Motion perception following simultaneous adaptation to smooth pursuit eye movement and retinal motion

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This dissertation is submitted for the degree of PhD.

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September, 2010. Cardiff.

The research was funded by the ESRC.

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Summary

This study employed adaptation paradigms to explore visual motion processing during smooth pursuit eye movement. Two classes of model, classical models and reference signal models, employ estimates of retinal motion and pursuit to estimate head-centred world motion. The pursuit estimate in classical models is purely extra-retinal. In reference signal models the pursuit estimate is additionally modulated by retinal feedback. Chapters 2 and 3 investigated the motion aftereffect (MAE) following adaptation to simultaneous retinal motion and smooth pursuit. In chapter 2 adaptations to either horizontal retinal motion or vertical smooth pursuit respectively resulted in retinal or extra-retinal MAE. Simultaneous orthogonal adaptation to both motions resulted in a unidirectional MAE that bisected the individual MAE directions. Adaptation to a head-centred motion signal (perceived direction) was not supported by the recorded directions for adapting motion and resulting MAE. An explanation employing separate lower level adaptations was favoured. Chapters 3 and 4 examined motion perception following collinear motion adaptation. Additionally, the retinotopic nature of retinal motion adaptation was exploited to limit the effects of retinal sensor adaptation during the test phase. The two classes of model then make differing predictions: Reference signal models predict a pursuit estimate that is modulated by retinal motion, whilst classical models do not. In chapter 3 varying the background motion during adaptation did alter the physical eye movement. However, the properties of the resulting MAE were not modulated by retinal feedback and a classical model was supported. Chapter 4 used a moving test to quantify the perceived stability of a background during smooth pursuit; using a two alternative forced choice paradigm and staircase procedure. Either a phantom velocity aftereffect or a modified reference signal model was suggested as modulating the Filehne illusion in Experiment 6. Two control experiments failed to find evidence for phantom adaptation. Experiment 9 demonstrated a potential retinotopic location bias for background motion when applying a reference signal model, background motion above the test area did not alter perceived stability judgments.

Declaration/Statements

DECLARATION

This work has not previously been accepted in substance for any degree and is not concurrently submitted in candidature for any degree.

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STATEMENT 1

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Acknowledgements

Mostly, I would like to thank Tom Freeman for giving me the opportunity to work towards a PhD, and for his continued help and guidance throughout. He was an excellent supervisor during the three years, always available at short notice, and willing to spend a long time looking at various aspects of the work. I would also like to thank the ESRC for funding my research. I enjoyed my three years in the School of Psychology at Cardiff, which provided a pleasant, supportive and often fun atmosphere in which to work. The facilities and staff are excellent.

I should like to thank everyone I shared an office or a beer with over the three years. Mainly I'd like to thank Emma Bridger, Emer O'Connor, Rachael Elward, Tracey Herlihey, Carl Hodgetts, Marieke Stiel and Hilary Watson for their friendship. The variety of people, backgrounds and attitudes helped to make it as interesting a time as you could hope for, always fun and always something different going on. I was lucky to study with a large group of genuinely nice people and I could easily list several more here.

I would also like to thank my family, Niamh for always being there and Cónán who only arrived during the PhD, but has managed to make everyday more fun. I'd also like to thank my Mum and Dad for taking the strain and doing so much more than anyone could reasonably expect. I am looking forward to more free time to spend with all of you.

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Chapter 1: General Introduction

The current thesis presents an investigation into aspects of visual motion processing, specifically the relationship between retinal motion and eye movements. The physical patterns of light that are focussed onto the retina are altered during an eye movement. In order to build an accurate representation of the visual world, the visual system must take into account the effects of self-motion on perception.

Afferent and Efferent Signals

Visual stability, or space constancy, is the visual systems ability to maintain a view of the outside world that does not jump about and move with every eye movement (Duebel, Bridgeman & Schneider, 1988; Stark & Bridgeman, 1983). During an eye movement visual stability can be achieved, or the velocity of a target can be estimated, by interrogating retinal information and internal estimates of self motion. The terms afferent and efferent denote the different origins for these signal types. Afference relates to the neural inflow of information from sensory organs, whilst efferent signals travel away from the central nervous system.

The afferent signals referred to in this thesis relate to retinal information, although the term could encompass proprioceptive information, such as that from the muscles around the eye. Additionally, whilst some vertebrates have retinal cells specialised for motion detection (Barlow and Hill, 1963; Barlow & Levick, 1965), evidence suggests that motion-specific processing in humans occurs after the retinal ganglion cell level at later stages in the visual processing hierarchy (Bach & Hoffman, 2000). Despite the suggested absence of specific motion processing units at the retina, retinal motion is defined here as the afferent signal arising from retinal stimulation. Afferent retinal motion has two sources; retinal motion that is created during self motion and retinal motion that is created through the external movement of objects in the world. Afferent retinal signals are further classified to denote this. Exafferent retinal motion refers to signals generated by the motion of external objects, whilst reafferent signals relate neural inflow as a consequence of our own movement (von Holst & Mittelstaedt, 1950).

Considering the simple case of a smooth pursuit eye movement, an internally generated estimate of eye velocity could provide the necessary information to differentiate between exafference and reafference. An early suggestion considered the efferent signal as the "effort of will" required to produce an eye movement (Helmholtz, 1867, cited by Bridgeman, Gaunt, Plumb, Quan, Chiu, Woods, 2008), an endogenous extra-retinal signal. Later the pattern of neuronal excitation producing the eye movement, termed corollary discharge, was suggested as providing the effort of will feedback (Sperry, 1950). The idea that an image of the efferent signal could be created, called efference copy, was proposed in the same year and similarly refers to neural outflow (von Holst and Mittelstaedt, 1950). von Holst and Mittelstaedt suggested that the signal sent to control the extra-ocular muscles is additionally copied to the perceptual centre of the brain. Evidence for an extra-retinal efferent copy was provided by surgically inverting the head of a fly (von Holst and Mittelstaedt, 1950, in Rosenbaum, 2009). This reversed the relationship between visual motion and the internal estimate of physical motion during flight. Flying to the right provided inaccurate feedback that the fly was moving to the left. In trying to compensate for the incorrect feedback and regain it's heading, the fly travelled in circles, in a positive feedback loop. The fly moved normally in darkness. The motion perception mechanisms of the fly had been distorted in ways which could not be predicted by changes to retinal motion alone.

Combining Afferent and Efferent Signals: Models of head-centred motion perception.

Sensory signals relating information about our physical movements, as well as information regarding external object motion, are required in order to preserve a stable and accurate view of the world, and to estimate external motion. During smooth pursuit, a simple way of achieving both space constancy and an estimate of motion for moving objects is to combine the velocity estimates derived from afferent and efferent sources.

A smooth pursuit eye movement will cause world stationary objects to move in the retinal image. Because the eye velocity and retinal velocity are equal and opposite, adding together retinal and extra-retinal estimates of these respective motions provides a method for achieving perceptual stability. Additionally, for an object moving in the world, the exafferent portion of the retinal signal will remain after the cancellation process. This non-cancelled portion of the retinal motion signal could then provide the necessary information to derive an estimate of object motion.

Whilst combining information from afferent and efferent sources can provide a reasonable estimate for the motion of both stationary and moving objects, these estimates can differ. Two visual illusions are commonly cited as demonstrating this persistent error in visual processing. The first is the Aubert-Fleischl illusion, in which an object is perceived as moving more slowly when pursued (Aubert, 1886; Fleishcl, 1882; cited by Ernst, 2010). The second is the Filehne illusion, which describes the illusory motion of a stationary background during pursuit (Filehne, 1922, cited by Mack and Herman, 1973). Both of these illusions suggest that the pursuit speed estimate is typically smaller than the retinal speed estimate. The Filehne illusion is further detailed in section 1.3.1, and was employed in chapter 4 to examine the changes in perceptual stability that can be observed following adaptation.

Figure 1.1 shows a simple schematic detailing the combination of retinal information and eye velocity estimates to generate perceived motion. This diagram also illustrates the focus of chapters 2, 3 and 4. The experiments reported in chapter 2 investigate the motion aftereffect (MAE - see section 1.3.2) which follows simultaneous adaptation to retinal motion and repetitive smooth pursuit. Chapter 2 investigates the level at which the adaptation of retinal and extra-retinal signals occur, when both are presented simultaneously. Evidence is provided for adaptation at a lower level of motion processing, before the signals are integrated to provide the perceived direction. Chapters 3 and 4 then investigate the nature of the eye velocity estimate during pursuit. The aim of these chapters was to differentiate between two competing models of motion perception during pursuit, namely the "classical model" and the "reference signal model". The classical model suggests that the pursuit estimate is based on a purely extra-retinal signal whereas the reference signal model proposes that the extra-retinal signal is mediated by retinal feedback.

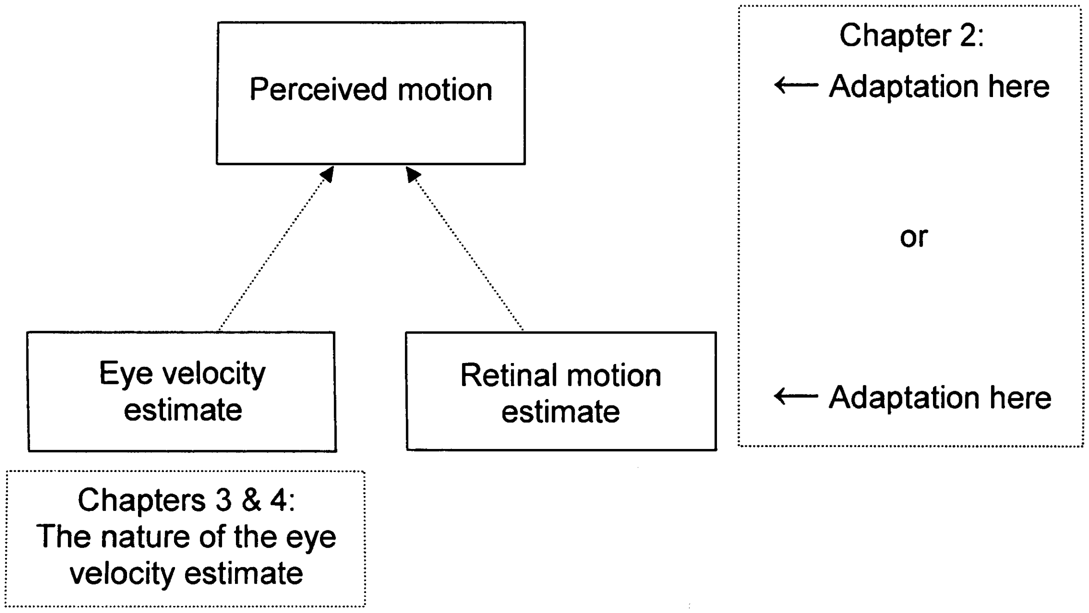

Figure 1.1: Perceived motion can be derived from internal and external sources of information. Extra-retinal efferent signals inform the eye velocity estimate, whilst our sensory system introduces afferent motion signals to estimate retinal motion. Some models suggest that the retinal motion estimate also informs the eye velocity estimate; this is examined in the experiments of chapters 3 and 4.

Although they are discussed as two separate models in this thesis, Wertheim (1994) grouped them together into one approach that he termed inferential perception theories. Inferential perception models calculate object and background motion by employing estimates of pursuit eye movement to cancel retinal motion. Classical and reference-signal models differ in their conception of how the pursuit estimate is derived. Whilst this thesis concentrates on inferential motion perception, another class of models, termed 'direct perception' by Wertheim, suggest an alternative approach to motion perception. Direct perception theories propose that only retinal motion is required for the calculation of object motion and the maintenance of perceptual stability. A brief examination of direct perception is therefore included in this review for completeness.

Classical Models

Retinal motion is created during a smooth pursuit eye movement. If the observer and object are otherwise stationary, then the retinal motion created is in the opposite direction, but of a similar magnitude, to the eye movement. Where the object is moving, the retinal motion created by an eye movement is added to the motions already existing in the retinal image. The original proponents of the Classical Models of motion perception considered the efferent extra-retinal signal and the portion of the retinal signal created during an eye movement (the reafferent signal) to be approximately equivalent, and able to cancel one another (Sperry, 1950; von Holst and Mittelstaedt, 1950; Jeannerod, Kennedy & Magnin, 1979). A vector sum of these two will therefore result in no perceived motion from self-induced motion, when there is no noticeable net difference between the two velocity estimates. Figure 1.2 provides a schematic for the classical model, in which estimates for the retinal and pursuit signals are produced, and then combined to represent a head-centred estimate of world motion.

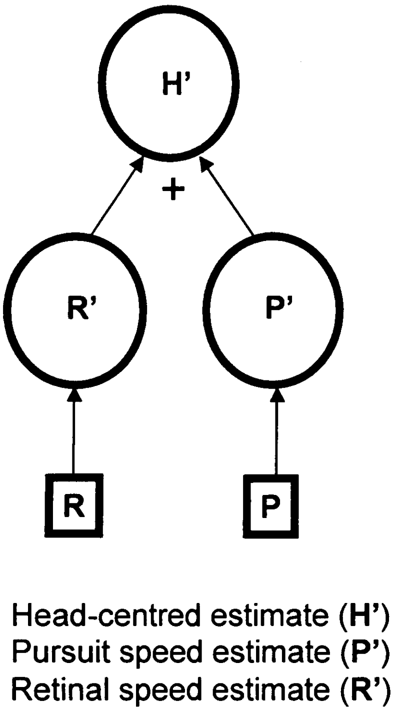

Figure 1.2 The Classical Model. A head-centred estimate of world motion can be derived from the equation $H' = R' + P'$, where retinal (R') and pursuit (P') estimates are added to produce the perceived head-centred motion (H), an estimate of real world motion.

Many reports have suggested that an error in the eye movement estimate would produce an error in the head-centric interpretation of motion (Festinger, Sedgwick & Holtzman, 1976; Swanston and Wade, 1988; Swanston, Wade, Ono & Shibuta, 1992). Early accounts of the classical model assumed that retinal motion processing was veridical (e.g. Post & Leibowitz, 1985). Freeman & Banks (1998) demonstrated that the retinal motion estimate (R') is dependent on the properties of the viewed stimulus. In a series of experiments the spatial frequency of the displays were varied, with the result that related changes were observed for both the Aubert-Fleischl illusion and the Filehne illusion.

Properties that can alter the perceived speed of a stimulus have been shown to include the spatiotemporal properties of the stimulus (Smith & Edgar, 1994; Ferrera & Wilson, 1991, Bex, Verstraten & Mareschal, 1996), contrast (Thompson, 1982; Stone & Thompson, 1992; Blakemore & Snowden, 1997; Anstis, 2001; Thompson, Brooks & Hammett, 2005), eccentricity (Johnston & Wright, 1986), exposure to previous retinal motion (see adaptation section), and dot density (Watamaniuk, Grzywacz & Yuille, 1993) . A non-isotropic variation in perceived motion also occurs across the visual field (Raymond, 1994). Thus, the physical properties of the pursuit target, and the background over which pursuit takes place, could alter head-centred motion.

The most recent accounts of the classical model therefore derive head-centred motion ($\hat{H}$) by taking into account the potential limitations of both the R and P estimates using gain functions r and e to express the respective errors (Freeman and Banks, 1998, 1999; Souman, Hooge & Wertheim, 2005).

$$\hat{H} = rR + eP$$

The model as stated above assumes that the gain terms are fixed and independent of speed. However more recent work has questioned this assumption (Freeman, 2001; Turano & Massof, 2001; Souman & Freeman, 2008). For instance, Souman and Freeman (2008) compared velocity estimates for random dot patterns during pursuit and fixation using a two-interval forced-choice paradigm. Participants had to report which interval contained a dot pattern with the highest head-centred velocity. A non-linear variant of the model, in which the gain terms e and r depended on eye speed and retinal speed, respectively, was found to best predict the estimates for both retinal velocity and eye velocity.

Two visual illusions experienced during smooth pursuit, the Aubert-Fleischl illusion and the Filehne illusion are often cited as demonstrating the differing size of the retinal and pursuit estimates (Mack & Herman, 1973; Freeman, 2001). Both illusions are explained by the extra-retinal signal only being large enough to partially compensate for the retinal motion induced during smooth pursuit. When combining the signals, the classical model suggests that any excess signal during the cancellation process should represent an approximation of world motion. This is because, having removed the effect of eye movement on retinal motion, any remaining retinal motion represents exafference and can be used to estimate the motion of external objects.

Classical models suggest that motion perception during smooth pursuit is determined by the sum of two independent retinal and extra-retinal signals. The purely extra-retinal nature of the pursuit speed estimate has been questioned (Wertheim, 1987, 1994; Haarmeier & Thier, 1996; Haarmeier, Bunjes, Lindner, Berret & Thier, 2001). The fixed nature of the extra-retinal estimate has been suggested as a weakness, with more recent reference signal models replacing the extra-retinal signal with a continuously optimised estimate of smooth pursuit, an estimate capable of matching the visual signal.

Reference signal models

Wertheim (1987) reconsidered the nature of the extra-retinal pursuit estimate in order to accommodate the differing perceived motions of large and small background patterns when viewed during similar eye movements. Size is not the only background property that can influence perceived motion, other properties such as luminance, contrast and spatial frequency can also (Thompson, 1982; Raymond, Shapiro, & Rose, 1984; Smith & Hammond, 1985). The influence of these background properties on motion perception have led to claims that efference copy based estimates of eye movement alone would fail under most conditions (Dash, Dicke, Chakraborty, Haarmeier and Thier, 2010). A successful compensation process may therefore need to rely on retinal information. Such feedback would form a self-referential circularity or 'strange loop' with retinal information being used to help interpret itself (Wertheim, 1987). Wertheim suggested that the visual differences reported for the larger background pattern could be explained by the inclusion of additional vestibular and optokinetic information within the pursuit estimate. Thus Wertheim's suggested pursuit estimate is not exclusively derived from an efference copy/corollary discharge, but from a range of sources. The concept that retinal motion comprises a part of an extra-retinal signal is clearly an oxymoron, so for this reason the extra-retinal signal of the classical model was replaced by a reference signal (Wertheim, 1994). Reference signal models combine extra-retinal, retinal and vestibular information to generate a single compound signal from which eye velocity is estimated (Brenner & van den Berg, 1994; Crowell & Andersen, 2001; Goltz, DeSouza, Menon, Tweed & Vilis, 2003; Haarmeier, Bunjes, Lindner, Berret & Thier, 2001).

There are also reasons to suspect that pursuit estimates are not subject to continuous visual recalibration. Two visual illusions demonstrate situations in which recalibration does not occur. The Filehne illusion (Filehne, 1922; more detail below) describes the perception that a background is moving during smooth pursuit. A similar illusion relates a paradox in perceived speeds for a moving object. When pursued it appears to move more slowly than when viewed with stationary eyes. This is the Aubert-Fleischl illusion is again attributed to an under-estimate of pursuit (Aubert, 1886; Fleishcl, 1882; cited by Ernst, 2010; Dyde and Harris, 2008). Both illusions can be attributed to an underestimation of pursuit velocity (Mack and Herman, 1973). A lack of continuous recalibration may be suggested when such illusions demonstrate a consistent mismatch between retinal and pursuit estimates.

As stated by Sumnall, Freeman and Snowden (2003) "The current lack of detail in many of the reference-signal models makes it quite difficult to devise appropriate experiments" (p. 1717). With this lack of detail in mind, Figure 1.3 presents a possible schematic for a simple reference signal model.

As with Figure 1.2, retinal and extra-retinal signals again provide information to estimate head-centred motion. In comparing this model with the classical model presented in the previous section, it can be seen that the main difference is in the nature of the pursuit speed estimate. In figure 1.3 the pursuit estimate is a function of both extra-retinal and retinal information. Retinal motion thus provides information for its own interpretation, and corresponds to a feed-forward signal that forms a referential circularity within the perceptual system ('a strange loop' according to Wertheim, 1994). The model excludes the influence of vestibular feedback, which is included in some reference signal models (Wertheim, 1994), because the head was stationary in all experiments reported in this thesis.

As mentioned in the classical model section, retinal motion processing has often been assumed to be veridical, whilst evidence suggests this is not the case (Freeman & Banks, 1999). A major problem with the evidence for reference signals to date is that the properties of the retinal stimulus that affect the R input into P′ could also change R′ (Freeman & Banks, 1998; Sumnall, Freeman and Snowden, 2003). The term 'properties' is used in its most general sense here, and so could refer to adaptive state, which is the issue central to the current thesis, as well as more obvious spatiotemporal factors such as spatial and temporal frequency content. So far research has failed to determine which of the two models is most appropriate because it has failed to exclude the potential for R′ to directly alter H′, despite claims to the contrary. Chapters 3 and 4 investigate the reference signal and classical model using a motion adaptation technique that limited the potential for R′ to influence the outcome. When the direct influence of retinal motion on perceived head-centred motion can be excluded, experiments in which the two models make differing predictions for the outcome can be designed.

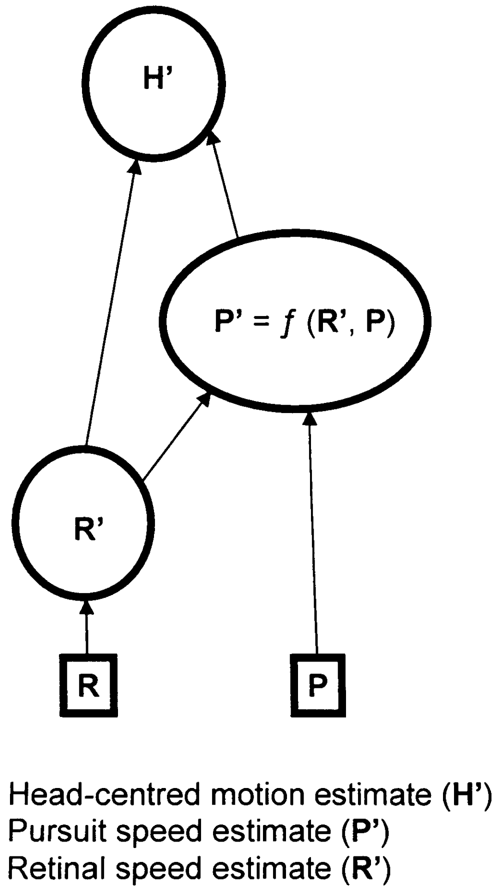

Figure 1.3 The Reference Signal Model. To estimate head-centred motion, estimates of both retinal motion and smooth pursuit eye movement are combined. The purely extra-retinal signal of the classical model is replaced by a reference signal. The reference signal is a function of both retinal motion and the pursuit eye movement.

It should also be noted that the term reference signal is often used interchangeably with a purely extra-retinal signal (e.g. Li, Brenner, Cornelissen and Kim, 2002) with the classical model sometimes referred to as the reference signal in its simplest form (Dash et al, 2009). As defined here, the classical model considers that retinal, extra-retinal and vestibular information are processed in parallel whilst a reference signal combines these separate sources of information into a single signal. The properties of a reference signal therefore differ to those of a purely extra-retinal signal, with some models also allowing a reference signal to be shaped by cognition (Mergner & Rosemeier, 1998).

Reference signals allow for the recalibration of an eye movement estimate. The physical motion of the eye can be altered through development, disease or fatigue (Ludvigh, 1952a). If the pursuit estimate were independent of retinal feedback, eye movement estimates would become inaccurate over time (Haarmeier, Bunjes, Lindner, Berret and Thier, 2001). With an increasing disparity between an eye movement estimate and the associated eye movement, the perception of the world would become increasingly unstable. Another error would occur as a result of the same eye movement over differing backgrounds, visual scenes which vary in respect to their spatial frequency or contrast can produce different perceptions of motion. Dash et al (2009) suggest that a classical model is likely to fail under most conditions since it does not take into account the changes between different visual scenes. The action of a reference signal is proposed to ameliorate these potential errors.

A change in the magnitude of a reference signal has been hypothesised by Haarmeier, Thier & colleagues as necessary to maintain a stable percept by adjusting for error in the pursuit estimate. The whole-field flow of retinal motion during an eye movement provides a source of information about the eye's velocity assuming that the world is largely stationary (Crowell & Andersen, 2001). This could ameliorate differences that develop between the pursuit and retinal motion estimates. When retinal feedback suggests that the pursuit estimate is not sufficient to completely cancel retinal motion (under the stationary world assumption), then the reference signal is considered to be inappropriately small by the visual system. In this case, the claim is that the observers increases the reference signal accordingly (Haarmeier et al, 2001). Equally, a decrease in magnitude would be expected when retinal feedback suggests the pursuit estimate is too large. In this way, retinal motion will lead to a recalibration of the reference signal. As a result, reference signal experiments often manipulate the background motion during an eye movement, thereby changing the amount of retinal feedback (Brenner and van den Berg, 1994; Haarmeier & Thier, 1996, Haarmeier, Bunjes, Linder, Berret and Thier, 2001).

There are a number of studies that support this idea. Brenner and van den Berg (1994) investigated the situations under which reliable eye velocity information could be obtained from retinal flow. Under the majority of circumstances they reported no change in perceived velocity whilst the relative motion between the background and the pursuit target was maintained. Relative motion was found to modulate estimates of the eye movement. Brenner & van den Berg suggested that the extra-retinal signal could both inform the visual system about the viability of employing relative motion and, when retinal motion was deemed inappropriate, could then provide a direction and minimum speed for any given eye movement. This conclusion was drawn from conditions in which the background motion, during an eye movement, was manipulated to the extent that it no longer resembled a static background. This included conditions for which the background retinal motion was in the same direction as pursuit. Under these circumstances, extra-retinal information would show that the background motion could not be consistent with the eye movement. The extra-retinal signal would then provide the only means of estimating the direction and minimum speed of the eye movement.

Simultaneous adaptation evidence for reference signal models

Adaptation experiments in which observers pursue an object over a moving background have provided a means to investigate the claims of reference signal models. Adaptation paradigms in which retinal and extra retinal signals could adapt have also been applied consistently throughout the current thesis.

Crowell & Andersen (2001) investigated adaptation to simulated retinal motion, recreating the retinal flow fields that would be experienced during self motion and showed that extra-retinal signals are most informative in an absence of sufficient retinal motion. Such claims do not compromise the premise that retinal motion modulates a reference signal pursuit estimate. It could be claimed that the pursuit estimate is extra-retinal in the absence of useful retinal information, and improved by retinal feedback when such feedback is available. By the model shown in figure 1.3, where $P' = f(R', P)$, these situations could be represented as a zero input for R′. The implication is that head-centred motion is then related to pursuit speed.

Crowell and Andersen (2001) examined the effect of adaptation on navigation judgements. Other adaptation paradigms have focussed on the use of a reference signal in the maintenance of perceptual stability and in the estimation of object motion. The motivation for chapters 3 and 4 was provided by several studies from Haarmeier, Thier and colleagues (Haarmeier & Thier, 1996; Haarmeier, Bunjes, Lindner, Berret & Thier, 2001; Dash et al, 2009) and a study providing an alternative view of the data by Freeman (2007).

Following exposure to conditioning stimuli Haarmeier and Thier (1996) reported a modification of the Filehne illusion. The conditioning stimuli manipulated the amount of retinal motion during either smooth pursuit or fixation using a two-alternative forced choice adaptive staircase procedure. The relationship between the PSS and retinal slip (slip = retinal motion - eye velocity) can be seen to approximate sigmoid functions (Figure 1.4), with the upper asymptotes achieved when the conditioning stimuli shows no retinal slip (retinal motion - eye velocity = 0). In line with the suggestion of Brenner and van de Berg (1994), perceived stability judgements do not appear to be altered by conditioning stimuli containing positive retinal motion. The lower asymptote would presumably also signify a cut off for extreme negative retinal motion. At this point retinal slip could also be deemed inappropriate for the given eye movement (in pursuit conditions). Conditions containing pursuit eye movements (ETCS - eyes tracking conditioning stimulus) show a larger variation in the PSS than the fixation conditions (ESCS - eyes stationary for conditioning stimulus). However, the modification of the Filehne illusion is mainly determined by retinal slip, with modification of the PSS resulting from the oculomotor system being a secondary factor (Haarmeier & Thier, 1996). Critical to Haarmeier & Thier's argument was a control experiment that used stationary test patterns to test for the effects of retinal motion sensor adaptation. They found no MAE in this case, which led them to conclude that the changes in PSS reflected the dynamic nature of the space constancy mechanisms, presumably a reference signal recalibration.

Haarmeier et al have consistently demonstrated that changes to head-centred perception follow pursuit over backgrounds of varying motion. Interestingly, the studies claim to have excluded the adaptation of retinal motion sensors, thus enabling a direct examination of the effects of retinal motion on the reference signal. Referring back to figure 1.3 it can be seen that when retinal motion adaptation can be excluded, then any retinal mediation of the head-centred estimate following adaptation must be due to the action of the retinal portion of P′. Since this approach offers the ability to discriminate clearly between the two models, a similar method is employed in chapters 3 and 4.

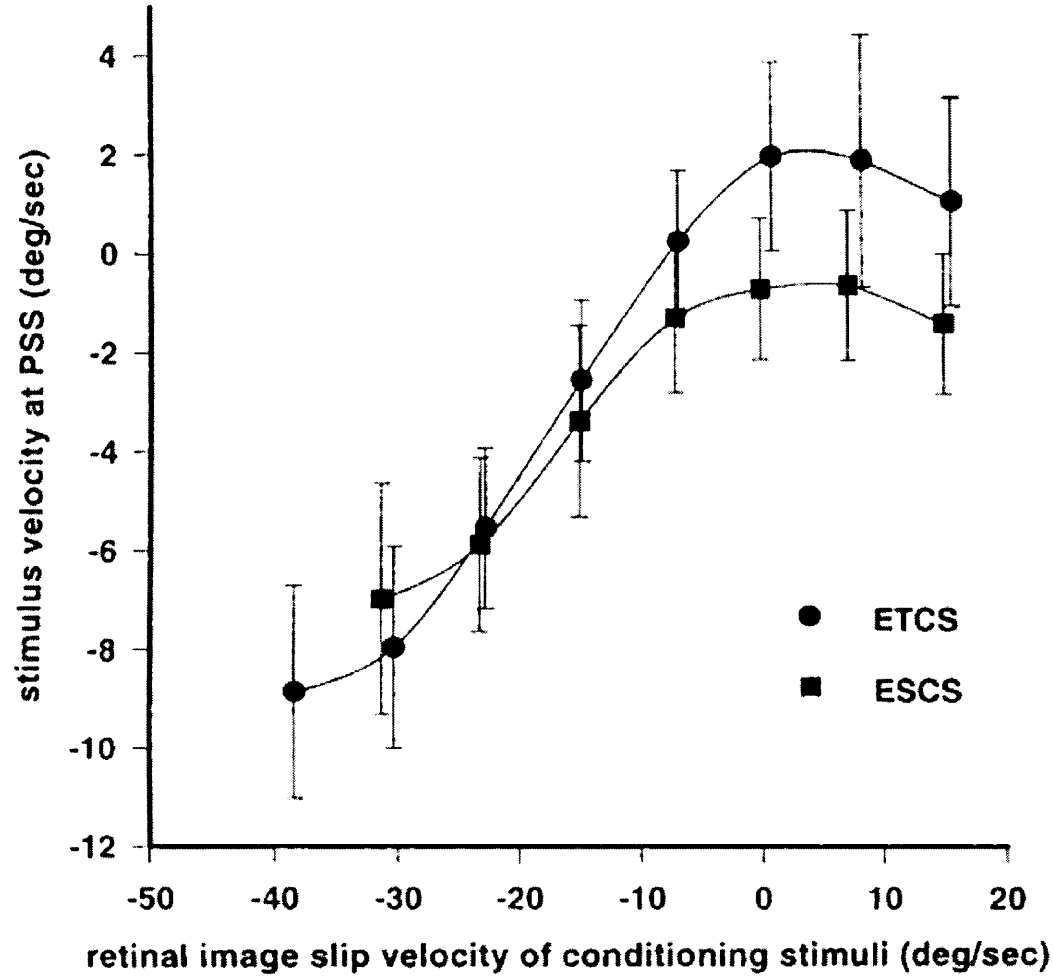

Figure 1.4: Reproduced from Figure 4, Haarmeier and Thier (1996), page 746. Conditioning stimuli modifies the Filehne illusion (error bars represent ±1 SE). Pursuit conditions (Eyes tracking conditioning stimulus: ETCS) show larger variation in PSS across conditions than fixation conditions (ESCS). Both curves can be described by sigmoid functions, with the upper asymptote of each at approximately 0 deg/s retinal slip.

Haarmeier and Thier (1996) demonstrated no MAE was present when a stationary test was employed. This control measure cannot address potential changes to the apparent speed of a moving test following adaptation. Similarly, Haarmeier et al (2001) claimed that retinal motion adaptation had been excluded by employing equal amounts of stimulus motion in opposing directions. Such motion-balanced stimuli result in no net motion visible for a post-adaptation stationary pattern. Having equal motion in both directions results in no imbalance between opponent-process motion detectors, and therefore no MAE is generated (MAE section 1.3.2). Unfortunately, whilst motion balancing would result in no MAE for a stationary test pattern, it does not prevent motion sensor adaptation (Freeman, 2007). Whilst there may be no opponent-process disparity, opposing banks of sensors still adapt. Freeman (2007) showed that this adaptation can alter the velocity judgements for both retinal motion and smooth pursuit eye movements independently. This change in perceived velocity is produced by a close relative of the MAE, the velocity aftereffect, in which adaptation alters the perceived velocity of a moving pattern (Thompson, 1981; Smith & Hammond, 1985). The changes to perceived stability reported by Haarmeier and colleagues could arise from separate adaptation of either the pursuit estimate or the retinal estimate; both signals will alter the head-centred motion estimate. The reported changes can be explained by either the classical model or the reference signal model. This thesis tests the claims of the two models by attempting to eliminate the potential for retinal motion adaptation by exploiting the retinotopic nature of retinal motion adaptation.

Optokinetic potential model: A reference signal model or a classical model?

The optokinetic-potential model (Post & Liebowitz, 1985) proposed that retinal motion altered the extra-retinal signal output, via competition between the reflexive (OKN) and voluntary (smooth pursuit) eye movement systems. This introduces a means by which the properties of the background act to alter the overall magnitude of the extra-retinal signal. Changes to the extra-retinal signal, interpreted as changes due to antagonistic or synergistic reflexive eye movement interference, have been found to alter the perceived velocity of a target (Raymond, 1984). In line with this finding, pursuit over an optokinetic background also significantly changes the gain of smooth pursuit eye movements (Yee, Daniels, Jones, Baloh and Honrubia, 1983; Masson, Proteau and Mestre, 1995; Hutton, Crawford, Kennard, Barnes & Joyce, 2000). Background motion affected the speed of eye movements in Chapter 3. If the extra-retinal signal and the OKN signal antagonistically interfere with one another, both the eye movement velocity and the perceived velocity could be reduced.

Other evidence has not demonstrated support for the optokinetic potential model, since predicted changes to optokinetic potential did not alter perceived speed when background contrast and spatial frequency were manipulated (Sumnall, Freeman & Snowden, 2003). Sumnall et al used a speed matching procedure to estimate the perceived speed of pursued and non-pursued moving patterns, whilst contrast and spatial frequency were varied. However, the study reported no significant change to the eye movements across pursuit conditions as a result of OKN.

Optokinetic potential models are of interest as they potentially explain changes to eye movements over various backgrounds in terms of competition between eye movement signals. The optokinetic potential model's dependence on visual factors suggests that it can be taxonomically related to the reference signal model (e.g. Freeman, 2007). However, whilst the physical eye movement is altered, the extra-retinal origin of the pursuit estimate can be maintained. The optokinetic model could equally be envisaged as supplementing a classical model. Whilst the background alters the OKN, this is not retinal feedback. Both optokinetic nystagmus and smooth pursuit eye movement are generated by retinal image motion. Both classical and reference signal models are only superficially concerned with the initial generation of eye movements.

Whilst both classical and reference signal models consider the role of extra-retinal and retinal information in estimating eye movement velocity, other models suggest that extra-retinal signals are unnecessary. Direct perception models suggest that all of the information required for visual perception is available within the afferent retinal signal.

Direct Perception models

Since the influence of an eye movement on the retinal flow field is to add a constant to all retinal motion, it has been suggested that it is the invariants in the flow field that contain the most relevant information for visual perception (Gibson, 1950). Additionally, self-generated motions create predictable patterns of retinal motion (e.g. expanding, contracting or translating). These optic flow fields provide a major source of information for several models of self-motion perception (Perrone, 2004).

An observer moving through an environment can employ the focus or flow of expansion for locomotion, guiding their heading direction by aligning it with a target (Gibson, 1955; Warren, Kay, Zosh, Duchon & Sahuc, 2001). Bruggeman, Zosh and Warren (2007) suggested that optic flow is involved in the recalibration of visuo-locomotor mappings under instances of displaced vision. Others have disputed the role of optic flow in the visual guidance of walking (Rushton, Harris, Lloyd & Wann, 1998) instead suggesting that it is involved in the recalibration of egocentric space (Held & Freedman, 1963; Brandwood, Rushton & Charron, 2009). Parallels can be drawn between employing retinal motion for egocentric recalibration of locomotion and the retinal recalibration of world motion via a reference signal.

The most recent models of this type are flow parsing models, which separate optic flow due to self-motion and that due to object motion (Rushton & Warren, 2005; Warren & Rushton, 2007, 2009). Separately processing these components allows for self-motion and object-motion to be disambiguated in terms of relative motion to a background. Some models suggest that only when retinal motion becomes ambiguous will extra-retinal signals be employed.

Dual-mode Models

There is evidence for hybrid models, which disambiguate retinal motion using an extra-retinal signal, but otherwise rely on direct perception. Such models have been termed 'dual-mode' (Wertheim, 1994). It has been suggested that observers may use extra-flow-field variables (extra-retinal signals) to help resolve a percept when there is ambiguity in the flow field (Warren & Hannon, 1990). van Boxtel, Wexler and Droulez (2003) demonstrated a task in which participants were either immobile or active within a scene, but experienced the same optic flow in both conditions. Optic flow alone was able to provide 3D structure perception, but when participants were active the inclusion of extra-retinal information increased participant accuracy. Mack and Herman (1978) provide evidence for the use of both classical and direct model mechanisms to control perceptual constancy during an eye movement. During pursuit, the interval for which a background was displayed, the size of the background, and the relative motion between the target and background were varied. These manipulations resulted in large changes to perceived stability. Mack and Herman concluded that relative motion allowed for an object-relative percept that employed retinal information directly, whilst reducing object-relative saliency resulted in a subject-relative evaluation of motion (Mack and Herman, 1978). Similar results were obtained by Crowell and Andersen (2001) who found that the direction of prior retinal motion altered perceived self-motion significantly in a simple scene, although had little effect in a more complex 3-D scene. Again the use of a purely extra-retinal signal as a trigger for a more complex reference signal was hypothesised. An interesting, if tangential, study examined haptic and visual recalibration, when the relative reliability of each was manipulated (Burge, Girshick and Banks, 2010). The results suggested reliability-based recalibrations occur, which are highly dependant on the most reliable source of information. This may offer insight into dual-mode models of motion perception, with the best motion estimate being employed for either perception or recalibration.

