's perception of object motion differs from the onscreen trajectory. If observers are able to parse self-motion then the object's trajectory will be biased and will *not* match the onscreen trajectory. However, if observers have a reliable source of information about the onscreen trajectory – i.e. they can judge it in relation to the horizontal edge of the screen – then they could use this information may alter their perception or their judgement.

In order to overcome this confound, the angular extent of the flow stimulus had to be reduced. The stimulus was modified so that the full circumference of the annulus was completely visible, which was constrained by the height of the projected image. Unfortunately, this slightly reduced the maximum eccentricity of flow stimulus, but was effective in removing the cardinal edges from the display. In the experiments I conducted after this point[6], no visible horizontal or vertical edges were present in the projected image.

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[6] The reader should note that I refer to the chronological order in which I ran the experiments, which does not necessarily match the order that experiments are presented herein. Experiment 1.3b (Appendix B) was conducted at the same time and therefore suffers from the same caveat.

Experiment 1.1 – Full statistical results for Interaction

Interaction between Flow direction and Target eccentricity

Table B1 – Results of within-subjects ANOVA of Experiment 1.1 showing significant interactions at each flow eccentricity.

16.5 cm radius: $F\,(1, 5) = 76.633$, $p < 0.001$
20 cm radius: $F\,(1, 5) = 50.765$, $p = 0.001$
25 cm radius: $F\,(1, 5) = 109.405$, $p < 0.001$
30 cm radius: $F\,(1, 5) = 33.317$, $p = 0.002$
35 cm radius: $F\,(1, 5) = 49.724$, $p = 0.001$
40 cm radius: $F\,(1, 5) = 18.237$, $p = 0.008$

Experiment 1.1b - Flow eccentricity control study (Scaled)

Experiment rationale

Using a peripheral stimulus that was appropriately scaled with increasing retinal eccentricity, this experiment sought to replicate the relationship between flow eccentricity and relative tilt seen in Experiment 1.1. In the experiment reported in the main body, relative tilt magnitude appeared to decrease with increasing flow eccentricity, indicating that the contribution of flow to the parsing process declines with the increasing retinal eccentricity of the flow. However, cortical representation of the retina is not uniform or equal across the visual field (Anstis, 1998). A stimulus presented in central vision will be over represented in terms of the neural area activated by the stimulus in comparison to the same stimulus presented in peripheral vision (Mora et al., 1989). The cortical magnification factor provides a measure of the number of millimetres on the cortex that equates to one degree of visual angle on the retina (Anstis, 1998). This measure can be used to equate visual stimuli for neural area such that peripheral stimuli are scaled according to the reciprocal of the magnification factor (M-scaling). In the present experiment, the flow stimuli across the different eccentricity conditions were scaled using the M-scaling method described by Rousselet, Husk, Bennett and Sekuler (2005). This meant that the onscreen dimensions of the flow annulus and diameter of the dots increased with retinal eccentricity.

The predictions of this study were identical to those in Experiment 1.1, and an interaction between flow direction and target eccentricity was expected for each flow eccentricity indicating a peripheral contribution to flow parsing. In addition, based on the findings of Experiment 1.1, a decline in relative tilt magnitude was expected with increasing flow eccentricity. If the results do not demonstrate a decline in relative tilt magnitude with increasing flow eccentricity then this would suggest that the decline seen in Experiment 1.1 was due to the fact that the size of the flow band was not scaled in order to account for the decreasing neural area stimulated by the flow with increasing eccentricity of the stimulus.

Methods

Participants.

The same six participants who sat as observers in the unscaled version took part. Participants completed this study after Experiment 1.1, but they remained naïve to the experimental hypotheses until after both experiments were completed.

Apparatus and Stimuli.

A modified version of the near peripheral stimulus as in the unscaled radius manipulation (Experiment 1.1) was used in this study. In this experiment, the width of the flow annulus was scaled with eccentricity using M-scaling. The width was calculated using the method described by Rousselet et al. (2005) where the flow width was 14 degrees (10 cm) at a radius of 22.78 degrees eccentricity and increased by the factor M with each eccentricity. The inner radius of the peripheral flow ring was varied in five conditions: 16.8 cm (equivalent to the flow stimulus used in Experiment 1.1), 20 cm, 25 cm, 30 cm, 35 cm, Table B2 provides the respective eccentricity in visual angle for each flow eccentricity.

