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Investigation into factors affecting perceptual stability of the world during smooth pursuit eye movements

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Abstract

During pursuit eye movement, a stationary background projected on the retina shifts in the direction opposite to that of the eye movement. This complicates the perception of objects because during an eye movement the retinal and head-centric motions differ. Nevertheless, our visual system is somehow able to compensate for the added eye motion so that the world is perceived as stable. The eye movement compensation is traditionally assumed to consist of a combination of a retinal motion signal and an extra-retinal estimate of eye velocity (Von Holst & Mittelstaedt, 1950; Sperry, 1950). This view has been expanded upon by a number of researchers in the last few decades with the introduction of vector addition-like models. However, it is not well known how closely the eye movement compensation mechanism follows the rules of vector algebra. Evidence for the presence of a signal coming from the moving eye has come from a variety of neurophysiological and perceptual research on the cortical Medial Superior Temporal (MST) area in primates.

Previous studies have shown that the spatio-temporal structure of the background plays an important role in the perceptual accuracy of the velocity of a moving object in the visual field. Background characteristics have been shown to influence not only the retinal signal, but also the extra-retinal signal to some degree. The current thesis provides new information on factors that affect the degree of compensation for retinal motion during smooth pursuit eye movement. The findings are based on several experiments that were designed to use a range of pursuit target and stimulus dot velocities across different backgrounds and

stimulus exposure times, in order to reveal details about how the retinal and extra-retinal signals are combined. Participants were asked to determine the direction of a moving stimulus by rotating an arrow on the screen. In a separate experiment, participants were also asked to assess the speed of a stimulus using a magnitude estimation task. A linear vector model was developed to separate the retinal and extra-retinal signal contribution to the overall compensation. This model was used to assess the degree of perceptual stability across different visual conditions.

Generally, the data indicate that the perceived stimulus motion is well predicted by a vector subtraction mechanism postulated to be occurring in the human brain. However, in situations where there is weak visual stimulation, participants' estimates of motion are less accurate and tend to follow the retinal image motion. In the current thesis I identify how the type of background, directions of eye movements, and stimulus velocities relative to the eye movements affected participants' perceptual performance. Based on the data and the model fitting, it was concluded that the visual system appears to utilize the eye-movement related signal differentially depending on the retinal motion content.

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Chapter I. Introduction

1. The problem of “eye rotation”

Our visual sensory systems are continuously activated as a result of our own actions and changes in the external environment. It is important that we are able to distinguish movements generated by ourselves from those occurring in the external world. This includes assessing which objects are moving and which are stationary in order to effectively navigate our way through the environment.

Retinal image motion may result from objects moving in the environment, or from our own movements. When we move around, these sources of retinal image motion are combined. If the environment is still and we move our eyes, the surrounding world remains perceptually stable although it moves on the retina; and if something moves in the environment and we move our eyes, most of the time we only perceive the movement caused by the external object. We are usually not aware of the motion pattern occurring on our retina caused by our own movement. Eye movements complicate the perception of motion from retinal images because these images are shifted by the rotational component added by the eye movements (the “eye rotation problem”). It is not entirely clear how the visual system can differentiate between the movements resulting from our own actions from those that happen around us.

The current thesis attempts to provide new information on the phenomenon of perceptual stability during self-motion. Specifically, it investigates how well people estimate the direction of an external moving stimulus during eye movements. In other words, it examines the degree of cancellation of the retinal image motion caused by eye movements in different situations. These situations

are defined by experimental conditions that include varying directions and speeds of the moving external object and eye movement (to manipulate the combined retinal image slip). The conditions are also varied by introducing additional background information to the external moving object. The questions of interest are how the directions and speeds of the external object and our eye movement (in combination) affect the ability to estimate the motion of the external object, and whether varying background information changes the accuracy of our perception. What affects how well the movement of the external object is retrieved from the combined retinal image motion? The findings will add to our understanding of how the retinal image slip caused by our eye movements is compensated for so that we perceive the world as stable during our eye movements.

2. Early theories on motion perception during eye movements

Understanding the mechanism in the visual system that derives the veridical direction of moving objects during eye movement has been the focus of interest for many vision scientists. The idea of a cancellation signal evoked by the rotating eye was first voiced independently by Bell in 1823 and Purkyne in 1825. They observed that an afterimage on the retina does not move when the eye is pressed by a finger, but moves with an eye movement. This effect is the opposite with external images – during eye movement stable images in the environment move across the eye's retina, but they are perceived as stationary, yet appear to move when the eye is pressed (Bridgeman, 2007). The concept of a cancellation signal from the moving eye was further developed by Helmholtz (1866) who considered the sensory-motor signal in addition to perception, initiating the formulation of the “Inferential theory” (1866), i.e., that the world's stability in the presence of

eye movements is maintained by an internal monitoring of ongoing and planned eye movement. The idea of a signal produced by the moving eyes, cancelling the self-induced retinal image slip, was the beginning of a theory that has dominated the explanation of the eye rotation problem. Because the signal is generated by the moving eyes themselves, it will be referred to as “the extra-retinal” signal throughout the current thesis.