The next section considers the effects of adaptation on the perception of motion, illusory motion, and more persistent errors in motion processing (the Filehne Illusion). The Filehne illusion is a persistent error in motion processing which suggests a perceptual under-constancy in the efferent estimate (Mack and Herman, 1978). When considered with the evidence supporting dual-mode models, this under-constancy could suggest a reason for the apparent dominance of reliable retinal information in providing motion estimates. The retinal motion estimate generally produces a stronger signal than its extra-retinal counterpart.

The effect of lenses

The retinal image of a distant object which is offset is closer to the centre of the eye with a convex lens in place, than if the lens was not present. This is because of the refraction through the lens results in an apparent displacement of the source object. As the image is closer to the centre of the eye with the lens in place, a lower amplitude eye movement will be required to centre on the object. The relationship between retinal image and estimated eye movement under these circumstances remain. This could alter the perceived background motion during pursuit which would have consequences for the reference signal model. However, the basic relationship between R and P would not be altered under the classical model.

An interesting paper by Rushton & Cox (1987) used two lenses to affect limited image stabilisation. A high powered convex lens was employed to focus the image at the centre of the eyeball (globe). An additional similarly strong concave contact lens was used to refocus the image on the retina. Within a limited field of view some image stabilisation was achieved. This would change the relationship between the retinal and extra-retinal cues. The planned eye movement would no longer result in the expected outcome... feedforward and feedback models of motor control change the eye movement with regards retinal feedback. The physical change to the eye movement would additionally change the estimate of the eye movement, the efference copy. This copy would then become appropriate for the retinal motion. The classical model would be maintained by the behavioural change. This offers advantages over the reference signal model, which instead of altering the now dysfunctional behaviour changes how that behaviour is perceived.

Adaptation, aftereffects and the Filehne illusion

As already suggested by the discussion of the work of Haarmeier and Thier, motion adaptation is a key tool for trying to understand the basic mechanisms of motion processing. Adaptation has proved invaluable for the non-invasive investigation of motion perception (Mollon, 1974), and was employed in all of the experimental chapters reported here. Following a period of adaptation, our perception of the world can be briefly perturbed, resulting in a variety of visual illusions. Such perceptual changes can be employed to reveal the underlying mechanisms of visual information processing.

Adaptation occurs when individuals are involved in an activity, such as viewing constant motion, which results in a decreased sensitivity to the viewed property. A reduction in sensitivity following visual motion has been attributed to fatigue (Sekuler and Pantle, 1967), where the responding neurons become unable to sustain their firing rates. However, fatigue accounts do not consider the utility of adaptation.

Changes to the functioning of the visual system supplement the analysis of information, removing redundant repetition and increasing the ability of the visual systems to encode changes in the adapted property, matching our response to sensory information with the environment (Clifford, Webster, Stanley, Stocker, Kohn, Sharpee & Schwartz, 2007). Rather than just being a deleterious affect of neuron fatigue, adaptation can be considered as playing a more functional role. Given a limited dynamic range for various groups of neurons, an adjustment in sensitivity to certain aspects of the scene is essential for perception (Smirnakis, Berry, Warland, Bialek & Meister, 1997). An example is dark adaptation. When in poorly illuminated conditions, an increased sensitivity to dim objects is more useful than high acuity information for brighter objects (Barlow & Foldiak, 1989). The change in apparent velocity following motion adaptation can also be attributed a functional process. Motion adaptation is accompanied by increased sensitivity to discriminate speed (Bex, Bedingham & Hammett, 1999; Krekelberg, Wezel and Albright, 2006; Clifford & Langley, 1996). It has also been noted that the visual systems sensitivity to directions of motion differ from sensitivity to the direction of an adapted motion (Phinney, Bowd, & Patterson, 1997).

Chapters 2 and 3 employ the MAEs which following periods of retinal and extra-retinal adaptation. Whilst both the retinal MAE and the extra-retinal MAE are examined in isolation, the MAE specifically investigated in chapter 2 examines a combined MAE comprising both retinal and extra-retinal adaptation. The nature of retinal and extra-retinal signal combination, in eliciting the unidirectional combined MAE, is studied. Chapter 3 employs the extra-retinal MAE to investigate the nature of the smooth pursuit eye movement estimate, whilst attempting to exclude the influence of the retinal MAE. The experiments investigate changes to the properties of the emergent MAE, given adaptation to smooth pursuit over backgrounds with differing motion. The MAEs of chapters 2 and 3 are replaced by the Filehne Illusion for chapter 4. The perceived stability of the background was measured, and the relationship between retinal and extra-retinal signals that follows adaptation to smooth pursuit eye movements over a moving background was again investigated. The results of experiment 1 in chapter 4 are proposed as demonstrating the action of a phantom velocity aftereffect (VAE). This phantom VAE is induced in a previously unadapted central homogenous area. This sub-section outlines previous findings, to relevant illusory effects, that impact on later experimental chapters.

The Filehne illusion

As previously discussed, the Filehne illusion describes the illusory motion of the background during a smooth pursuit eye movement. The Filehne illusion does not result from motion adaptation, and represents a permanent error in motion processing. It is often taken as evidence that the pursuit eye movement is underestimated, and as such is unable to fully cancel the retinal motion created during smooth pursuit. Since the size of the illusion was quantified by Mack and Herman (1973, 1978), it has been used in several adaptation experiments to investigate the mechanisms of perceived stability (Haarmeier & Thier, 1996; Haarmeier, Bunjes, Lindner, Berret & Thier, 2001, Freeman, 2007; also chapter 4).

The Filehne illusion was first reported by Filehne, following an investigation in which he pursued his moving finger at various speeds (1922, cited by Mack and Herman, 1973). By manipulating the absolute motion of an illuminated background during the pursuit of a luminous point, Mack and

Herman were able to determine the point at which the background appeared stationary. To estimate the magnitude of the Filehne illusion, the point of perceived stationarity was compared to the points at which the background was perceived to be moving, both with and against the direction of pursuit. They provided evidence to confirm that the pursuit estimate was too small to cancel the retinal motion created during an eye movement. The compensatory background motion was always in the direction of the eye movement, suggesting a case of perceptual under-constancy.

A second claim in the Mack and Herman paper was that the adjacency of the background to the pursuit point altered the Filehne illusion. When the background was closer to the pursuit point, the Filehne illusion was stronger. In the original study, the test involved the removal of the fixation point during pursuit, which resulted in a drop in the eye movement velocity; this adjacency claim was tested by de Graff & Wertheim (1988). They displayed the background through a moving window, a paradigm frequently employed in the current thesis. By moving the window with the fixation point, the adjacency of the background and pursuit point could be manipulated without altering the exposure time. Since the pursuit point was always visible, it also helped to maintain a constant pursuit eye movement. Additionally, the same retinal area was exposed to the background motion during pursuit.

The properties of the viewed stimulus, such as display time and spatial frequency, have been found to alter the size of the Filehne illusion and invert it (Wertheim, 1987). This finding led to the suggestion that the extra-retinal signal, traditionally considered responsible for compensating the retinal motion created during an eye movement, should be replaced by a reference signal. In drawing this conclusion, it is also necessary to consider that the perceived motion of the background can change as a result of adaptation. Whilst the Filehne illusion illustrates persistent errors in visual processing, other more temporary illusions result from adaptation.

The Motion Aftereffect (MAE)

The point was made earlier that one needs to rule out changes to retinal sensor output in order to make unequivocal statements about post-adaptation changes to perceived stability and how these differentiate between classical and reference-signal models. For this reason, the next sections highlight some of the important properties of the MAE, some of which are utilised in the experiments reported in this thesis. This includes the identification of the 'extra-retinal' MAE which has been almost completely overlooked.

After viewing continuous motion in one direction, the Motion Aftereffect is a percept of illusory motion in the opposite direction. Adaptation in several cortical locations can result in an MAE, as a result there are several ways to both elicit and test for an MAE (Mather, Verstraten, & Anstis, 1998). Early models of the MAE consider that the populations of neurons that are stimulated by an adapting motion have a subsequently reduced firing rate (Sutherland 1961, Mather, 1980). Sutherland proposed the opponent-process model. A decrease in the firing rate of cells that have been exposed to previous motion alters the relationship between variously tuned motion detectors. Figure 1.5 shows a small section of the sensor layer and opponent energy layer. There are two sensors depicted, tuned in opposite directions. The light grey arrows feeding the opponent energy layer are excitatory, whilst the dark arrows are inhibitory. Adaptation alters the strength of signal, either at the sensor layer or the opponent energy layer, triggering a false motion response. The MAE arises as all non-adapted cortical units respond more vigorously when a test pattern is displayed.

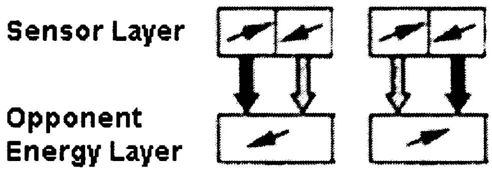

Figure 1.5: The sensor layer contains retinal motion sensors that respond vigorously in one direction, whilst inhibition will occur for motion in the opposite direction. The opponent process model of the MAE suggests that fatigue, following excitation by motion in one direction, will lead to an imbalance between the opposing motion detectors. One unit provides a stronger post-adaptation response; the imbalance is then interpreted as motion. (Reproduced from Mather and Harris, 1989, The Motion Aftereffect, Figure 7.1, page 159)

The required reduction in the firing rate of motion sensitive cells, following prolonged exposure to moving stimuli, has been observed in the rabbit retina ganglion cells (Barlow & Hill, 1963). Electrodes inserted into the rabbit retina recorded a post-adaptation response that fell below the baseline firing rate. Additionally, the recovery from sub-baseline firing followed a time course that could coincide with that of a decaying MAE.

Low level adaptation and fatigue models are not sufficient to account for the differing properties of MAE. Adaptation occurs at various stages in the motion processing hierarchy, with the final MAE potentially being a cumulative percept from several adapted sites. Evidence for MAE from adaptation at later levels of motion processing has been provided from several experiments examining interocular transfer (Wohlgemuth, 1911; Tao, Lankheet, van de Grind & Wezel, 2003; Steiner, Blake & Rose, 1994), the effects of attentional modulation - either by distracting attention (Chaudhuri, 1990, Georgiades & Harris, 2000) or by attending to specific stimulus components (Lankheet & Verstraten, 1995). An MAE can also be viewed after a period of time which would be sufficient for the recovery of any neuronal imbalance, ruling out a fatigue explanation. A particularly resilient MAE, that follows adaptation to a moving spiral, has been reported the day after exposure (Masland, 1969). Storage experiments insert a period of darkness between adaptation and test which extends the decay time for an MAE, beyond that reasonably expected by low level fatigue of the sensor or opponent energy layers. An fMRI study confirmed that following adaptation, during the dark stage of storage, MT+ activation was reduced (Culham, Dukelow, Vilis, Hassard, Gati, Menon & Goodale, 1999). Following the storage phase, when the test pattern was displayed, MT+ activation rebounded in MAE conditions - to a much greater extent than that recorded during control sequences. Transcranial magnetic stimulation of MT has also been found to reduce both the perception and storage of MAE (Theoret, Kobayashi, Ganis, Capua and Pascual-Leone, 2002).

The presence of a visible stationary surround during adaptation and test has been shown to increase the percept of an MAE (Strelow and Day, 1971; Day and Strelow, 1971). The MAE in turn was severely reduced or completely diminished when the test did not include a background. Whilst the absence of a background reduced the MAE it did exhibit storage, the delayed restoration of the background would again result in a strong MAE. It is suggested that two mechanisms are responsible for this MAE, as the adaptation of both the target and the stationary background were found to be independent of one another (Strelow & Day, 1975). Strelow and Day suggest the adaptation of relative motion detectors acted in the generation of such MAE.

The context in which motion is viewed will change the perception of motion, and exert an influence on MAE. Relative motion provides one such context, the relationship between various differential motions, such as a moving target and background, can affect our ability to accurately estimate motion (Lappin, Donnelly & Kojima, 2001). Whilst the relative motion of objects can alter the perceived motion in a scene, it can also generate illusory motion in a physically stationary stimulus, called induced motion (Duncker, 1929, cited by Anstis & Casco, 2006). Duncker noted that induced motion was in the opposite direction to the motion of the background, and that the perceived motion of a target combined both induced motion and target motion. When the speed of the inducing pattern is increased, the amount of induced motion decreases (Reinhardt-Rutland, 1988). Tyler and Torres (1972) demonstrated that at low temporal frequencies, movement detected at the fovea is more sensitive to relative motion than to absolute motion, whilst a separate system sensitive to higher frequencies, but insensitive to relative motion, extends into the periphery. Stimuli that comprise of patterns that provide induced motion are very effective at generating MAE (Swanston & Wade, 1992, Ashida & Susami, 1997). Whilst induced motion can produce a motion aftereffect, it is interesting to note that a motion aftereffect is also capable of producing induced motion in neighbouring patterns (Anstis & Reinhardt-Rutland, 1976).

Peripheral retinal motion (a moving background) has been used to induce an MAE in a stationary central target (Swanston & Wade, 1992; Wade, Spillman and Swanston, 1996). Two flanking gratings were employed to provide induced motion in a stationary central grating. Following adaptation an MAE was observed in the central pattern, in the opposite direction to the induced motion. Wade et al (1996) additionally showed that the presence of the central pattern was not essential for adaptation. The properties of the MAE they reported varied with complicated interactions between different regions of retinal stimulation. This effect of surround modulation on central MAEs was further investigated by Murakami and Shimojo (1995), MAE strength was found to increase as the adapting stimulus was moved further into the periphery. Given the finding of a weak central MAE in Chapter 2, the second experiment moved the adaptation and test patterns into the periphery. This approach was further supported by findings that the motion required to null an MAE increased in the periphery when adapting to drifting gratings (Wright, 1986) or expanding motion (Price, Greenwood and Ibbotson, 2004). Price et al also examined the differences between concrete MAE, such as those discussed so far, and phantom MAE. The perceived motion of both increased in the periphery. Whilst the concrete MAE showed well defined spatial frequency and velocity tuning, the tuning for phantom MAE was much broader and not easily defined. Several studies have examined the phantom MAE.

The phantom MAE, visual phantoms, and phantom motion processing

Given the induction of MAE in a non-moving central target (Swanston & Wade, 1992), it is perhaps not surprising that MAE can also be witnessed in retinal regions exposed to a homogenous field during adaptation. When an MAE can be viewed in an area that has not been exposed to retinal motion during the adaptation phase, it is termed a phantom or remote MAE (Von Grünau & Dube, 1992; Snowden & Milne, 1997; Price, Greenwood & Ibbotson, 2004).

One type of phantom MAE has been induced between remote patterns. An illusory pattern can be seen to extend across an occluded area between two gratings; this has been termed the induced grating effect (McCourt, 1982). When gratings or stripes are displayed either side of a central homogenous area, the blank area becomes filled with an illusory pattern (Weisstein, Maguire & Berbaum, 1977; McCourt, 1982). Weisstein et al demonstrated that the illusory stripes could be animated by moving the surround. Following adaptation to these illusory moving stripes, a physical test placed in the central area elicited a phantom MAE. The visual phantom images described here have been associated with increased activity early in the visual system, specifically in V1 and V2 (Meng, Remus, & Tong, 2005). Such low level activity could additionally cause adaptation at cortical locations further along the visual pathway, but the direct adaptation of higher level mechanisms has also been shown to result in phantom MAE (Snowden & Milne, 1997).

Phantom MAEs are not confined just to areas in which illusory patterns have previously been observed. Another phantom MAE can be generated in a previously homogenous region which was perceived as such. Evidence suggests that such phantom MAE result from the adaptation of global motion processing mechanisms. Global motion processing occurs relatively late in the visual processing hierarchy. It has been demonstrated that neurons in MST are sensitive to rotating and translating optic flow patterns (Duffy & Wurtz, 1991) whilst lesions in V5/MT have been shown to inhibit global motion processing (Newsome and Pare, 1988). Phantom MAE can be partially explained by the properties of neurons at the later stages of motion processing. Whilst the receptive field sizes of neurons are precise at V1, their size increases during subsequent stages of motion processing (Zaksas & Paternak, 2005). Since the neurons that are sensitive to complex patterns of motion have larger receptive field sizes, Snowden and Milne

(1997) predicted that adaptation to optic flow patterns should produce phantom MAE. By adapting to motion in two non-adjacent quarters of a circle, Snowden and Milne tested for phantom MAE in the two non-adapted quarters. As predicted, MAE were reported for rotation, expansion, contraction and translation in areas that had not been previously exposed to motion.

The stimulus employed by Snowden and Milne (1997) used dot patterns presented in a circular shape, with two quarter sections missing. The test stimulus could therefore be placed in quarter sections that had been exposed to retinal motion or not. Stimuli such as these could be interpreted as containing occluded areas. The resulting MAE suggests that the processing of global motion patterns still occurs in areas which appear to be occluded. The assimilation of various related motions across the whole visual field could help the visual system to process ambiguous motion. A noted problem with local motion sensors is that they can only detect motion perpendicular to the orientation of a contour. This was termed the aperture problem (Marr & Ulman, 1981). To solve the aperture problem, the early level processing of several small receptive fields require integration, whilst separate areas with differing motions need to be segmented (Braddick, 1993). Integration allows a reduction in noise by averaging the responses from several receptors. Integrating motion from several areas will be useful when such motion is related, i.e. when a background is occluded. Additionally, areas showing different motions would need to be segmented and processed as separate motions, as integration would then lead to error.

Warren and Rushton (2008) showed that the perceived trajectory of a target object was altered by radial optic flow patterns consistent with forward motion. When a flow pattern was displayed in either the upper or lower hemifield, the motion of a target in the opposing hemifield gained an additional motion component. This again suggests that motion processing is altered as a result of global motion processing in potentially occluded areas, the effect was prescribed to phantom flow parsing. Brown & Weisstein (1991) provided evidence that the visibility of a phantom pattern was greatly reduced when depth cues suggested that homogenous areas represented the ground, rather than the figure (occluding object). Whilst it does not appear to have been directly tested, it is reasonable to suspect that patterns which do not appear to be occluded will result in segmented motion processing. Such a pattern was employed in the second experiment of chapter 4, and successfully reduced the phantom motion adaptation reported in the first experiment.

Retinal image displacement accounts for several MAE and other similar phenomenon (Anstis & Gregory, 1965; Mather, Verstraten & Anstis, 1998; Murakami & Cavanagh, 2001; Tolhurst & Hart, 1972). Whilst retinal motion adaptation is a central theme in the MAE literature, and differing patterns of retinal motion result in traditional, induced, and phantom MAE, adaptation to smooth pursuit eye movement also produces illusory motion.

The extra-retinal MAE

Whilst the retinal MAE has been extensively investigated, a less known variant arises from the adaptation of eye movements. Adapting an extra-retinal signal, such as the efference copy, would offset a motion detection system in a similar way to that proposed for the retinal MAE. Extra-retinal MAE have been induced under conditions which have provided negligible retinal motion and are seen following repetitive smooth pursuit and saccadic eye movements in the dark (Chaudhuri, 1991). Following adaptation participants were required to fixate a target point, which displayed illusory motion in the opposite direction to pursuit. Chaudhuri proposed that an extra-retinal signal was the causal mechanism for this MAE. Specifically, if a fixation task followed repetitive smooth pursuit, a signal would be required to suppress any residual after-nystagmus eye movement. After-nystagmus eye movements are of smaller amplitude than the adapting eye movement, but continue to be made when a period of smooth pursuit is followed by no visible stimulus (Muratore & Zee, 1979). A fixation task would require that this signal is suppressed, an action which could result in the observed illusory motion.

Further evidence for an extra-retinal MAE was provided by Freeman, Sumnall, & Snowden (2003), who demonstrated an MAE following prolonged vertical nystagmus. The test occurred in an area of the visual field that had not previously been adapted to retinal motion, given participant's ability to fixate a central blank area. Eye movement recordings confirmed that participants were largely able to complete the task successfully. Extra-retinal signals were confirmed as adding a non-visual component to the MAE. In the concluding paragraphs, Freeman et al raised the point that the MAE reported by Mack, Hill and Kahn (1989) could result from adapting retinal and extra-retinal signals; this possibility is discussed in the next sub-section and investigated in chapter 2.

Freeman & Sumnall (2005) investigated the extra-retinal MAEs that follow reflexive and deliberate pursuit eye movement. They found that the MAE induced by reflexive MAE are diminished following a period of storage, but that deliberate pursuit eye movements are not. The potential suppression of after-nystagmus eye movement, thought to generate the reflexive extra-retinal MAE, had decayed during the storage period. It is suggested that the phylogentically older reflexive eye movement system does not adapt higher cortical regions, unlike deliberate pursuit. The storage of deliberate eye movement MAE indicates a level of cortical adaptation not present for reflexive eye movement, the likely candidate for this was deemed to be MST (Freeman and Sumnall, 2005). One interesting finding in the study showed that the extra-retinal MAE following deliberate oblique pursuit changed direction as the signals decayed. This finding, both with and without a storage period, led to the conclusion that both cortical and sub-cortical areas were adapted during pursuit.

Since these studies severely limited the amount of retinal information available, the visual system would be required to rely more heavily on extra retinal information. Other models would suggest that the adapted signal is not purely extra-retinal. Reference signal models would claim that the adapted signal comprised both retinal and extra-retinal information. Whilst the MAE following eye movement could result from extra-retinal or reference signal adaptation, for simplicity it will be referred to here as the extra-retinal MAE.

Retinal motion signals and extra-retinal signals can adapt in such a way as to provide separate MAE. What are the perceptual consequences when a participant adapts to both retinal motion and smooth pursuit eye movement simultaneously? Several studies have examined adaptation to multiple sources of motion, although the majority have employed stimuli containing differing retinal motions.

Combined MAE

Whilst the MAE considered so far have detailed adaptation to motion in one direction, neither activity, adaptation, nor perception, are limited to unidirectional motion. Both individual and multiple MAE can be observed following adaptation to stimuli containing multiple retinal motions. The illusory motion observed is contingent on the various properties of the adaptation and test stimulus (von Grunau, 2002). These properties reveal information about the site of adaptation, with static MAE revealing lower level adaptation whilst dynamic MAE are considered to reveal adaptation at higher levels of processing (Verstraten, van der Smagt & van de Grind, 1998). Altering the stimulus properties, during adaptation and test, can reveal multiple locations for adaptation. An additional advantage to multiple motion stimuli is that their individual properties can be varied independently. Such a paradigm, employing low and high speed stimuli, with static and dynamic tests, demonstrated that different populations of neurons process motion speeds separately (Verstraten, van der Smagt, Fredericksen & van de Grind, 1999). Static tests revealed an MAE direction favouring the slower moving component, whilst dynamic tests revealed the direction as tending toward the faster component. The study confirmed that differing adaptation sites are integrated post-adaptation, with the nature of the test pattern determining the influence of various adapted neural populations in the perceptual experience.

Interocular transfer has long been held as demonstrating adaptation at differing regions within the visual cortex (Wade, Swanston & de Weert, 1993). Using a variant of the principle, Riggs and Day (1980) presented differing motion directions to each eye and reported a traditional MAE in each for monocular testing. Interestingly, a test viewed with both eyes resulted in a single binocular MAE. The direction of the binocular MAE was contingent on the combined directions of the alternating motions, demonstrating a single MAE as a result of two separable adaptations. Multiple MAE must result from adaptation in differing populations of neurons, unidirectional MAE could result from either adaptation at differing sites being integrated, or alternatively, from a single adaptation at a higher level of visual processing. Verstraten, Fredericksen & van de Grind (1994) demonstrated an MAE whose properties suggest adaptation at the later integrator level. They employed transparent motion, for which two patterns appear to move through one another. Following adaptation to transparent motion, a unidirectional MAE was observed in the opposite direction, consistent with a vector average of the retinal motions. The two retinal motion patterns were chosen because they yielded MAE with differing time courses. If individual adaptation sites produced signals combined by an active integration process, then the differing recovery rates would result in a change to the MAE direction. This did not occur, the direction remained the same over the time-course of the MAE. Verstraten et al (1994) concluded that the locus of adaptation was at some stage which followed the combination of separate motion signals.

The differing loci of adaptation for Verstraten et al (1994) and Riggs and Day (1980) may reflect differences between the separate interleaved presentation and concurrent presentation employed in the two studies. It could also demonstrate the well known finding that changing the properties of the test stimulus will reveal adaptation at different sites within the visual cortex (Verstraten, Fredericksen, van Wezel, Lankheet, van de Grind (1996); Culham, Verstraten, Ashida & Cavanagh, 2000; Maruya, Watanabe & Watanabe, 2008).

Whilst the two studies described above combined two retinal motions in differing directions, Chapter 2 was motivated by a study which adapted eye movement and retinal motion. Mack, Hill and Kahn (1989) investigated the unidirectional MAE that followed adaptation to stimuli combining vertical smooth pursuit over horizontal screen motion. During an eye movement, the visual system needs to combine both retinal and extra-retinal information to generate a representation of world motion. For orthogonal vertical pursuit and horizontal screen motion, retinal motion is moving in an oblique direction. Mack et al reported that the MAE was opposite to the horizontal direction of motion perceived by participants during adaptation. This led them to suggest that adaptation to a head-centred motion signal had resulted in the MAE. In chapter two this is termed the 'Perceived-Direction Hypothesis'. As with the previous examples, the MAE direction is not opposite to the retinal motion direction, as would be expected for the traditional MAE. It is also not opposite to the eye movement, as with a purely extra-retinal MAE. As an alternative to the perceived direction hypothesis, which represents adaptation after the signals are integrated, it is also possible that the unidirectional MAE resulted from two separate adaptations, one retinal and one extra-retinal.

The velocity aftereffect (VAE)

A close relative of the MAE is the velocity aftereffect. Instead of illusory motion in a static or dynamic test, adaptation results in a change to the apparent velocity of a moving stimulus. This change to the perceived motion of a subsequently viewed moving stimulus was first reported by Wohlgemuth (1911) and has been termed the Velocity Aftereffect (Thompson, 1981; Thompson, 1998). The VAE is dependent on the velocity of the stimulus during adaptation and test, rather than on their spatial or temporal frequency

(Thompson, 1998). The speed of the adaptor and test do not share a linear relationship with the apparent motion of the test (Carlson, 1962; Smith, 1985; Thompson, 1998). When the test is slower than the adapting motion, the apparent motion of that test is suppressed, whilst increasing the test speed increases the percept of motion (Thompson, 1981; Smith and Edgar, 1994). Unlike the MAE, the VAE demonstrates broad directional tuning, the apparent motion of a test is altered when it moves in the same, or in the opposite, direction to the adapting stimulus (Smith & Hammond, 1985; Thompson, 1981). Adaptation has been shown to increase sensitivity in discriminating small changes in the velocity of test patterns, although this is at the expense of accurately perceiving the total motion (Clifford & Langley, 1996).

The velocity aftereffect has been shown to influence the Filehne Illusion, both in a traditional manner and via the action of a proposed extra-retinal VAE (Freeman, 2007). Both illusions are central to the fourth chapter of this thesis, which ascribes the changes recorded in the magnitude of the Filehne illusion to a phantom velocity aftereffect.

Focus of the dissertation

The studies presented in this thesis employ adaptation to investigate some of the mechanisms responsible for maintaining motion perception during smooth pursuit. Chapter 2 investigates the properties of the MAE that follow simultaneous adaptation to orthogonal retinal motion and smooth pursuit. The MAE direction bisects the area between a retinal MAE and an extra-retinal MAE. This could suggest that the two signals adapt separately, with differing populations of neurons adapting to signals that are retinal or extra-retinal in origin. The signals from these sources would then be integrated post-adaptation at a later stage in the visual processing hierarchy. Alternatively, adaptation could occur at this later stage of processing, with the perceived direction of motion providing the source for motion adaptation. The experiments aim to determine whether adaptation occurs at an early component level or at a later perceived motion level. Since chapter 2 provides evidence for the adaptation of separate signals, chapters 3 and 4 then examine the nature of the pursuit motion estimate.

The nature of the pursuit estimate in the classical model differs from that in the reference signal model. Chapters 3 and 4 exploit the retinotopic nature of retinal motion adaptation to find whether retinal feedback modulates the pursuit estimate. The test patterns were located in areas unexposed to preceding retinal motion. The aim was to ensure that the retinal motion sensors in the test location were not adapted. These experiments were conducted with the potential for phantom after-effects considered. Chapter 3 examined the MAE that follows repetitive smooth pursuit eye movement, termed the extra-retinal MAE. This could have been a misnomer, had the results suggested that the illusory motion resulted from adaptation of a reference signal. In anticipation, they did not. Chapter 4 employed the Filehne illusion as a logical progression from the MAE experiments. As discussed, the Filehne illusion has been successfully employed to investigate changes to perceived stability in several studies (Mack and Herman, 1973; Haarmeier & Thier, 1996; Freeman, 2007). Despite these studies, a question remained as to whether a reference signal or an extra-retinal signal provided the cancellation process with the requisite input to estimate head-centred motion. Whilst Freeman (2007) showed that a classical model fully accounted for the observed changes to perceived stability, via separable changes to retinal and extra-retinal signals, this finding did not exclude the potential action of a reference signal. Chapter 4 therefore investigates perceived stability in an area unexposed to previous retinal motion. The argument advanced agrees with the previous findings of Freeman (2007), and excludes the reference signal as influencing perceived stability, as shown by the Filehne illusion in Chapter 4.

Chapter 2: The motion aftereffect following orthogonal retinal motion and smooth pursuit eye movement

Abstract

Adaptation to retinal motion can yield illusory motion in the opposite direction, the motion aftereffect (MAE); adaptation to smooth pursuit eye movements also elicits an MAE. When the adapting stimulus contains orthogonal retinal motion and smooth pursuit, the direction of the MAE is not opposite to either adapting motions. Mack, Hill & Kahn (1989, *Perception*, 18, 649-655) suggested that the MAE direction following adaptation to smooth pursuit and retinal motion is determined by the perceived motion during adaptation. An alternative to this is a vectorial combination of separate component MAEs resulting from adaptation to both types of motion. To differentiate between these two hypotheses, perceived direction during adaptation and during test was measured. Stimuli consisted of moving random dot patterns presented centrally (about the pursuit target) or peripherally (10° from the target). All stimuli were presented in the dark on a black background. The pursuit target obeyed a sawtooth wave (period 1s) consisting of constant upward motion (4 deg/s) and abrupt return. The retinal motion of the dot pattern was horizontal (4deg/s). Adaptation could consist of retinal only (R-only), pursuit only (P-only) or both simultaneously (R+P). Experiment 1 investigated central adaptation although the reported frequency of MAE was low in the R-only adaptation condition. In

Experiment 2 adaptation with retinal motion in the periphery was investigated. For both experiments the perceived direction during adaptation could not predict the perceived direction during test. Experiment 3 examined the magnitudes of the component-MAE. The results do not support the perceived motion hypothesis. A model of the vector sum hypothesis is developed. We show it provides only a partial explanation of the results.

Introduction

After a period of watching unidirectional motion, a stationary test pattern will appear to move in the opposite direction (the motion aftereffect - MAE). When a stationary fixation point is provided during the adaptation period, the MAE is presumably a consequence of adapting to retinal motion. When the fixation point is removed, the observer is likely to follow the adapting stimulus with a pursuit eye movement. Adaptation now combines signals related to eye movement and retinal motion, both of which can independently give rise to MAE (Chaudhuri, 1990, 1991; Freeman & Sumnall, 2005; Freeman, Sumnall, & Snowden, 2003).

There are two ways in which retinal motion can occur during an eye movement. When a pursuit eye movement does not accurately follow a target, retinal slip is created between the eye and the stimulus. However, this type of retinal motion is often too small and variable to account for any subsequent MAE following pursuit (e.g. Chaudhuri, 1991; Freeman, Sumnall & Snowden, 2003), and is sometimes in the wrong direction (Morgan, Ward and Brussell, 1976). A more influential source of retinal motion during an eye movement is that created by other objects visible in the scene, we call this object-dependent motion. Object-dependent motion occurs when the eye and any visible object move at different velocities. When object-dependent retinal motion arises from objects that are earth-stationary, a number of studies have shown that the retinal motion created during adaptation with an eye movement induces MAE in a central test (Mack, Goodwin, Thordarsen, Benjamin, Palumbo, & Hill, 1987; Mack, Hill and Kahn, 1989; Wade, Spillman & Swanston, 1996).

When tracking moving stripes either over stationary stripes or over stripes moving in the opposite direction, induced motion has been credited with creating the reported MAE (Morgan et al, 1976). They also reported that MAE of longer duration occurred following the eye movement 'tracking' conditions, and that MAE were reported in an eye unexposed to the tracking target. Whilst the results could be due to induced motion in the centre test pattern from the surround, another possibility is that an MAE related to the repetitive eye movement was responsible for the illusory motion. Research has since demonstrated that tracking eye movements create MAE which is independent of retinal motion (Chaudhuri, 1990, 1991; Freeman et al, 2003; Freeman & Sumnall, 2005). This is termed the extra-retinal MAE, as the illusory motion does not originate from retinal stimulation but from the oculomotor system. There are some important properties of extra-retinal MAE that differentiate it from its retinal counterpart. First, the extra-retinal

MAE is not retinotopic (Chaudhuri, 1991), though it should be noted that adapting to specific patterns of retinal motion, such as expansion, produces a retinal MAE which is also not retinotopic (Grunau and Dube, 1992; Snowden and Milne, 1997; Price, Greenwood & Ibbotson, 2004). Second, adapting to repetitive oblique pursuit eye movements gives rise to extra-retinal MAE whose direction can change over time (Freeman & Sumnall, 2005). The observed change of direction for the oblique extra-retinal MAE suggests that this unidirectional MAE arises from the adaptation of separate horizontal and vertical eye movement mechanisms. Following adaptation, the mechanisms have differing recovery rates. Third, the extra-retinal MAE exhibits storage, that is, the extra-retinal MAE is still experienced when a relatively long period of darkness is inserted between the adaptation phase and the presentation of a test pattern. It should be noted that only deliberate, pursuit-like eye movement gives rise to MAE that exhibit storage. When executing a reflexive nystagmus eye movement to the same adapting stimulus the MAE is found to dissipate over the storage period (Freeman & Sumnall, 2005).

Given that MAE can arise from object-dependent retinal motion and from repetitive smooth pursuit eye movements, predicting the perceptual consequences of adapting to both motions at once is potentially quite complicated. Whilst one motion could triumph as a 'winner takes all' signal and veto the other motion, evidence from adaptation studies suggests that this does not happen, with the judgements reported indicating that the signals instead combine (Haarmeier et al. 1996, 2001; Dash et al, 2009; Freeman, 2007;

Mack, Hill and Kahn, 1989). One possibility is that adapting to both retinal motion and pursuit creates two 'component' MAEs that combine via a vector sum. Figure 2 shows two outcomes for a particular example, namely smooth pursuit over a stationary background. In this case, the image of the stationary background moves across the retina at a rate equal and opposite to the physical motion of the eye (figure 2.0a). The two component MAEs that could result from smooth pursuit over a stationary background are therefore in opposite directions to each other. If they are also of similar magnitude then, assuming a linear vector combination of the two, there will be no net illusory motion (figure 2.0b). The test pattern will appear stationary as the retinal and extra-retinal components cancel one another. However, when the components have different magnitudes they will no longer fully cancel one another and so illusory motion will result. The direction depends on which component magnitude is larger. For instance, an MAE in the opposite direction to the eye movement occurs when the extra-retinal component has a greater magnitude (figure 2.0c).

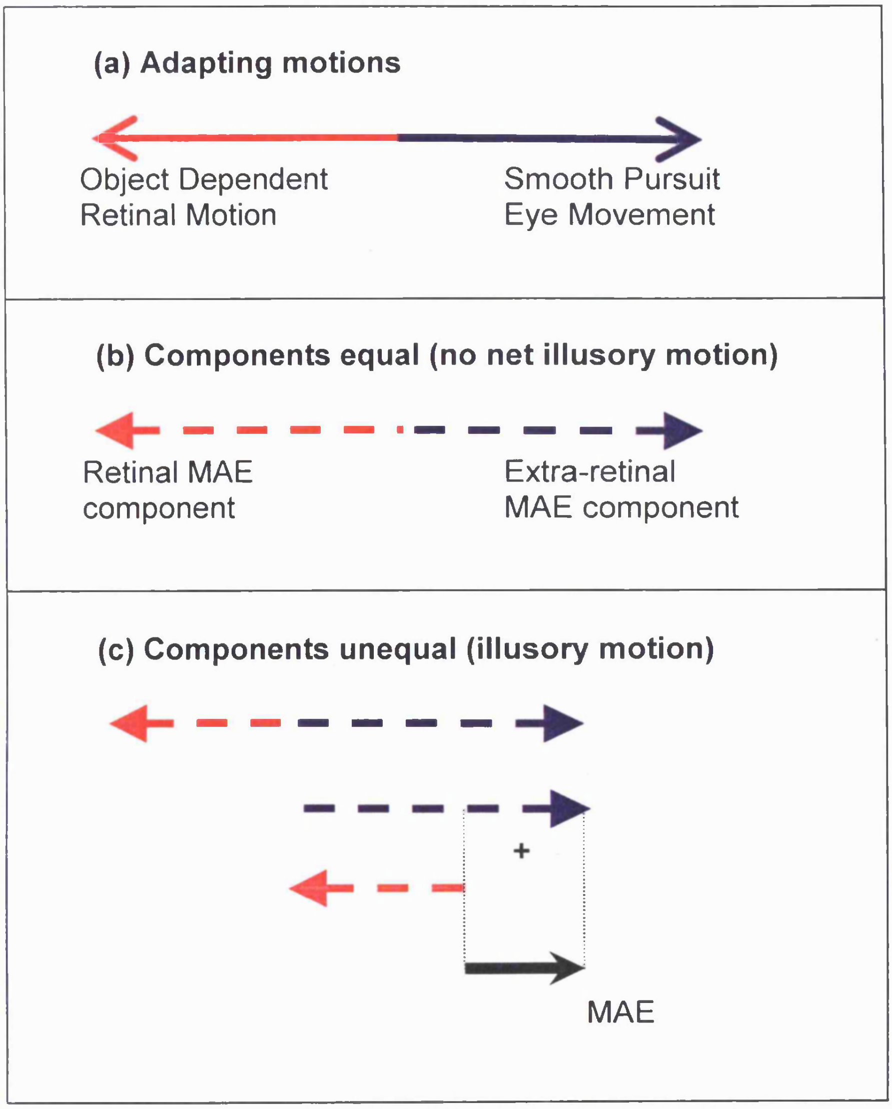

Figure 2.0. (a) Following adaptation to a repetitive smooth pursuit eye movement over a stationary background, then the consequence of adapting to two motions within the motion channel or motion sensitive neuron populations could conceivably lead to: (b) No illusory motion; the separate adaptations which would result from induced motion and from eye movement are approximately equal, they motion balance. (c) Illusory motion in one of two directions; when one motion provides a stronger adapting stimulus, illusory motion will result from the difference that remains following vector summation.