Table B2 – Details of the flow eccentricity conditions including the M-scaling factor and width of the flow annulus for each flow eccentricity.

Inner radius of flow annulus (cm)	Visual angle of radius (degrees)	M-Scaling factor	Width of flow annulus (cm)	Width of flow annulus (degrees)
16.8	22.78	1	10.00	14.04
20	26.57	1.14	11.43	15.95
25	32.00	1.36	13.29	18.38
30	36.87	1.53	15.33	20.97
35	41.19	1.70	16.96	22.98
40	45.00	1.84	N/A (18.40)	N/A (24.70)

The largest eccentricity employed in Experiment 1.1 (45 degrees) could not be used in this version of the experiment as the width of the scaled flow annulus meant that the stimulus exceeded the height of the projected image and introduced clear visible edges to the display. Dot size was also scaled for eccentricity using the same method.

Design.

The design was identical to Experiment 1.1, except that there was one fewer level of the eccentricity manipulation (45 degrees radius condition). This resulted in a total of 180 trials, which were randomly ordered and completed by each participant in a single experimental session.

Procedure.

Identical to Experiment 1.1 (Page 66).

Results

The effects reported in Experiment 1.1 were all replicated. As before, there was a significant difference in the magnitude of relative tilt difference between Expanding and Contracting flow conditions, with a larger magnitude in the Expanding case (F (1, 5) = 244.375, p <0.001). There was also a significant interaction between flow eccentricity and flow direction (F (4, 20) = 9.430, p <

0.001) as predicted if the results of Experiment 1.1 were not due to the fact the flow was not scaled for retinal eccentricity.

Figure B3 shows that that magnitude of relative tilt difference reduces with increasing flow eccentricity. The decrease in relative tilt for expanding flow in this study was much the same as in the unscaled version (Experiment 1.1 slope = -0.367). However, there was a less noticeable decrease in relative tilt magnitude observed for contracting flow in this experiment with a slope of 0.436 here but 0.520 in Experiment 1.1.