The concept of the extra retinal signal was supported by Von Holst and Mittelstaedt (1950) and Sperry (1950) who described the stabilizing mechanism in terms of “efference copy” or “corollary discharge” theory respectively. They proposed that a copy of the motor command to move eyes (efference copy) is also sent to the sensory-motor processing centres in the brain (a “comparator”), where it is compared with the actual sensory feedback coming from retina. This efference copy signal supposedly arrives at the “comparator” at the same time as the retinal motion signal from the retina, whereby it is subtracted from the self-generated (re-afferent) sensation. In other words, the stability of the world during eye movements is the outcome of a comparison between two neural signals, one coming from the eye muscles and one coming from the retina. If the two signals cancel each other, one will perceive no movement, and if they don’t, the remainder of the information about the changing scene that is not due to the eye movement is then perceived by the observer. In sum, the perceptual stability of the world is thought to be achieved by a comparison of the actual sensory input with an internal estimate of the eye movement.

During pursuit eye movement a stationary background sweeps over the retina in the direction that is opposite to the eye movement. The Efference Copy (EC) / Corollary Discharge (CD) theories would maintain that an extra-retinal signal generated by the eye movement cancels this re-afferent motion, resulting in the perception of a stable background. However, this stabilization mechanism, where the re-afferent motion signal and the extra-retinal signal combine, often seems to be inaccurate as evidenced by a number of observations. Sometimes during eye movement, an external object that is actually stationary seems to move in the opposite direction to the eye movement (Filehne Illusion; Filehne, 1922).

Similarly, when pursuing a target, it seems to move slower than when viewed with eyes stationary (Aubert-Fleischl phenomenon; Aubert, 1886; Fleischl, 1882). These two perceptual oddities suggest that the interaction of the retinal and extra-retinal signals do not completely cancel each other, indicating that the cancellation mechanism as described by EC/CD is not a complete explanation of the eye-movement cancellation process.

An alternative view to EC/CD on the perception of motion during eye movement is based on the “Direct perception theory” originally put forward by Gibson (1966, 1979). This theory disregards the concept of an extra-retinal signal (Gibson, 1968). It assumes that motion perception can be derived directly from the external world that manifests itself via the optic array; Gibson was interested in the information provided by the optic array. For example, when one moves forward through the environment, a pattern of motion is projected onto the retina. The fixed point in the image coinciding with the direction in which the person is moving (focus of expansion) appears motionless, but the rest of the visual

environment projected onto the retina is moving away from that point and increases in speed as it reaches the peripheral part of the visual field. In other words, motion radiates out from a fixed point that corresponds to the direction of heading. When the eyes move, the motion pattern projected onto the retina changes because the pattern of the array sweeps across the retina, but the optic array itself is not affected by eye movement. Only head movement or body rotation would cause changes in the optic array. The optic array is central to Gibson's theory and represents the distribution of light from a particular viewpoint, containing information about the surroundings and the relative position of the observer to the surroundings. However, Gibson's theory cannot account for the effects of eye movements on the retinal image and the fact that the brain only has access to the retinal velocities, not the optic array.

Both the Inferential and Direct theories of perceptual stability during eye movement have led to the notion that perhaps there are two distinct modes of perception, sometimes called a "dual-mode" theory (Wertheim, 1994). This theory is based on concepts originally considered by Wallach (1959) who tried to explain the phenomenon of center-surround induced motion. Wallach noted that stationary objects appear to move when their large surrounding background moves, regardless of whether or not one engages in eye movement. As a result, Wallach suggested that there may be object-relative and subject-relative cues affecting our perception of motion. The object relative cues relate to the displacement of parts of the visual field relative to one another, while subject-relative displacement is the apparent shift of the entire content of the visual field relative to the observer. Induced motion often occurs as a result of object-relative

motion; which object is perceived as moving depends on the relationship between them, not their actual (subject-relative) motion.

Using the dual-mode theory analogy, the object-relative and subject-relative cues cause the visual system to operate in either the direct or the inferential perceptual mode, respectively (Wertheim, 1994). In everyday life, the direct mode of perception seems to dominate because objects move in relation to the large background pattern (extra-retinal input is not required for veridical percepts). On the other hand, the inferential mode is regarded as a back-up system which kicks in if the object-relative cues are absent (such as in a totally dark environment), and makes use of extra-retinal signals. Illusions then occur when eye velocity is underestimated in the efference copy. Although the “dual-mode” model of motion perception brings the Direct and Inferential theories together, it has an implicit and incorrect assumption: perception is always veridical if the visual system uses the direct mode (information in the optic array is sufficient), and always impaired when the visual system uses the inferential mode (because extra-retinal signals are not always exact), often producing the Filehne Illusion. However, the Filehne Illusion is not always of the same magnitude and varies in size. Wertheim suggests that the varying size of the Filehne Illusion is an indication of how the visual system works; it depends on the eye-movement signal to a larger degree when the amount of visual information in the environment is reduced.

3. Types of eye movements

Physiological along with psychophysical experiments have identified two types of voluntary eye movements: saccades and pursuit. The main difference between

saccades and pursuit lies in how these eye movements manifest themselves physically - saccades are fast and ballistic while pursuit is slow and more controlled (e.g., Erkelens, 2006; Krauzlis, 2004). Saccades typically occur when one needs to locate an object in the environment. Pursuit, on the other hand involves tracking a single target in the scene, keeping its image centered on the fovea and minimizing its retinal image motion. These types of eye movements were thought to have different neuronal as well as perceptual characteristics. However, recent evidence suggests that they may not be entirely independent oculomotor systems that use different visual information or that have different functional organization (Krauzlis, 2004). Neurons related to smooth pursuit have been found to carry extra-retinal signals. For example, Newsome, Wurtz and Komatsu (1988) observed that neurons in the Medial Superior Temporal (MST) area of the brain continued to fire during smooth pursuit even after the pursuit target had been eliminated (retinal image slip was removed). In addition, responses of MST cells correlated with motion on the screen, not with image motion on the retina, during smooth pursuit eye movements (Inaba, Shinomoto, Yamane, Takemura & Kawano, 2007). Most psychophysical research on extra-retinal signals has therefore been conducted using smooth pursuit eye movements.