The above describes what we refer to as the component hypothesis. An alternative to this is the perceived-motion hypothesis, which holds that the primary drive for adaptation is the perceived motion experienced during adaptation rather than post-adaptation changes to earlier sensory processes. The perceived-motion hypothesis is based on the idea that the visual system needs to compensate for the retinal motion generated by self-motion, allowing the observer to determine how objects are moving with respect to the ego (Champion & Freeman, 2010; T.C.A. Freeman, 2001; T. C. A. Freeman & Banks, 1998; T.C.A. Freeman, Champion, Sumnall, & Snowden, 2009; T.C.A. Freeman, Champion, & Warren, 2010; T.C.A. Freeman & Fowler, 2000; Haarmeier et al., 2001; Haarmeier & Thier, 1996; Krukowski, Pirog, Beutter, Brooks, & Stone, 2003; Naji & Freeman, 2004; Nefs & Harris, 2007; Perrone & Krauzlis, 2008; Rushton & Warren, 2005; Souman, Hooge, & Wertheim, 2005b, 2006; Sumnall, Freeman, & Snowden, 2001; Turano & Massof, 2001; Wallach, 1987; Warren & Rushton, 2009; Wertheim, 1987, 1994). This type of hypothesis was favoured by Mack et al (1989), who studied the perceived direction of MAE following adaptation to vertical pursuit over a stimulus moving horizontally on the screen. In their study the subsequent MAE moved horizontally, suggesting that the MAE was opposite to the perceived motion of the adapting stimulus (as opposed to the oblique object-dependent retinal motion that the vertical pursuit produced). However, they did not measure the perceived motion during adaptation, a point that is central to the current experiments (see below). Moreover, they did not consider how the extra-retinal MAE might influence their results, in part because Chaudhuri's pioneering finding yet to be published. Thus they only considered one of the two possible component aftereffects that could be elicited by their adaptation sequence, namely that related to object-dependent retinal motion.

Mack et al's results contrast with an earlier report by (1965), who found that only the direction of retinal motion predicted the MAE following eye movement (it is important to note that the pursuit eye movement in Anstis & Gregory's study was extremely slow at 0.75 deg/s, which probably explains the dominance of retinal motion). The perceived motion hypothesis suggests that the primary drive for adaptation is not changes to individual components themselves but rather the perceived motion in the adapting stimulus. Further support for this hypothesis comes from self-motion adaptation studies. Harris, Morgan & Still (1981) and Wallach & Flaherty, (1975) found that when retinal expansion and forward self-motion were combined during adaptation; the perception of a contracting MAE was considerably reduced compared to a no self-motion condition. Assuming their displays simulated an earth-stationary scene as observers were pushed to and fro on a moving trolley, the reduced MAE could be explained in terms of a reduction in perceived motion in the self-motion conditions. Further evidence comes from Durgin, Gigone & Scott (2005), who found that the perceived speed of flow fields is reduced during active self motion (walking) and passive self motion (sitting on a moving cart). Note that the reductions reported for the MAE when self-motion and adapting motion complement each other could also be explained by the Component MAE Hypothesis, assuming that extra-retinal MAE extend to vestibular processes.

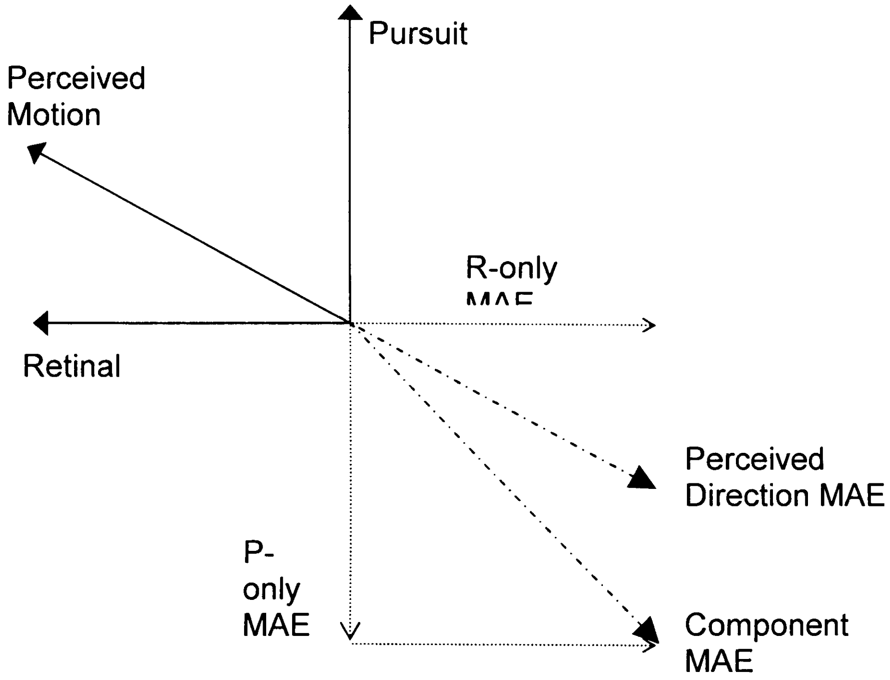

Figure 2.1: Figure showing the adaptation directions and potential MAE. The two hypotheses make differing predictions as to the direction of the resulting MAE. The Perceived direction MAE is opposite to the perceived motion. The Component MAE results from a vector sum of the two component MAEs (R-only and P-only)

The paradigm developed here makes use of the fact that the perceived direction of retinal motion is distorted during pursuit eye movement (Festinger et al, 1976; Becklen et al, 1984; Swanston and Wade, 1988; Souman et al., 2005a, b). Figure 2.1 shows predictions of the component-MAE and perceived-direction hypotheses when the adapting retinal motion and pursuit are orthogonal, as is the case in the current chapter. For the sake of argument the predictions assume that adapting eye movements are accurate, a point that is developed in the Results section. According to the Component MAE Hypothesis, upward pursuit and leftward retinal motion produce rightward retinal MAE and downward extra-retinal MAE, respectively. Assuming that the magnitude of the component MAEs are the same, this will yield an overall MAE directed obliquely as shown. The perceived motion hypothesis, on the other hand, predicts an overall MAE that depends on the motion perceived during adaptation. This in turn depends on the relative accuracy of the motion signals that encode eye velocity and retinal velocity. Several studies have shown that the visual system underestimates eye velocity relative to retinal velocity (Filehne, 1922; Freeman and Banks, 1998; Mack and Herman, 1973; Turano and Heidenreich 1999; Wertheim, 1994; Haarmeier, Bunjes, Lindner, Berret & Thier, 2001). In particular, for orthogonal motions like those shown in Figure 2.1, the perceived motion of non-pursued objects during a smooth pursuit are biased towards the direction of retinal motion (Festinger et al, 1976; Becklen et al, 1984; Swanston and Wade, 1988; Souman et al., 2005a, b). It is therefore likely that if an MAE is based on the perceived direction then the retinal signal will be overrepresented. Hence the perceived motion hypothesis predicts an overall MAE that is biased towards horizontal, as shown in Figure 2.1.

In the current study observers adapted to orthogonal pursuit and retinal motion of equal speed whilst making concurrent judgements about the velocity perceived during adaptation. These were then compared to judgements of the perceived velocity of MAE. In the first two experiments we measured perceived direction only. The perceived motion hypothesis predicts an MAE in the opposite direction to the perceived direction of motion seen during adaptation. As a check, we also included separate pursuit-only (P-only) and retinal-only (R-only) adaptation conditions to determine whether the essential ingredients for the Component MAE Hypothesis were in place. In anticipation, the results of first two experiments did not support the perceived motion hypothesis. But in order for the component hypothesis too fully explain the results, a linear vector model determines that the magnitude of the extra-retinal MAE must be considerably greater than the retinal MAE following central adaptation (Experiment 1), whilst being about the same following peripheral adaptation (Experiment 2). This prediction was tested in the final experiment, which measured the speed of the MAE produced by the P-only and R-only conditions, using a magnitude estimation technique.

Experiment 1: Central Retinal Adaptation

Method

Participants

Twenty five undergraduate psychology students at Cardiff University, with normal or corrected to normal vision, took part in experiment 1 for course credit. Four participants did not experience an MAE during the experiment and were excluded. All participants provided informed written consent and were fully debriefed after completing the experiment.

Stimuli

Stimuli were generated on a PC using a Radeon 9800 Pro graphics card and presented on a Viewsonic P225F 19 inch monitor. The visual stimuli were generated using PASCAL in the Delphi 2006 suite and the powerful graphics functions of the open graphics library, OpenGL. The screen was viewed binocularly through a red gel absorptive filter to reduce screen glow. Both adaptation and test were presented on a black background in a dark room. A chin rest and forehead bar maintained a stationary head at a constant viewing distance of 57.3 cm.

There were three conditions: retinal-only adaptation, pursuit-only adaptation and simultaneous adaptation that combined retinal motion and pursuit. We refer to these as R-only, P-only and R+P. The adaptation conditions were achieved using the stimuli illustrated in Figure 2.2. Each consisted of a random dot pattern (density of 1 dot/deg) comprising dim red dots (radius 0.1 deg) and a larger fixation point (radius 0.2 deg). The random dot pattern was presented within an annulus window (inner radius 0.5deg, outer radius 5 deg). When retinal motion was required in the R-only and R+P conditions (left and right panels in Figure 2.2), the random dot pattern moved to the left within the window at a speed of 4 deg/s (red arrows, Figure 2.2). When pursuit was required in the P-only and R+P conditions (middle and right panels), the fixation point, annulus window and dots all moved vertically upwards at 4 deg/s (blue arrows, Figure 2.2). On the screen, therefore, the dots moved obliquely up and to the left in the R+P condition, so assuming accurate pursuit, the retinal motion was identical to the R-only condition. Adapting motions were executed using a sawtooth wave signal consisting of a 1s sweep of adapting motion followed by an abrupt return (Figure 2.2 inset). Position was therefore a sawtooth function of time. A new random dot pattern was generated on each sweep.

Following 50s adaptation, a central fixation point was displayed for 1s to aid accurate stationary fixation. The fixation point was then removed and replaced by a stationary annulus test pattern for 5s (see bottom right panel of Figure 2.2). Participants were instructed to keep their eyes stationary during this period at the centre of the annulus. The dimensions of the test annulus (inner radius 1 deg, outer radius 4 deg) were smaller than the adaptation annulus so that the test pattern covered an area 'inside' the adaptation pattern. The reduced size helped ensure that the entire test area had been strongly adapted by retinal motion, even if fixation or pursuit were somewhat inaccurate. In addition, the reduction mitigated possible edge effects, such as the 'peculiar MAE' confined to the edge of a test grating reported by Murakami and Shimojo (1995), which they attributed to small fixation errors during adaptation.

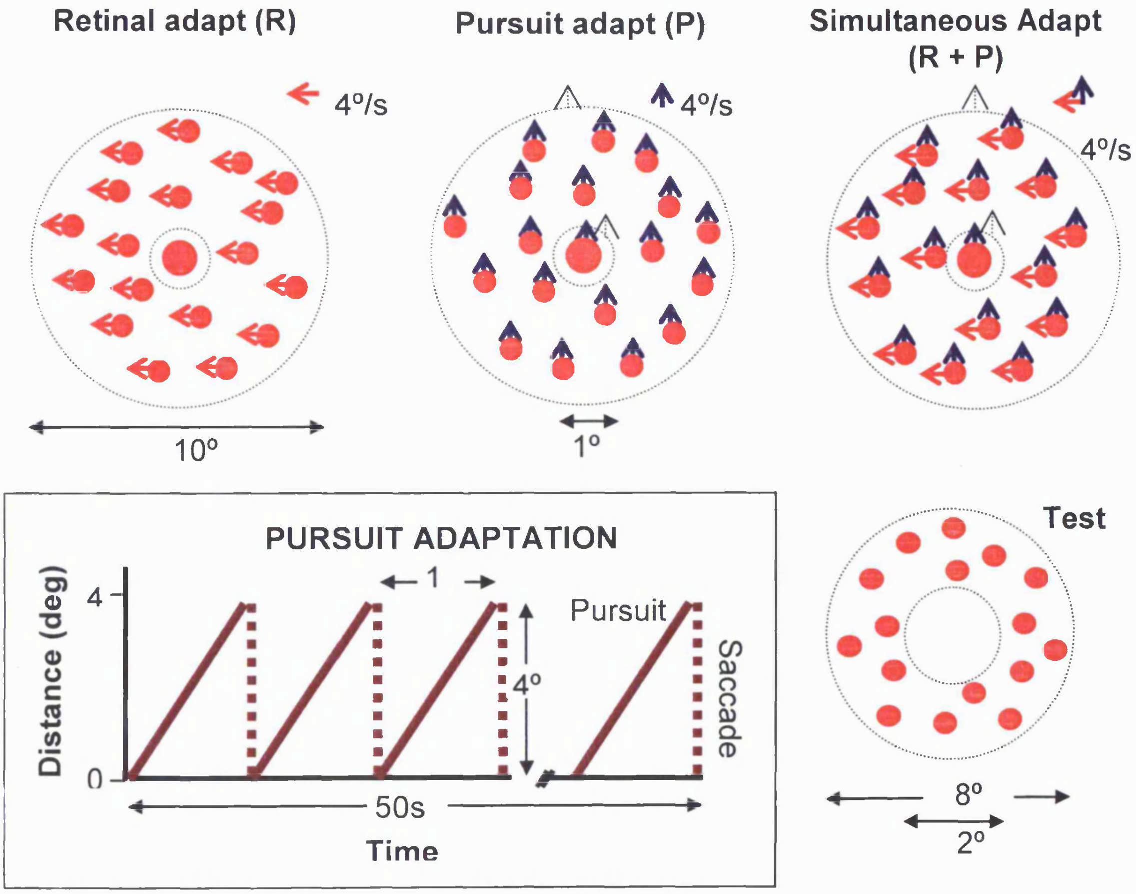

Figure 2.2: Schematic representation (not to scale) of the stimuli, adaptation phase motions and test. Note the red dots were presented on a black background in a dark room. Inset: Illustrates distance-time graph for an ideal eye movement trace during adaptation.

Procedure

During both adaptation and test, perceived direction was recorded using a purpose-built potentiometer pointing device attached to a table in front of the observer. The potentiometer was a 3-turn 5 volt potentiometer, the data from which were sampled using the I/O channels of a National Instruments Data Acquisition Card (NIDAQ card, BNC-2110, 16-Bit, Sampling rate: 4MS/s) attached to the PC. The potentiometer pointing device consisted of an arm mounted on a box that could be rotated horizontally to indicate perceived direction. Physical stoppers could be placed in several positions to limit the arc of rotation as required (see Figure 2.3). The plane of rotation was approximately at right-angles to the screen.

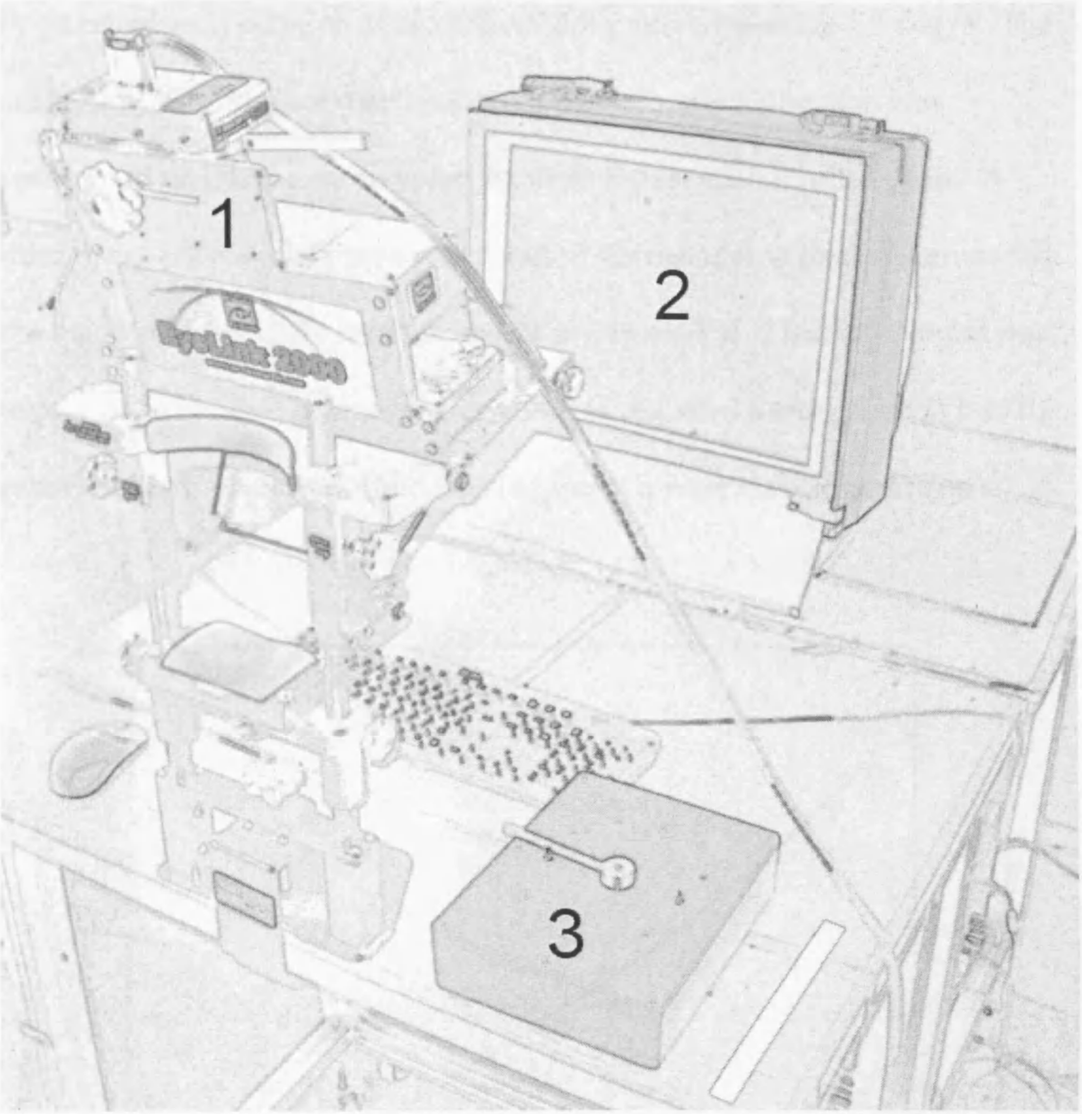

Figure 2.3: The laboratory set up. (1) Eyelink 2000 eye tracker, chin rest and forehead bar, as used in experiment 3 (2) 19" CRT monitor with red gel filter (3) The potentiometer pointing device with 2 stoppers to limit rotation to the top 180° arc.

Participants were therefore required to map perceived direction seen in one plane onto felt direction in another. For this reason, all participants completed a calibration run prior to data collection, using the pointing device to indicate the direction of 15 dot pattern motions ranging from -112.5° to 202.5° in 22.5° steps. The calibration stimuli followed the same presentation format as the test in the main experiment, except that the central fixation point remained visible and the random dot pattern moved at 0.5 deg/s. The calibration stimuli were displayed for 3 seconds. Each direction was presented twice and a mean voltage calculated for each direction pair. A third order polynomial curve was fitted to the calibration data to summarise the mapping separately for each observer (Figure 2.4). This polynomial was then used to convert potentiometer voltages obtained during the test into the reported MAE perceived directions (degrees) for the main experiment.

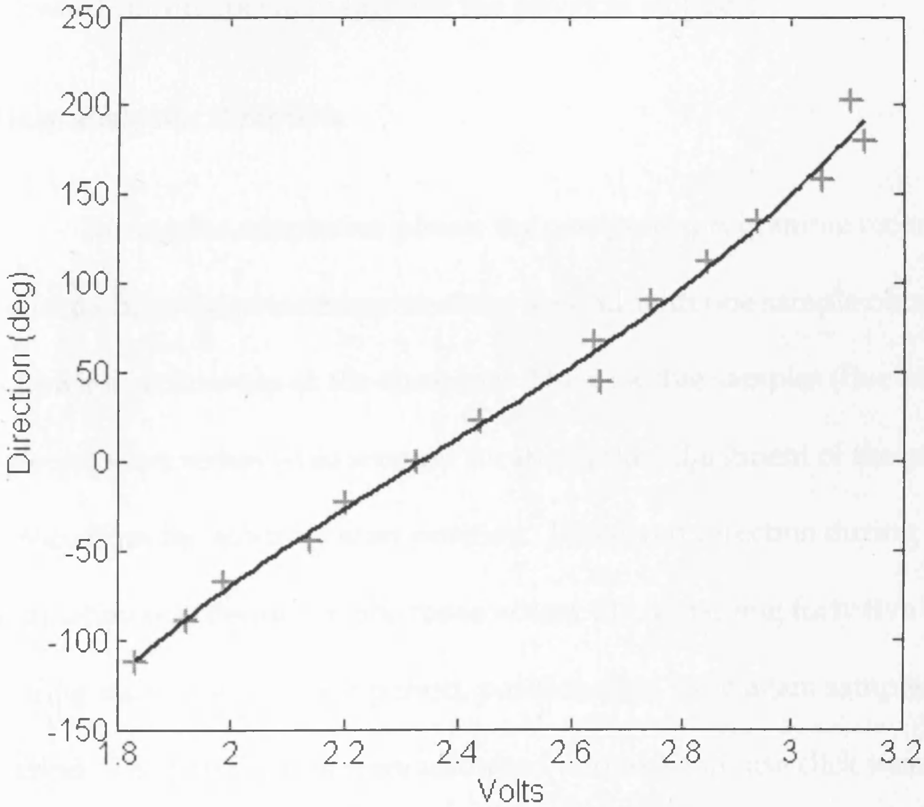

Figure 2.4: Third order polynomial fitted to calibration data for one participant. This was then applied as a look-up for potentiometer readings in the main experiment.

There were four replications of the three adaptation conditions. The 12 trials were presented in random order. Each started with 50s of light adaptation to a bright homogeneous screen (luminance). Adaptation to motion followed for a further 50s, during which participants continuously indicated the direction of the adapting motion using the pointing device. Observers then indicated the perceived direction of the stationary test. They were allowed to take as long as they needed to set the pointing device even though the test only appeared for 5s. Once satisfied, observers terminated the trial with a mouse click. Participants were also given the option of indicating that they experienced no MAE by leaving the pointer bar in the arbitrarily leftward starting position (against the physical stopper).

Data analysis: Direction

During the adaptation phase, the computer programme recorded the adjustment of the potentiometer every second with one sample obtained following each sweep of the stimulus. The first five samples (five adaptation sweeps) were removed to account for the initial adjustment of the pointing device from the arbitrary start position. Perceived direction during adaptation was defined as the mean across the remaining forty five samples. During the five second test period, position data were again sampled every second. The participants were informed to make a mouse click when they were happy that the pointer indicated the direction of the MAE. This click terminated the trial and polled the potentiometer for a sixth and final voltage. The direction of the MAE in each trial was calculated from this final sample only. When observers did not experience an MAE the trial was discarded from the analysis. Data were averaged over the remaining trials for each observer.

Two observers made one anomalous direction setting each in their allotted twelve trials, reporting an average direction opposite to the actual adapting motion. We attributed these to a mistake and deleted the two trials from the analysis.

Eye movement recording and analysis

Eye movements were recorded for all participants in all trials using an ASL series 5000 head-mounted eye tracker sampling at 60 Hz. The eye movements were analysed in MatLab using a combination of custom-built and ASL eye tracker software. The eye movement data were first smoothed with a Gaussian filter (SD = 16 Hz). Velocity and acceleration profiles for the data from both x and y channels were then obtained by separately differentiating each channel. The centre of a saccade was defined as a zero-crossing in the acceleration profile where the related velocity exceeded a threshold of 35 deg/s above or below the pursuit target speed. If a saccade was detected in either the X or Y channel, then samples ±83ms either side were removed from both X and Y velocity profiles. Eye Blinks were also removed. A sample eye movement recording for one fifty second adaptation phase (60Hz * 50s = 3000 samples) for the R+P condition is shown in Figure 2.5. The top trace represents the horizontal eye movement component including slight movement along the x-axis suggestive of the oblique pursuit eye movements in the R+P condition. The bottom trace shows the vertical component (sawtooth wave). The black sections indicate 'good' eye movements, whilst saccades are indicated in red. The red sections correspond to detected saccades and were removed from the analysis as stated. The eye speeds (Pythagoras' Theorem) and directions (arctangent) were calculated from the X and Y recordings. Adaptation phase eye movement outliers were removed trial by trial (2 standard deviations from mean eye velocity).

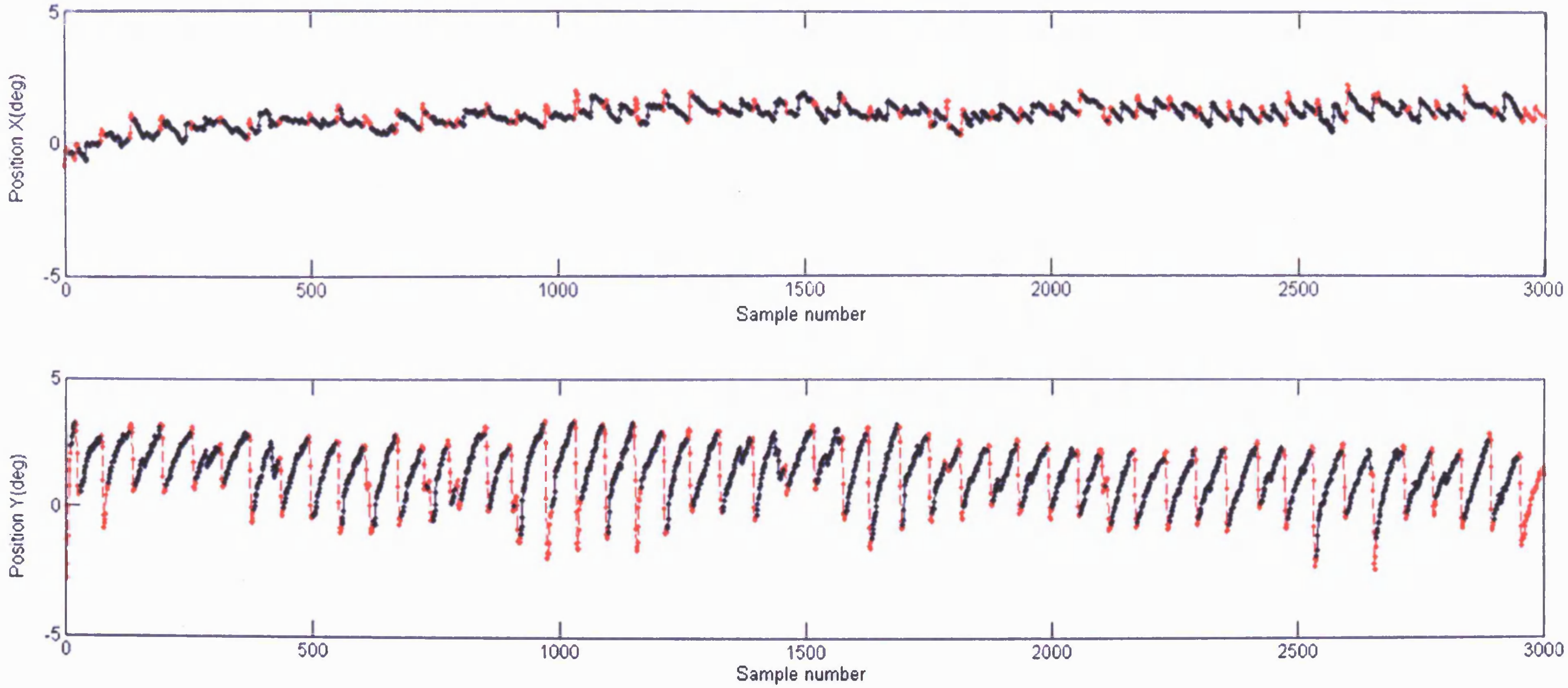

Figure 2.5: Eye movement traces in the X and Y channels for one sample adaptation period (R+P condition). Red sections highlight areas removed from the analysis. Black areas indicate smooth pursuit eye movement.

Results and Conclusions

Figure 2.6 plots the mean perceived direction during the three adaptation conditions (solid arrows) and during MAE (dotted arrows), averaged across observers. Different coloured arrows correspond to the results for different adaptation conditions. The directions reported during R+P adaptation (solid black arrow) agree with previous findings (Mack, Hill and Kahn, 1989) and indicate that the combination of retinal motion and pursuit in the display yield a mean perceived direction that tends toward the retinal motion (horizontal). Individual settings are shown as dots. The critical test of the hypotheses is the R+P condition, shown in black. According to the perceived motion hypothesis, the MAE should be opposite to the direction perceived during adaptation. This prediction is shown in grey. The actual MAE reported following R+P adaptation deviates significantly from the prediction ($t(19) = 7.1$, $p < 0.001$; note that $df \neq 20$ as one observer reported no MAE in this condition). On this basis the data do not support the Perceived Direction Hypothesis. Whether they support the Component MAE Hypothesis is discussed later.

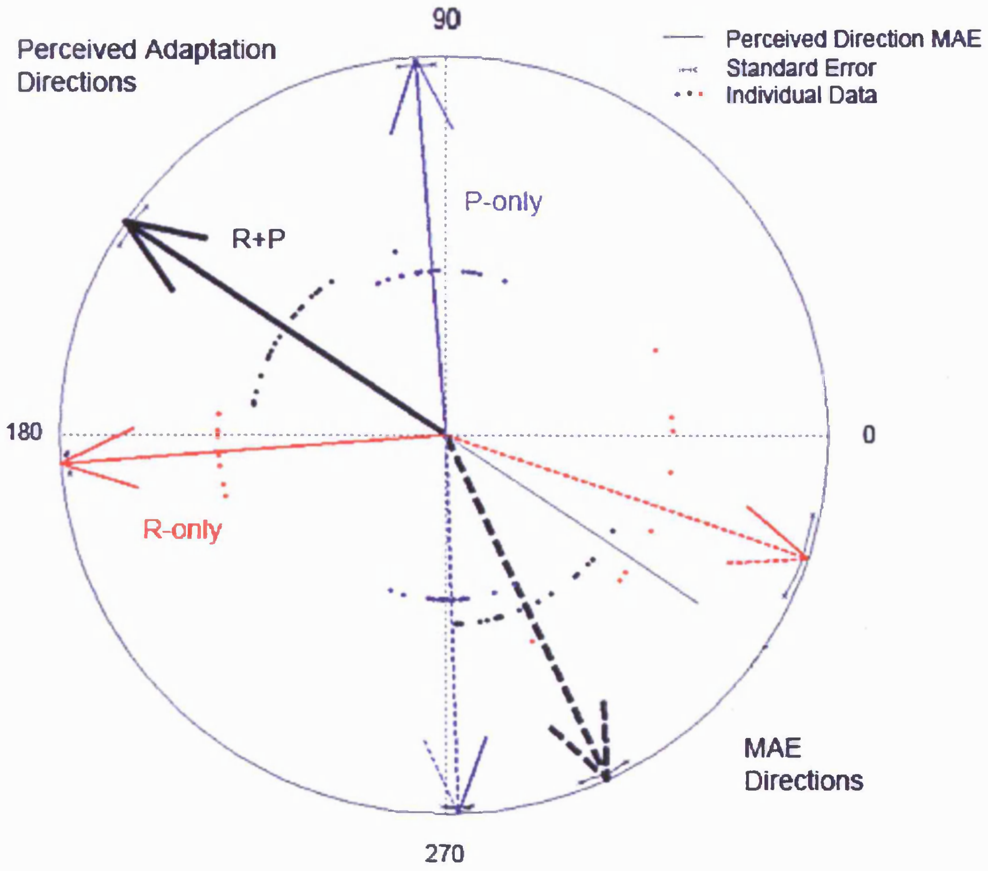

Figure 2.6: Mean perceived directions during adaptation and test. The solid arrows represent the perceived adapting directions, with the dotted arrows showing the mean reported MAE. At the end of each mean direction data arrow, the grey lines with plus symbols at the extremes indicate 1 standard error, whilst the dots represent individual data points.

Figure 2.6 also shows the perceived directions for the R-only and P-only conditions. Each produced an MAE, confirming previous reports that adaptation to pursuit by itself can give rise to illusory motion (Chaudhuri, 1991a, 1991b; Freeman and Sumnall, 2005). In the P-only condition (blue arrows), MAE direction was opposite to the direction of motion indicated during adaptation (t(19) = -0.7, p=0.47, ns); the same was also true for the R-only adaptation (t(7) = -2.17, p >0.05). Across all observers, MAE for the R-only condition was reported in only 24% of trials, compared to 67% for the P-only and 78% for the R+P condition. This suggests that the R-only adaptation produced a relatively weak MAE which led to the more variable judgments of direction evident in the figure.

Mack et al (1989) described a relative motion explanation for their MAE whilst doubting its applicability. To further limit the potential role of relative motion in the current study, all experimentation was conducted in a dark room. With only the stimulus visible this excluded extraneous visual field information that would have provided relative motion between stimuli and surround. However, with the exception of the P-only condition, the adaptation stimulus did contain some relative motion between the pursuit/fixation point and the dot pattern. Relative motion has been demonstrated as effective in generating strong MAE percepts and so the infrequent retinal MAE reports during experiment 1 showed that the relative motion within the stimulus was successfully reduced.

A relatively weak R-only component MAE is consistent with an R+P MAE biased towards the P-only component as reported. Examining individual results, the R+P direction data contained six participants whose R+P directions suggested a strong extra-retinal MAE influence with little or no retinal component influence (MAE mean direction -83°). Experiment 2 was designed to strengthen the R-only MAE, specifically by placing retinal adaptation and test stimuli in the periphery. Given a stronger retinal component, the Component MAE Hypothesis would predict that the mean R+P MAE direction would move anti-clockwise. The change in MAE direction is predicted due to an increased similarity in magnitude for R and P components.

Eye movements

Figure 2.7 shows a summary of the eye movements for one observer in the three adaptation conditions. The 2D histograms were constructed from the x and y velocity components and are plotted in this Cartesian space. The pursuit target is shown as a white cross. For this observer, fixation in the R-only condition was reasonably accurate, as was pursuit in the P-only condition. However, the introduction of orthogonal retinal motion in the R+P condition caused the eye movements to deviate slightly away from the horizontal pursuit target, gaining a small horizontal component with the direction of retinal motion.

These trends were similar across all observers. Figure 2.8 plots the mean x and y velocities collated across observers. In the R-only condition, observers were able to hold their eyes reasonably still. In the P-only condition, eye movements were vertical (92°, calculated using inverse tan from the mean velocities of the X and Y components) and at a slower speed than the pursuit target (gain = eye speed/target speed; mean pursuit gain = 0.74). In the R+P only condition, the eyes deviated away from vertical due to the influence of the surrounding retinal motion (114° mean direction, gain =

0.67). Pursuit eye movement is known to be altered in the presence of a moving background (Suehiro, Miura, Kodaka, Inoue, Takemura, Kawano, 1999; Masson et al., 1995; Niemann and Hoffmann, 1997).

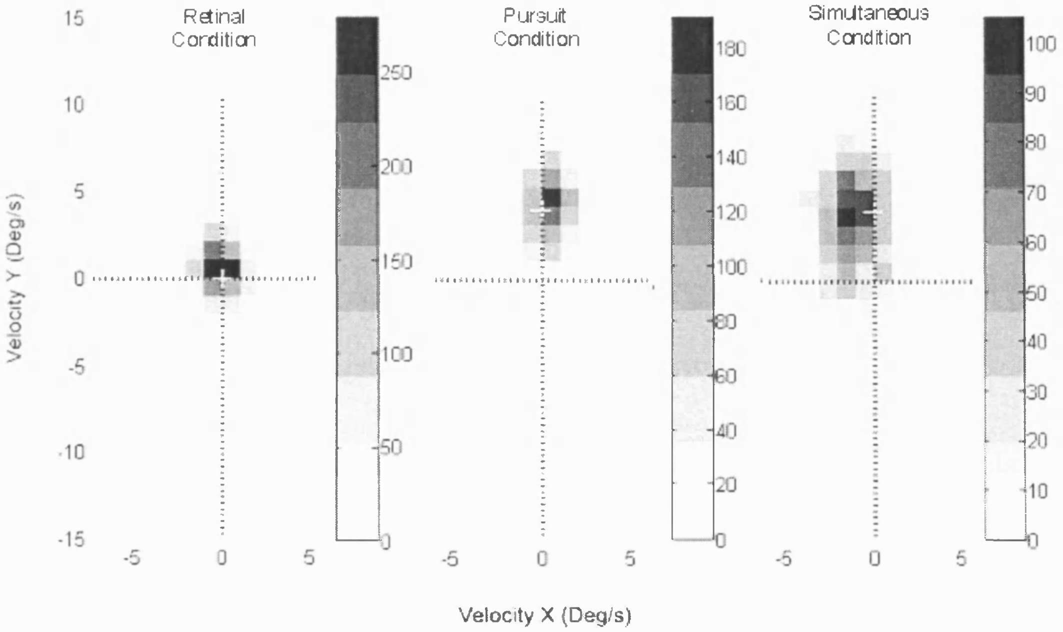

Figure 2.7: Sample eye movement velocity 2d histograms. One adaptation period per condition is shown for one observer with good eye movements. White plus indicates the velocity of the target/fixation point. The 1 deg^2 bins are shaded darker as the number of (five sample moving average) eye velocities falling within them increase.

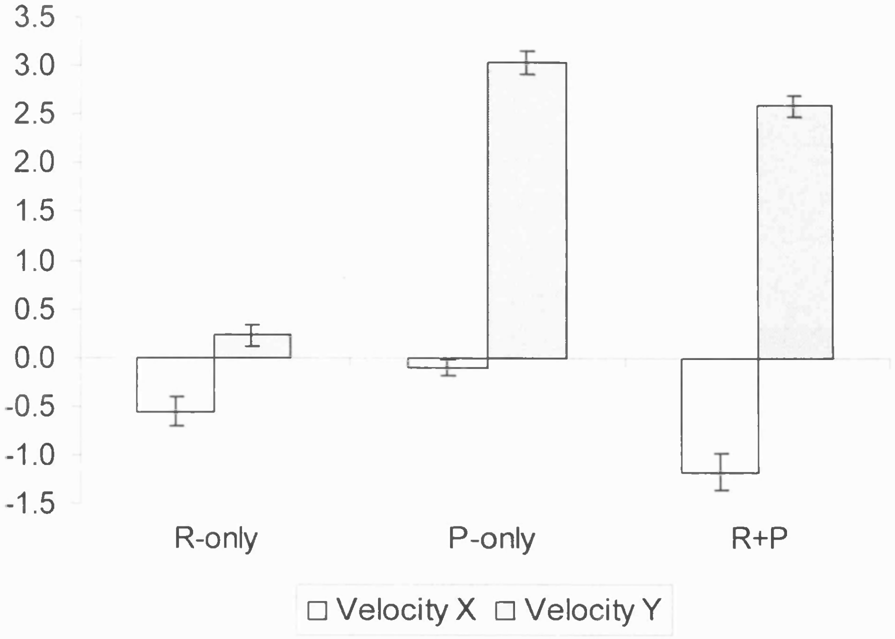

Figure 2.8: Mean adaptation phase eye movement velocities in the X and Y planes for all participant trials reporting an MAE in experiment 1. The average eye movements in the X (white bars) and Y (grey bars) directions are shown for the three adaptation conditions (R-only, P-only and R+P).