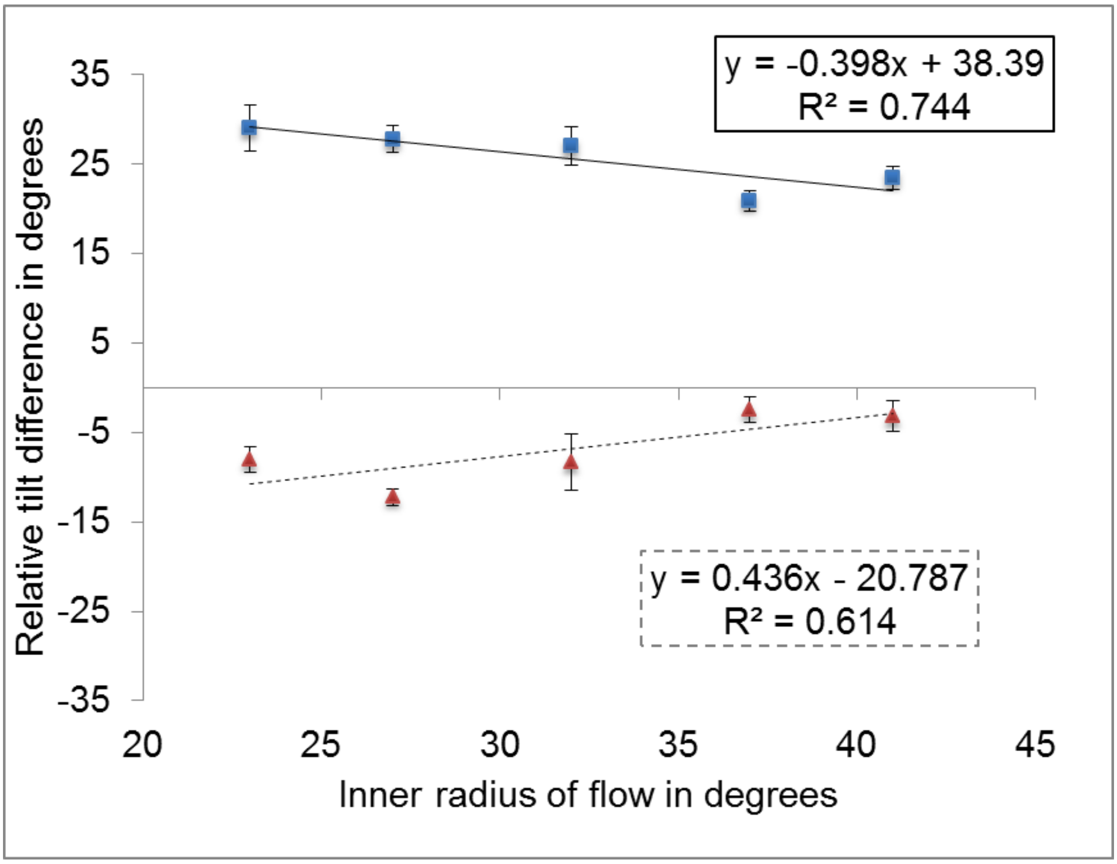

Figure B3 – Relative tilt difference in degrees as a function of flow direction and flow eccentricity. Error bars show within-subject *SE*.

Figure B4 shows the data from Experiment 1.1 and the present study on the same axis to allow a comparison of the two datasets. Regression analysis was conducted to assess whether the decline in relative tilt magnitude with increasing flow eccentricity in this experiment was significantly different from the decline observed in Experiment 1.1. For each participant the data from Experiment 1.1 and this experiment was regressed separately to obtain the slope of the regression line in each study. A paired-samples t-test was then conducted to determine whether there was a significant difference between the slopes. This analysis was run separately for Expanding and Contracting flow conditions. The t-test revealed that there were no significant differences in the slope of the regression line between the two datasets (Expanding: *t* (5) = 0.138, *p* = 0.896, *n. sig*; Contracting: *t* (5) = 0.403, *p* = 0.704, *n. sig*).