Pursuit eye movements are slow, typically with a velocity less than $30^\circ/\text{s}$, and comprise two stages, often called open and closed loops. The open loop stage is approximately the initial 150 milliseconds during which the eye accelerates from being stationary to capturing the image of the moving target onto the fovea. During this time period the visual signals have not had time to travel through the visual system yet, and therefore are not getting any feedback from the eye

movement that would influence the retinal image (Lisberger & Westbrook, 1985; Krauzlis & Lisberger, 1994). Thus it is believed that this initial stage of smooth pursuit is not affected by extra-retinal signals that would otherwise alter the retinal image motion. The second stage, the closed loop, is characteristic of steady-state eye tracking, during which the pursuit and the optokinetic systems interact, correcting for eye velocity to compensate for retinal slip. The optokinetic system allows holding the image steady on the retina during sustained eye-rotations, whereas smooth pursuit allows keeping the image of the moving target on the fovea. It the closed loop stage of smooth pursuit that the eye movement signal reaches higher brain areas and interacts with the visual information.

Perceived stimulus motion during the open loop stage of smooth pursuit may significantly differ from that during the closed loop stage, because it relies mostly on a retino-centric (image motion on the retina), as opposed to head-centric (motion in the scene relative to observer) frame of reference. The closed loop stage is influenced to a large extent by the eye movement signal which cancels the re-afferent motion (e.g., Bradley, Maxwell, Andersen, Banks & Shenoy, 1996). The types of cells carrying visual and extra-retinal information as well as the cortical site where the transformation from retinal to head-centric parameters takes place has been mainly identified through psycho-physiological studies on animals, and will be discussed later in section 5.1.

4. Early psychophysical studies of the extra-retinal signal

Many studies investigating the degree of perceptual stability during pursuit eye movements measured the strength of the Filehne Illusion (FI) by presenting a

background stimulus (often consisting of a patch of dots or a grating) moving in the same direction as the pursuit eye movement (e.g., Mack & Herman, 1978; Wertheim, 1987; de Graaf & Wertheim, 1988). The velocity of the background stimulus is adjusted so that it compensates for the illusory background motion until the background is perceived as stationary. It is assumed that if the background is actually stationary with respect to the head, it will be perceived to move with the same adjusted velocity but in the opposite direction. Most of the studies used stimuli that were either stationary or moving collinearly with the eyes. The studies demonstrated that the FI can be modified by different stimulus display configurations. For example, Mack and Herman (1973) showed that during eye movement, a compensatory velocity must be added to the stationary background until it is perceived stationary during a 500 ms exposure, but they also observed that increasing the stimulus presentation time from 0.2 to 1.2 second leads to smaller FI effects (Mack & Herman, 1978). Further, after eliminating relative motion cues in the short presentation, a much lower loss of stability was reported. Mack and Herman (1978) concluded that shorter presentation of the stimulus and close adjacency of the stimulus to the target leads to a greater loss of background stability during smooth pursuit. These findings were essentially in support of the notion that the visual system may use two different modes of perception because a large patterned background (which dominated the visual stimulation) decreased the FI.

De Graaf and Wertheim (1988) further identified that it was the stimulus exposure duration, not the stimulus-target adjacency that is critical for the strength of the FI, supporting earlier findings by Wallach (1985) and Mack and Herman

(1978). They varied exposure time of a stimulus (a patch of random white dots) but maintained the adjacency of stimulus and target constant. They found that longer stimulus presentation increased the extra-retinal signal more than the visual signal. This interpretation was later extended by other researchers who suggested that extra-retinal signals may have a slower time course, and increase over the course of eye movements (Grigo & Lappe, 1999). These studies all implied that the extra-retinal signal is weaker than the retinal signal, causing under-estimation of the eye movement velocity which in turn leads to perceptual errors such as the FI. If the estimated eye speed is lower than the actual eye speed, the extra-retinal signal encoding the eye velocity is also reduced, causing incomplete compensation for retinal motion, ultimately leading to the illusory backward motion.

While these studies emphasize the importance of the visual display characteristics (e.g., size and exposure time) in veridical perception, there is also evidence for other factors, such as the age of observers or the presentation of stimuli to the visual periphery. Wertheim and Bekkering (1992) reported that older people tend to experience an inverted FI (the dots appeared to move in the direction of the eyes) under conditions that evoke a classical FI in younger participants. In addition, a very large FI has been noted when background stimuli were presented to the retinal periphery (Ehrenstein, Mateef & Hohnsbein, 1986). This is an interesting observation, since the extra-retinal signal has traditionally been assumed to encode 80% of the eye velocity (relative to the head) and was assumed to dominate perception (Wertheim, 1994). The perceptual changes as a result of

aging and retinal eccentricity are more difficult to explain simply by the combination of retinal image motion and an eye movement signal.