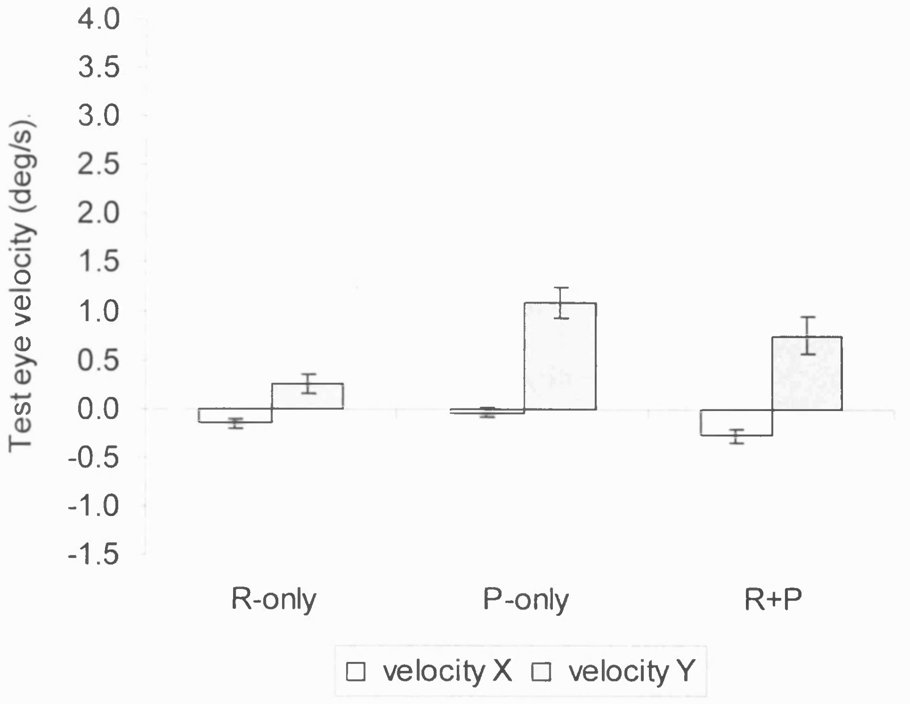

Figure 2.9: Mean test phase eye movement velocities in the X and Y planes for all participant trials reporting an MAE. The average eye movements in the X (white bars) and Y (grey bars) directions are shown during test following the three adaptation conditions (R-only, P-only and R+P).

The mean eye movements during the test phase can be seen in Figure 2.9. Any eye movement during the test phase is a potential source of perceived motion, the associated retinal slip could be misperceived. However, all trials, including those with eyes moving in the opposite direction or with near stationary eyes, report similar directions for the MAE. This suggests that the reported MAEs were unrelated to the actual small eye movements made during test. This was confirmed in a further analysis, by comparing the MAE directions for the 50% of trials with the lowest test phase eye velocities in the X direction to those with the fastest test phase eye velocities. No significant difference existed for the MAE directions reported in these two groupings (t(63) = 0.76, n.s.). A final confirmation that test eye movements did not affect the results was obtained by excluding those trials with a vertical motion exceeding 1 deg/s at test. This resulted in eye movements during the test phase having a mean speed of 0.4deg/s (SE = 0.1) and an average MAE direction of -88.2° (SE = 2.1).

Assuming the eye movements are accurate then we can predict the relative magnitudes of the component MAEs from the direction of the R+P MAE. Figure 2.10 shows the line along which the R+P MAE lies (blue line). Since the magnitudes of the component MAEs are unknown, the predicted speed of the R+P MAE using the Component MAE Hypothesis is also unknown. Nevertheless, it has to be the case that the pursuit component is larger than the retinal component, as shown in the figure. Had the two component magnitudes been the same, the resulting MAE would be opposite to the angular bisector of the two adapting motions (-45°). The reported results deviate toward the pursuit component.

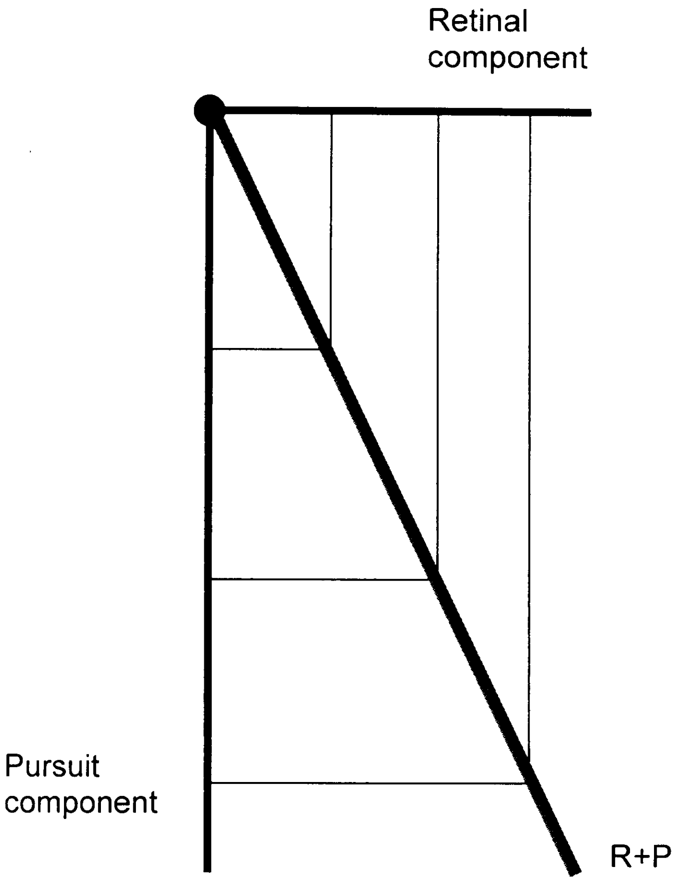

Figure 2.10: Figure illustrating the relative strengths of the R and P components which could produce the R+P MAE direction reported. Since the absolute magnitude of the components in unknown, it is only possible to know that the P component is larger than the R component.

The above discussion assumed that pursuit was accurate. However the results of the eye movement analysis show that oculomotor control during adaptation was not perfect. As discussed above, the perceived directions reported by observers do not support the perceived-motion hypothesis, but the inaccurate eye movements may have important ramifications for predicting the data on the basis of the Component MAE Hypothesis. According to the Component MAE Hypothesis, the MAE following R+P adaptation is the sum of two vectors, as discussed earlier in Figure 2.0. One vector corresponds to an MAE component related to the adapting retinal motion and the other to an MAE component related to the adapting pursuit. Inaccurate pursuit will change the velocity of the adapting motions. This issue is taken up in the final experiment and the model section.

The results provide evidence that the retinal component was considerably weaker than the pursuit component. The direction of the R+P MAE was found to be heavily influenced by the pursuit direction, suggesting less influence for a retinal component. This is affirmed by the low report frequency and the high variability of direction reports for the R-only condition. Experiment 2 repeated experiment 1 except for a change to the placement of the retinal motion pattern. This change was implemented in order to increase the strength of the retinal component. An increase in retinal MAE strength following adaptation predicts that the R+P mean direction in experiment 1 will be displaced in an anticlockwise direction toward the retinal component for experiment 2. A higher report frequency and more consistent direction reports for the R only condition are also predicted.

Experiment 2: Peripheral Retinal Motion Adaptation

Introduction

Previous research suggests that placing retinal motion in the periphery is likely to increase the magnitude of retinal MAE. The velocity needed to null a peripheral retinal MAE is greater (Wright, 1986). Moreover, evidence indicates that the effect of surround modulation for MAEs also increases with eccentricity (Murakami & Shimojo, 1995). The potential increased strength of peripheral MAE was also suggested by Morgan et al (1976) as one possible explanation for the induced MAE reported when both centre and periphery showed no speed differences during adaptation. However, the extra-retinal MAE could also influence the results reported by Morgan et al. By moving the central adaptation and test dot patterns 10° into the periphery, this experiment aimed to increase the incidence of retinal MAE through peripheral adaptation and test.

Method

Participants

Sixteen students were recruited in the same way as Experiment 1.

Stimuli and Experimental Design

The stimuli were the same as Experiment 1 with the exception that the centre of the adapting pattern was placed 10 deg to the right of the fixation point, subtending +5 deg to +15 deg along the horizontal axis (see Figure 2.11). During the calibration and the test phase the pattern was also displayed peripherally (calibration/test subtended +6 to +14 deg).

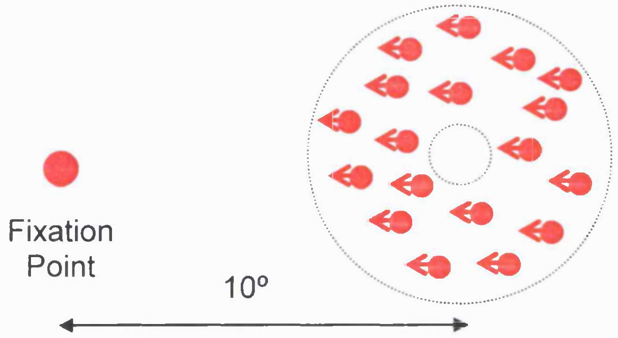

Figure 2.11: The adaptation conditions. Apart from the peripheral placement of the annulus window containing the random dot pattern, the three conditions replicated experiment 1.

Results and Conclusions

Peripheral adaptation successfully increased the frequency of MAE reports for the R-only condition, with participants reporting an MAE for 52% of trials (compared to only 24% in experiment 1). The report frequencies for the P-only MAE (53%) and the R+P MAE (69%) both decreased from experiment 1. The increase for R-only MAE and decrease for P-only MAE reports resulted in comparable frequencies following peripheral adaptation. This contrasts with the differences reported between the two components in experiment 1.

Figure 2.12 plots the mean perceived directions during adaptation and test. The predicted MAE directions from the perceived-motion hypothesis were calculated as in experiment 1. The mean perceived direction prediction and MAE direction are shown on Figure 2.12 as dashed black arrow and thin black line respectively. The reported MAE directions for the R+P condition significantly differed from the predictions (t(12) = 2.23, $p < 0.05$). This does not support the Perceived Direction Hypothesis. The P-only and R-only conditions were not significantly different from the directions opposite to the perceived adapting motions (t<2, P>0.05, ns) and conformed to the directions expected for retinal and extra-retinal MAE.

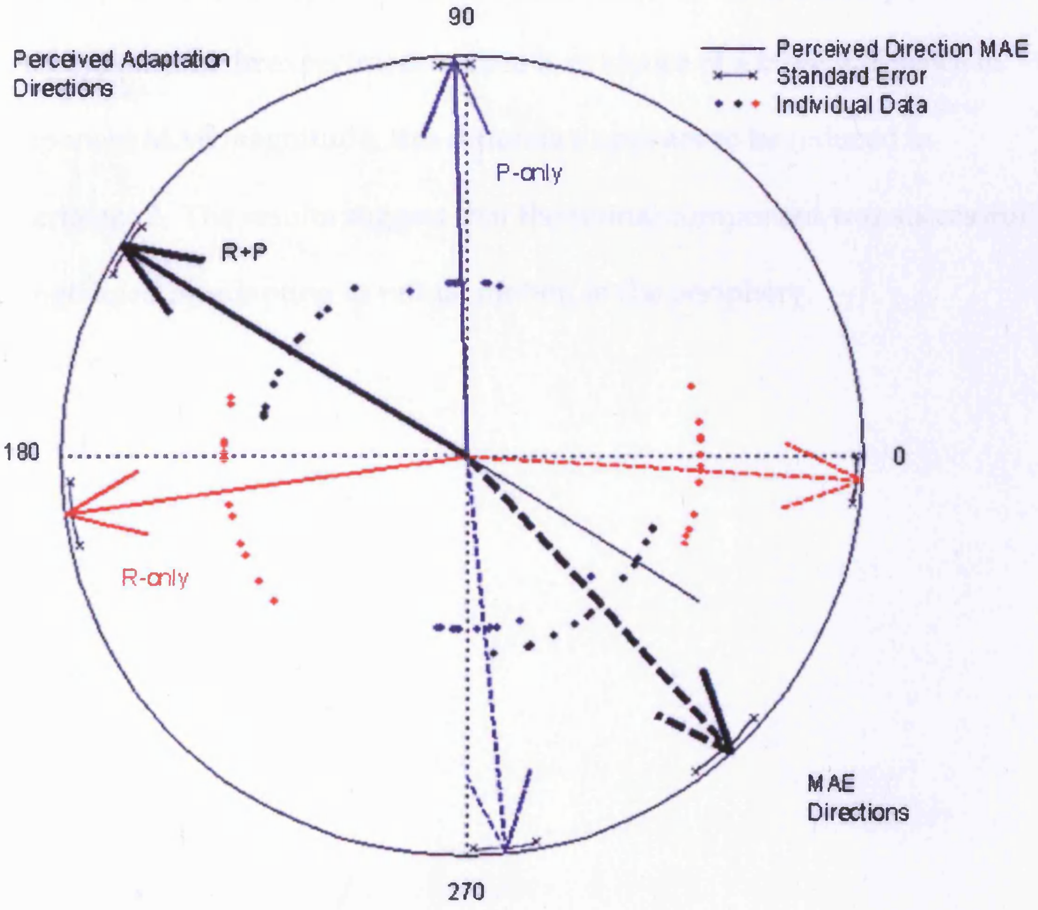

Figure 2.12: Mean perceived directions during adaptation and test for experiment 2.

As predicted, a stronger retinal component led to the mean direction for the R+P condition (black dashed line, Figure 2.12) changing from experiment 1. The R+P direction in Figure 2.12 suggests a more equal representation of both components, with the mean direction having moved in an anti-clockwise direction from that shown in Figure 2.6. Despite this change, the direction was still significantly different from that predicted by the Perceived Direction Hypothesis. The perceived direction during adaptation in both experiments 1 and 2 were similar, whilst the MAE direction varied considerably. Whilst not supporting a Perceived Direction Hypothesis, these changes can be accommodated within the Component MAE hypothesis. In experiment 1 there is evidence of a large difference in component MAE magnitude, this difference appears to be reduced in experiment 2. The results suggest that the retinal component was successfully strengthened by adapting to retinal motion in the periphery.

Eye movements

The smooth pursuit eye directions were close to vertical, averaging 90° and 96° for R+P and P-only conditions respectively. Figure 2.13 shows the adaptation phase eye movements, it can be seen that participants maintained relatively stationary eyes in the R-only fixation condition. Peripheral pattern placement showed a reduction in eye movement gain during adaptation for both the P-only condition (gain = 0.63, SE = 0.09) and the R+P condition (gain = 0.59, SE = 0.03). These pursuit gain reductions maybe reflected in the reduced MAE report frequencies previously reported.

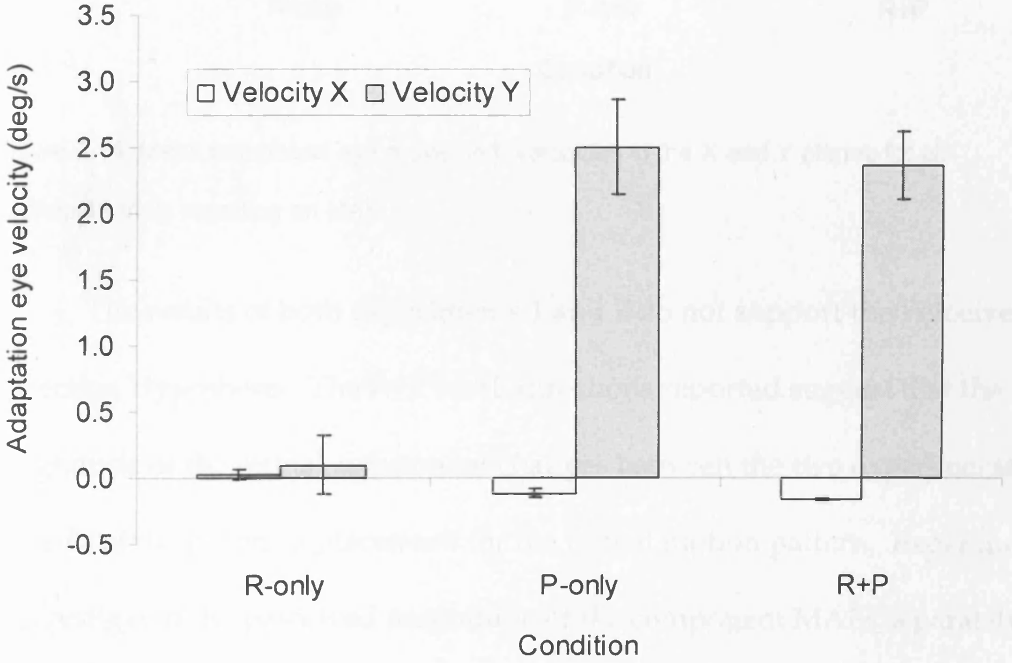

Figure 2.13 Mean adaptation phase eye movement velocities in the X and Y planes for all participant trials reporting an MAE in experiment 2. As before, the average eye movements in the X (white bars) and Y (grey bars) directions are shown during test following the three adaptation conditions (R-only, P-only and R+P).

Unwanted eye movement during the test phase was also reduced (see Figure 2.14; cf. Figure 2.9). The peripheral placement of the random dot patterns during adaptation and test showed that the moving background had less influence on the physical motion of the eye.

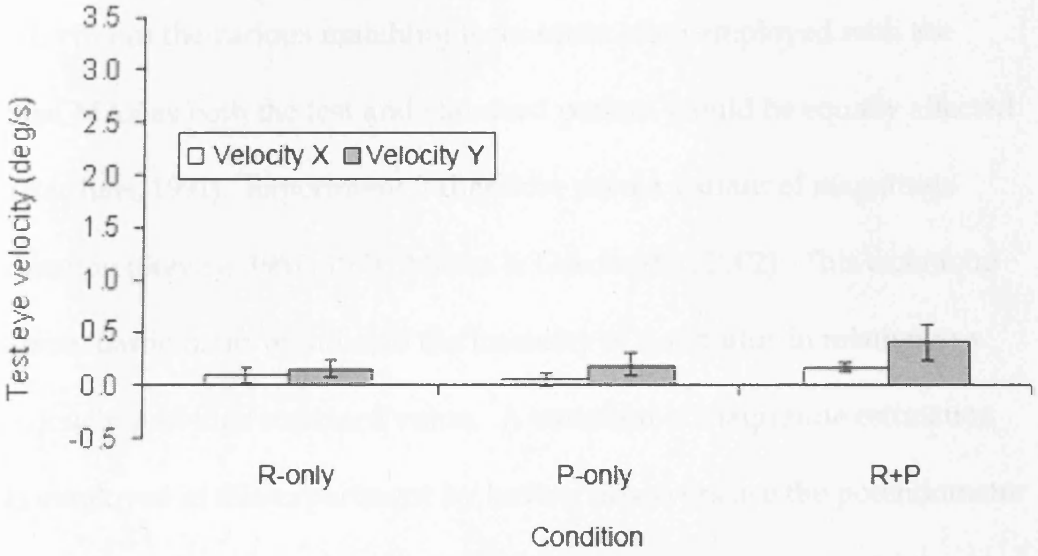

Figure 2.14: Mean test phase eye movement velocities in the X and Y planes for all participant trials reporting an MAE.

The results of both experiments 1 and 2 do not support the Perceived Direction Hypothesis. The R+P MAE directions reported suggest that the magnitude of the retinal component changes between the two experiments as a result of the differing placement for the retinal motion pattern. Experiment 3 investigated the perceived magnitude of the component MAEs separately by having observers report the perceived speed of the MAE.

Experiment 3: Component MAE Magnitudes

Introduction

The properties of the extra-retinal component complicate attempts to measure its speed. The whole field, non-retinotopic nature of the extra-retinal MAE vitiates the various matching techniques often employed with the retinal MAE as both the test and standard pattern would be equally affected (Chaudhuri, 1991). Experiment 3 therefore used a variant of magnitude estimation (Stevens 1957, 1971; Marks & Gescheider, 2002). This technique requires participants to indicate the intensity of a stimulus in relation to a previously provided standard value. A variation of magnitude estimation was employed in this experiment by having observers use the potentiometer as a speedometer. This allowed participants to provide estimated values in relation to a previously presented range of speeds.

From the previous experiments it was hypothesized that peripheral adaptation should increase the retinal MAE magnitude. This was suggested by both the direction of the R+P MAE and the increased frequency of MAE reports peripherally. Also, an interaction was expected between the location of the adapting pattern and the type of adapting motion. Peripheral adaptation to retinal motion was expected to produce faster MAE reports in the R-only condition as suggested by Experiment 1. In comparison, no such increase in adaptation strength was expected for the P-only condition.

Method

Participants

Sixteen students with normal or corrected to normal eyesight participated. All participants gave informed written consent.

Stimuli and experimental design

The P-only and the R-only conditions from experiments one and two were employed. The R+P condition was excluded. Two replications for all four conditions were presented in random order.

Procedure

Perceived MAE speeds were recorded with the potentiometer pointing device used in Experiments 1 and 2. Participants were asked to use the unseen pointing device as if it was a 'car speedometer' to indicate speeds. The motion of the pointing device was limited to a 180° rotation in an upper arc around the zenith. Instead of making direct numerical estimates of speed, a full range of reference speeds were provided in a training/calibration phase before the perceived MAE speeds were collected. At the start of each calibration phase, participants were instructed to indicate stationary (0deg/s) by moving the potentiometer bar to touch the left-hand stopper and the fastest speed (4deg/s) by rotating it to the right-hand stopper. The initial range setting occurred whilst appropriate actual screen motion was displayed. Following this a range of calibration speeds from 0 deg/s to 4 deg/s in 0.8 deg/s steps were displayed, in a random order, both centrally and peripherally. The calibration was repeated to obtain two recordings at each speed. These were averaged and a third order polynomial fitted to act as a calibration curve for the experimental voltage readings. These could then be employed to act as a look-up to translate the MAE speeds indicated during the test phase. Unlike the previous experiments, no response was required during adaptation.

Eye Movement recording and analysis

Using a new eye tracker, eye movements in the current experiment were recorded using an SR Research Eyelink 2000 tower mount eye tracker at 1000 Hz. The eye movements were analysed in MatLab using custom developed software.

MAE data preparation

Any trials not reporting an MAE speed were removed. Data were averaged across the two replications for each participant. Only participants with speeds registered in all four conditions were included for the ANOVA.

Results and Conclusions

Figure 2.15 shows the perceived speeds for the retinal and pursuit conditions, both centrally and peripherally. Pursuit MAE were consistently reported as faster than retinal MAE. A two-way ANOVA found a main effect of adapting motion (retinal/pursuit), $F(1,7)=5.70$, $p \leq .05$, cases with missing data were excluded. The placement of adaptation and test in the periphery suggest MAE magnitude increases for both retinal motion and pursuit, although these increases only tend towards significance, F(1,7)=4.32, p = 0.076. There was no significant interaction, F(1,7)=1.23, p=0.303. Whilst an increased peripheral MAE speed was expected for retinal motion, higher speeds were reported peripherally for both retinal motion and smooth pursuit.

The low frequency of R-only MAE reports in experiment 1 was not found for the central adaptation condition in this experiment, with retinal and extra-retinal MAE reported in 69% of trials for central adapt. For the peripheral adaptation, a retinal MAE was reported in 50% of trials whilst a pursuit MAE was reported in 78% of trials.

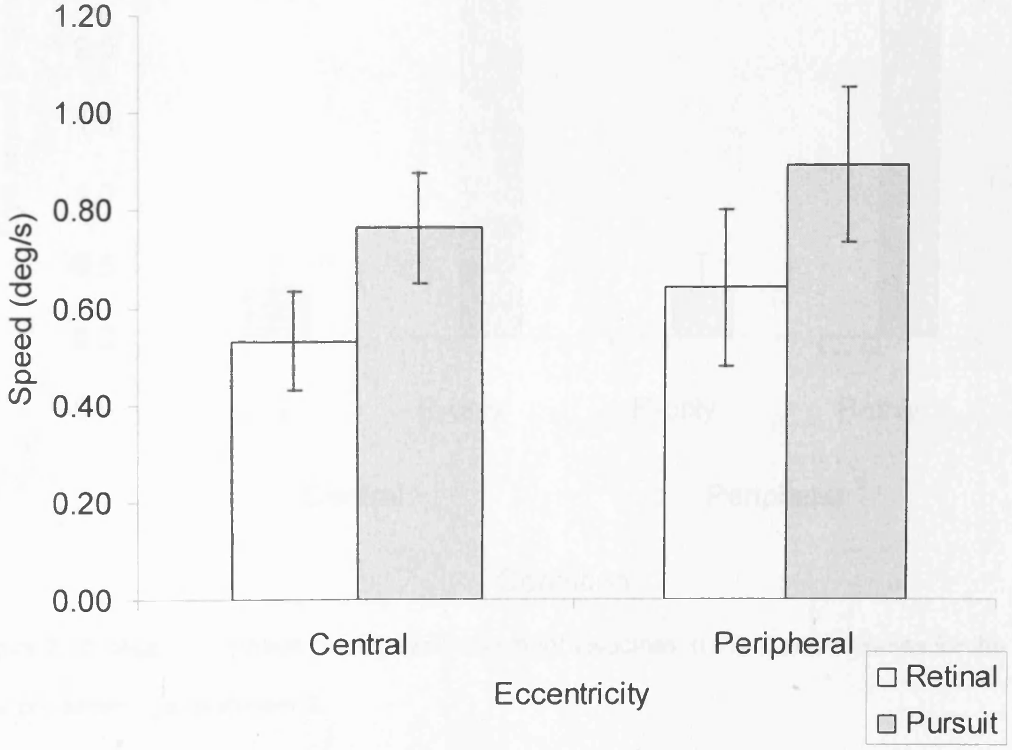

Figure 2.15: Perceived speeds (MAE magnitude) for experiment 3. MAE reported speeds were below 1 deg/s for all conditions, but were consistently higher for the pursuit condition.

The eye movements again confirmed that participants pursued in pursuit conditions and fixated in fixation conditions (see Figure 2.16). The eye data showed a small leftward eye movement induced by the surrounding dot pattern in the central fixation condition (mean = 0.21deg/s (SE = 0.06)) with the next largest being a mean leftward eye movement of 0.12deg/s (SE = 0.05) in the peripheral pursuit condition. The smooth pursuit eye directions were close to vertical, averaging 90.4° (SE = 0.8) central and 91.8° (SE = 1) peripheral.

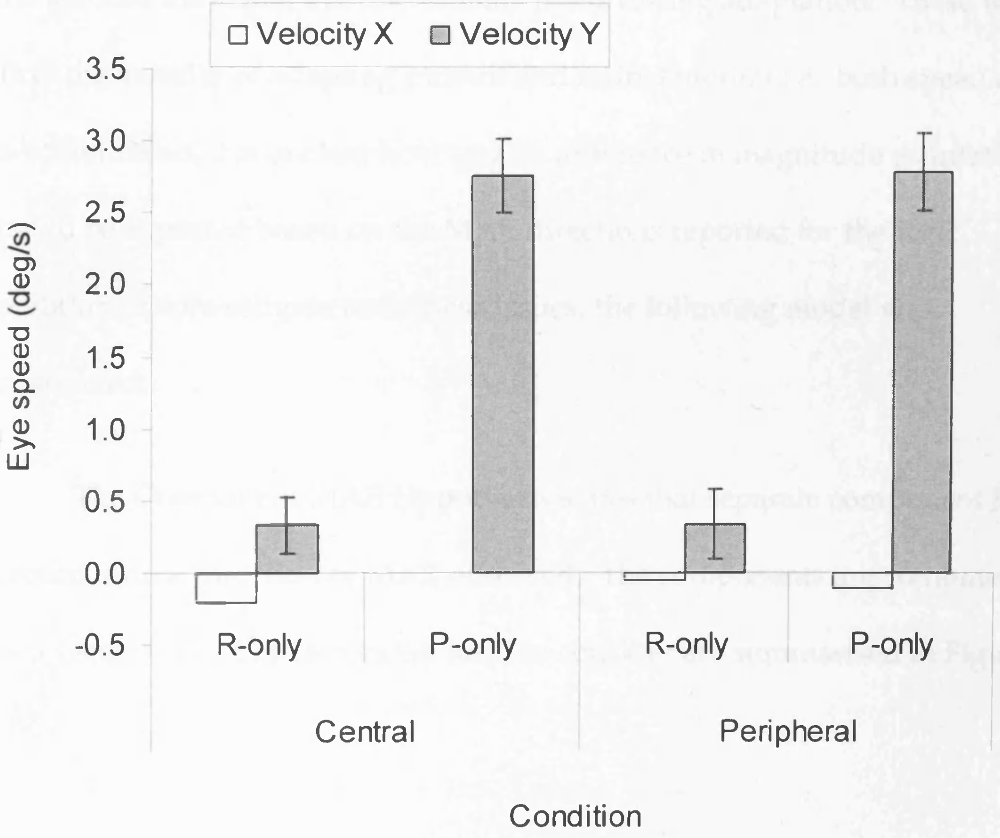

Figure 2.16: Mean adaptation phase eye movement velocities in the X and Y planes for the four conditions in experiment 3.

Modelling the Component MAE Hypothesis

Experiments 1 and 2 did not support the Perceived Direction Hypothesis. This section investigates whether the data support the Component MAE Hypothesis. On the basis of Experiments 1 and 2, this hypothesis predicted an interaction between MAE component type (R-only and P-only) and location (central and peripheral) in Experiment 3. However, none was found. The results did show that the P-only condition produced an MAE that appeared faster, but this was only expected for the central condition (Experiment 1). Importantly, the predicted interaction did not take into account the actual eye movements made during adaptation. These will affect the velocity of adapting pursuit and retinal motion i.e. both speed and direction. Also, it is unclear how large a difference in magnitude estimates should be expected based on the MAE directions reported for the R+P condition. To investigate both these issues, the following model was constructed.

The Component MAE Hypothesis states that separate component MAE account for the direction of MAE observed. The components are combined via a vector sum. The factors we need to consider are summarised in Figure 2.17.

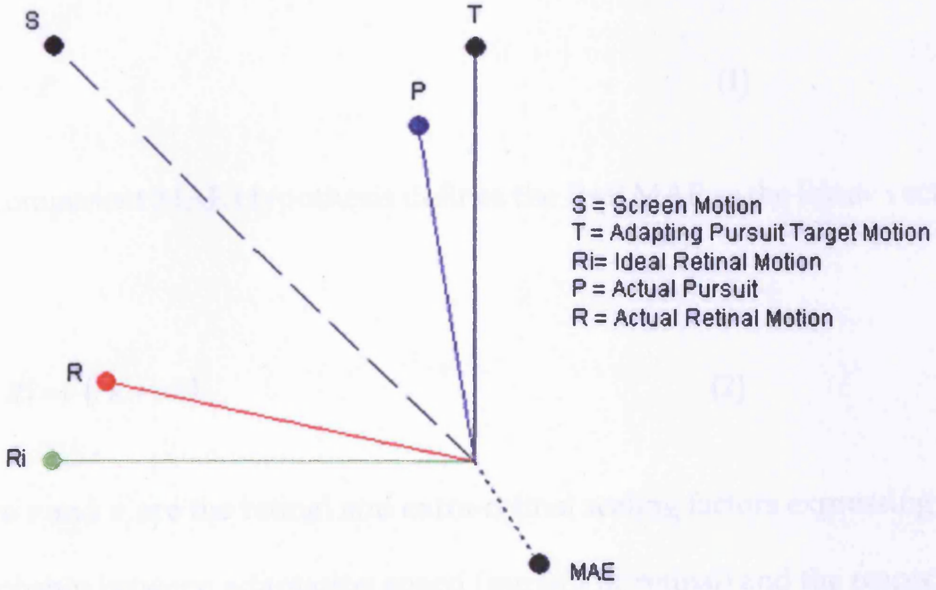

Figure 2.17: Factors affecting the component MAE. The actual pursuit eye movement (P) alters the adapting retinal motion (R). The relative velocity of the two components determines the resultant retinal MAE and pursuit MAE. A vector sum of component MAE results in the R+P MAE (MAE) shown.

Consider a pursuit target motion (T) moving vertically at 4deg/s with an 'ideal' background retinal motion (R_i) moving orthogonally at 4deg/s. 'Ideal' means the retinal motion that would be produced by an accurate eye movement and so R_i is equivalent to the relative motion between the pursuit target and the background. The combination of orthogonal motions results in head-centred motion (H) which is the angular bisector of R_i and T. Head-centred motion is an approximation of screen motion. If the pursuit eye movement is not accurate, the actual eye movement (P) would produce retinal motion (R). These produce component MAEs that combine to produce an overall R+P MAE shown as a dotted line on the figure.

By definition, the vectors R, H and P are related by:

$$R = H - P \qquad (1)$$

The Component MAE Hypothesis defines the R+P MAE as the linear vector sum:

$$M(R,P) = -(rR + eP) \qquad (2)$$

Where r and e are the retinal and extra-retinal scaling factors expressing the relationship between adaptation speed (pursuit or retinal) and the respective magnitude of the individual component MAEs. The values are negative because the MAE is in the opposite direction to the adapting motion.

Substituting (1) into (2) gives:

$$M(R,P) = -(r(H - P) + eP) \qquad (3)$$

Which gives:

$$M(R,P) = -(rH + (e - r)P) \qquad (4)$$

Equation (4) shows that when the scaling factors are identical ($r = e$), the MAE vector is independent of actual pursuit. However, Experiment 3 showed differences in the perceived speed of the different types of component MAEs. This suggests that $r \neq e$, in which case the actual velocity of eye movements do matter.

One way to estimate the scaling factors is on the basis of the data in Experiment 3. Assuming that magnitude estimates (E) are equal to the magnitude of the component MAEs, then $r = \mathrm{E}/|R|$ and $p = \mathrm{E}/|P|$. Note that observers were able to fixate accurately, and so $|\mathrm{R}|$ is equal to the adapting speed of 4deg/s. However, pursuit during adaptation was not accurate so $|\mathrm{P}|$ = gain*P, where gain relates the velocity of the eye movement to the velocity of the target. Combining the eye movement data from the P-only condition of Experiment 3 with the magnitude estimates, the mean e across observers was 0.76/(0.66*4) = 0.28 for the central condition and 0.89/(0.69*4) = 0.32 for the peripheral condition. Similarly, the mean r was 0.53/4 = 0.13 for the central condition and 0.64/4 = 0.16 for the peripheral condition. For the statistical tests in the next paragraph, individual participant gains were used to calculate predicted MAE.

Having set the MAE scaling factors, the model was then used to calculate the predicted R+P directions for the first two experiments. The means of the Component MAE predictions are represented in Figure 2.18 as a dashed red arrow for central adaptation and a dashed blue arrow for peripheral adaptation. For experiment 1, the mean direction from the predictions was -52°, the predicted directions significantly underestimated the actual directions reported in experiment 1 ($t(19)=-3.1$, $p<0.01$). So even with actual eye movements included, the direction settings and magnitude estimates in the central adaptation condition together do not support the Component MAE Hypothesis. For experiment 2, the mean of the model predictions was -56° and the individually predicted directions did not significantly differ from the directions reported by the observers (t(13)=1.3, p=0.21, N.S.). Hence the combination of perceived MAE direction and magnitude estimates in the peripheral condition can be predicted by the Component MAE Hypothesis. Importantly, as discussed in earlier sections, both component model predictions provide better estimates than their perceived direction equivalents. Possible reasons for the failure of the component MAE to quantitatively predict the direction of R+P MAEs found in Experiments 1 is taken up below.

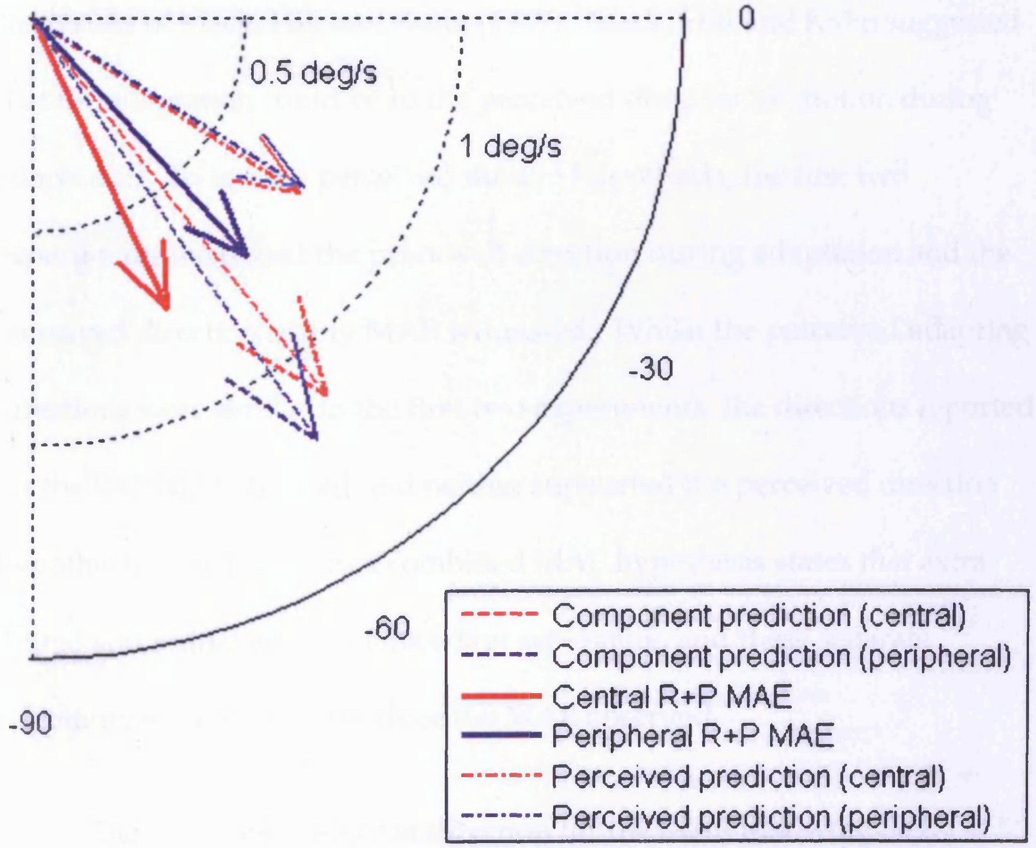

Figure 2.18 shows the mean predicted MAE and actual mean MAE directions from experiments 1 and 2. The R+P MAE velocities predicted by the component MAE hypothesis

for central adaptation (dashed red arrow) and for peripheral adaptation (dashed blue arrow) are similar. The arrows for both the R+P MAE directions (solid arrows) and for the almost identical Perceived Direction Hypothesis predictions (dash-dot arrows) indicate direction only. Arrows relating information from experiment 1 are red, and for experiment 2 the arrows are blue.

Discussion

This study investigated the unidirectional MAE that follows adaptation to orthogonal retinal motion and smooth pursuit eye movements. The MAE direction was neither opposite the retinal motion direction, nor opposite the eye movement direction, but resulted from a combination of both, replicating the results of Mack, Hill and Kahn (1989). Mack, Hill and Kahn suggested that the adaptation could be to the perceived direction of motion during adaptation. To test the perceived motion hypothesis, the first two experiments measured the perceived direction during adaptation and the perceived direction of any MAE witnessed. Whilst the perceived adapting directions were similar in the first two experiments, the directions reported for the R+P MAE differed and neither supported the perceived direction hypothesis. The alternative combined MAE hypothesis states that extra-retinal and retinal components adapt separately, and these separate adaptations combine to produce the MAE observed.