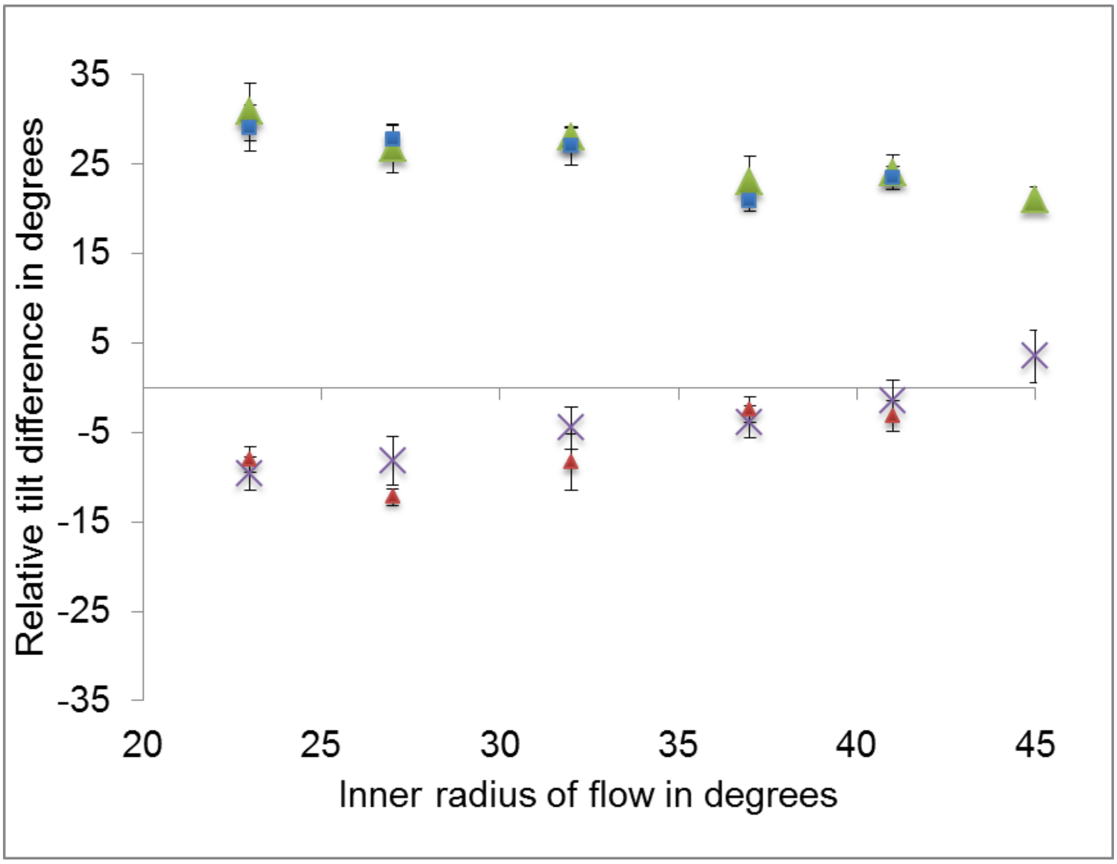

Figure B4 - Composite data from Experiment 1.1 and 1.1b. Unscaled experiment data = green triangles (Expanding) and purple crosses (contracting), Scaled experiment data = Blue squares (Expanding) and red triangles (contracting). All error bars show within-subject *SE*.

Interpretation

As in Experiment 1.1, the magnitude of relative tilt decreases as the eccentricity of the flow stimulus increases, for both expanding and contracting flow. Comparing the results of this experiment with the unscaled version, there do not appear to be any differences in the contribution of peripheral flow to flow parsing, as might have been expected if the results of Experiment 1.1 were accounted for by differences in cortical magnification between the different flow eccentricities.

Experiment 1.3b - Radial flow configuration: Paradigm development

Experiment rationale

This experiment was motivated by the need to determine whether the location of the Far peripheral stimulus is the reason smaller effects were found for this condition. This study was undertaken prior to Experiment 1.3. Experiment 1.3 is reported in the main body as it employed a more rigorous methodology. The aim of both studies was to determine whether flow configuration played a critical role in the findings of Experiment 1.2. Namely, that the far peripheral stimulus did not illicit a relative tilt as strong as the near peripheral stimulus. The peripheral monitors, displaying the Far peripheral stimulus, are only located on the left and right of the head and do not therefore provide self-motion information above and below the observer. It could be the case that above/below visual field stimulation is critical for identifying self-movement and flow parsing using visual flow in the far periphery, or full field motion might be required i.e. all around us. These two differences between the Near and Far peripheral conditions used in Experiment 1.2 required investigation to ensure that the Near-Far effect seen in Experiment 1.2 represented differences in flow parsing between these retinal regions. Furthermore, testing portions of the visual field allowed for the relative contribution of each area to be assessed to see whether there are any notable differences.

Methods

Participants.

Five participants (3 male) took part in all conditions, with an age range from 24-30 years (M = 26.00, *SD* = 2.35). In the Left/Right flow condition, there were two additional participants (1 male; age range 24-30, M = 25.75, *SD* = 2.07). All individuals were postgraduate students at Cardiff University.

Apparatus and stimuli.

The near peripheral stimulus used in Experiment 1.2 was modified so that sections of flow were excluded from the display by overlaying a black rectangle in front of the flow stimulus (Figure B5). In the Above/Below and Left/Right conditions longest dimension of the rectangle subtended the entire height/width of the projected image. This produced two visible bands of flow, either at the top and bottom of the screen or to the left and right. From the nearest screen edge, each band of flow extended 18cm (10.73 degrees) towards fixation. Otherwise the flow stimulus was identical to the Near stimulus in Experiment 1.2.

The probe was presented at a fixed eccentricity of 4 degrees (6.64 cm) from fixation and had a starting position of either -45 degrees or +135 degrees, where 0 degrees is defined as vertically upwards. The two potential target locations were the same as in Experiment 1.3.