Haarmeier and Their (1996) discovered that the FI can be modified by information unrelated to the retinal image motion and eye movement. They measured the FI in trials that were interleaved with “conditioning” trials in which high retinal slip was generated by a background moving horizontally at a constant velocity. The “conditioning” background velocity preceding a test trial was predictive of the size and direction of the FI. A large FI occurred when the background velocity in the conditioning trial was in the direction opposite to the eye movement. When the background in the conditioning trials moved in the same direction as the eyes, the FI was quite small and invariant, and a strong inverted Filehne Illusion was achieved only when the preceding stimuli moved in a direction opposite to eye movements. In other words, the changes in the FI were attributed to the retinal image slip of stimuli in preceding experimental trials. Other studies also found asymmetrical changes of responses, although in different experimental contexts. For example, Wallach, Becklen & Nitzberg (1985) found the perception of motion is more accurate when the stimuli move in the same direction as the eyes. Similarly, Brenner (1993) also found that background motion opposite to the eye movement affects perception to a larger degree than a background moving in the same direction as eyes. Although these findings do not explain the exact mechanism for the perceptual changes, they imply that motion perception is dependent on the unique interaction of the presented visual information and extra-retinal signals.

The incomplete cancellation of the eye-movement-induced retinal image motion has been an attractive explanation of the FI (illusory perception of motion during eye movement). The hypothesis is that oculomotor activity is under-estimated by the visual system and thus is under-represented in the extra-retinal signal. This under-registration hypothesis has been supported by the Aubert-Fleischl phenomenon (Aubert, 1886; Fleischl, 1882; Dichgans, Korner & Voigt, 1969; Mack & Herman, 1973), i.e., when the perceived speed of a pursued object is slower than when the object is viewed with eyes stationary. When the object is pursued, its velocity cannot be estimated from the retinal image motion because there is almost no retinal image motion, and can only be derived mainly from the extra-retinal signal generated by the moving eye (Wertheim, 1981).

The above hypothesis explaining the Aubert-Fleischl (A-F) phenomenon cannot account for situations when the stimulus is of low spatial frequency. For example, Dichgans, Wist, Diener and Brandt (1975) reported the A-F phenomenon is less evident for stimuli of low spatial frequency than it is for stimuli of higher spatial frequency. Wertheim (1994) suggests that high spatial frequency gratings are less optokinetic than low spatial frequency ones when they are observed with eyes stationary. This means that low spatial frequency gratings induce a higher reference signal and have larger motion thresholds which leads to slower speed perception (this also supports the higher perceived stationarity of larger stimuli). When high and low frequency gratings are tracked by the eyes, there is no flow across the retina and no visual modulation of reference signals occurs. Freeman and Banks (1998) point out that when a test and standard grating are presented in two intervals wherein the eyes are stationary (and where the spatial frequency of

the test grating is varied), the matching speed increases as the spatial frequency decreases. Thus retinal gain, which refers to the estimation of retinal speed by the visual system, changes depending on spatial frequency. However, the effect of spatial frequency was not as strong when the test grating had been viewed during smooth pursuit eye movement. Moreover, as the eye movement speed increased, the effect of spatial frequency weakened (Freeman & Banks, 1998). Becklen, Wallach & Nitzberg (1984) also showed that if there is another stimulus in addition to the pursued one, its direction of motion is misperceived toward its retinal image motion during eye movement. In summary, these findings imply that visual information contributes to the eye movement compensation process in a number of different ways.

5. Eye movements and self-motion

The previous sections have described research concerning eye movement compensation arising when simple uniform motion occurs in two-dimensions. These studies assume that the observer is static in the environment and this is a great simplification of what happens in the real world. A more challenging problem for the visual system arises when a person moves through the environment, and simultaneously moves their eyes (e.g., Regan & Beverly, 1982; Warren & Hannon, 1988). When a person is stationary and only their eyes move, eliminating the self-motion generated retinal signal would be relatively easy because the motion on the retina is largely uniform. It is uniform in the sense that the majority of the motion elements have the same speed and direction (rightward eye movement will produce a uniform retinal motion to the left in the central part of the visual field). It is therefore possible to just cancel all of the image motion.

The image on the retina however becomes more complex when the observer moves through the environment while at the same time moving their eyes, as it will now contain multiple directions and speeds. The directions and speeds are a function of the (unknown) distances to the objects in the world and the observer's heading direction. In this moving observer situation the resulting retinal image motion cannot be removed altogether. Only the eye movement induced retinal flow has to be cancelled, while the retinal image motion component resulting from translation needs to remain in order for the visual system to extract features such as the observer heading and the relative depth of points in the field. Figure I.1 portrays the retinal image generated by the eye movement and observer's forward movement (Perrone & Krauzlis, 2008). The retinal image during eye rotation is made complicated by the observer's movement. The radial image motion generated during forward translation of the observer with no eye movement is combined with the uniform image motion during eye movement. The resulting image motion generated during simultaneous forward translation and smooth pursuit contains multiple directions and speeds. It is made up of the vector sum of the vector representing image motion during eye movement and the vector generated by the observer's forward motion (assuming no relative motion of objects within the visual scene). In order to have access to the self-motion vectors, the visual system must remove the pursuit vectors. The question is how does the human brain perform the vector subtraction required to solve this complex problem?

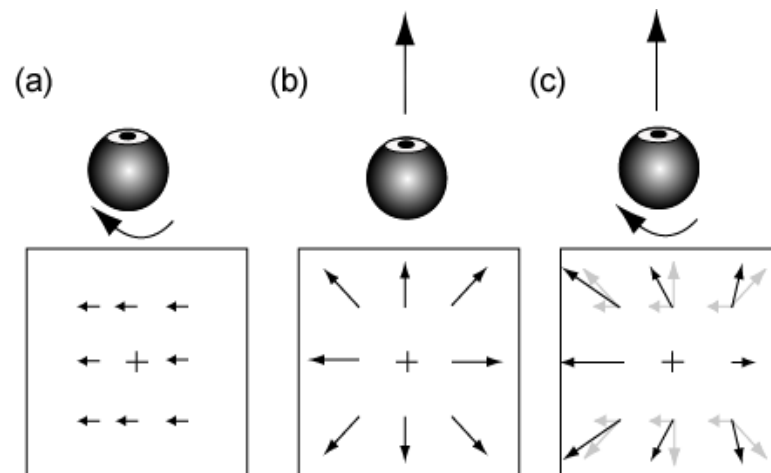


Figure 1.1. Complexity introduced by motion of the observer.