The observed change in direction for the MAE following R+P adaptation was however concordant with variations observed in the R-only MAE between the two experiments. Experiment 1 found the R-only MAE infrequently reported, so the R+P MAE direction was strongly influenced by the pursuit component. Several participants reported R+P MAE directions in which the retinal component appears to have negligible influence, with the directions instead being comparable to those reported in the P-only condition. Experiment 2 successfully increased the reports for the R-only component via adaptation and test in the periphery. The direction of the R+P MAE also suggested an increased retinal component.

When the current study was initially piloted the retinal MAE was found to be weak in agreement with previous research (Day and Strelow, 1971; Wade et al, 1996). Often no MAE was observed in an unstructured visual field. Whilst this suggested a successful reduction in relative motion, a poorly reported retinal MAE also offered an opportunity to test the Component MAE hypothesis. A faster and more compelling percept for MAEs in the periphery was observed during the piloting and testing of this study, and confirmed by Experiment 3. Some previous evidence had suggested that the periphery could be more susceptible to illusory motion. Surround modulation of the MAE is stronger peripherally (Murakami & Shimojo, 1995) and the velocity required to null a retinal MAE is greater peripherally (Wright, 1986). In an unstructured visual field, without surround modulation, the retinal MAE was reported over twice as frequently when adaptation occurred peripherally compared to central vision between experiments 1 and 2. The stronger retinal MAE in the periphery provided an opportunity to test the Component MAE Hypothesis by manipulating the

R+P direction between experiments 1 and 2. Whilst a stronger R component would not change the R+P MAE direction if the Perceived Direction Hypothesis were correct, the direction would change if the components did determine the MAE direction.

For a combination of MAE components to predict the directions reported in both of the first two experiments, the magnitude of the extra-retinal MAE would need to be greater than retinal, although their relative difference would be considerably smaller in experiment 2. This was partially confirmed by experiment 3. Extra-retinal MAEs were consistently perceived as faster than their retinal counterparts. This was the case for both central and peripheral conditions, however, the expected interaction was not found. This may be due to the retinal MAE being weak and poorly reported in the first experiment, a finding widely replicated when piloting experiment 1, but not replicated for the third experiment. The relative speed of pursuit and retinal MAE speeds reported for both the central and peripheral conditions of experiment 3 were similar.

Whilst the component MAE model successfully predicted the directions from experiment 2, the predicted directions for experiment 1 were significantly different from the MAE directions reported. The R+P MAE directions reported in experiment 1 suggested a weak retinal component, with some directions similar to a P-only MAE. The predicted directions for experiment 1 may have deviated from those observed due to the retinal component suggested by magnitude estimation. The predictions rely on the estimates being similar to the actual influence of the components during the trials. Unfortunately, the estimated magnitude of the centrally adapted retinal MAEs in experiment 3 had differing properties to those reported for experiment 1. Whilst R-only MAEs were reported in 24% of trials for experiment 1, their magnitude was estimated in 69% of trials for experiment 3. This high level of reporting suggests an increased saliency for the retinal MAE when participants are asked to estimate magnitude. Employing a large R-only MAE magnitude estimate to represent a weak R-only MAE would produce a difference in the same direction as that found for the predicted directions and central R+P MAE.

The change in saliency may suggest a different judgment is being made during magnitude estimation of the MAE. The motion of the MAE is illusory, and as such is not bound to position as it would be via Newtonian mechanics -whilst the stimulus appears to be in motion, the motion is not physically bounded to its position. It has been reported that under certain conditions position can shift in one direction, whilst perceived motion is in another (Bulakowski, Koldewyn & Whitney, 2006). Naive observers, unaware of the properties of the MAE may reduce their estimates as the test pattern did not changing location despite an apparent motion. This could lead to reduced differences in magnitude estimates between conditions.

The P-only MAE and the R+P MAE frequency decreased with the peripheral placement of the adapting retinal motion and the test pattern. As extra-retinal MAE are not retinotopic (Chaudhuri, 1991), the effects of eye movement adaptation are independent of the test placement. The eye movement analysis provides an explanation for the reduction in MAE reports. The physical eye movement was reduced when the retinal motion was displayed peripherally in Experiment 2. The difference between eye movement gains in Experiment 1 and 2 may reflect the placement of the retinal motion either around the pursuit target or in the periphery. The pattern providing retinal motion had a horizontal speed component that matched the pursuit target. When estimating, initiating and maintaining a smooth pursuit, less sensory information will be provided by a single foveal dim red dot with a peripheral dot pattern than when the whole stimuli is presented centrally. Smooth pursuit improves when more information is available to the visual system. As the number of dots in a pursuit pattern is increased, variations in the eye direction and speed are decreased (Osborne and Lisberger, 2009).

Overall, given the predictable nature of the target trajectory, the gains of the smooth pursuit eye movements were low. Predictable stimuli increase the accuracy of pursuit (Stark, Vossius & Young, 1962; Dallos & Jones, 1963; Yasui & Young, 1984). However, the gains of vertical pursuit are known to be lower than for horizontal pursuit (Rottach et al, 1996). Different brain structures drive vertical and horizontal pursuit with the effect present even in young children (Gronqvist, Gredeback & von Hofsten, 2006). Plus pursuit over a background results in around a 20% reduction for vertical pursuit, with similar reductions reported between differing background structures (Collewijn & Tamminga, 1984). Participants were also required to attend a perceived motion direction which differed from the pursuit direction. Tasks designed to distract attention from the pursuit target also reduce the accuracy of tracking movements (Brezinova and Kendell, 1977). Given these previous findings, the pursuit gains reported in this study, with psychophysically inexperienced participants, would seem to be reasonable.

Whilst extra-retinal MAE magnitudes were greater than retinal MAE, it is known that retinal speed estimates are greater than eye movement estimates. This is illustrated by the Aubert-Fleischl phenomenon, where an object's motion is perceived as slower when pursued (Aubert, 1886; Fleischl, 1882) and the Filehne illusion in which a stationary background appears to move in the opposite direction to an eye movement (Filehne, 1922). This illusory motion of the background in the opposite direction to the eye movement suggests that the cancellation of retinal motion is not fully accomplished because the pursuit speed estimate is lower. This finding was confirmed in the current chapter. The perceived direction of adapting motion tended toward the retinal motion in the first two experiments. Again this suggests that retinal speed estimates influence the perceived direction more than extra-retinal estimates. However, the relative magnitudes of retinal and extra-retinal signals following adaptation differ, as illustrated by their comparative influence on the reported direction of the R+P MAE. The current data therefore suggest a difference between the size of extra-retinal and retinal signals during eye movement and the magnitude of the component MAEs they produce. This suggests differences between the adaptation of eye movement and retinal motion. Following a pilot experiment, the test phase fixation point was initially considered as potentially increasing the relative strength of the pursuit component in the R+P condition to explain the noted difference. As the fixation point was presented in an area previously unexposed to the adapting retinal motion it was considered that only the pursuit component would act upon it. The results suggest that the removal of the fixation point during test did not reduce the pursuit components influence on the R+P condition. The pursuit component consistently produced a stronger percept of illusory motion than the retinal component across the three experiments. Separate mechanisms for eye movement and retinal motion speed estimation, with separate adaptation profiles is perhaps not very surprising as there is no reason to assume that the two motion estimates have matching characteristics.

This study successfully differentiated between the two proposed models, showing that the Perceived Direction Hypothesis could not accommodate the directions reported for the R+P MAE. The MAE direction could be explained through a vector sum of adapted retinal motion and smooth pursuit eye movement components using peripheral adaptation. Potential changes in the magnitude of the R-only MAE may provide an explanation for the failure of the component MAE model to predict the results of experiment 1. Whilst the R+P MAE can be generated by the adaptation of two low level signals, this will not fully exclude a potential role for adaptation further along the motion processing pathway, processing that eventually provides the perceived direction. However, the results here confirm that the separate components produce separable MAE, and that these can be combined to predict a single illusory percept. There remains debate as to the nature of the components that are being adapted. The nature of the pursuit speed estimate is investigated in the next two chapters.

Chapter 3: The pursuit speed estimate: Extra-retinal aftereffects and the influence of retinal motion.

Abstract

Chapter 2 provided evidence that both retinal and extra-retinal signals can adapt separately to produce individual sources of illusory motion. In this chapter the nature of the pursuit speed estimate is investigated. As discussed in Chapter 1, the pursuit estimate could either be derived from a purely extra-retinal signal or from a reference signal which is additionally modulated by retinal motion. The experiments presented here employed an adaptation paradigm using collinear retinal motion and smooth pursuit to test the two models. The effects of retinal motion adaptation were limited by the placement of the test in an area not coincident with the adapting motion. Through excluding the effects of local retinal motion adaptation from the test phase, the properties of the extra-retinal MAE were examined in isolation. Retinal motion during adaptation would not alter the properties of an MAE whose origin is purely extra-retinal, but the properties of an adapted reference signal would change. In pursuit conditions, the adapting stimuli consisted of a moving pursuit target and a surrounding random dot pattern producing retinal motion in either the same or opposite direction. In fixation conditions, the pursuit target remained stationary and the dot pattern moved as before. In separate sessions observers judged the direction or speed of any MAE they experienced during Experiment 4. This was refined in Experiment

5, with participants reporting both speed and direction in each trial. Perceived direction was assessed using an adjustable rod that could be rotated in the direction of the MAE. Perceived speed was assessed using the same device, this time in a manner akin to a speedometer. In both cases, perceived direction and perceived speed were calibrated against physical motion prior to the collection of data. The results showed few reports of MAE in any of the fixation conditions and in pursuit conditions that contained retinal motion in the opposite direction. Conversely, most observers reported salient MAE when retinal motion moved in the same direction as pursuit. The results are explained by measured changes to the eye movement that were dependent upon the comparative velocity of the background; an alteration to the physical eye movement will change the extra-retinal signal. The research presented here suggests that an extra-retinal pursuit speed estimate results in the MAE that follows adaptation to repetitive smooth pursuit eye movement over various background motions. The reference signal account of the pursuit speed estimate was deemed unsatisfactory as no evidence was found to suggest that retinal feedback modulated the size of the pursuit speed estimate.

Introduction

The previous chapter showed that when retinal motion and pursuit eye movement are orthogonal, the R+P MAE that results comprises two components, one related to the retinal motion and one related to smooth pursuit. The MAE that follows adaptation to smooth pursuit was employed in the experiments presented here, to examine the influence of background motion on the smooth pursuit estimate. The issues addressed in this and the next chapter fit into the wider context of how the visual system interprets retinal motion during pursuit.

When we visually pursue a moving object its image is maintained on the fovea, the high acuity area of the retina. A pursuit eye movement thereby increases the amount of visual information available about the target. However, moving our eyes creates a flow of retinal motion that is tied to self motion rather than motion in the surrounding environment. The various sources of retinal motion need to be identified and interpreted to help inform the perception of a stationary world which contains moving objects.

When we make an eye movement, one of the proposed mechanisms to recover head-centred motion is to employ an internal estimate of self motion. This internal estimate can be envisaged as an extra-retinal copy of the efferent signal that initiates the eye movement, an 'efference copy' (von Holst & Mittelstaedt, 1950), or the outflow of neural activity, which is termed 'corollary discharge' (Sperry, 1950). Both terms relate similar concepts, and here they will be referred to simply as extra-retinal signals. Classical models of motion perception consider the extra-retinal signal and the portion of the retinal signal created during an eye movement (reafferent signal) to be approximately equivalent to one another. These two signals can then be used to cancel one another. Both signals produce a separate estimate of motion, one for retinal motion (R′) and the other for the pursuit eye movement (P′) (Freeman & Banks, 1998). Since pursuit causes retinal motion in the opposite direction, when there is no noticeable difference between the two estimates, the resultant of a vector sum is no net self-motion percept during the eye movement.

There is a question as to whether the pursuit estimate is purely extra-retinal in origin. If the relationship between the physical eye movement and the extra retinal estimate decreases over time, either due to disease, development or fatigue, it will no longer be appropriate to cancel the retinal slip created during an eye movement (Haarmeier, Bunjes, Lindner, Berret and Thier, 2001). Therefore, reference signal models replace the extra-retinal signal with a composite signal which is a function of both retinal and extra-retinal information (Figure 3.1b). Reference signal models combine extra-retinal and retinal information to estimate eye velocity (P′) (Crowel & Andersen, 2001; Haarmeier & Thier, 1996; Goltz, DeSouza, Menon, Tweed & Vilis, 2003; Dash, Dicke, Chakraborty, Haarmeier & Thier, 2009). Retinal information is therefore used to provide feedback as to the suitability of the reference signal pursuit estimate.

Figure 3.1 recreates the figures for the classical model and the reference signal model introduced in chapter 1. Two motion estimates (R′ + P′) are transformed into a head-centred motion estimate (H′). The inclusion of an adaptation box in Figure 3.1 is intended to indicate that P′ will solely modulate H′ (for both models) when R is constant and local R′ adaptation can be excluded. The magnitude of P′ during adaptation will be determined by the extra-retinal signal only for the classical model, whilst it will additionally be modulated by R′ for the reference signal model. With local retinal motion sensor adaptation controlled for, P′ will only be influenced by adaptation R′ if the eye movement estimate into H′ is a reference signal.

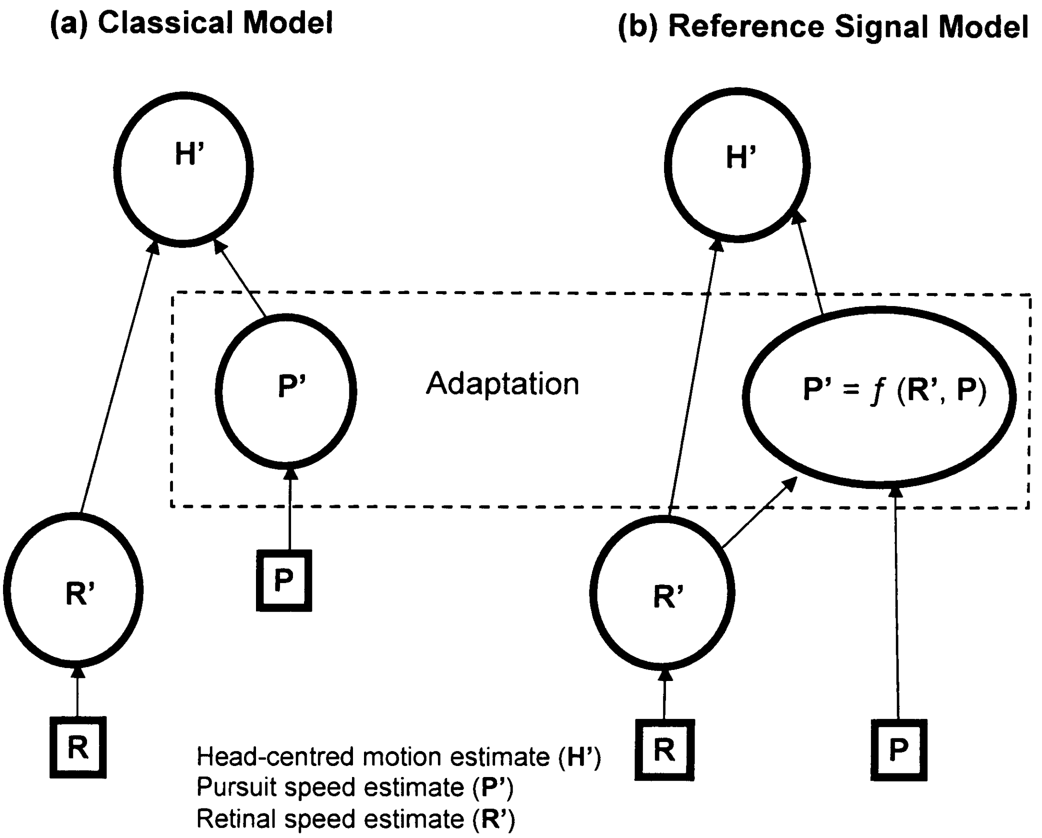

Figure 3.1: The Classical Model and the Reference Signal Model. Both estimate head-centred motion from retinal and extra-retinal information. The origin of the classical model pursuit speed estimate is purely extra-retinal. A Reference Signal Model replaces the extra-retinal signal with a pursuit speed estimate calibrated by retinal feedback, a reference signal. Since adaptation and test patterns are spatially non-coincident in this and the next chapter, the adaptation box has been used to illustrate the exclusion of retinal motion adaptation as a factor in altering head-centred motion perception.

In estimating head-centred motion, any excess signal during this cancellation process allows for the estimation of external physical motion. Persistent errors have been shown to occur in this estimate. The illusory motion of a stationary background during smooth pursuit, known as the

Filehne Illusion, is thought to represent a perceptual under-constancy of the eye movement estimate (Mack and Herman, 1973). Mack and Herman manipulated the physical motion of the background across trials, until the amount of motion required for the background to be perceived as stationary could be estimated. The motion required in the background to attain this point of subjective stationarity has to have the same magnitude as the Filehne illusion in order to cancel the perceptual effect. Haarmeier and Thier (1996) employed a two-alternative forced-choice method in which participants had to report whether the background motion was left or right. Previous responses were used to inform future background motions via an adaptive staircase procedure. Haarmeier and Thier showed that the Filehne illusion could be changed by the speed of the background motion in previously viewed conditioning stimuli.

Haarmeier et al (2001) again quantified changes to the point of subjective stationarity, following observation of backgrounds whose motion was manipulated to be substantially different to that expected during an eye movement. The repeated perception of either too much or too little background motion was considered to act on the reference signal, whose gain would be modified to help attain background stability during pursuit. When the background was manipulated to move too much in the same direction as pursuit, this was envisaged as indicating that the reference signal would be too high to fully cancel background motion. Likewise, when the background was moving against pursuit, this represented a reference signal that was too low. When retinal feedback suggests that a reference signal magnitude is incorrect the size of the reference signal is modified to correct any imbalance. In the current study background motion is again manipulated, so that it provides either too little or too much background motion, for any given eye movement.

Some conditions in this study provide background motion in the same direction as the eye movement. If such positive retinal motion conditions are in an extended range of 'reference signal too high' velocities, then a compensatory gain change would result in the magnitude of the reference signal being decreased. The range of conditions tested in the current study was not directly tested by Haarmeier et al (2001). However, the results of Haarmeier et al (1996) showed a decrease in reference signal magnitude for positive retinal velocities compared to those observed for negative retinal slip. Negative retinal slip occurs when a small reference is not sufficient to cancel the retinal effects of pursuit. The hypothesised increase in the reference signal would then alter the point of subjective stationarity in later tests. The results of Haarmeier and Thier (1996), who employed backgrounds moving in the same direction as pursuit, suggest no large magnitude change when retinal motion has a greater velocity than the eye movement in the velocity range tested. In an alternative reference signal model Brenner and van den Burg (1994) proposed that when a background motion is in the same direction as pursuit (positive retinal image slip) then retinal motion would be disregarded. This is because retinal motion could not be a useful source of information about the eye movement if it can not be related to the physical motion of the eye. The extra-retinal signal alone would then provide the best estimate concerning the speed and direction of an eye movement (Brenner and van den Burg, 1994). In more general examples of this type of model, some authors also include vestibular information related to head and body movement, because any self motion will create a change to the afferent retinal motion (Wertheim, 1994).

It is unclear from the experiments of Chapter 2 which type of signal is being adapted, largely because the retinal motion displayed during adaptation was orthogonal to the pursuit. Reference signal models consider conditions with collinear motion, and would not make predictions for orthogonal motion. This is because orthogonal retinal motion is not created by the action of smooth pursuit. In this chapter the retinal motion displayed during adaptation was therefore made collinear with the pursuit. In this circumstance, the pursuit component of the R+P MAE could be based on either extra-retinal adaptation per se or a reference signal that combines eye velocity and retinal motion.

Some previous studies that have examined adaptation to R and P have placed the retinal motion shown during adaptation and test in the same retinotopic location (Haarmeier & Thier, 1996; Haarmeier et al, 2001; Freeman, 2007; Dash et al, 2009). Under these conditions, it has not been possible to differentiate between the predictions of a classical model and a reference signal model since local retinal motion sensor adaptation (R' adaptation in Figure 3.1) cannot be excluded as an explanation for any subsequent aftereffect. But retinal motion adaptation is known to be retinotopic (Wohlgemuth, 1911; Sekuler and Pantle, 1967; Masland, 1969; Knapen, Rolfs and Cavanagh, 2009), so one way to prevent local R' adaptation is to place the adaptation and test patterns in different locations. In the current chapter, the effect of combining pursuit with retinal motion that is non-coincident with the subsequent test is investigated for static pursuit-induced MAE. In the next chapter, the same manipulation is used to investigate how simultaneous adaptation changes perceived stability when the eyes move during the dynamic test phase.

The MAE which follow adaptation to eye movement, even in the absence of retinal motion, are considered to be of extra-retinal origin (Chaudhuri, 1990, 1991). However, it is possible that the MAE following repetitive smooth pursuit eye movement over a visible background results from the adaptation of a reference signal. Whilst a reference signal represents a composite signal employing both smooth pursuit and retinal information, when retinal information is unavailable, a reference signal could only consist of a purely extra-retinal input. The classical model predicts no change to the properties of the resulting MAE as a result of background motion during adaptation. When retinal feedback differs across conditions the size of a reference signal will vary and thereby the amount of illusory motion observed will differ between conditions. Establishing which model best describes the transformation of the component signals into head-centred motion relies on the test not being affected by adapted local retinal motion sensors.

Unfortunately, placing adapting retinal motion and subsequent test in different retinal locations does not exclude the possibility of phantom retinal MAEs. As discussed in Chapter 1, phantom MAEs can be observed in areas that have not been exposed to previous adapting retinal motions, although they are usually reported when viewing dynamic tests (von Grunau & Dube, 1992; Snowden and Milne, 1997; Culham, Verstraten, Ashida & Cavanagh, 2000; Price, Greenwood & Ibbotson, 2004). To determine whether phantom MAE played any role in the current study, fixation conditions were employed which contained no eye movements. For these, participants adapted to retinal motion that matched that present in the pursuit conditions. The fixation conditions also tested whether non-retinotopic adaptation created induced motion MAE (Wade, Spillman and Swanston, 1996). The induced MAE requires the pattern providing retinal motion to be visible during the test period, this did not occur in the current experiment. Unlike the phantom MAE, for the fixation conditions, an induced MAE would be in the same direction as the adapting retinal motion. Moreover, the directions of induced MAEs become more difficult to predict when adaptation includes smooth pursuit. However, as is the case for phantom MAE, the fixation conditions would reveal the presence of any induced motion MAE.

To summarise, the current chapter thus investigated whether the strength of adaptation was altered by artificially manipulating the background motion during pursuit adaptation. The stimulus in the current chapter was designed to exploit the retinotopic nature of retinal motion adaptation by placing the test pattern in an unadapted retinal region. Additionally, the removal of the adapting pattern during the test phase was designed to further reduce the chance of MAE due to adapted retinal motion sensors (Day and Strelow, 1971; Wade, Spillman and Swanston, 1996).

The nature of the pursuit estimate was examined by measuring the perceived speed and direction of the pursuit MAE following simultaneous collinear adaptation. Collecting the direction of the MAE allowed confirmation that the MAE conformed to the direction expected for a pursuit induced MAE, opposite to the adapting smooth pursuit eye movement. In the first experiment speed and direction were collected in separate blocks. Having confirmed the viability of the measurement methods, both speed and direction were collected following each trial for the second experiment. The two models make differing predictions concerning the MAE speed; an extra-retinal signal is a function of the eye movement alone, whilst a reference signal is also contingent on the background motion. A finding that the MAE does not vary as a function of retinal motion would support the idea of a purely extra-retinal pursuit speed estimate. Conversely, if feedback from retinal motion changes the strength of adaptation, then this would support reference signal models. Specifically the magnitude of a reference signal would be increased in conditions for which background motion was excessively opposite to pursuit e.g. (-16, 8), and either decreased or remain constant in the conditions for which background motion is in the same direction as pursuit e.g. (16, 8) or (8, 8).

Experiment 4

Method

Participants

Eight undergraduate psychology students at Cardiff University, with normal or corrected to normal vision, participated for course credit. Informed written consent was gained and a full debrief followed the experiment. Stimuli and experimental design

Stimuli were generated using Borland Delphi and OpenGL and displayed on a 19″ PC monitor in a dark room as in the previous chapter. A chin rest/head support ensured a constant viewing distance of 70cm.

There were four smooth pursuit conditions and four eye stationary conditions. Both are represented in figure 3.2. The adapting stimuli consisted of a single target point either moving vertically at 8°/s for the pursuit conditions or remaining stationary in the fixation conditions. Surrounding the target was a dim red random dot pattern with a constant density of 1 dot/deg^2. The surrounding dot pattern was contained within an annulus window (inner radius 5 deg, outer radius 10 deg). The target dot had a radius of 0.2° whilst all other dots had a radius of 0.1°.

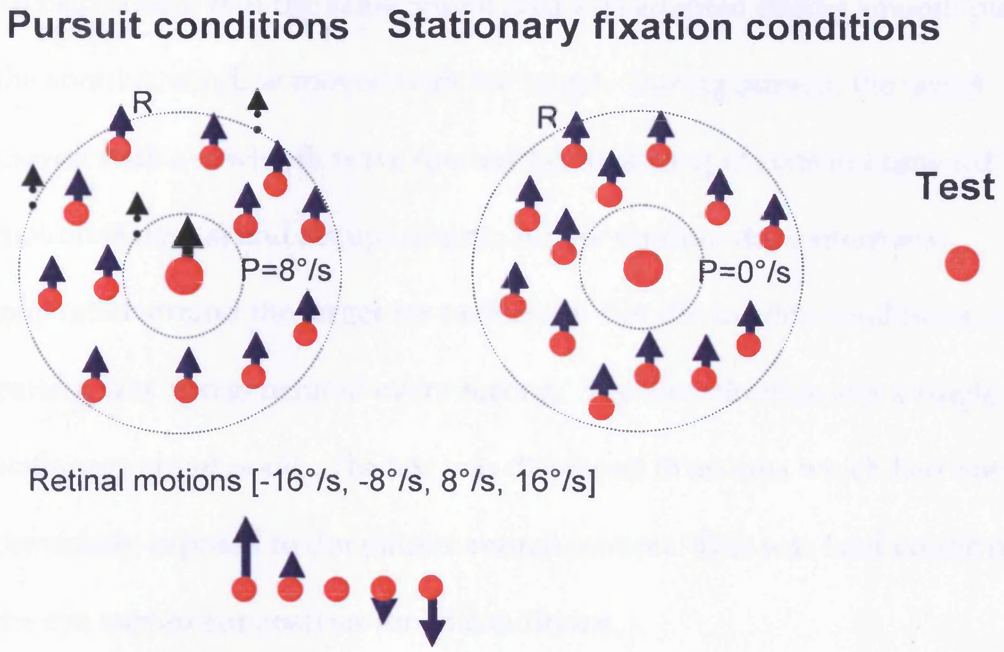

Figure 3.2: Schematic representation (not to scale) of the stimuli, adaptation phase motions and test. The red dots were presented on a black background in a dark room, the dot circles represent the invisible annulus window within which retinal motion was displayed (inner annulus 5°, outer annulus 10°)

The random dot pattern moved upwards or downwards within the window to provide retinal motion in all eight conditions (Figure 3.2). The four adaptation condition velocities were represented using the notation (R, P), where R refers to retinal motion and P to pursuit. The four adaptation conditions with smooth pursuit contained retinal motion in the range -16 deg/s to 16 deg/s, specifically: (R, P) = (-16, 8), (-8, 8), (8, 8) or (16, 8) deg/s. The same retinal motions were displayed during fixation conditions: (R, P) = (-16, 0), (-8, 0), (8, 0) or (16, 0). Positive velocities refer to upward retinal motion, whilst negative velocities correspond to downward motion; note that for the (R, P) = (-8, 8) condition, the dot pattern was stationary on the screen.

To help ensure that the same retinal area was adapted during smooth pursuit, the annulus window moved with the target. During pursuit, the target moved with a sawtooth wave (period 1s) consisting of constant upward motion (8 deg/s) and abrupt return. A new random dot pattern was generated around the target for each cycle. For the fixation conditions, a new pattern was also generated every second. The test stimulus was a single stationary target point. The test was displayed in an area which had not been previously exposed to dot pattern retinal motion. This was later confirmed by the eye movement analysis for all conditions.

Procedure

Directions and speeds were recorded via a purpose built, table mounted potentiometer pointing device registering increasing voltage when rotated. Speed or direction trials were run in separate sessions, the rotation of the pointing device was limited to the upper hemifield by two stoppers in speed trials, but complete rotation was limited by only one stopper for direction trials. Each session started with a calibration phase. Participants used the pointing device to indicate either several real screen directions or speeds, as appropriate. For the direction calibration, participants were asked to report the directions of a moving dot in eleven randomly presented directions, twice each for 22 calibration measures. The calibration directions ranged from -112.5° to 112.5° in 22.5° steps. For the speed calibration the potentiometer rotation was limited to a 180° rotation around the zenith. As in experiment 3 of chapter 2, participants were asked to imagine the potentiometer as a 'car speedometer'. By rotating the bar, participants indicated perceived speeds. Participants were shown the fastest speed and asked to set the speedometer to the maximum, and then readjust to minimum for a stationary dot. Thus the full range of rotation was used. Participants then reported dot speeds from 0 to 8deg/s in 1.6°/s steps. The order of presentation was randomised for both calibrations. A third order polynomial curve was fitted to the calibration voltages for direction and speed separately. This allowed the transformation of experimental voltage readings into the perceived direction or speed of MAE.

Every experimental trial began with the pointer reset to an arbitrary start position (pointing leftward). The screen was illuminated for 50 seconds before each trial, to allow previous adaptations to decay. The adaptation phase was then presented for fifty seconds. Participants were either required to pursue a moving target or fixate a stationary one. The test stimulus consisted of a single stationary point displayed for 5 seconds following adaptation. All direction trials were presented in one session, whilst speed trials were presented in a second session. The orders of sessions were counterbalanced, and the orders of conditions within each session were randomised. Participants reported either the direction or speed of any MAE, or indicated no MAE seen.

Eye Movement recording and analysis

Eye movements were recorded for all participants in all trials using an SR Research Eyelink 2000 tower mount eye tracker at 1000 Hz. The majority of the analysis was the same as for Experiment 3 in Chapter 2. A saccade was defined as an eye movement 30 deg/s above or below the pursuit speed. Trials in which MAE were reported were analysed separately from those in which no illusory motion was reported. Each participant completed two repetitions of each trial. Trials were separated into those which reported an MAE and those which did not. Within participant means were calculated before calculating between participant means.

Direction and speed data preparation

Potentiometer voltages were polled every second during the test. Participants were asked to report when they were happy with their final speed or direction recording via a mouse click. This mouse click initiated the final voltage reading. This setting alone determined the perceived MAE speed or direction for that trial. Trials in which no MAE was reported were removed from the analysis. MAE frequency counts were taken. Data were averaged across the two replications to produce a mean speed and mean direction for each participant. Whilst the direction data allowed for a full range of direction reports, the results indicate that a simple binary categorisation of up or down would have been sufficient. This binary up/down grouping was simply achieved by rating those directions above the horizontal as up and below as down. The mean downward direction for all pursuit conditions was -86.5° (se = 5.1°) and the mean upward direction was 97.3° (se = 2.3°).

Results and Conclusions

Perceived Direction

Figure 3.3 plots the percentage of trials in which observers reported an MAE for each condition, and the percentage of trials reporting no illusory motion. MAE are categorised by the reported direction of illusory motion, either up (light bars), down (dark bars), or no MAE seen (dotted bars). The first four (R, P) conditions correspond to those containing eye movement adaptation, whilst the last four show the results for the fixation conditions. Only the two pursuit conditions which contained positive retinal motion resulted in frequently reported MAE [(8, 8), (16, 8)]. The majority of reported directions were opposite to the direction of smooth pursuit as expected. MAE reports were infrequent when the adaptation phase retinal motion and eye movements were in opposite directions [(-16, 8), (-8, 8)].

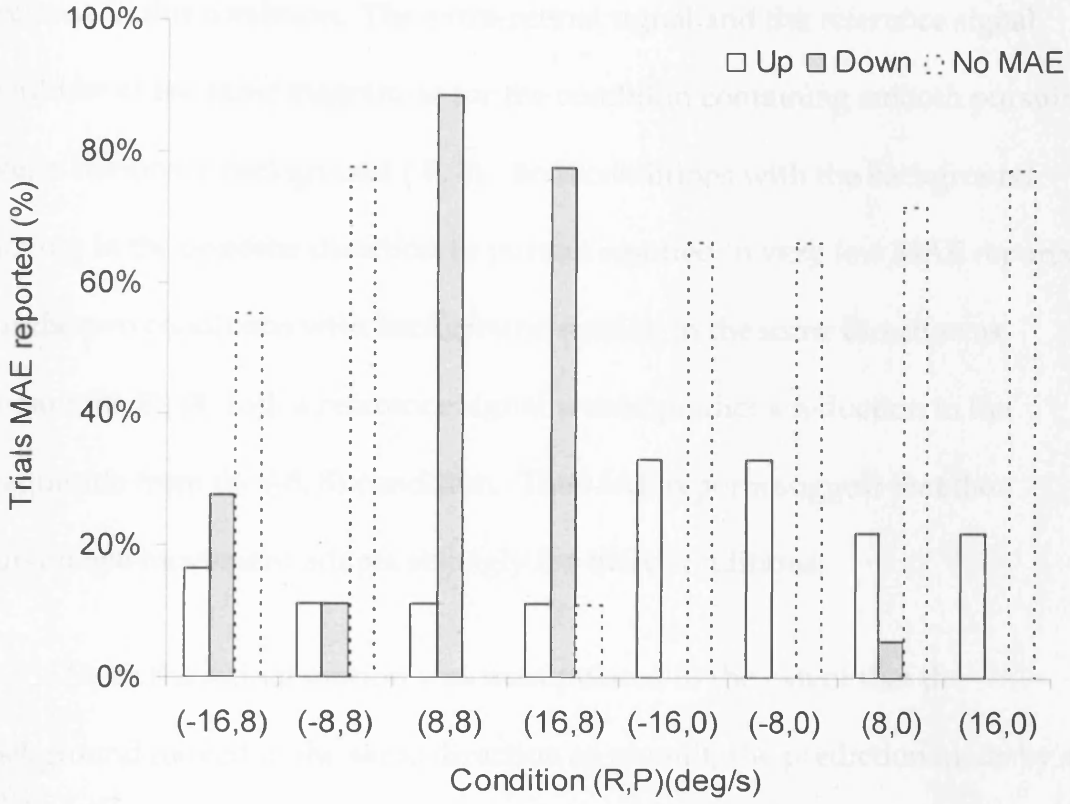

Figure 3.3: Percentage of trials in which an MAE direction was reported. The MAE resulting from the four conditions containing pursuit are shown on the left hand side of the bar chart. The grey bars represent downward MAE report frequency whilst white bars correspond to upward MAE; the dashed bars indicate trials for which no MAE was reported.

Whilst the MAE differs across the pursuit adaptation conditions, the observed pattern of change seen in figure 3.3 is not that predicted by a reference signal model. As discussed in the introduction, the magnitude of a reference signal would be increased in the condition for which the background motion is excessively opposite to the direction of pursuit (-16, 8). Increasing the magnitude of the signal should increase the amount of adaptation, which in turn would lead to increased reports of pursuit MAE. A reference signal is not supported as the MAE reports were observed to decrease in this condition. The extra-retinal signal and the reference signal would be of the same magnitude for the condition containing smooth pursuit over a stationary background (-8, 8). Both conditions with the background moving in the opposite direction to pursuit resulted in very few MAE reports. For the two conditions with background motion in the same direction as pursuit [(8, 8); (8, 16)], a reference signal would predict a reduction in the magnitude from the (-8, 8) condition. The MAE reports suggest that the pursuit eye movement adapts strongly for these conditions.

Since the retinal motion was manipulated to the extent that the background moved in the same direction as pursuit, the prediction made by a reference signal model could be either one of no change (Brenner and van den Berg, 1994), or a decrease in magnitude (extending the predictions made by Haarmeier et al, 2001), between the (8, 8) and (16, 8) conditions. This would depend on how the visual system interpreted retinal motion, in relation to an eye movement in the same direction. However, the results do not support either reference signal model, with a large increase in MAE reports observed for the two conditions. Assuming that the eye movement was the same in each condition, these results would not be predicted using a classical model either. However, as described below, the properties of the eye movement differ in line with the properties of the MAE.

The four conditions on the right of Figure 3.3 show the results for adaptation without eye movement. Recall that these conditions were designed to test for the existence of non-retinotopic MAEs which could be induced by peripheral retinal motion adaptation. Phantom MAE would be in the opposite direction to the adapting retinal motion, whilst induced MAE would be in the same direction. However, in the four fixation conditions illusory motion was reported infrequently. This suggests that non-retinotopic adaptation cannot account for the results of the pursuit conditions. The results for fixation adaptation do show some consistent reporting in the direction data but this doesn't seem to be predicted by either of the non-retinotopic MAEs considered. If they were responsible, then two of the fixation conditions should have resulted in upward MAE and two in downward MAE. This is not the pattern seen. Experiment 4 therefore seems to have successfully isolated the pursuit MAE. The preponderance of up directions in the fixation conditions is indicative of a response bias.

Perceived Speed

Figure 3.4 shows perceived MAE speeds, with the results for the four pursuit adaptation conditions again shown on the left. The increase for the reported perceived speeds in the conditions with positive retinal motion corresponds with the increased MAE reports in Figure 3.3. If retinal feedback were to influence the pursuit speed estimate via a reference signal, the conditions in which fast MAE were reported here should have instead resulted in the slowest MAE. As the gain of a reference signal is altered to maintain the balance between retinal motion and the eye movement estimate, then these conditions should again have reported the opposite effect to that observed. Excess negative retinal motion did not result in faster pursuit MAE (-16, 8) and positive retinal motions did not result in slower MAE [(8, 8), (16, 8)].