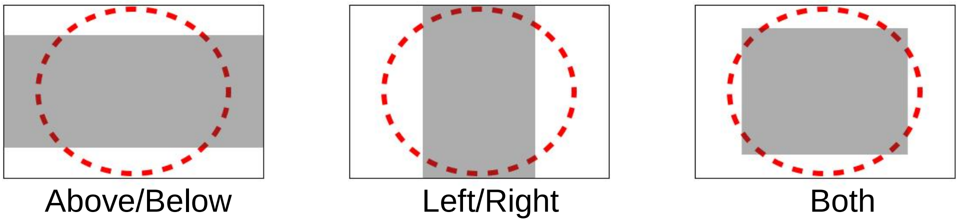

Figure B5 – Schematic representation of the three flow configurations.

Design

Three conditions: Above/Below, Left/Right, Both. The order of conditions was randomised across six participants. There were 17 possible tilt locations from a range of ±16 degrees in 2-degree steps.

Procedure.

Procedure was the same as for Experiment 1.3 and the peripheral flow was displayed in one of three configurations (see Figure B5).

Results

Prior to analysis, the difference in relative tilt between the two target locations (Above and Below fixation) was calculated for each condition. It was anticipated that the Both flow configuration would replicate the results of Experiment 1.2 and show a larger difference in relative tilt for Expanding than Contracting flow. Although there is a trend towards this finding, this was not a significant difference ($p > 0.05$).

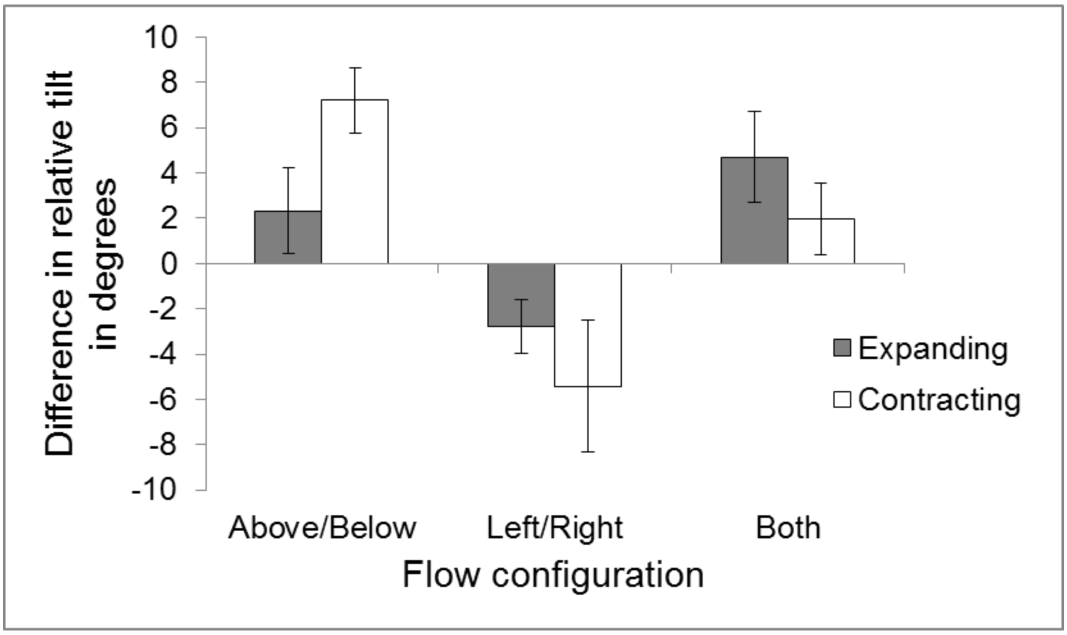

Figure B6 – Differences in relative tilt as a function of flow configuration and flow direction. Error bars show within-subject *SE.*

If flow from different portions of the retina equally contributes to the effects seen in the Near peripheral condition of Experiment 1.2 then the two partial flow conditions should show the same pattern, but this is not the case (see Figure B6). The results did not show a consistent pattern across the three flow configurations. A 3 x 2 within-subjects ANOVA confirmed that there were differences between the flow configurations (*F* (2, 8) = 5.607, *p* = 0.030).