(a) Representation of the retinal image motion caused by a pursuit eye movement to the right with static dots in the background. The flow field is largely uniform in speed and direction. (b) Image motion generated during forward translation of the observer with no eye movement. The image motion radiates out from a point in the middle of the visual field coinciding with the direction of heading. (c) Image motion generated during simultaneous forward translation and smooth pursuit to the right. The image motion is made up of the vector sum of the vectors in (a) and (b) and contains multiple directions and speeds. (From Perrone & Krauzlis, 2008)

Whether or not the human visual system can actually perform the vector subtraction required to solve this problem of retrieving heading direction during eye movement has been investigated by many researchers to date (e.g., Warren & Hannon, 1988; Royden, Banks & Crowell, 1992; Stone & Perrone, 1997). It has also been shown that visual information may be used to some extent to compensate for the eye movements and under certain circumstances, heading direction can be recovered from optic flow displays modified by simulated eye movement, using only visual stimuli (Li & Warren, 2000; Warren & Hannon, 1988; Crowell & Andersen, 2001; Stone & Perrone, 1997, Longuet-Higgins & Prazdny, 1980). For example, it has been shown that it is theoretically possible to recover heading from optic flow alone when depth variations are present in the scene that help separate rotational from translational flow (Longuet-Higgins &

Prazdny, 1980). Others have shown that people are able to estimate their heading direction more accurately during pursuit eye movement than when they are presented with displays contaminated by a simulated eye movement. This indicates the importance of the extra-retinal information (Banks, Ehrlich, Backus & Crowell, 1996; Royden, Cahill & Conti, 2006). Heading judgments were more accurate in real eye movement conditions in contrast to simulated eye movements on a visual display, when pursuit speed was increased (e.g., Royden, Banks & Crowell (1994). Extra-retinal eye movement information is required for accurate perception in situations when translation and rotation are not well specified by optic flow alone, (van den Berg & Beintema, 2001). It is now generally agreed that extra-retinal signals, such as those produced by eye movements, help resolve the retinal perturbation to the expansion flow field caused by eye movements and that the reafferent motion cancellation process is required.

5.1 Neurophysiological research on motion perception

The eye movement compensation mechanism requires brain cells that respond to optic flow stimuli such as those produced by forward motion and also respond to image motion caused by the movement of the eyes (Bradley, Maxwell, Andersen, Banks & Shenoy, 1996). Higher motion processing areas such as the MSTd and VIP have been identified as being able to process such image motions, but just how these areas represent and code for the velocity vectors underlying the eye-movement cancellation is currently unknown. The solution to the eye rotation problem requires the equivalent of vector subtraction to occur somewhere in the brain – the visual system needs to subtract vectors representing the retinal image

motion due to eye movements from the combined retinal image motion. But where do the vectors come from? How are they represented in the brain?

Early physiological studies on cats and monkeys have provided insight about how visual motion could be analyzed in the brain. It was discovered that the visual pathway is largely hierarchically organized and visual information is processed through stages in this orderly fashion (Hubel & Wiesel, 1962, 1965). Based on numerous physiological experiments, a motion perception pathway has been identified, which includes the middle temporal area (MT) and the medial superior area (MST) of the extrastriate cortex.

Middle Temporal lobe

Evidence for MT as an area where motion is processed by the visual system was first found in primates (Dubner & Zeki, 1971; Maunsell & Van Essen, 1983a). MT neurons that receive input largely from V1 neurons, are also organized into columns, but unlike some V1 cells, they are nearly all sensitive to a particular direction of motion (Albright, Desimone & Gross, 1984). MT neurons also have substantially larger response fields than neurons in area V1 (Movshon & Newsome, 1996). In general, they have been classified as two types, the component and the pattern type. The component type responds to motion of one-dimensional objects such as a single oriented lines or gratings. Pattern cells respond to motion of a two-dimensional pattern, often formed by superimposing two independently moving gratings or lines. Movshon, Adelson, Gizzi and Newsome (1985) and Rodman and Albright (1987) identified these two types of MT cells based on their differential responding to moving gratings and plaid

stimuli. For example, a moving pattern stimulus composed of two sinusoidal gratings that have different orientations but are similar in contrast and spatial frequency is perceived as one moving pattern only (Movshon et al., 1985; Adelson & Movshon, 1982). On the other hand, if these gratings have differing contrast and spatial frequency, they are perceived as two component gratings moving over one another (Adelson & Movshon, 1982). Besides their direction selectivity, most of the MT cells were also found to be selective for speed and binocular disparity (Maunsell & Van Essen, 1983a, 1983b), but not for stimulus shape or colour (Maunsell & Van Essen, 1983a; Zeki, 1974). The ability to respond to individual velocities that combine into a complex motion has led to the conclusion that the MT is a site for integrating visual motion.