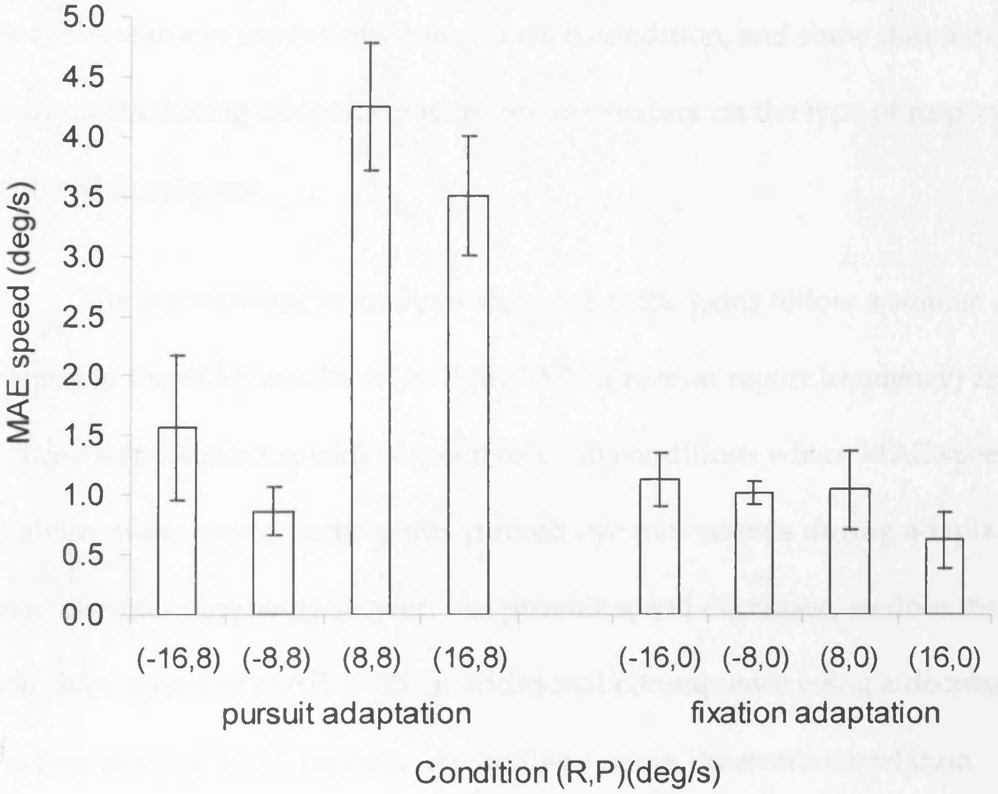

Figure 3.4: Average MAE speed. The reported MAE speeds follow a similar pattern to the report frequency shown in figure 1. Error bars indicate ±1 standard error.

As the pursuit component of the classical model is based on a purely extra-retinal signal it predicts no change in MAE visibility or speed across conditions given similar adapting eye movements. The speed and frequency data show that there are considerable changes between the conditions. The classical model requires similar changes to the eye movements during the adaptation phase.

Eye Movements

The speed of the physical smooth pursuit eye movements are illustrated in figure 3.5 (Direction trials) and Figure 3.6 (Speed trials). Both plot the mean eye movement gain for each condition, and show that the eye movements during adaptation were not dependant on the type of response required during test.

The eye movement analysis shows that the gains follow a similar pattern to the MAE results from figure 3.3 (direction report frequency) and figure 3.4 (perceived speed) respectively. In conditions where MAE speed or visibility were lower, participants pursuit eye movements during adaptation were also comparatively slower. As pursuit speed decreases, so does the perceived speed of MAE, with an additional consequence being a decrease in the frequency of MAE reports. An analysis using Pearson's correlation coefficient confirmed a significant relationship between the eye movement gain during adaptation and the perceived speed of the MAE ($r(42)=0.45$, $p<0.01$).

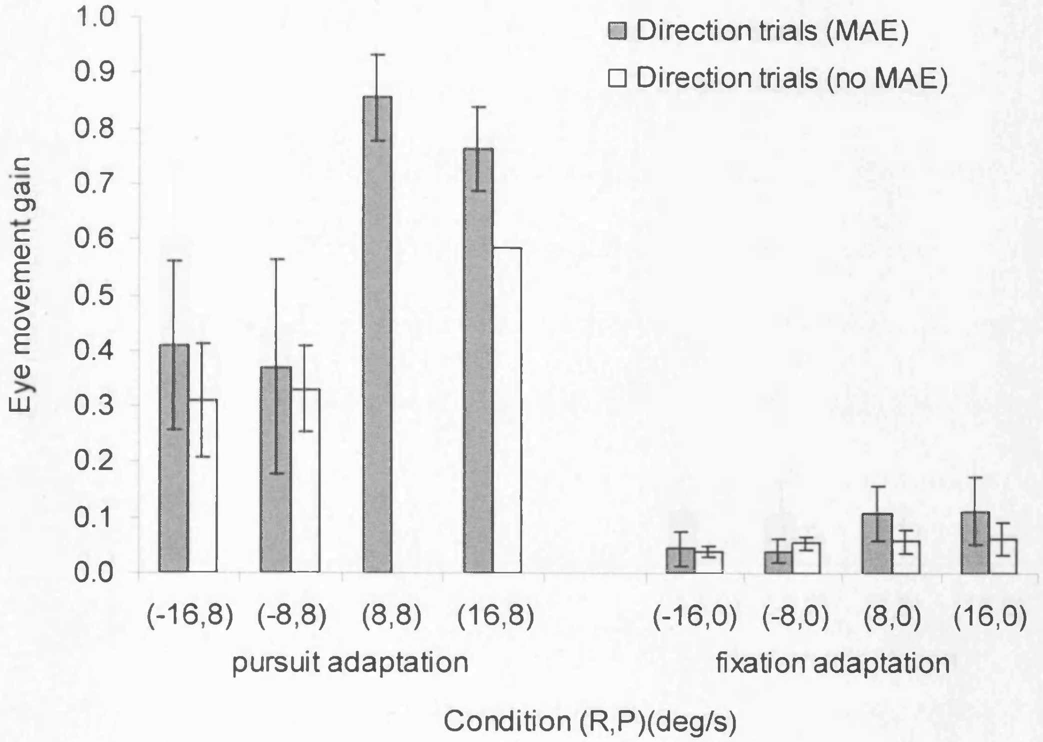

Figure 3.5: Mean eye movement gains during MAE direction trials. For the (8, 8) condition all participants reported an MAE, similarly, for the (8, 16) condition only one participant reported no MAE.

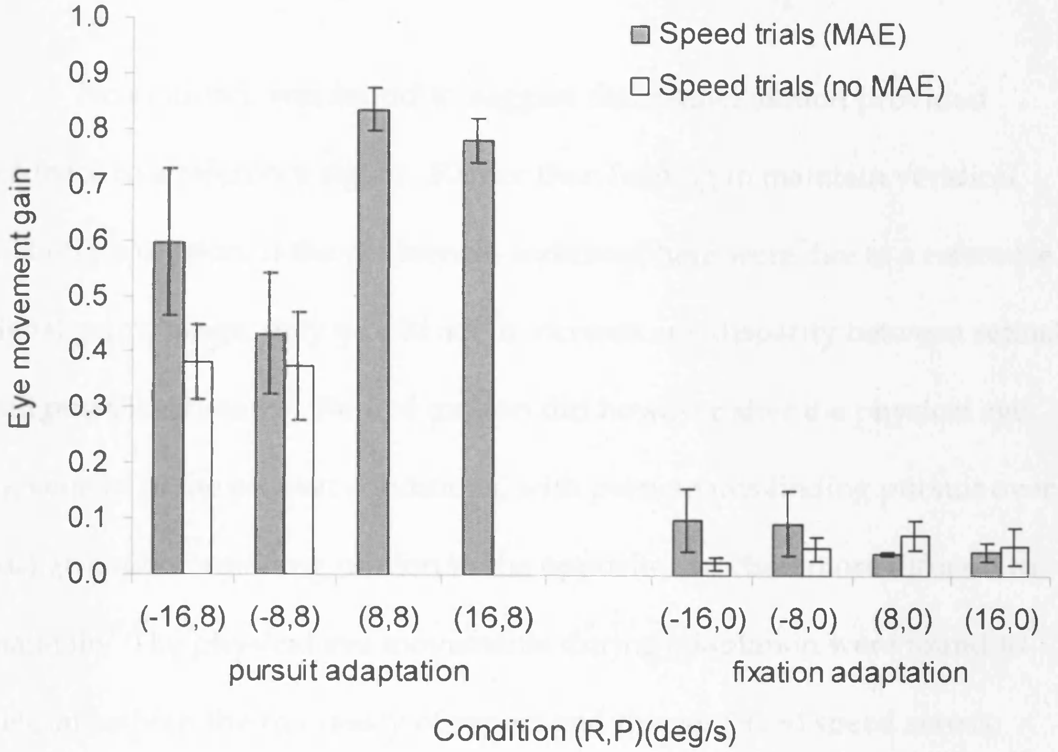

Figure 3.6: Mean eye movement gains during MAE speed trials.

Additionally, the trials in which no MAE were reported had significantly slower adaptation phase eye movements (M=2.6, SD=1.5) than for those in which MAE were witnessed (M=5.0, SD=1.8); (t(38) = 4.3, $p < 0.01$). High gains were recorded in the conditions with positive retinal motion that reported consistent MAE.

The eye remained largely stationary for the test phase in all conditions. The largest mean eye movement was 0.14 deg/s (gain = 0.02) in the (-8, 8) test. All other test phases had an average eye movement speed below 0.1 deg/s.

Summary

No evidence was found to suggest that retinal motion provided feedback to a reference signal. Rather than helping to maintain veridical motion perception, if the differences indicated here were due to a reference signal gain change, they would act to increase any disparity between retinal and pursuit estimates. Retinal motion did however alter the physical eye movement in the pursuit conditions, with participants finding pursuit over backgrounds containing motion in the opposite direction more difficult to maintain. The physical eye movements during adaptation were found to determine both the frequency of report and the perceived speed across conditions. The results support an extra-retinal account of the pursuit MAE.

The results indicate a large difference in the reported pursuit MAE characteristics between the (-8, 8) and the (8, 8) conditions. In order to examine the area in which these differences occurred, the range of adaptation speeds are changed for Experiment 5.

Speed and direction were collected separately in the current experiment. This meant that speeds reported for the MAE in the direction opposite to pursuit could not be differentiated from those reported for MAE in the same direction as pursuit because judgements of speed and direction could not be related on a trial-by-trial basis. The upward MAE are unlikely to have arisen from a compelling percept of illusory motion, given the consistent direction of smooth pursuit during adaptation. The perceived speeds reported in such trials were likely to be slower. Since upward MAE were only reported infrequently, the proposed effect on speed data may have resulted in a small reduction in the reported speeds for Experiment 4. Experiment 5 collected the speed and direction data at the end of every trial.

Experiment 5

Experiment 5 examines the differences between the MAE properties reported in Experiment 4 across a reduced range of retinal motions. Participants were also required to report both the speed and direction of MAE in the same trial. Experiment 5 otherwise replicates Experiment 4.

Method

Participants

Sixteen undergraduate psychology students at Cardiff University participated. As one participant only reported one weak MAE in one condition and none in the others, an additional participant was recruited to replace them.

Stimuli and experimental design

Except for a change in the range of adapting motions, the adapting stimuli and test were generated in the same manner as Experiment 4. The adapting motions for pursuit conditions were (R, P) = (-8, 8), (-4, 8), (0, 8), (4, 8) or (8, 8). The fixation conditions contained equivalent retinal motion.

Procedure

Before the main trials, direction and speed calibrations for each participant were completed with real screen motion as before. Whilst speed calibration was again limited to 180°, the physical constraint on rotation of the potentiometer bar was then removed in the main experiment so that speed and direction could be reported within the same trials. At the end of every test phase participants were required to indicate the speed of MAE as per experiment one. Then, following a mouse click, a new screen with two arrows (indicating up or down) prompted participants to report the direction of the MAE whose speed they had just given. All other details were the same as the first experiment.

Results and Conclusions

Perceived direction

Figure 3.7 shows the direction and frequency of MAE reports for the new range of adaptation speeds, employing the same format as for Figure 3.3. The majority of MAE reports for the pursuit conditions were opposite to the pursuit eye movement during adaptation. A similar frequency of MAE reporting followed adaptation to retinal motions within the range -4deg/s to +8deg/s. As in Experiment 4, the (-8, 8) condition resulted in a reduced number of MAE, with MAE reports decreasing by just under a factor of 2 compared to the other pursuit conditions.

The results for the fixation conditions again showed little evidence of phantom aftereffects or induced motion MAE. There were infrequent MAE reports following purely retinal adaptation, many of which had incorrect direction reports, again suggesting little influence of both phantom MAE and induced motion MAE. The perceived directions reported seem to reflect a similar response bias to that found in Experiment 4. The response bias was confirmed by the inclusion of a (0, 0) condition for which the adaptation phase consisted of fixating a stationary pattern. This should have produced no motion adaptation but the results show MAE directions and report frequencies similar to the other fixation conditions.

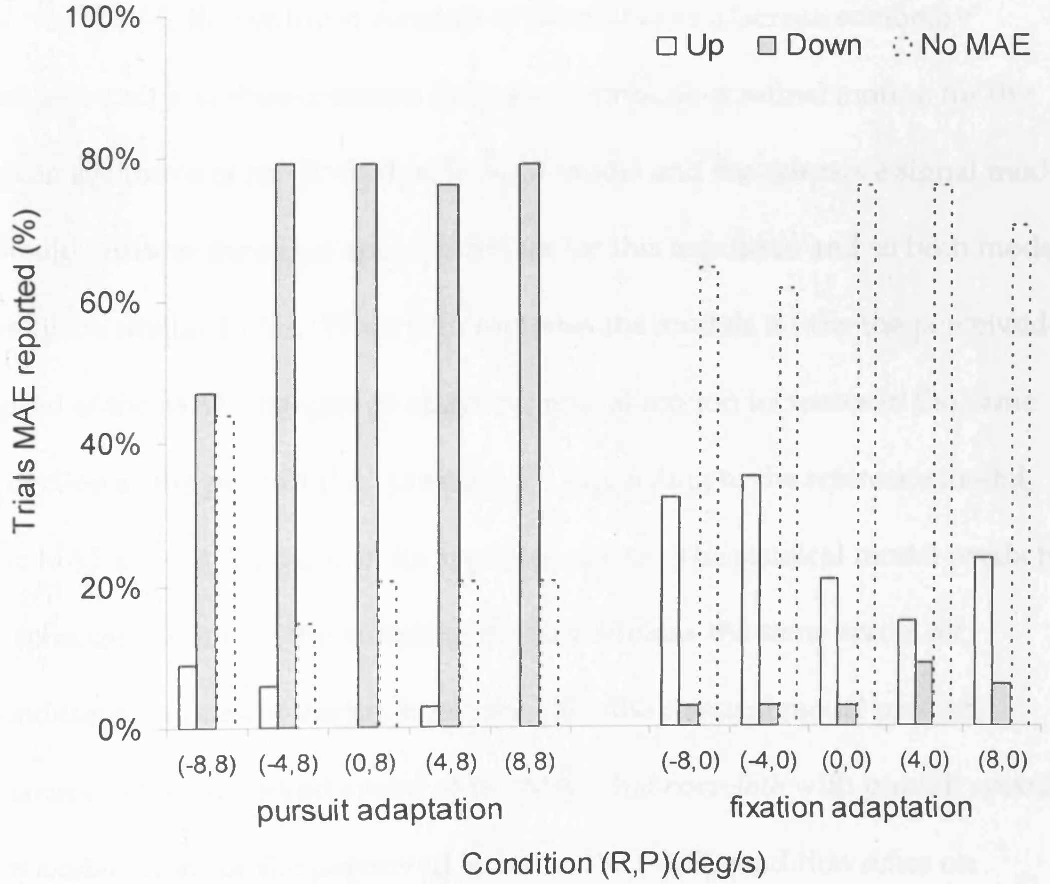

Figure 3.7: Percentage of trials reporting an MAE, and their direction.

Perceived Speed

In Figure 3.8 the speed of MAE for the pursuit adaptation, in the expected direction (down), can be seen to increase with the speed of retinal motion adaptation. A repeated measures one-way ANOVA tested for differences in the reported speeds of the MAE across the pursuit conditions. The analysis revealed significant differences, $F(1, 13) = 24.9$, $p < 0.01$. Bonferroni corrected post hoc tests showed that the (-8, 8) condition differed significantly from the (4, 8) and (8, 8) conditions ($M = -1.93$, $M = -1.89$ respectively, $p < 0.05$). No significant differences were found between the other conditions.

The (-8, 8) condition consists of pursuit over a 'screen stationary' background, and thus contains the correct amount of retinal motion for the given eye movement. Both the classical model and the reference signal model should indicate the same speed estimate for this condition and so both models predict a similar MAE. What differentiates the models is how the perceived speed of the MAE changes as adapting retinal motion increases in the same direction as the pursuit (i.e. positive R). According to the reference model, the MAE should decrease in its apparent speed. The classical model predicts no change, assuming the adapting pursuit remains the same across all conditions. If pursuit varies, however, then the classical model predicts changes to the perceived speed of the MAE that correlate with pursuit speed. An explanation for the perceived speed in the (-8, 8) condition relies on changes to the physical eye movement. The other four conditions show no significant differences in speed or eye movement.

The fixation conditions (Figure 3.8) suggests that MAE speeds depend on the speed and direction of adapting retinal motion. The MAEs were consistently perceived as faster in the opposite direction to the adapting retinal motion. This suggests some non-retinotopic adaptation. However, similar MAE reports were obtained in the (0, 0) baseline condition, which as pointed out above, should have produced no MAE. This questions whether the fixation conditions offer any compelling evidence of non-retinotopic motion adaptation overall, especially if combined with the low report frequencies discussed above.

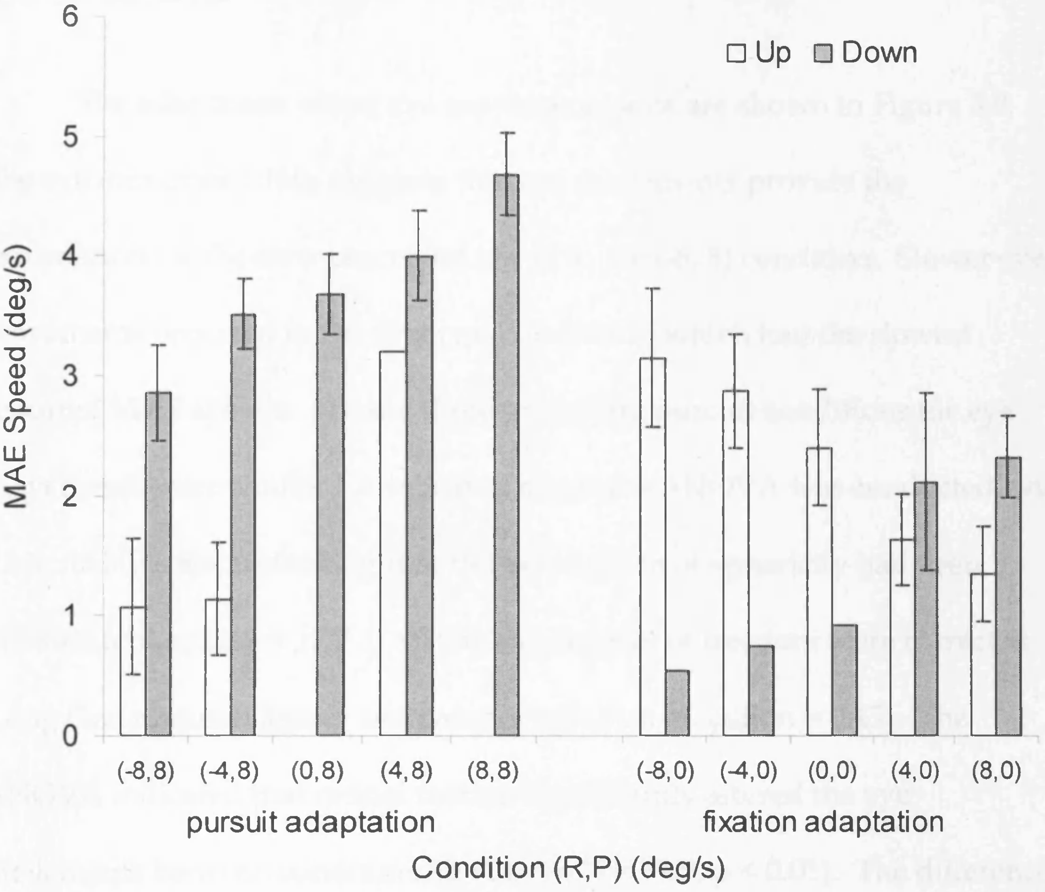

Figure 3.8: MAE speed for the five pursuit conditions (left hand bars) and the five eye stationary conditions (right hand bars). The grey bars represent the reported mean speed for downward MAE whilst white bars are the mean speeds for upward MAE reports

Eye movements

The adaptation phase eye movement gains are shown in Figure 3.9. The eye movement data suggests that eye movements provide the explanation for the slow perceived speed in the (-8, 8) condition. Slower eye movements occurred in the first two conditions, which had the slowest reported MAE speeds. For the three remaining pursuit conditions the eye movements were similar. A repeated measures ANOVA was conducted, with a Maunchly's test indicating that the assumption of sphericity had been violated (chi-square = 17.7, p <0.05), the degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity (epsilon = 0.45). The ANOVA indicated that retinal motion significantly altered the eye movements between conditions (F (1.8, 18.1) = 31.9, p < 0.01). The difference in speed between the conditions with retinal motions between 0deg/s and +8deg/s were not significant (all p>0.9). The two conditions with negative retinal motions produced significantly different eye movements from each of the other four conditions (for all 8 comparisons, p<0.02). These results can support the classical model. Adaptation phase pursuit eye movements are again altered as a result of background motion in the opposite direction. The significantly reduced eye movement gains in the negative retinal motion conditions alter the likelihood of an MAE being experienced. This is detailed further below, and the effect of eye movement gain on reported MAE speed is illustrated by the line fit to the data in figure 3.10. It can be noted that for few MAE are reported when eye movement gain falls below 0.5.

The eye movement recordings indicated that the mean eye speeds did not exceed 0.2 deg/s (gain < 0.03) in any fixation condition. An analysis of the eye movements during the test phase, found that the eyes remained largely stationary in all conditions. The largest mean eye movement was 0.31 deg/s (gain = 0.04) in the (8, 0) test.

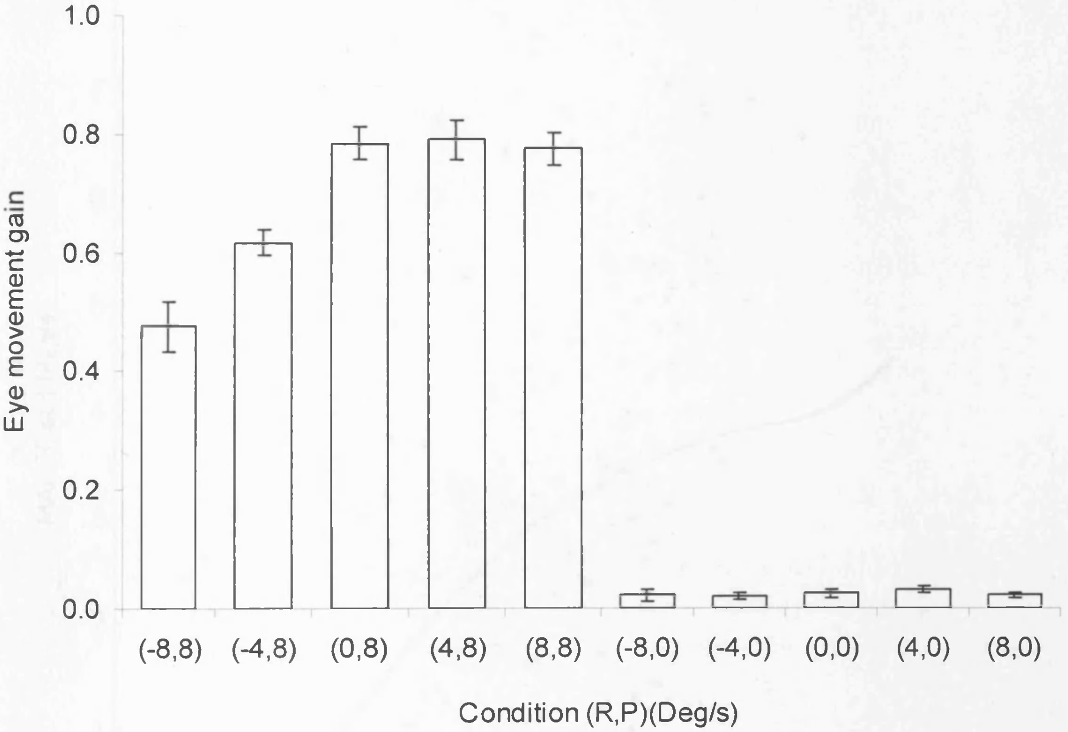

Figure 3.9: Eye movement gains for the 'down only' MAE, Experiment 5. Error bars represent ±1SE.

Figure 3.10 plots the MAE speeds against physical eye movement gains for the pursuit conditions. It can be seen that MAE reports did not occur at eye movement gains below 0.4. In order to elicit an MAE, this suggests that either the eye movement gain needs to exceed 0.4, or that eye speed needs to be greater than 3.2deg/s. The solid line on Figure 3.10 indicates a Gaussian kernel estimate of MAE speed as a function of the eye movement gain. The width of the Gaussian Kernel (SD = 0.139) was determined using a leave-one-out cross-validation technique (Hastie, Tibshirani, Friedman, 2001; Ludwig, Mildinhall, & Gilchrist, 2007).

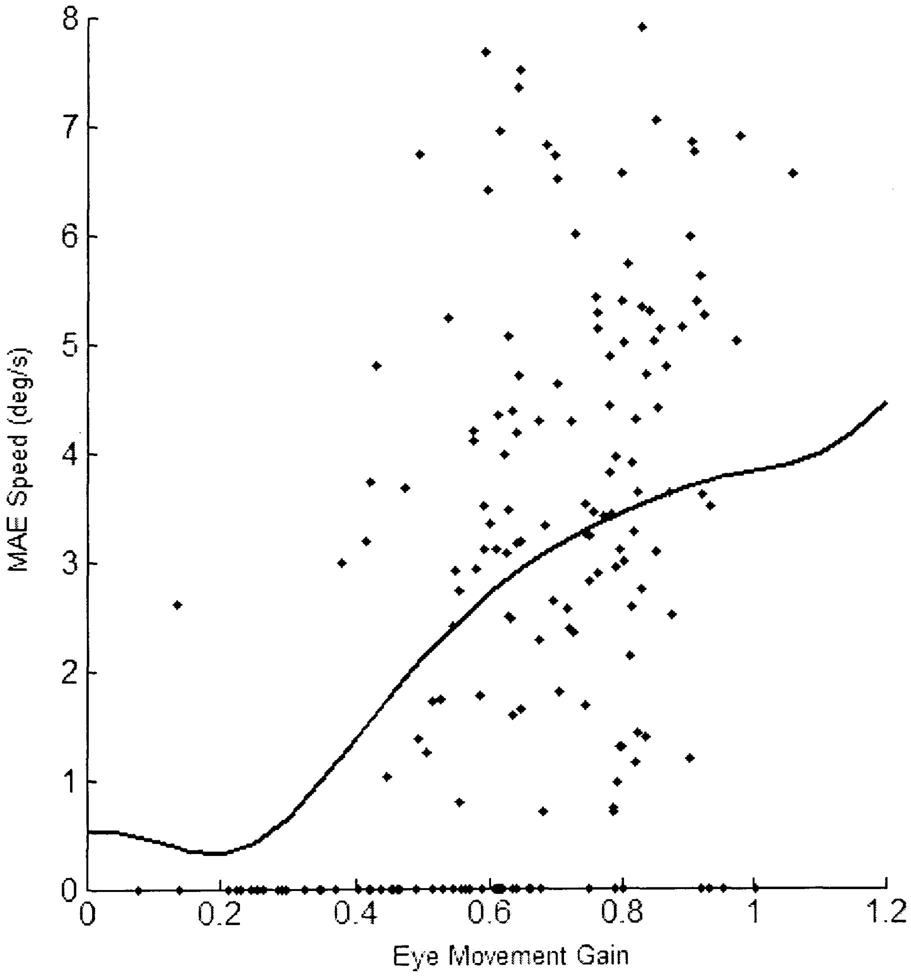

Figure 3.10: Scatter plot showing the eye movement gain and raw MAE speed data. Solid line indicates kernel estimate of MAE speed as a function of eye movement gain using a Gaussian Kernel (SD = 0.14).

The slow physical eye movements that were recorded for the (-8, 8) condition resulted in the lower MAE report frequency as reported. The eye gain for pursuit in this condition was only just above 0.4 with a mean of 0.48 for seen MAE. Whilst eye movements in the (-4, 8) condition were slowed by retinal motion that opposed pursuit, the number of MAE reports were similar to those reported in the other three conditions. The mean gain for reported MAE in the (-4, 8) condition was 0.62, thus the eye movement velocities were still within a range capable of successfully generating MAE.

Summary

The recorded properties of the MAE correlate with the pursuit eye movement speeds. The results provide evidence that the MAE following adaptation to collinear retinal motion and smooth pursuit eye movement are purely extra-retinal in origin when adaptation and test areas are spatially non-coincident. The results support the prediction of the classical model.

The reference signal model is not supported. When the background moved in the same direction as a given eye movement, the reference signal magnitude should decrease. When the background moved in the opposite direction to pursuit, the reference signal should have increased. The changes observed for the MAE are in the opposite direction.

The conditions in which eye movements varied also showed a change in the perceived speed of the MAE. In the three conditions with similar eye movements a (non-significant) increase in speeds was reported. This is again opposite to the pattern of MAE speed that a reference signal would predict.

There was no indication that a reference signal gain change altered the pursuit MAE in any condition.

Discussion

As discussed in the introduction, controls for retinal motion adaptation in previous studies have been insufficient (Freeman, 2007) and therefore a question has remained as to which model best accommodates the observed changes to perceived stability that follow adaptation. Recent papers have favoured different models (classical: Freeman, 2007; reference signal: Dash et al, 2009). The changes have been attributed to either separate retinal and extra-retinal signal adaptations or changes in the gain of a reference signal. This chapter approached the problem using an alternative adaptation paradigm, employing the MAE that follows repetitive smooth pursuit to examine the properties of the adapted pursuit estimate signal. The next chapter employs the paradigm from previous studies.

The novel methodological technique developed in this chapter involved the physical separation of the adapting pattern and test stimulus locations. This separation was designed to utilise the retinotopic nature of retinal motion adaptation. Retinotopic MAE are most often reported when a static test pattern is employed (Wohlgemuth, 1911; Sekuler and Pantle, 1967; Masland, 1969), although dynamic test stimuli can also demonstrate retinotopic adaptation (Knapen, Rolfs and Cavanagh, 2009). In the current chapter, removing the influence of adapted retinal motion sensors, whilst additionally using a single-point static test, allowed an investigation into the pursuit eye movement estimate in isolation. Given the same eye movements across conditions, a reference signal would be altered through retinal feedback, whilst a purely extra-retinal signal would result in an MAE whose properties are constant.

The properties of the reported MAE were found to alter across conditions in both experiments. However, in no condition could these changes easily be attributed to a reference signal. The conditions resulting in infrequently reported and low speed MAE were the conditions for which a reference signal should have been largest. The two conditions producing weak MAE contained retinal motion in the opposite direction to the pursuit eye movement. The (-16, 8) condition in Experiment 4 represented a situation for which a 'reference signal too low' would be indicated, using the terminology of Haarmeier et al (2001). The (-8, 8) condition should result in an unchanged reference signal, since the condition featured the correct amount of reafference during the eye movement. Conversely, the conditions representing 'reference signal too high', in which afferent feedback would lead to a reduction in the magnitude of a reference signal, provided frequently-reported MAEs with higher perceived speeds. An alternative reference signal model suggests no reference signal gain change when the velocity of retinal motion is greater than pursuit (Brenner & van de Berg, 1994). No change occurs under these conditions since retinal motion would be deemed an unreliable indicator of eye movement speed. The increases found for MAE speed, with increasingly positive retinal motion, do not conform to the predictions made by reference signal models.

Whilst a reference signal model predicted the opposite change to that observed, the classical model predicted no change in MAE given similar eye movements across conditions. The eye movement analyses showed that opposing retinal motion had a profound effect on the physical movement of the eye during adaptation. Studies have previously reported reduced pursuit gain for eye movements over textured backgrounds, with eye movement reductions of around 10% horizontally and 20% vertically in humans (Collewijn and Tamminga, 1984; Masson, Proteau & Mestre, 1995) with similar deficits also found in monkeys (Ilg, Bremmer & Hoffman, 1993). The detrimental effect of a background on pursuit is further increased when the background drifts. The reduction in eye movement gain is then dependent on the relative velocities of background and target (Kodaka, Miura, Suehiro, Takemura & Kawano, 2004; Worfolk & Barnes, 1992). These findings agree with the eye movement analysis of the current chapter, eye movement gains were reduced for smooth pursuit when the retinal motion pattern was in the opposite direction. Backgrounds moving in the same direction as pursuit have also been shown to increase the pursuit speed (Suehiro, Miura, Kodaka, Inoue, Takemura & Kawano, 1999; Lindner, Schwarz & Ilg 2001). Whilst the fastest smooth pursuit eye movements were reported for positive retinal motions, the advantages of a background moving in the same direction to pursuit seemed limited. The changes in eye movement matched changes in both the frequency and speed reports of the MAE across conditions. Large changes to the pursuit gain, when the background motion is manipulated, are thought to demonstrate a direction-specificity of optokinetic reflex suppression (Lindner & Ilg, 2006). Such a suggestion lends support to the optokinetic-potential model of Post and Liebowitz (1985). Post and Liebowitz suggested that retinal motion would change the extra-retinal output, due to competition between the reflexive (optokinetic nystagmus) and voluntary (smooth pursuit) eye movement systems.

It should be noted that for both the classical model and the reference signal model, a change to the physical eye movement would alter the internal estimate of pursuit. However, in Experiment 5, the mean MAE speeds increased across three conditions for which the adaptation phase eye movements were similar. Whilst this increase was not significant, a reference signal model would predict the opposite effect. Whilst the physical eye movements would alter the extra-retinal estimate in both signals, the additional influence of retinal motion inherent to reference signal models was again not indicated.

The fixation conditions provided evidence that non-coincident adaptation and test successfully reduced the potential for retinal motion adaptation. The fixation conditions in Experiment 4 revealed no evidence for retinal motion adaptation. The pattern of response in Experiment 5 is potentially open to more interpretation, for both the pursuit and the fixation conditions there is a pattern which superficially indicates non-retinotopic adaptation. In considering the bearing of this on the issues outlined in this chapter, we need to consider three findings. Firstly, the frequencies of MAE report in the fixation conditions were low. Secondly, the (0, 0) fixation condition produced similar MAE reports to the other fixation conditions despite a complete absence of adapting motions. Thirdly, the differences in speed were not significant. The weight of evidence therefore suggests that adaptation to retinal motion was largely retinotopic in nature for the stimuli used in this chapter. Furthermore, had weak non-retinotopic adaptation featured in the second experiment, this would not lead to a significant change in the conclusions when the direction of the effect are considered. A phantom MAE would easily be accommodated by the classical model, combining with the pursuit in a manner similar to that reported in chapter 2.

In summary, this chapter provides evidence that the MAE following repetitive eye movements, over a non-coincident background whose motion is manipulated, result in MAE whose origin is extra-retinal. Whilst eye movements are affected by the background, no evidence was found for a gain change to a reference signal. In order to further investigate the two competing models, the next chapter investigates perceived stability judgements when adaptation and test are again non-coincident. Changes to the Filehne illusion similar to those reported by Haarmeier et al would support a reference signal account. The placement of the test pattern in an area non-coincident to the adapting pattern should eliminate the influence of adapted retinal motion sensors. Unsuccessful measures to eliminate adaptation to retinal motion have led to the previously reported studies failing to differentiate between the two competing models. Since this chapter provides evidence that the size of the pursuit speed estimate remains unaltered by adaptation phase retinal motion, the prediction for the next chapter is that perceived stability judgements will not change as a result of the background motion during adaptation.

Chapter 4: Perceived stability following adaptation to simultaneous smooth pursuit eye movement and spatially non-coincident retinal motion.

Abstract

Comparing estimates of retinal motion and smooth pursuit helps compensate for the retinal effects of eye movement. Recent models claim that the pursuit estimate is based on a reference signal that combines retinal and extra-retinal motion components. Part of the evidence on which this claim is based involves showing changes to perceived stability following simultaneous adaptation to pursuit and retinal motion. However, this change could equally be accounted for in a classical model via adaptation of the inputs, such as changes to the retinal motion sensing of speed (the velocity aftereffect). In the current chapter these two types of model were tested using retinal motion adaptation that was spatially non-coincident with the test stimulus, thus ruling out any changes in perceived stability due to local retinal motion adaptation. In Experiment 6, observers simultaneously adapted to a pursuit target moving along a central blank strip and flanking retinal motion. Pursuit and retinal motion executed left-right triangle waves, either in-phase (pursuit and retinal motion in the same direction), or 180 degrees out-of-phase (pursuit and retinal motion in opposite directions). Test stimuli consisted of dot stimulus pursuit over a background, all presented within the strip. Perceived stability was assessed by adjusting the background motion using interleaved staircases to yield the point-of-subjective-stationarity (PSS). The

results showed significant changes to perceived stability, with both in-phase and out-of-phase conditions altered so that the PSS described an inverted U-shaped function symmetrically about R = 0 deg/s. To explain these results using a reference signal the retinal feedback would need to indicate only discrepancies in the speed, and not the velocity, of any pursuit estimate. However, the classical model would require non-coincidental retinal adaptation to induce a retinal VAE in the central test area. Two control experiments failed to find evidence for a retinal VAE, and therefore failed to support the classical model. An additional experiment demonstrates an additional change is required to the reference signal model, one which requires motion at specific background locations. Overall it is concluded that a modified reference signal model can account for the observed changes in perceived stability.

Introduction

The last chapter found no evidence that MAE following adaptation to simultaneous pursuit and retinal motion resulted from the changes to a reference signal. Whilst the MAE varied as adapting retinal motion was manipulated, the reported changes mirrored changes to the physical eye movements. It was concluded that the MAE found in chapter 3 was extra-retinal in origin, and therefore supported the classical model. Given that the use of non-coincident retinal motion adaptation proved to be a successful way of excluding local retinal motion sensor adaptation in the previous chapter, a natural progression was to employ the same type of adaptation to investigate the changes in perceived stability reported by Haarmeier, Thier & colleagues (Haarmeier & Thier, 1996; Thier, Haarmeier, Chakraborty, Lindner & Tikhonov, 2001; Dash, Dicke, Chakraborty, Haarmeier, Thier, 2009).

As discussed in Chapter 1, Haarmeier, Thier and colleagues used the changes in perceived stability brought about by simultaneous adaptation to pursuit and retinal motion as providing support for a reference signal (Thier, Haarmeier, Chakraborty, Lindner & Tikhonov, 2001). Adaptation and test trials were intermixed. Observers judged the motion of a background stimulus whilst making a pursuit in all trials. The test trials were used to determine the background motion that appeared to be stationary to the observer during pursuit. In the absence of the adaptation, Haarmeier et al found observers reported that the background appeared to move against the eye movement. This well-established finding is the Filehne illusion (Mack and Herman, 1973, 1978; Freeman, Crowell & Banks, 2000). In the adaptation conditions, the Filehne illusion changed. The adapting retinal motion was manipulated so that it did not correspond with pursuit over a stationary background. The background was moved either in the same direction as pursuit or in the opposite direction to pursuit. These conditions were termed 'reference signal too high' and 'reference signal too low' respectively (Haarmeier et al, 2001). When the background moved in the same direction as a given eye movement the Filehne illusion increased. When the background moved in the opposite direction to pursuit the size of the Filehne illusion reduced and even inverted. Haarmeier et al attributed these effects to changes in the observer's estimate of eye velocity, brought about by the influence of the adapting retinal motion on the extra-retinal signal.