Critique

The results from the two partial conditions are not in line with a peripheral contribution to flow parsing, which is at odds with the results obtained in Experiment 1.1 and 1.2 which used full field stimuli. The apparent lack of a peripheral contribution seen in the present study might stem from the reduction in the visual area of the flow stimulus in the above/below and left/right conditions, or it may be a result of the way in which flow was occluded in these two stimuli.

In much the same way as in Experiment 1.0 (Appendix B), clear horizontal and vertical edges were introduced to the display. As I noted in the critique to Experiment 1.0, this presents a problem when observers are reporting perceived trajectory. Eagle-eyed readers may question why the evaluation of this previous experiment did not prevent the same issue arising in this study – simply put: the two experiments were run in parallel. As such, the critique found on Page 233 is equally applicable to this study and the reader may wish to refer to this earlier section.

For the present study, investigating the effect of flow location on relative tilt, the introduction of edges in the display was equally not desirable. In order to overcome this confound, the stimulus was redesigned. In Experiment 1.3, *segments* of flow were employed rather than *sections*. The critical difference being that no cardinal orientations were present in the display. The flow was divided into quarters along two lines that diagonally subtended the projected image. Comparing the results of Experiment 1.3 and 1.3b, it is clear that the stimulus used in this study was far from optimal. Thus, the development of the stimulus produced a much more effective means by which to test the effect of flow location.

Experiment 1.4 - Radial flow Speed Discrimination: Alternative analysis

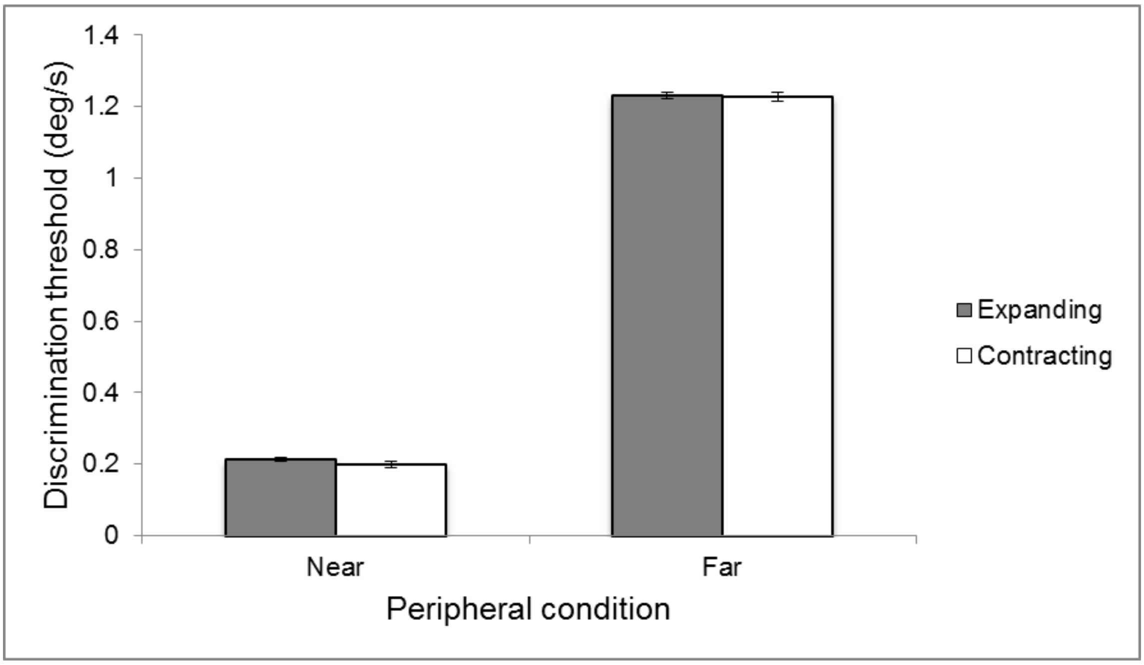

Figure B7 Discrimination threshold in degrees/s for each Peripheral condition and flow direction. Error bars show within-subject *SE*.