The role of MT in the perception of motion has been examined in many studies. For example, Newsome and Pare (1988), using motion coherence stimuli, found that an ibotenic acid lesion in area MT of a macaque monkey raised the coherence threshold for random dot kinematograms four times. In another experiment, Newsome, Wurtz and Komatsu (1988) revealed that MT neuronal activity was significantly reduced when retinal input was briefly removed during eye movement. Similarly, Newsome, Wurtz, Dursteller and Mikami (1985) found that lesions to monkeys' MT cells that encode inputs from the peripheral visual field lead to impairment in the ability to perceive motion and to initiate smooth pursuit. They suggested that damage to MT cells disabled smooth pursuit initiation because in order to track a moving object, one needs to be able to detect it first. Born, Groh, Zhao and Lukasewycz (2000) provided further evidence that MT cells can differentiate the relative motion between an object and its background.

They showed that cells with center-surround receptive fields respond best to local motion contrast, while some MT neurons without the center-surround properties respond best to large fields moving in the same direction.

Previous studies of motion sensitivity showed that MT neurons are speed tuned and respond selectively to a particular speed of an object, such as a moving bar or edge (Maunsell & Van Essen, 1983a). These neurons were tested with a range of spatial and temporal frequencies using gratings to specifically map out their response profiles (Perrone & Thiele, 2001; Priebe, Cassanello & Lisberger, 2003). For example, Perrone and Thiele (2001) demonstrated that many MT neurons have inseparable (fixed) spatiotemporal receptive fields and their response profiles are elongated and oriented in the spatio-temporal frequency domain which indicates the neuron's preferred speed. However, the mechanism of how the actual speed is extracted from the individual MT outputs is currently not known.

In summary, MT neurons have been regarded as being responsible for the local integration of pattern motion on the retina caused by moving stimuli in the visual field. Because of their responsiveness to local retinal image motion, MT cells provide visual information to pursuit system and thus play role in pursuit initiation (Newsome, Wurtz & Komatsu, 1988). In order to look at a moving object and initiate pursuit, the visual system uses signals derived from the retinal image motion of the object of interest (Lisberger, Morris & Tychsen, 1987). An increasing amount of evidence now suggests that these signals are generated by the motion pathway which includes area MT, but also area MST which is adjacent to area MT and receives most of its input from area MT (e.g., Zeki, 1974;

Maunsell & VanEssen, 1983). Single neuron studies have explored a possible role of these areas in smooth pursuit and found a population of pursuit cells that are activated during smooth pursuit of a dot against a black background (Komatsu & Wurtz, 1988a). It is not well understood yet how these cells are involved in signal processing of eye position or eye velocity during pursuit, but there is a suggestion that area MST is specifically involved in distinguishing self-motion from the image motion of the stationary background that also moves on the retina during pursuit (Inaba, Shinomoto, Yamane, Takemura & Kawano, 2007; Page & Duffy, 1999; Celebrini & Newsome, 1994). This distinction is important for maintaining stability of the world during eye movement.

Medial Superior Temporal lobe

There are a variety of MST neurons which are selective for different types of complex motion, such as that generated by eye rotation or translation. For example, cells in the dorso-medial region of MST (MSTd) have large visual response fields (Komatsu & Wurtz, 1988a; Tanaka, Sugita, Moriya & Saito, 1993), and respond best to large-field patterns such as expansion or rotation (Tanaka & Saito, 1989; Duffy & Wurtz, 1991). They have therefore been ascribed a role in the determination of heading and self-motion and their properties support this function (Perrone & Stone, 1998). In addition, some MST neurons are responsive to pursuit eye movements. Early experiments by Newsome and colleagues (1988) suggested that the activity of pursuit MST cells was related to an extra-retinal input because MST neurons, unlike MT neurons, continued to fire in the absence of retinal stimulation, implying that pursuit eye movement was driven by extra-retinal signals. Area MST has therefore been implicated as a

possible site for integrating retinal motion with the motion of the eye (Newsome et al., 1988; Thier & Erickson, 1992).

Some studies have provided additional evidence that area MST is the likely site for combining optic flow and eye movement information because MSTd neurons are sensitive to eye position (Bremmer, 1997; Squatrito & Maioli, 1997) and some selectively respond to direction of pursuit eye movement (Dursteler, Wurtz & Newsome, 1987; Komatsu & Wurtz, 1988). Researchers also showed that MSTd cells may be comparing the extra-retinal with the retinal signals (Haarmeier, Thier, Repnow & Petersen, 1997; Haarmeier, Bunjes, Lindner, Berret & Thier, 2001), and that these signals are used to differentiate between external and self-induced motion (Erickson & Thier, 1991; Ilg, Schumann & Thier, 2004). In sum, MSTd neurons respond to various types of motion such as expansion, contraction, translation or their combination, which are components of optic flow, and their behavior has been emulated by a number of computational models (e.g., Crowell & Andersen, 2001; Perrone & Stone, 1992; van den Berg, Beintema & Frens, 2001; Pack & Mingolla, 1998).

Bradley, Maxwell, Andersen, Banks and Shenoy (1996) recorded the responses of a single MSTd cell to optic flow stimuli during smooth pursuit. The responses were recorded in two conditions presenting identical visual but different extra-retinal input. One condition presented an expanding optic flow pattern during pursuit in a preferred or not preferred direction while the second presented a combination of expansion and translation, while the eyes were stationary (simulating the retinal image motion of the eye movement condition). When the

monkeys made an actual eye movement the neurons responded to the focus of expansion of the presented optic flow pattern and seemed to be ignoring the effect of the eye movement. This suggests that these neurons were somehow able to compensate for the changed retinal image flow field. However, the compensation was only partial.