Haarmeier et al (2001) argued that motion balancing was critical to explaining the effects they found. In their experiments, the adaptation consisted of back and forth eye movements across a moving background. In all conditions, the motions were therefore 'balanced'. This means that in any one adaptation run, observers made both leftward and rightward pursuit, and simultaneously were exposed to rightward and leftward retinal motion. They showed that motion balancing produced no MAE in stationary stimuli viewed without eye movement. They argued that this demonstrated that the changes in perceived stability could not have arisen from adaptation of retinal motion sensors, as would need to be the case for an explanation based on the classical model (recall that the results of Chapter 2 do not support the idea that adaptation occurs at the stage where retinal motion and pursuit estimates are combined, but the data there could not differentiate between adaptation of pursuit estimates based on reference signals or purely extra-retinal signals). The problem with Haarmeier et al's argument is that it overlooks the fact that to judge perceived stability, the observer needs to compare two motion estimates. Hence what one needs to know is how simultaneous motion adaptation affects speed estimates, be they retinal, extra-retinal or reference, as opposed to how static objects containing no physical motion appear to move. Whilst adaptation that is motion balanced would produce no MAE in a stationary test, it does not follow that a test involving motion will remain unaffected by previous motion adaptation for the following reasons.

When a test pattern contains motion, it can be subject to a Velocity Aftereffect (VAE). The VAE results in an apparent velocity change for a moving stimulus following adaptation (Thompson, 1981). Motion balancing is likely to be ineffective, as the velocity aftereffect has been found for tests that move either in the same or opposite direction to the adapting motion (Thompson, 1981; Smith and Hammond, 1985). Whilst motion balancing results in no net adapting motion, this does not mean that the sensors remain unadapted. Mechanisms sensitive to both the adapting directions become adapted. The absence of MAE is because the net effect cancels; but the test stimulus used to investigate the VAE probes only one set of sensors, in one direction. The same is true for the test used to probe perceived stability, because the retinal motion is in one direction and hence probes only one set of sensors. The VAE is therefore an important consideration in understanding how simultaneous adaptation, motion-balanced or otherwise, affects perceived stability. Freeman (2007) demonstrated that perceived stability judgements, given a motion balanced stimulus, are subject to VAE. The VAE was found to alter the perceived speed of the background motion whilst similar changes to the perceived speed of the eye movement were also inferred (Freeman, 2007). His model combines an extra-retinal VAE with a retinal VAE in an antagonistic relationship. Note that this antagonistic relationship arises because of the geometry of the situation (ie. opposite component motions), as opposed to being intrinsic to the compensation mechanism itself.

Freeman (2007) showed that retinal adaptation decreases the PSS whilst extra-retinal adaptation increases it. Hence a classical model can account for the modification of the Filehne illusion reported by Haarmeier et al, without the need to invoke a reference signal. This does not mean that a reference signal could not explain the data; Freeman's argument is rather one of parsimony. But since each model remains plausible, there is clearly a need to differentiate between them and so the experiments in the current chapter aim to test both.

As Haarmeier and colleagues argue, an approach that excludes retinal sensor adaptation would allow the two models to be differentiated. The experiments presented here therefore use the adaptation procedure used in the previous chapter, where the retinotopic nature of retinal motion adaptation was shown to be a useful tool. The format of the stimuli ensured that the motion of the adapting background remained spatially non-coincident with the test background (Figure 4.2 & Figure 4.8). Successfully eliminating the influence of retinal motion adaptation during a perceived stability judgement allows the influence of background motion on the pursuit estimate to be examined in isolation.

Predictions from the two models

The predictions for classical and reference signal models for the conditions investigated in Experiment 6 are shown in Figure 4.1. The classical model predicts that the PSS will not change as a result of manipulating the adaptation background, so long as the eye movements are similar across conditions. This assumes that any retinal adaptation effects are entirely retinotopic. In the experiment the pursuit adaptation remained fixed, so the classical model predicts the PSS should rise from baseline and then remain constant as shown in Figure 4.1.

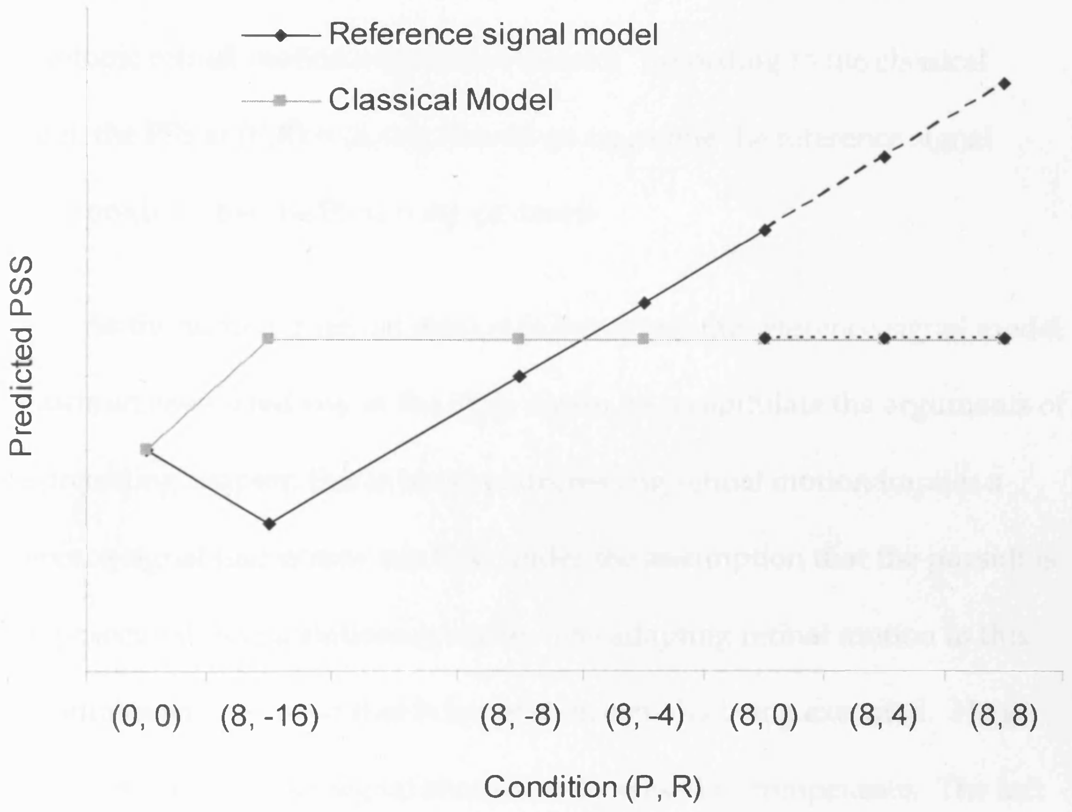

Figure 4.1: Predictions for the point of subjective stationarity as adapting retinal motion is manipulated. When eye movement remains constant, the classical model predicts no modification of perceived stability as adaptation of R' is retinotopic. The reference signal is dependant on the global retinal motion, feedback about the background motion results in a reference signal gain change and predicts a monotonic increase for the PSS across R'.

A reference signal, on the other hand, should be modulated by retinal feedback as discussed in the preceding chapter and the General Introduction. When the retinal motion is greater than expected for pursuit over a static scene (condition (P, R) = (8, -16)), the gain of the reference signal should be increased to compensate because the adapting retinal motion mimics what would happen if the eye had moved faster. Hence the PSS should lower and can go negative, in accord with the results of Haarmeier et al (2001). This highlights the first key difference between the two models when non-retinotopic retinal motion adaptation is used. According to the classical model, the PSS at (P,R) = (8,-16) should go up, while the reference signal model predicts that the PS should go down.

As the adapting retinal motion is increased, the reference signal model predicts an associated rise in the PSS. Again, to recapitulate the arguments of the preceding chapter, this is because decreasing retinal motion implies a reference signal that is now too low, under the assumption that the pursuit is being executed over a stationary scene. The adapting retinal motion in this case mimics an eye speed that is lower than actually being executed. Hence the gain of the reference signal should be decreased to compensate. The fact that the reference-signal model predicts a rise in PSS, and the classical model does not, is a second differentiating feature between the two models.

A third differentiation occurs for the condition (P, R) = (8, -8). This condition corresponds to adapting to a pursuit eye movement made over a static background. According to the reference-signal model, there should be no need to adjust the gain of the reference signal, so the PSS should be the same as baseline. Conversely, the PSS should remain above baseline according to the classical model.

The predictions of the reference signal model when the adapting retinal motion is in the same direction as the pursuit are unclear, mainly because this represents the situation in which the direction of retinal motion does not correspond to pursuit over a static scene, whatever its speed. One possibility it that the reference signals gain continues to be turned down so that the PSS continues to rise. Another possibility is that the retinal motion is ignored by the mechanism in the reference signal that correlates eye movement and reafference. Brenner & van den Berg (1994) suggest that when retinal motion is in the same direction as the eye movement the reference signal relies on extra-retinal information only. Hence, the PSS should follow the predictions of the classical model when $R > 0$.

Experiment 6

Introduction

The experiment was designed to take advantage of the retinotopic nature of retinal motion adaptation. As discussed, when retinal motion adaptation can be successfully excluded the two models make differing predictions about the modification of the Filehne illusion.

Method

Participants

Four adults with normal or corrected to normal vision participated, including the author and the thesis supervisor. The remaining two participants were naïve to the experimental hypothesis and financially rewarded for their participation. Informed written consent was gained and a full debrief followed the experiment.

Stimuli and Procedure

The stimuli were generated, displayed and viewed using the same methods as Chapter 3. The adaptation and test stimuli consisted of dim red dots (0.1° radii) presented at low luminance. The adaptation and test stimuli were designed so that retinal motion during the adaptation phase would be spatially non-coincident with the test stimulus (Figure 4.2). The background flanked the pursuit target and was constrained within two rectangular areas (16° wide, 8° high) symmetrically extending from 4.5° above and below the pursuit target. This created a 9° homogenous black central area around the pursuit target in which the test background would later be displayed. The invisible windows, through which the background was displayed, moved with the pursuit target. This ensured that the retinal location of the background remained consistent during pursuit.

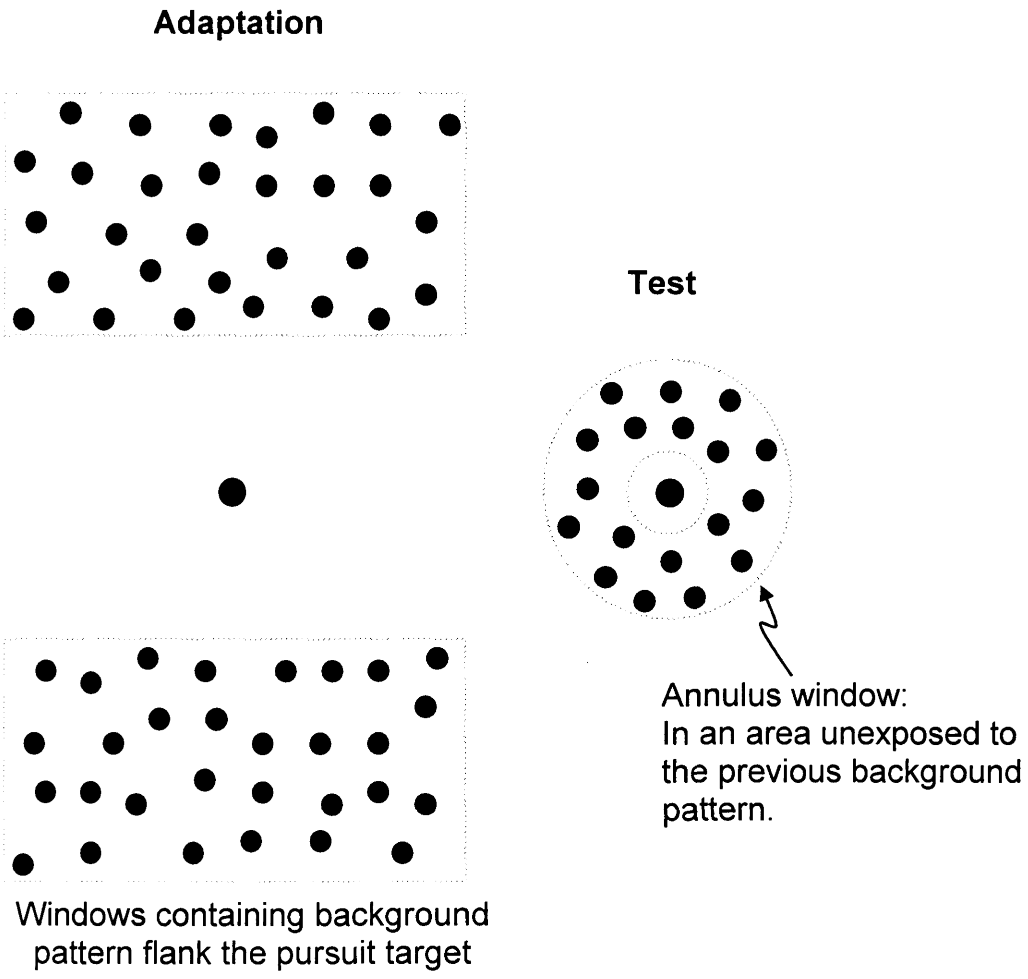

Figure 4.2: Representation of the Stimulus Configuration. Dotted lines represent the invisible windows through which the dot patterns were displayed. The windows and the pursuit target moved together. Adaptation dot pattern motion was determined by the condition, the test background dot pattern was adjusted via a staircase.

Figure 4.3 shows a schematic illustrating the motion of the adapting stimuli. A single target point performed two second sweeps to the left and then right (triangle wave at 8°/s, period 4s). In the middle of each sweep, the adaptation background (a random dot pattern with a constant density of 1 dot/deg) was displayed for 400ms with an additional 100ms ramp each side (shown as dot-dash rectangles). The stimulus allowed for the simultaneous adaptation of pursuit and retinal motion.

For the six experimental conditions the adaptation background would move, with or against the pursuit target. The adaptation velocities are represented using the notation (P, R). As in the previous chapter P and R refer to pursuit and retinal motion respectively, in deg/s. The six experimental conditions for the first experiment were (8, -16), (8, -8), (8, -4), (8, 0), (8, 4) or (8, 8). Negative velocities refer to retinal motion in the opposite direction to pursuit. The speed of background motion was constant within each condition; the pursuit target had a constant 8 deg/s speed across conditions. Figure 4.3 includes representations of two adaptation conditions [(8, -8), (8, 4)]. The initial adaptation phase lasted 60 seconds, an initial 52 seconds of motion was followed by an 8 second top-up. A short but perceptible gap occurred between the initial adaptation phase and the first top-up stimulus, which served to prepare participants for the test phase. An 8 second top-up then preceded every trial. During the adaptation, top-up and test phases, all participants were required to visually pursue the target point accurately.

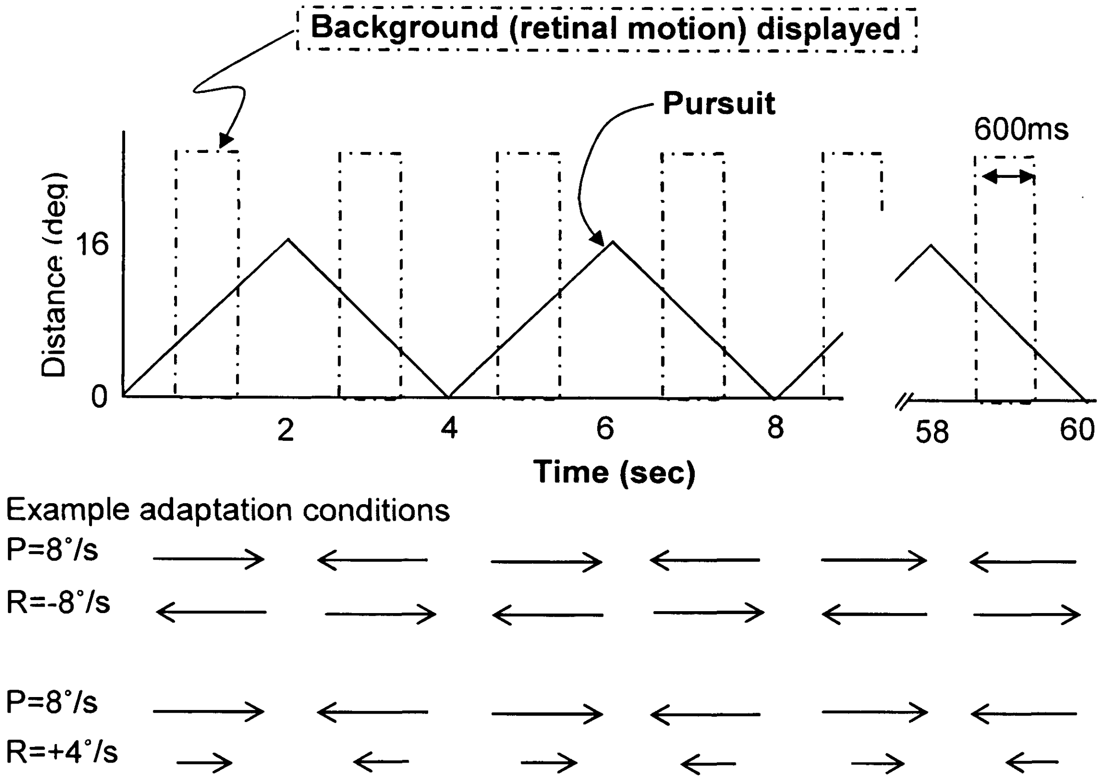

Figure 4.3: This schematic represents smooth pursuit and retinal adaptation, overall motion of the adaptation phase contains no net motion direction due to 'motion-balancing'. Observers simultaneously adapted to a pursuit target and retinal motion. Pursuit (continuous) and retinal motion (discontinuous) execute left-right triangle waves, either in-phase or out-of-phase. The example adaptation conditions show (8, -8) and (8, 4). Positive retinal motion indicates that the background is moving with the pursuit target.

A baseline condition was also included in which the adapting pattern was displayed, but contained no motion. This condition determined the baseline PSS for each participant. Participants were required to fixate a completely stationary pattern during adaptation and top-up. Whilst the fixation point was constantly visible, the background was displayed and removed with the same temporal frequency as during the six experimental conditions. The test phase followed an identical protocol to the other six conditions.

For the test, a fixation point would appear on the left or right of the screen. After one second the fixation point again became a pursuit target for two seconds, moving at 8 deg/s to either the right or the left. In the middle of this pursuit, a central background was displayed for 600ms, including a 200ms ramp. This test background was displayed in the previously blank central strip, in an area unexposed to the adaptation phase background motion. The background dot pattern was generated as for adaptation but placed around the pursuit target and constrained to an annulus window. The annulus window had an inner radius of 1° and an outer radius of 4° (Test pattern, Figure 4.2). The motion of the background was adjusted via a staircase procedure, described below. During the test, participants were required to judge whether the background was moving leftward or rightward, and to indicate the perceived direction of the background during pursuit via the mouse buttons. The next top-up trial would start immediately after test, and this continued until each staircase successfully terminated. Each of the seven conditions was presented in a random order. Two additional runs per participant were then completed in separate sessions.

Adaptive staircase procedure

Two independent interleaved staircases were employed. One staircase was assigned to leftward pursuit and one rightward. The starting value for each staircase was randomly designated to give a starting retinal motion for the background between -3 deg/s and -9 deg/s. For each trial, a staircase was chosen at random. The background motion on each trial of the staircase was determined by the participant's previous response. For each staircase the step size was 4° until the first reversal, 2° until the second reversal and thereafter a step size of 0.5° was implemented. The staircase terminated after ten reversals. The last eight reversals of each staircase were averaged to determine the threshold. Six thresholds were obtained per participant for each condition, these were then averaged. This method yields the point of subjective stationarity (PSS), at which the proportion of left and right judgements are equal. This procedure quantified the amount of motion required in a background for it to be perceived as stationary during smooth pursuit. Changes to the amount of motion required to null the Filehne illusion indicated the comparative size of the illusion across the various conditions.

Eye Movement recording and analysis

Eye movements were recorded and analysed as in Chapter 2, Experiment 3, except that a 150ms data segment was symmetrically removed around saccades and blinks.

Results and Conclusions

Eye movement analysis

The eye movement analysis was critical in providing an explanation of the results in Chapter 3. Eye movements could also provide an explanation for any results reported here. According to a classical model the extra-retinal signal correlates with eye movement speed. The extra-retinal signal also partially determines the size of a reference signal. It is therefore worth examining the eye movements, before considering the results in terms of the two models.

Figure 4.4 shows an example adaptation phase smooth pursuit eye movements recording, at 1000 Hz for the initial 52 seconds of adaptation. The top graph shows the motion-balanced triangle wave, as would be expected when accurate smooth pursuit of the target was maintained. The trace illustrates that the overall motion contains no net motion. Observers simultaneously adapted to a pursuit target and retinal motion. The pursuit target executed the continuous left-right triangle wave, evident from the eye movement trace, and also similar to the schematic from Figure 4.3. The discontinuous background motion was displayed in the centre of each sweep, it can be seen that the background display did not alter the course of the eye movement. The vertical eye movements were suitably minimal for a left-right pursuit target, and the vertical eye trace is shown in the bottom graph of Figure 4.4. Red sections indicate areas for which saccades or blinks were detected and removed from the analysis. Where a data point was removed from one of the eye movement traces, the corresponding point was removed from the other.

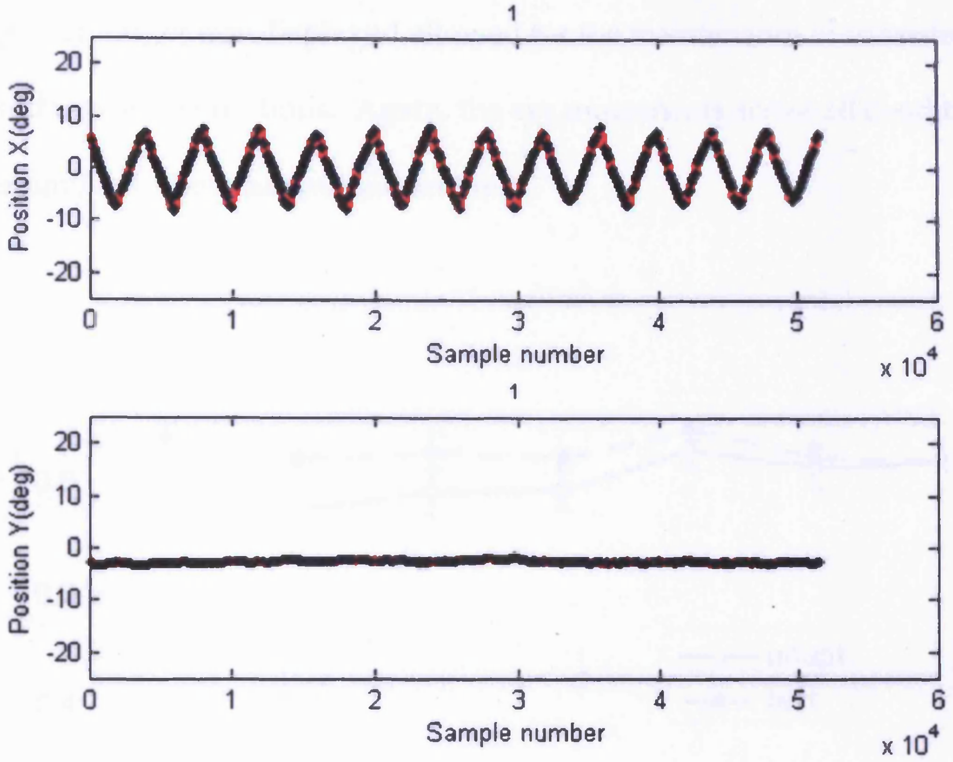

Figure 4.4: Example eye movement recording in the adaptation phase.

The eye movement gain from the six experimental conditions and the baseline condition are shown if Figure 4.5. In this figure, 'adapt' includes the eye movements from both the initial adaptation phase and the pre-test top-up phases. The baseline was a measure of the PSS after viewing a stationary pattern during the adaptation and top-up phases (0, 0). During the baseline adaptation participants were successful at keeping their eyes relatively stationary. The baseline test was identical to the test in the other six conditions, and the eye movements were similar across all.

Pursuing a target between two distracting motions could have resulted in less accurate eye movements as the distracter speed was increased. Whilst pursuing a target over a background in Chapter 3 resulted in changes to the accuracy of a smooth pursuit eye movement, the central blank area in which the pursuit target was displayed allowed for the maintenance of consistent pursuit between conditions. Again, the eye movements across all conditions were similar for both adaptation and test.

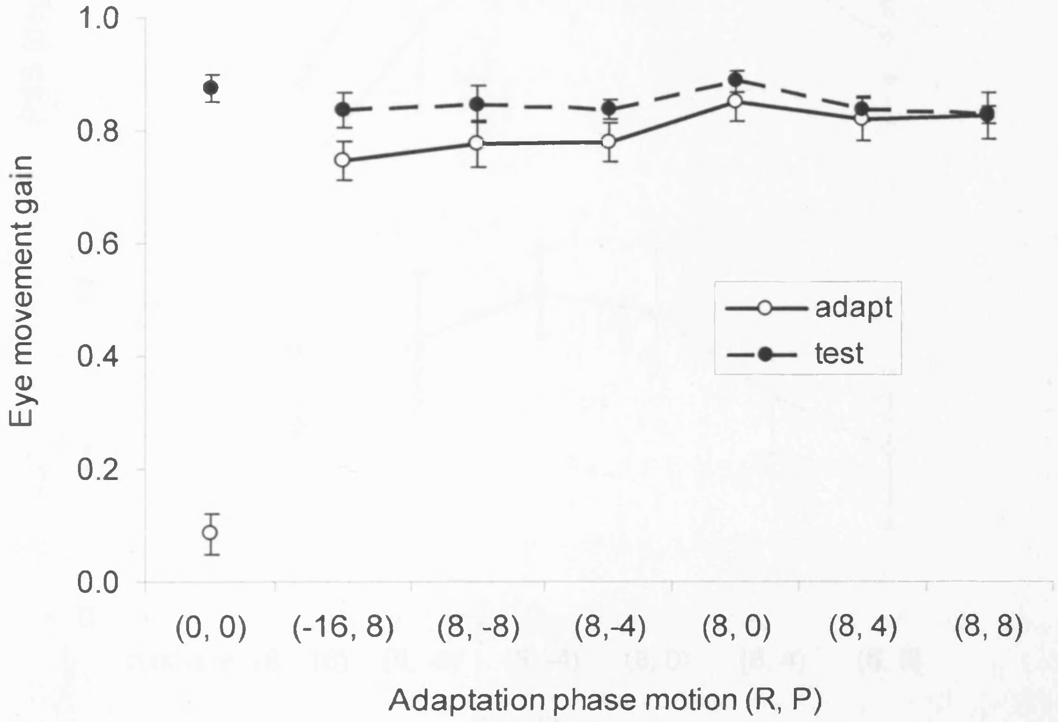

Figure 4.5: Eye movement gains for the baseline condition and the six experimental conditions.

Modification of the PSS

Figure 4.6 shows the baseline PSS for the four participants and the mean PSS after each adaptation condition. The baseline PSS ranged from 1.4 deg/s to 4.9 deg/s. Positive velocities denote background motion in the same direction as the eye movement, the classical Filehne Illusion.

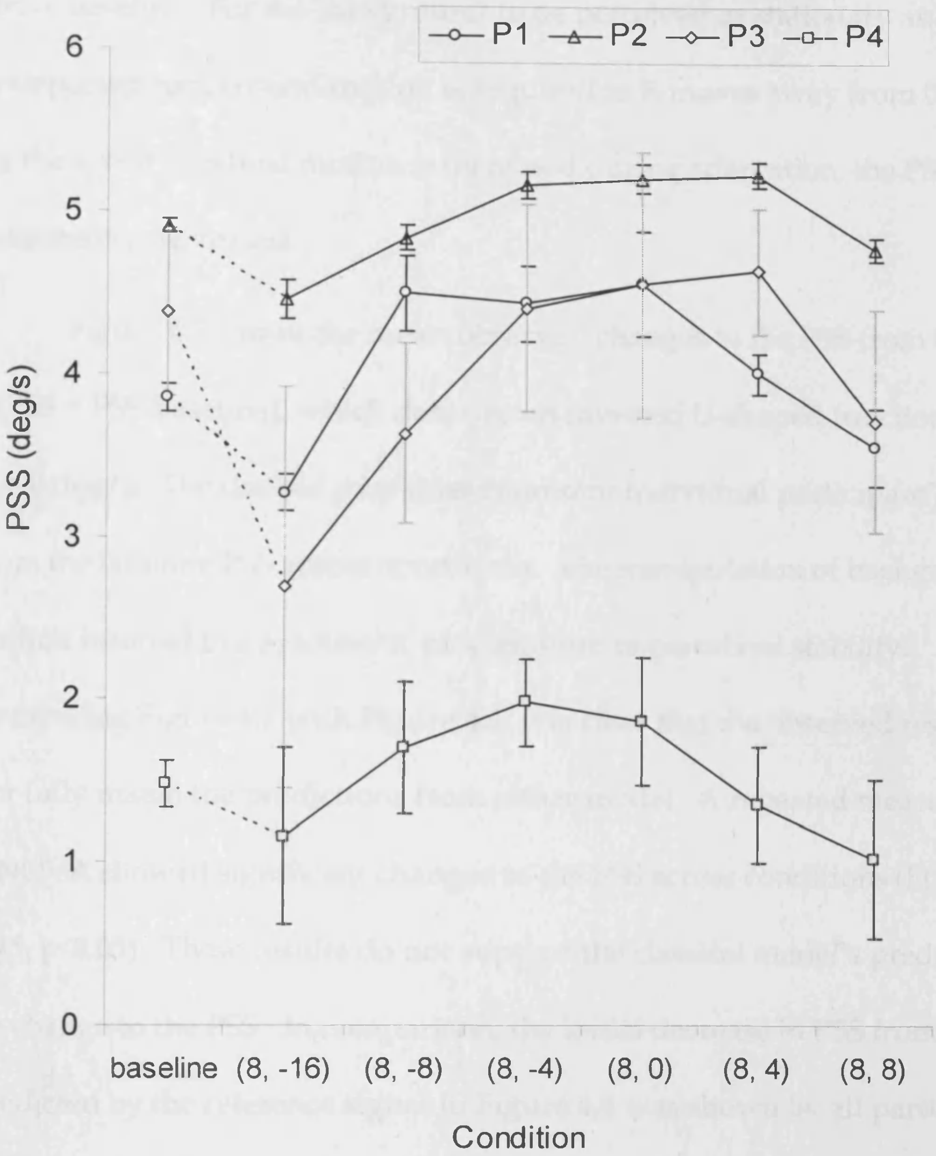

Figure 4.6: Individual participant results. The point of subjective stationarity is shown for all conditions, the baseline measures are shown as single points to the right.

Whilst the between participant stability baselines show considerable variation, the pattern of adaptation shown around the baseline were similar for all four participants. It can be seen that the PSS drops from baseline to (8, -16) as predicted by the reference signal model. Every participant then exhibited an inverted U-shape pattern of response, with the peaks centred approximately on R=0. Little or no retinal motion adaptation leads to a PSS above baseline. For the background to be perceived as stationary an increase in opposing background motion is required as R moves away from 0 deg/s. As the speed of retinal motion is increased during adaptation, the PSS is consistently decreased.

Figure 4.7 shows the mean observed changes to the PSS from baseline (ΔPSS = PSS-baseline), which describe an inverted U-shaped function around R = 0 deg/s. The dashed grey lines represent individual participant's change from the baseline PSS across conditions. The manipulation of background motion resulted in a systematic modification to perceived stability. Comparing Figure 4.7 with Figure 4.1, it is clear that the observed results do not fully match the predictions from either model. A repeated measures ANOVA showed significant changes to the PSS across conditions ($F(1.6, 4.8) = 7.45$, $p<0.05$). These results do not support the classical model's prediction of no change to the PSS. In comparison, the initial decrease in PSS from baseline predicted by the reference signal in Figure 4.1 was shown by all participants in Figure 4.7. Also, the PSS reported for the first three adaptation conditions are in line with the reference signal predictions and additionally conform to the findings of previous research (Haarmeier et al, 2001).

An interesting feature of the data is that for faster in-phase retinal motions a decrease in the PSS following the peak at R = 0 deg/s is shown. Adaptation to backgrounds with a retinal velocity greater than the eye movement resulted in perceived stability judgements similar to those conditions in which backgrounds moved at the same speed, but in the opposite direction.

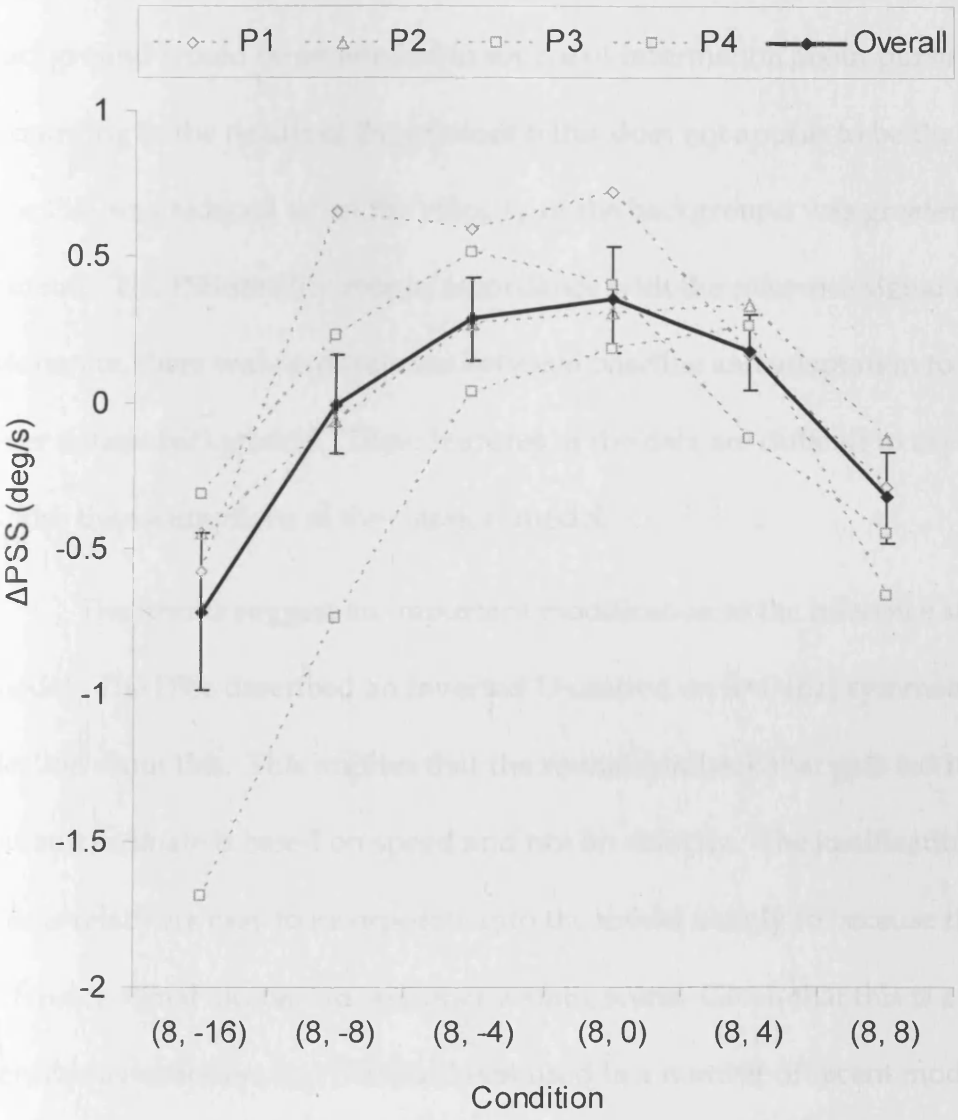

Figure 4.7: Absolute change in point of subjective stationarity from baseline (ΔPSS), following simultaneous adaptation to motion balanced retinal motion and smooth pursuit eye movements. The PSS forms an inverted U shaped curve that can be seen to vary around R = 0 deg/s. Error bars show ±1 standard error for the mean PSS.

Discussion

By extending the range of motion from previous research, this study investigated an adaptation space for which the reference signal is poorly defined. Brenner and van den Berg (1994) suggested that a reference signal could be replaced by an extra-retinal signal under such circumstances, since a background would be an unreliable source of information about pursuit. According to the results of Experiment 6 this does not appear to be the case. The PSS was reduced when the velocity of the background was greater than pursuit. The PSS steadily rose in accordance with the reference signal model. Moreover, there was no difference between baseline and adaptation to pursuit over a static background. These features of the data are difficult to explain under the assumptions of the classical model.

The results suggest an important modification to the reference signal model. The PSSs described an inverted U centred on R=0 that symmetrically decline about this. This implies that the retinal feedback that gets fed into the pursuit estimate is based on speed and not on velocity. The justification for this is relatively easy to incorporate into the model mainly to because the reference signal mechanism assumes a static scene. Given that this is a sensible assumption, one that has been used in a number of recent models of motion perception, direction is largely irrelevant: retinal motion is always opposite to pursuit during everyday viewing. The reference-signal computation exists to calibrate the magnitude of eye velocity (or its extra-retinal estimate) and consequent retinal motion (or its retinal estimate).

Hence the reference-signal mechanism need only take account of the speed of the retinal flow, not its direction

Can the classical model explain the results? It could do, but only if the non-coincident retinal motion adaptation gave rise to a non-retinotopic of 'phantom' VAE. The previous chapter did not find evidence for a phantom MAE, but it is possible that MAE and VAE behave differently. The requirement of a phantom VAE for the classical model account are further discussed and tested in the following experiments.

Control Experiments, Chapter 4

Introduction

Experiment 6 demonstrated a significant change to the point of subjective stationarity (PSS) as two flanking patterns, that provided adaptation phase retinal motion, were manipulated. The only way the classical model could explain these findings is if the retinal motion adaptation used in Experiment 6 induced a phantom VAE. As far as I am aware, there are no papers that report the requisite phantom velocity aftereffect. However, MAE can be observed in retinal areas that have not been directly stimulated during adaptation (Von Grünau & Dube, 1992; Snowden & Milne, 1997; Price, Greenwood & Ibbotson, 2004). Phantom MAEs are evident when using dynamic test stimuli. Such findings present the possibility that the apparent velocity of a moving test pattern can be altered by the non-coincident adaptation of motion sensors.

Whilst the test pattern was placed in a retinal location that was assumed to result in no aftereffect, the stimulus format may also have increased the likelihood of phantom adaptation in experiment 6. Placing a central test between two flanking adaptation patterns may have inadvertently resulted in the test being subject to induced retinal motion adaptation. It has been demonstrated that presenting a concentric ring pattern which contains two gaps during adaptation results in an observable MAE when the test is presented in the gaps (Snowden & Milne, 1997; Price, Greenwood and Ibbotson, 2004). The two control experiments reported here investigate the potential for the flanking pattern of retinal motion utilised by experiment 6 to influence the apparent speed of retinal motion during the test phase.