Motivated by the results from Bradley et al.'s (1996) single cell experiments, Page and Duffy (1999) examined a population of MST neurons and suggested that individual MST neurons do not compensate for eye movement very well (and cannot directly signal heading) because it takes a population of MST neurons to detect the correct heading direction. In their study many MST neurons showed a preferred location of the focus of expansion which could be used in determining the heading direction. Perrone and Stone (1998) demonstrated how maps of MST-like heading detectors could code for the location of the focus of expansion and hence the heading direction. A similar conclusion was reached by Paolini, Distler, Bremmer, Lappe and Hoffmann (2000), who showed that the computation of the heading direction is achieved by a cluster of neurons rather than a single neuron.

Neurons in MST also show activity during smooth pursuit in the absence of retinal stimulation and may respond to external head-centric rather than retinal motion, suggesting that perhaps area MST receives retinal signal from MT neurons and combines it with eye movement signals (Ilg, Schumann & Thier, 2004; Inaba, Shinomoto, Yamane, Takemura & Kawano, 2007; Inaba & Kawano, 2009). These extra-retinal signals help in perceiving the pursuit target as moving although there is no retinal information available (Ilg et al., 2004).

Strong support for involvement of area MST in self-motion and eye movement compensation processing comes from microstimulation studies by Britten and Wezel (1998, 2002). They trained monkeys to indicate perceived heading direction when presented with moving dot displays. Using a microelectrode they were able to locate and activate specific MST sites for detecting visual heading direction. Stimulating MST neurons that were tuned to leftward direction of movement produced an increase in “leftward” responses, suggesting there is a relationship between MST neural activity and heading perception. Activation of these neurons by electrical microstimulation while the monkeys performed a heading task introduces biases in heading perception – the selectivity of MST cells to optic flow changed and thus influenced the perceived direction of heading. In addition the induced biases were often larger during smooth pursuit. These findings support the notion that MST is involved in recovering heading from optic flow cues as well as by the compensation for pursuit eye movements.

Motion processing areas in humans

Researchers using functional magnetic imaging techniques on humans have identified areas homologous to the primate MT/MST (Huk, Dougherty & Heeger, 2002). Electroencephalography (EEG) and Magnetoencephalography (MEG) recordings supported the view that the MST area is involved in motion processing during eye movements, transforming eye movement induced retinal motion into perception of stable world (Thier, Haarmeier, Chakraborty, Lindner & Tikchonov, 2001). Strong evidence for the importance of MST in motion perception during eye movements comes from a study of a patient with bilateral lesions to large parts of the dorsal extra-striate cortex. The patient (RW) showed a complete lack

of eye movement compensation despite normal eye movements and normal motion perception when his eyes were stationary (Haarmeier, Thier, Repnow & Petersen, 1997). RW perceived the world as stationary only if it moved with his eyes, when the retinal image of the world was stabilized. However, when he moved his eyes across a stationary background, he experienced a 100% Fiehn Illusion. Because neurophysiological studies imply that visual information is transferred from retinal to head-centric co-ordinates within area MST (Andersen, Snyder, Bradley & Xing, 1977), Haarmeier et al. suggested that RW's lesions interfered with his ability to combine retinal and eye-movement signals.

In summary, physiological research on primates together with functional imaging research on humans has provided ample evidence that the perception of visual motion is based on a mechanism involving eye movement (extra-retinal) signals and that this mechanism is located in the later parts along the visual processing pathways, namely area MST. However, the exact mechanism of decomposing optic flow into rotational and translational components remains unclear, leaving the "eye rotation problem" unresolved. Unless it is revealed how this eye rotation problem is disentangled, it may be premature to look at the more complex, 3-dimensional scenario which would include the observer's body and head movement. The following section is a brief review of computational models of motion perception during pursuit that attempted to mathematically explain the interaction of visual and eye movement signals.

Chapter II. Models of motion perception during eye movement

Early theories of motion perception together with the neurophysiological studies have inspired the formation of models that try to explain the eye movement compensation process in more detail, but many of them were based on computations that were not biologically based, or do not include realistic stages of motion processing analogous to the visual processing pathway described in the physiological studies mentioned above. The following sections review how the original model of reafferent motion cancellation mechanism (formulated by von Holst & Mittelstaedt in 1950) has been expanded upon in the last 20 years.

1. Linear Model

The traditional theory (von Holst & Mittelstaedt, 1950) explaining visual stability during eye movement is built on the hypothesis that eye-movement information is used to generate a “copy” of the changes in retinal image motion (retinal signal) due to voluntary eye movement. The efference copy is equal to the shift in the retinal image motion but it has an opposite sign to the eye-induced retinal shift. The efference copy signal and the overall retinal signal must be added in order to cancel out the changes caused by eye rotation to achieve veridical perception of the external world. Thus, the head-centric perception (h) is equal to the sum of retinal (r) and extra-retinal (e) signals:

$$h = r + e \quad (\text{Equation 1})$$

This linear combination of extra-retinal and visual signal, however, was found to be too simple as it did not explain certain perceptual effects, such as the Filehne Illusion or the Aubert-Fleischl phenomenon (Freeman & Banks, 1998).