Control Experiments (7 and 8)

Method

Participants

The author and two adults with normal or corrected to normal vision participated in Experiment 7. The participants were naïve to the experimental hypothesis. Informed written consent was gained and a full debrief followed the experiment. For Experiment 8, the author and thesis supervisor acted as participants.

Stimuli and Procedure

The stimuli were generated as for experiment 6, and are represented in figure 4.8. The stimuli again ensured that adaptation phase retinal motion was not spatially coincident with the test stimulus. The background patterns flanked the test areas as in experiment 6 (16° wide, 8° high). The pursuit target was replaced by a stationary fixation point. The three experimental conditions for the first experiment were (0, 0), (0, 8) or (0, 16). Additionally the (0, 4) condition was included in Experiment 8. Adaptation remained motion balanced. A consequence of removing pursuit was the redundancy of the negative velocity coding conditions reported in experiment 6.

The test phase consisted of dim red dots displayed within two annulus windows (red dots in Figure 4.8) and a fixation point (represented as a black/red dot). Participants had to report whether the left or right hand patch was moving faster via a left or right mouse click. The speed of the comparison patch was fixed at either 8deg/s (Experiment 7) or at 4deg/s (Experiment 8). The motion of the test patches were controlled via two interleaved staircase procedures as for experiment 6. The starting point for each staircase was lowered to account for the different speed of the comparison patch in experiment 2, with one initiating above 4 deg/s and one below. Recording the display speeds and participant responses enabled calculation of the point of subjective equality for speed. The red dots in Figure 4.8 illustrate the test pattern for both controls. The fixed speed comparison patch was peripheral in Experiment 7. The comparison and test patch locations were swapped and the comparison patch was centrally located during Experiment 8.

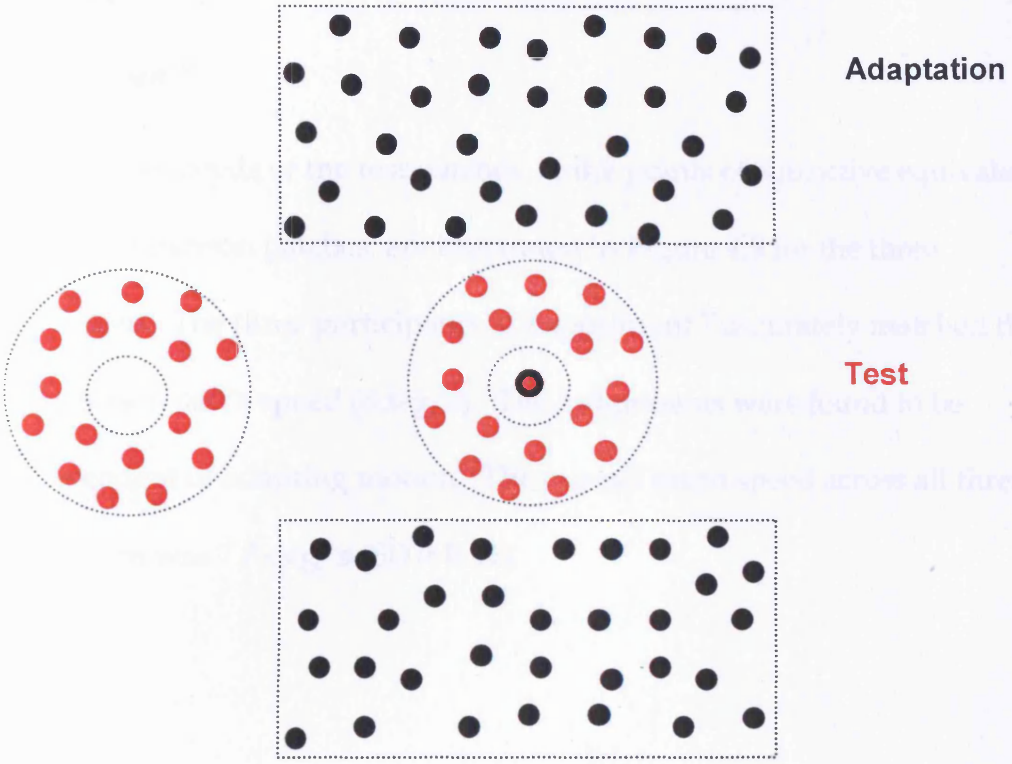

Figure 4.8: Representation of the Stimulus Configuration. Dotted lines represent the invisible windows through which the dot patterns were displayed. Whilst all dots were red, black dots here represent adaptation phase stimuli, whilst red dots represent the test phase. Adaptation dot motion was motion balanced and constrained within the stationary flanking windows. During the test phase one annulus patch motion was presented at a constant speed whilst the other was controlled via a staircase.

Results

Experiment 7

The speeds of the test patches, at the points of subjective equivalence to the comparison patches, are illustrated in Figure 4.9 for the three conditions. The three participants in Experiment 7 accurately matched the comparison patch speed (8deg/s). The judgements were found to be independent of adapting motion. The overall mean speed across all three conditions was 7.7 deg/s (SD = 0.54).

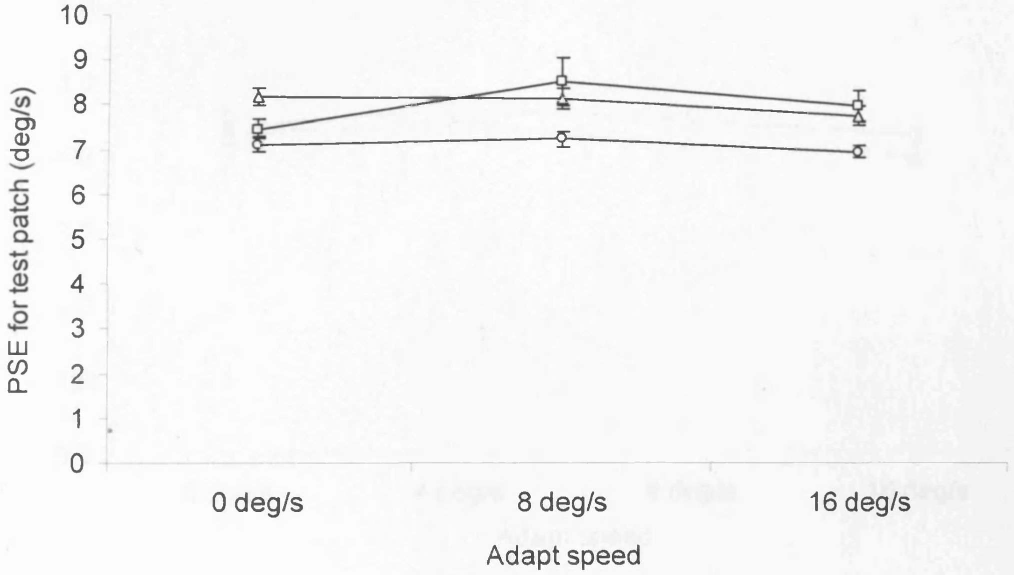

Figure 4.9: The point of subjective equivalence for the test patch, following simultaneous adaptation to motion balanced retinal motion without smooth pursuit eye movement. There is little change in PSE following adaptation, the test patch was judged to be moving at a similar speed to the comparison patch independently from the adaptation speeds.

Experiment 8

Figure 4.10 again shows the mean PSE for each participant following the different adaptation conditions. The speed of the adapting motion was found to have little consequence on the later judgement of test patch speed. The PSE across the four conditions were similar. The speed of the comparison patch for Experiment 8 was 4 deg/s. The speed of the two patches were judged to be equivalent when the test patch moved at a mean speed of 4.3 deg/s (SD = 0.2).

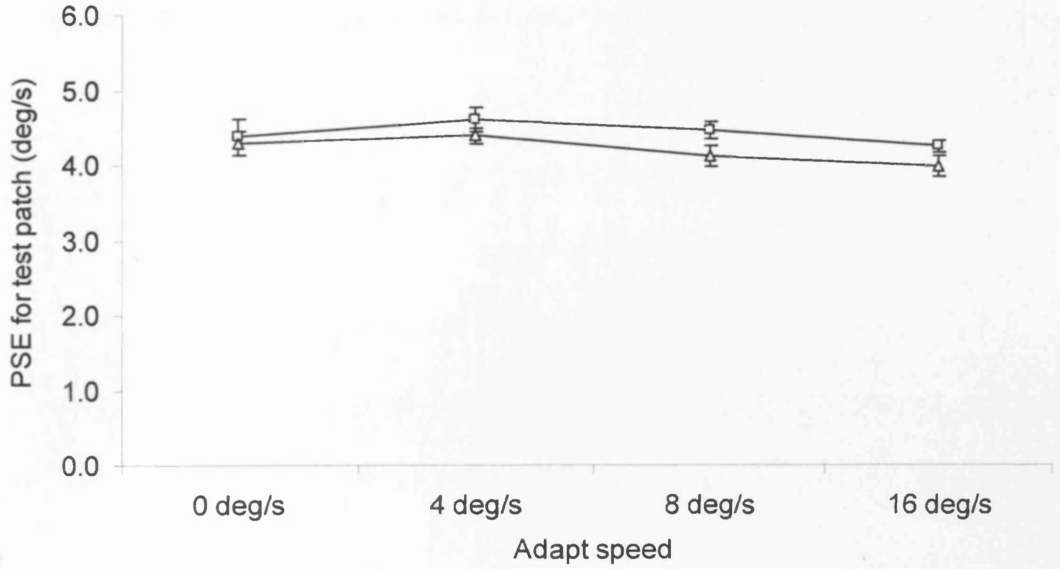

Figure 4.10: The point of subjective equivalence for the test patch. The test was judged to be moving at a similar speed to the comparison patch across conditions.

Conclusion

The results indicated no change for the apparent speed of a dot pattern following retinal motion adaptation. The slightly lowered equivalent speed of central test in Experiment 7 and raised equivalent speed of peripheral test in Experiment 8 illustrate small decreases in perceived velocity, which have previously been reported with increasing pattern eccentricity (Johnston & Wright, 1986). Control experiments 1 and 2 therefore provide no support for the hypothesised action of a phantom velocity aftereffect in the central test area. The classical model therefore cannot explain the results of experiment 6.

Both seem unlikely, so taken together, the results of all three experiments point to a modified reference signal model.

Experiment 9

Introduction

The results of the first experiment did not match the predictions made by the classical model. Moreover, the control experiment suggested that phantom motion adaptation had not occurred. Another method to further investigate the possibility of phantom motion induction had been suggested by past research with perceptually visible examples of induction between two patterned areas, such as the grating-induction effect (McCourt, 1982). When two gratings flank a central homogenous field, a phantom grating can extend for several degrees through the central blank area. A similar finding has been reported using light and dark stripe patterns to flank a central homogenous field (Weisstein, Maguire & Berbaum, 1977). Phantom stripes can be observed in the homogenous central region, when the actual stripes are animated, the phantom is also observed to move. When a physically present grating is displayed in the area previously subject to the illusory stripe motion Weisstein et al demonstrated a phantom MAE. Importantly, the induced stripe pattern in the central area, and the resulting MAE, were largely diminished by the removal of one flanker. This suggests that phantom motion adaptation could be diminished or removed with the removal of one of the adaptation patterns. This experiment investigated perceived stability when one of the flanking random dot patterns was removed. To maintain the overall amount of retinal motion, despite the removal of one flanker, the size of the remaining flanker was doubled.

Predictions

The two models again make differing predictions. The classical model predicts little change to the PSS across conditions. Since the global retinal motion of the stimulus remained unchanged, the reference signal model would predict an inverted U-shape curve as in Experiment 6.

Method

The same participants as Experiment 6 were employed. The retinal pattern flanking the test area in Experiment 6 potentially induced motion adaptation in the central test area. For Experiment 9 the adaptation background was constrained within a single upper rectangle (16° wide, 16° high) that extended symmetrically from 4.5° above the pursuit target (Figure 4.11). All other methods remained the same.

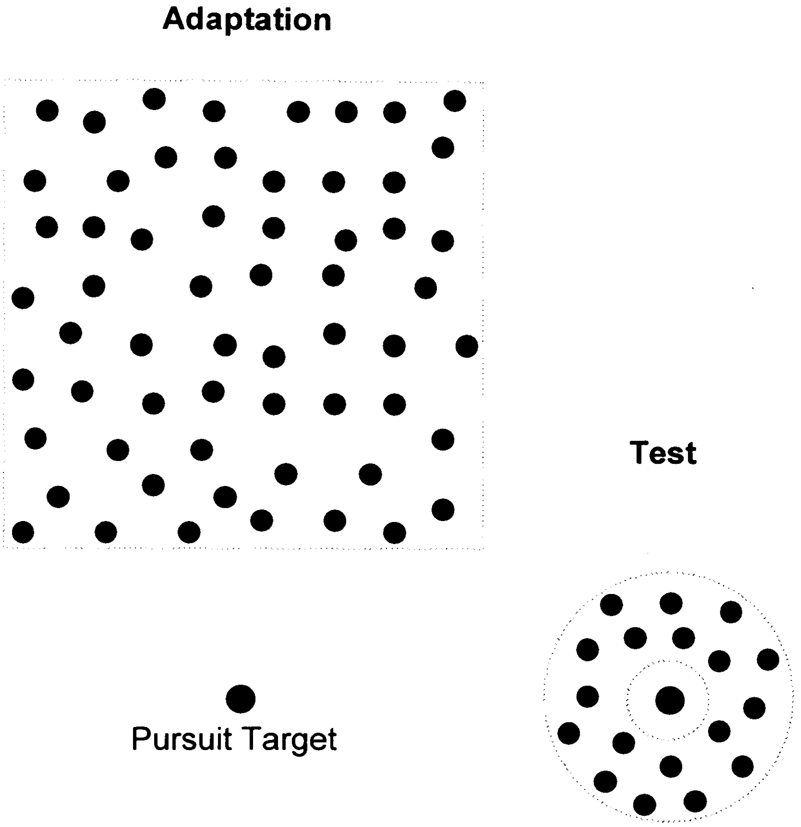

Figure 4.11: Representation of the Stimulus Configuration for Experiment 9. The flanking pattern from Experiment 6 was replaced by a single larger pattern. For test, the adaptation pattern was removed and the test pattern was positioned in an annulus window around the pursuit target as before.

Results

Figure 4.12 shows the baseline PSS for the four participants in the same format as Figure 4.6. Participant 4 shows a slightly inverted Filehne Illusion with a baseline PSS of -0.3 deg/s. The baseline PSS were in a similar range to that reported in the previous experiment. The inverted U-shape curves previously reported are less evident.

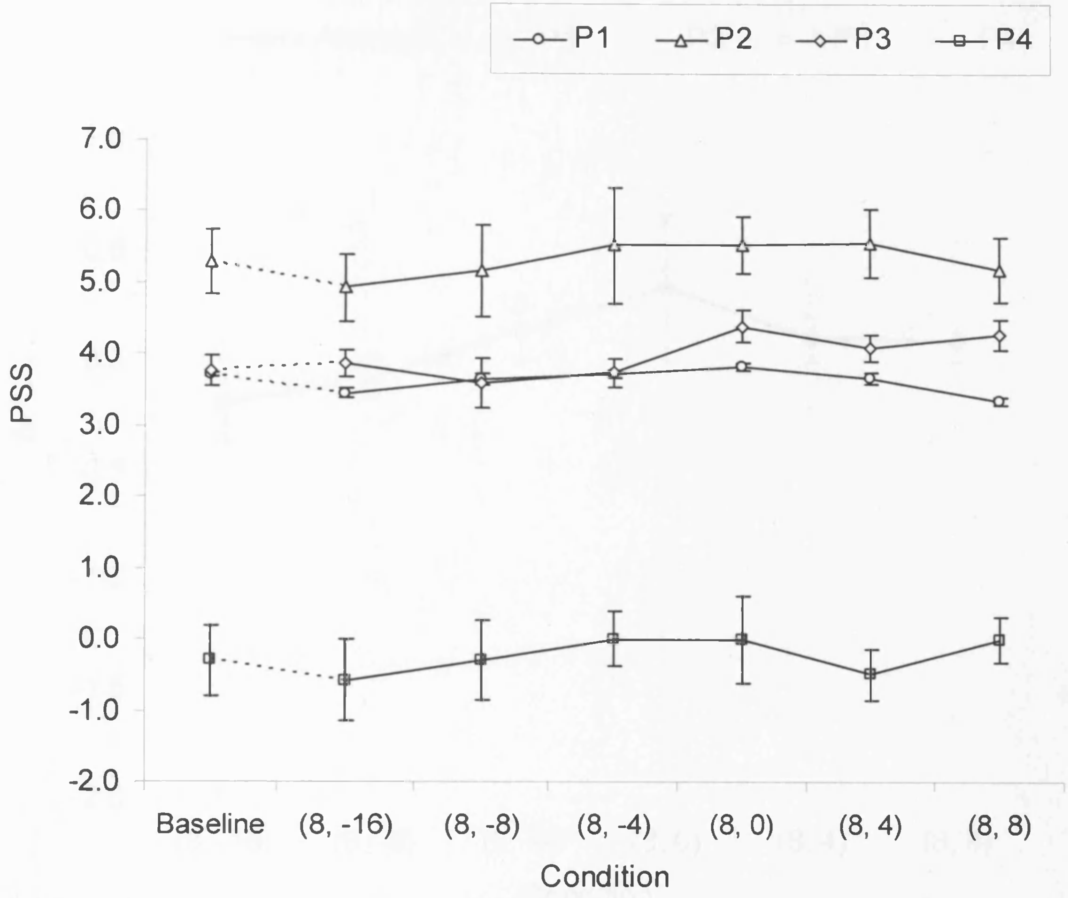

Figure 4.12 Individual participant results. The point of subjective stationarity is shown for all conditions, the baseline measures are shown as single points to the left.

Figure 4.13 displays the results of the current experiment in the same format as previously used for Figure 4.7. The U-shaped function apparent in the results of experiment 6 is reduced, with the ΔPSS showing little change between the conditions. A repeated measures ANOVA showed that the changes to the PSS across conditions were not significant (F(2.3,6.9) = 2.96, p=0.11). By the removal of one flanking pattern, with the entire retinal motion being displayed in a single window above the pursuit target, the effects of retinal motion on the PSS were severely reduced in Experiment 9.

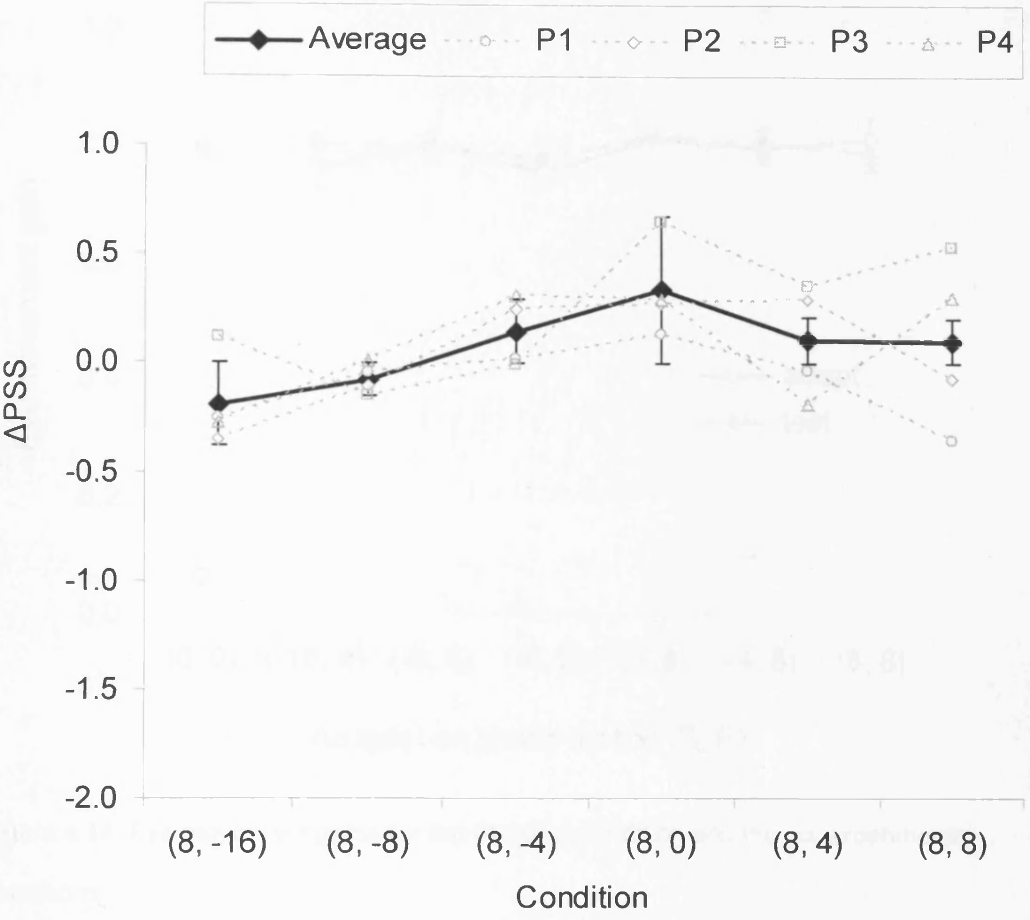

Figure 4.13: Absolute change in point of subjective stationarity, following simultaneous adaptation to motion balanced retinal motion and smooth pursuit eye movements. There is little change in PSS following adaptation.

Eye movement analysis

The eye movement analysis revealed that the eye movements across the two experiments were very similar. This is unsurprising; both experiments consisted of the same task, with retinal motion constrained to the periphery in each. Figure 4.14 shows the eye movement gains for Experiment 9.

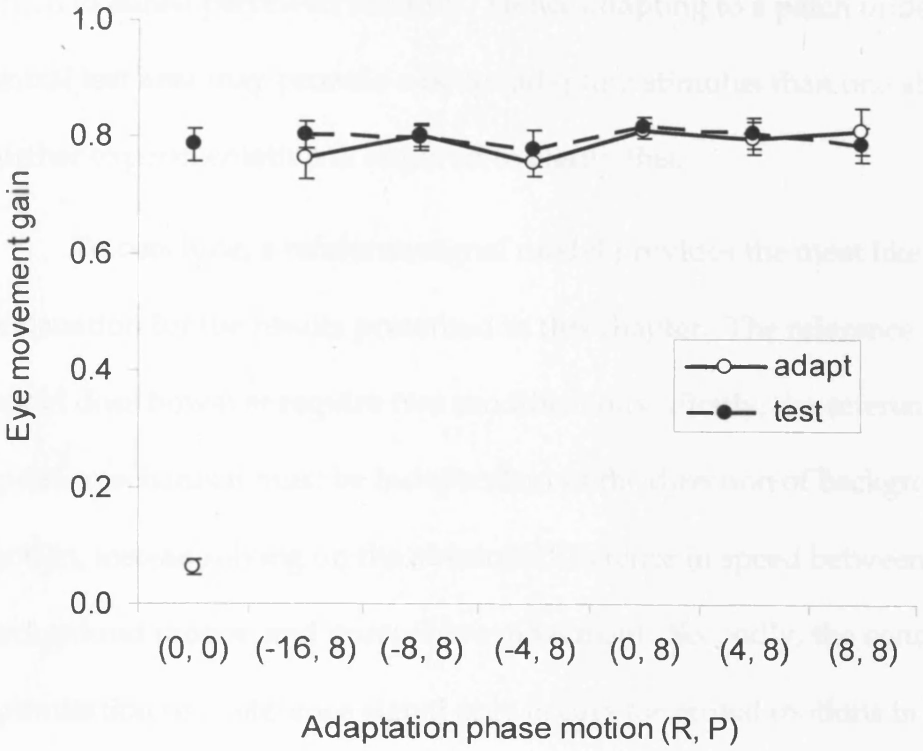

Figure 4.14: Eye movement gains for the baseline condition and the six experimental conditions.

Discussion

A change to the format of the adapting stimulus resulted in Experiment 9 reporting no significant change to the PSS. This presents a puzzle, because while there is clearly no evidence to support the classical model in the results of Experiments 6, 7 or 8, the results of Experiment 9 therefore suggest a second potential modification to the reference signal model, namely that the reference signal mechanisms are sensitive to the retinal location of the background retinal motion. This may be a reasonable modification. The sky is a largely featureless expanse, and when features such as clouds are present they are universally in motion. Compared to a textured stationary ground, the sky may make a poor choice for a reference by which to adjust perceived stability. Hence adapting to a patch underneath the central test area may provide a better adapting stimulus than one above. Further experimentation is required to clarify this.

To conclude, a reference signal model provides the most likely explanation for the results presented in this chapter. The reference signal model does however require two modifications. Firstly, the reference signal update mechanism must be independent of the direction of background motion, instead relying on the absolute difference in speed between background motion and pursuit eye movement. Secondly, the continuous optimisation of a reference signal only occurs for retinal motions in specific background locations.

Chapter 5: General Discussion

The previous chapters presented experiments that investigated the manner in which retinal and extra-retinal signals are combined. The combination helps inform the visual system about the motion of objects during smooth pursuit eye movement. The chapters employed various adaptation paradigms, examining adapting stimuli which presented orthogonal or collinear retinal motion and pursuit. Novel techniques were developed to measure the direction and magnitude of MAE using a purpose built pointing device. The device was built due to the nature of the extra-retinal MAE, which acts on all areas of the visual field, making traditional nulling or matching techniques difficult (Chaudhuri, 1991; Freeman, Sumnall and Snowden, 2003). The thesis also used a novel stimulus arrangement that aimed to reduce or remove the influence of adapted retinal motion sensors during the test phase.

The experiments in chapter 2 examined the origins of the MAE that follows simultaneous adaptation to orthogonal smooth pursuit and retinal motion. Adaptation to eye movement and retinal motion could result in extra-retinal adaptation, retinal adaptation or a combination of both. Two general origins were identified. The first was the perceived-motion hypothesis, suggesting that adaptation occurs after the perception of the adapting motion has been determined. Mack, Hill and Kahn (1989) reported an MAE following adaptation to a pursuit point that moved orthogonally to the background. The MAE was opposite to a direction that bisected the two adapting motions. One explanation offered for the MAE direction was that it was opposite to the direction of the perceived motion during adaptation, which is motion in a head-centred coordinate frame. The alternative hypothesis posited in chapter 2 suggested that such MAE result from a vector combination of lower level component adaptations. The component MAE hypothesis posited that separate retinal and extra-retinal MAE combined to form the unidirectional MAE percept reported by observers. Two experiments examined MAE directions, for a total of six adaptation conditions. Horizontal retinal motion only, vertical smooth pursuit only, and orthogonal retinal and pursuit motions simultaneously (R + P), each of which could either be presented in central vision (experiment 1) or 10 degrees peripherally (experiment 2). The perceived direction of motion was recorded in both the adaptation and test phases. Both experiments confirmed that adaptation to either signal could produce an MAE (R-only or P-only). Additionally, in the R+P condition, the direction of the MAE bisected the direction reported for the two component MAE. A third experiment measured the magnitude of the components generating the unidirectional R+P MAE, gaining speed estimates for the pursuit only and retinal only components. The speed estimates were again obtained using the pointing device, this time with observers asked to imagine the device as if it were a 'car speedometer'.

The experiments showed that the perceived direction of adapting motion did not predict the MAE direction. To test the component MAE hypothesis, a model was derived to estimate the R+P MAE from the first two experiments. The model used the magnitudes of the retinal and pursuit components from experiment 3 and the individual observer's eye movement data from the combined conditions of the first two experiments. The predictions were compared to the individual MAE directions reported by each participant. The component MAE model predicted the perceived directions from the second experiment. The model also outperformed the predictions created from the perceived direction hypothesis for experiments 1 and 2. However, the component MAE model failed to fully account for the directions reported in the first experiment. The inability to predict the R+P MAE directions from experiment 1 were potentially due to differences in the properties of the R-only MAE observed between experiment 1 and 3. In experiment 1 the retinal only MAE was reported infrequently. A weak retinal MAE was also suggested by the directions reported for the combined condition of experiment 1, with several R+P MAE directions similar to those reported for the extra-retinal pursuit only MAE. Overall, the results suggested a weak retinal aftereffect in experiment 1. This contrasts with the results obtained in experiment 3, for which the retinal MAE was reported frequently and with a similar apparent speed to that observed during peripheral adaptation. The component MAE hypothesis could only reasonably be expected to predict MAE when the measured speeds of the components are similar to those that produce the R+P MAE. Chapter 2 provided evidence that the two components could adapt separately, and that the MAE did not originate from adaptation to the perceived direction of motion. A motion signal comprising perceived direction information was not responsible for the R+P MAE. Chapters 3 and 4 looked at a related question, how is head-centred motion derived? Uncertainty exists as to the nature of the pursuit speed estimate, and so the later experiments were designed to examine the pursuit component in isolation.

As detailed in the introduction and in the experimental chapters, two current theories posit that accurate motion perception and perceptual stability are maintained during pursuit by comparing the afferent retinal signal to either a constant efferent extra-retinal signal (Jeannerod et al, 1979; Mittelstaedt, 1990, Freeman and Banks, 1998; Freeman, 1999, 2007) or a continuously calibrated reference signal (Wertheim, 1994; Haarmeier and Thier, 1996; Brenner & van den Berg, 1994; Crowell & Andersen, 2001; Haarmeier, Bunjes, Lindner, Berret and Thier, 2001; Goltz, DeSouza, Menon, Tweed, & Vilis, 2003; Dash, Dicke, Chakraborty, Haarmeier & Thier, 2009). The classical model of motion perception cancels the reafferent retinal motion produced during an eye movement through the use of a purely extra-retinal velocity estimate. A reference signal model also employs an extra-retinal signal, but one which is modulated in some manner by retinal feedback about the pursuit estimates efficacy. Recent evidence that the visual system does use an adaptable reference signal (humans: Haarmeier et al, 2001; monkeys:

Dash et al, 2009) has been confounded by a potential for retinal motion adaptation to influence the outcome of the test (Freeman, 2007). As a result, it had not been possible to differentiate the outcomes predicted by the two models. This led to the development of a stimulus format that could isolate the pursuit signal during test.

Chapter 3 again employed simultaneous adaptation to retinal motion and smooth pursuit, whilst limiting the effects of retinal motion adaptation. The stimulus format placed retinal motion during adaptation in an area that was not coincident with the test. This excluded retinal sensor adaptation as an influence on the properties of the emergent MAE. When retinal motion sensor adaptation can be eliminated as an influence on the test stimulus, classical models and reference signal models then make separate predictions when background motion has been manipulated during adaptation. The behaviour of a purely extra-retinal MAE (as predicted by the classical model) should be independent of background motion when presented in this way, whilst a reference signal MAE should be modulated by the background motion. However, peripheral retinal motion adaptation can produce phantom MAEs in a central test (Weisstein, Maguire, Berbaum, 1977), so control conditions were run to determine whether the adaptation stimuli induced phantom MAEs. This was achieved by providing a fixation point to keep the eyes stationary. The results for these control conditions suggested that the effects of retinal motion adaptation were successfully excluded by the stimulus arrangement. Any change in the MAE that resulted from changes in adaptation phase background motion should therefore indicate the modulation of a reference signal. As noted in the chapter, this prediction depends on the eye movements remaining reasonably consistent across conditions.

The results showed that the perceived direction and speed of the MAE depended on peripheral retinal motion. However, the recorded eye movements also depended on the adaptation conditions and were shown to correlate with the changes to the MAE. Retinal motion was found to alter the ability of participants to accurately pursue a target; this finding is consistent with other studies (Kodaka, Miura, Suehiro, Takemura & Kawano, 2004; Worfolk & Barnes, 1992; Collewijn and Tamminga, 1984; Masson, Proteau & Mestre, 1995). The extra-retinal estimate of the efferent signal generating an eye movement will partially (reference signal) or fully (classical model) determine the amount of pursuit signal adaptation. The changes in the properties of the MAE were not consistent with retinal motion feedback into a reference signal, with all changes being opposite to those predicted by that type of model. The classical model offers the best explanation for the results obtained in chapter 3.

Chapter 4 employed similar methods to those reported in chapter 3, but used a moving test pattern to investigate the influence of previous motion on perceived stability (e.g. Haarmeier et al, 2001; Freeman 2007). The Filehne illusion has been employed in several studies to quantify perceived stability and to thereby estimate changes to the retinal and pursuit speed estimates.

The method, first employed by Mack and Herman (1973, 1977), involves manipulating the actual motion of the background during pursuit to determine the point at which the background is perceived as stationary. This method has been used by Haarmeier and colleagues (Haarmeier & Thier, 1996; Haarmeier et al, 2001; Dash et al, 2009) and Freeman (2007) to measure the changes to the Filehne illusion that are observed following adaptation. As previously stated, the potential for retinal sensor adaptation to alter test phase motion has confounded previous attempts to clearly differentiate the models.

Using a variation of the non-coincident retinal motion stimuli developed successfully in chapter 3, chapter 4 again attempted to exclude the role of retinal motion sensor adaptation whilst quantifying the PSS. The placement of two background patches, flanking the central test area, was later determined to be a stimulus format that could potentially produce retinal motion adaptation in a central homogenous region. This suggested a failed exclusion of retinal motion adaptation in experiment 6 as one possible explanation for the consistent changes to perceived stability recorded for all the participants. Previous findings that employed analogous stimulus formats have shown that the perception of contiguous areas can be altered (Weisstein, Maguire & Berbaum, 1977; McCourt, 1982; Snowden & Milne, 1997). The changes to the point of subjective stationarity comply with a classical model outcome when retinal motion adaptation has influenced the perception. Two control experiments found no indication that phantom motion adaptation had occurred at two speeds (8deg/s and 4 deg/s). This ruled out the adaptation of low level retinal input into a classical model. For the changes to perceived stability in experiment 6 to be explained by the reference-signal model, the retinal feedback would need to be based on retinal speed not direction. Whilst the size of difference between the signals is important, intuitively the direction of each motion would also seem to provide useful information under conditions with positive retinal motion. However, it is a mechanical fact that retinal motion created by an eye movement is going to be opposite to the direction of smooth pursuit most of the time. Situations in which extra information about the direction of an eye movement would be useful are limited to ecologically unlikely conditions.

The classical model explanation, that inputs into the perceived stability system were altered through adaptation, was ruled out by the control experiments in chapter 4. The presence or absence of phantom VAEs influencing perceived stability judgments could now only reside as adaptation at later stages of the visual pathway, those directly related to perceived stability judgements.

Experiment 9 attempted to reduce the potential for retinal motion adaptation between two flanking dot patterns by removing one flanker. This method was suggested by the finding that the removal of one flanker largely reduced the phantom effect reported by Weisstein et al (1977). The size of the remaining flanker was doubled so that the same amount of retinal motion was present in the stimulus. This manipulation should not have altered any putative reference-signal, as the display still provided evidence for a change in the relationship between retinal motion and pursuit, the key ingredient to this type of signal and its modification during simultaneous motion adaptation. However, the results of Experiment 9 showed that displaying only one flanker largely abolished the changes to perceived stability found in Experiment 6. To explain this result, the reference signal is required to take into account the location of retinal motion. The flanker in Experiment 9 was placed above the test area. It may be that a sky in motion would be less successful as a reference signal recalibration stimuli than a ground in motion. Further experimentation is required to determine whether the ground provides a good reference signal recalibration stimuli. If retinal motion in a 'ground' location also acts as a poor adaptor, then neither the classical model nor reference signal model will easily explain the result. At that point a direct adaptation of retinal motion sensors specifically responsible for calculating world motion would be implicated. Experiment 9 needs to be replicated, replacing the 'sky' flanker with a 'ground' pattern, the next section details other potential areas for future research.

Future research

Chapter 3 replicated findings that an extra-retinal MAE can be observed following adaptation to a repetitive smooth pursuit eye movement (Chaudhuri, 1990, 1991). An interesting area of future enquiry could further define the conditions for which extra-retinal signals are most salient, again using the extra-retinal MAE. The section discussing dual-mode models in chapter 1 presented evidence that motion processing favours retinal motion information when it is deemed to be consistent and reliable. Purely extra-retinal estimates of pursuit are then employed when retinal information has been degraded or otherwise deemed unreliable. The basic characteristics of extra-retinal saliency, given a varying availability of retinal motion, are easy to demonstrate using the extra-retinal MAE. An observation that has not been reported to date is that the extra-retinal MAE can be stopped and restarted by varying the amount of retinal information available during test. This study has been piloted in an overly simple manner, through the use of a torch to illuminate the room whilst viewing an extra-retinal MAE. Adapting to repetitive smooth pursuit as in chapter 3, but with no background, produces a strong percept of illusory motion in a darkened lab. Providing and then removing retinal information, by turning a torch on and off, effectively stopped and then restarted the perceptual experience of the extra-retinal MAE. The effect can be observed several times during a single test period. Whilst this effect has only been demonstrated to one colleague, a full study could provide useful information on motion processing in poorly illuminated conditions. Measuring the duration or magnitude of an extra-retinal MAE, in the presence of varied retinal information, would provide details on the interplay between retinal and extra-retinal mechanisms and the motion perception system. Such a study could provide more evidence for the extra-retinal trigger suggested by Crowell and Andersen (2001), which suggests that at some point the illusory perception of extra-retinal motion would switch to a stationary percept informed by retinal motion. The transition could alternatively be a gradual one with the output of the adapted extra-retinal mechanism having less influence on the motion percept as the amount of available retinal information is increased.

Another potential method to examine the dual mode model could employ one of the visual stimuli that demonstrate bistable motion perception, such as 3-D structure-from-motion patterns (Andersen & Bradley, 1998). Such stimuli have two distinct interpretations as to the direction of their motion, and this direction percept can intermittently reverse. These illusions demonstrate a situation in which the interpretation of retinal motion is ambiguous. Dual mode models would suggest that the direction of retinal motion would be determined by an eye movement, with the extra-retinal signal determining the perception of motion. A reasonable hypothesis would suggest that the direction of ambiguous retinal motion would be perceived as opposite the extra-retinal signal detailing the eye movement. In a study examining saccadic eye movement and bistable motion perception, saccades did not cause switches to the perceived direction of motion, but potentially prolonged the current percept (Baker & Graf, 2010).

Summary

The experiments in chapter 2 examined whether the adaptation that results in an MAE following orthogonal retinal motion and pursuit was not related to the perceived direction of motion during adaptation. An alternative component MAE hypothesis was tested. This was better able to predict the direction of the resulting MAE.

The remaining chapters then examined whether a reference signal or extra-retinal signal was employed to derive head-centred motion when retinal motion and pursuit are collinear. The classical model was found to best describe the results from chapter 3, which investigated the extra-retinal MAE following adaptation to various retinal motions during smooth pursuit.

The results of chapter 4 could not be explained using the classical model, the control experiments found no evidence for adaptation of the retinal input into the perceived stability judgement. A modified reference signal model explanation of the results was preferred. The results suggested that perceived stability judgements rely on an absolute difference in speed between the eye movement and the background motion rather than their individual velocity estimates. Adaptation was found to modify perceived stability judgments when the adapting patterns flanked the test area in experiment 6, but not when the lower adaptation phase flanker was added to the top flanker in Experiment 9. Whilst the pursuit eye movement estimate remains a function of both retinal information and extra-retinal information, the location of the retinal motion information was found to be important. A modified reference signal was therefore deemed most capable of explaining the results.

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