Freeman and Banks developed the idea that head-centric perception is a linear combination of retinal and extra-retinal signals. These authors showed that perception is affected by erroneous retinal and extra-retinal signals. They adopted the traditional view that the extra-retinal signal is added to the retinal signal in a linear manner to achieve objective perception of the world, and thus the estimated eye velocity and retinal velocity are independent of each other. However, they proposed a model in which they describe the retinal and eye movement velocities in a vector form, where the retinal vector refers to the projection of a stimulus onto the retina during eye movement, and the extra-retinal vector refers to the eye movement velocity. Perceived head-centric velocity is then viewed as the sum of the two estimated velocities (see Equation 2) which are linearly related to the physical velocities. They also showed that perceptual accuracy may vary because the retinal and eye velocities are subject to estimation errors. As later pointed out by Freeman (2004), perceptual errors can only be evaluated by comparing them to some other, true standard. Comparing extra-retinal signals to retinal signals does not mean that the retinal signal is veridical (having a gain of 1). In other words, the retinal as well as the eye-movement information is subject to noise and therefore, the perceived head-centric motion is affected by both extra-retinal and retinal errors that reach the higher brain area where they are combined.

Specifically, Freeman and Banks' model assumes that head centric velocity of an object is the sum of true retino centric and eye pursuit velocities (Equation 1), but they point out that the retinal and eye velocities are estimated by the visual system and so they are both subject to errors. Therefore, the perceptual outcome will also reflect these errors and can be reformulated as:

$$h' = e' + r' \quad (\text{Equation 2})$$

These errors assume a linear relationship between the estimated and real velocities and can be expressed as:

$$e' = \epsilon e$$

$$r' = \rho r$$

Where the ϵ represents the extra-retinal signal gain and ρ represents the retinal signal gain. The head-centric velocity is then expressed as :

$$h' = \epsilon e + \rho r \quad (\text{Equation 3})$$

Freeman and Banks showed that these errors are dependent on the spatial frequency of the stimulus. In their experiment participants were asked to match the velocity of a test grating of varying spatial frequency (interval 1) to that of a standard grating (interval 2) during pursuit (0°/s, 3.1°/s, 6.2°/s and 9.2°/s). Freeman and Banks were therefore able to say that when the perceived velocity of the test (h'_1) matched the perceived velocity of the standard grating (h'_2),

$$h'_1 = h'_2$$

therefore, substituting the Equation 3 definition for h' we get:

$$\rho r_1 + \varepsilon e_1 = \rho r_2 + \varepsilon e_2 \quad (\text{Equation 4})$$

where ρr_1 and ρr_2 are the retinal signals, and εe_1 and εe_2 are the extra-retinal signals in the two intervals. The formula can be rewritten as:

$$\varepsilon/\rho (e_1 - e_2) = r_2 - r_1 \quad (\text{Equation 5})$$

which suggests that the individual gain parameters ε and ρ cannot be estimated from experimental data and the parameter of interest is the ratio of the two gains. It also implies that the effects of experimental factors on the perception of motion during pursuit cannot be uniquely linked to changes in either the retinal or extra-retinal signal (Freeman & Banks, 1998). In other words, any deviation of the ratio from 1 only indicates that the head-centric motion is not perceived veridically. This model was shown to describe the perceived velocity of not only collinear target-stimulus motion, but also other stimulus directions ranging from 0° to 360° relative to a target (Souman, Hooge & Wertheim, 2005).

Wertheim (1994) also modified the traditional theory of von Holst and Mittelstaedt (1950) that proposed that perception is the sum of retinal and extra-retinal signals. He substituted the concept of extra-retinal signal with that of a “reference signal” which may not be purely motor (as the traditional theory implies), but could comprise of visual as well as vestibular components

(Wertheim, 1994). This modification preserves the main idea that eye movement information is necessary to perceive objects in the environment veridically.

However, it also addresses the traditional theory's failure to distinguish between absolute object motion in the environment and relative motion of objects with respect to each other, which is a concept stemming from the Direct theory of motion perception (Gibson, 1966, 1979).

Wertheim's "reference signal" explains why the Filehne Illusion is not experienced normally during eye movements. When the head is stationary, the reference signal encompasses the efference copy as well as the visual and vestibular components. Thus, Equation 3 was expanded to reflect the additional components in the reference signal. The following equation represents errors as gains but the vestibular signal is omitted here,

$$h' = \rho r + (\epsilon e + \gamma r) \quad (\text{Equation 6})$$

where ρ is the retinal signal gain, ϵ is the purely eye movement-related signal gain and γ is the gain associated with the visual information that is proposed to be part of the overall reference signal (e.g., the relative motion of the eye and the external object). In this equation, the visual properties affect the retinal and extra-retinal signal differently and independently. The γr is encoded in the reference signal coming from the eye and so cannot be cancelled out by the retinal signal (ρr) prior to the signal combination stage. This equation is similar to Freeman and Banks' model (Equation 3) but adds visual and vestibular components as part of the extra-

retinal (compensation) signal. These additional components, however, cannot be experimentally quantified.

According to Wertheim, illusions only occur if eye velocity is not correctly estimated by the visual system. Under normal circumstances, in daylight, re-afferent motion on the retina produces an additional visual component that is compensatory to some extent. So even if the eye movement-related signal (ϵ_e) is undersized, the visual component of the reference signal (γ_r) increases the compensation. Wertheim's reference signal model also explains the phenomena of "object-relative" and "subject-relative" motion. While fixating on a small stationary stimulus, the large moving surroundings generate a reference signal, making the small stationary stimulus appear as moving. If one pursues the surrounding field, the small stationary stimulus appears to move in the direction opposite to the pursuit (just like in the Filehne Illusion). The visual and extra-retinal components of the reference signal interact in a non-linear fashion, depending on eye movement and background characteristics. Wertheim thus expanded upon the existing literature by suggesting that the reference signal is changeable, depending on the size of extra-retinal (eye movement) and visual signals. However, he did not expand on how the proportions of each signal interact with one another or what influences their interaction.

More recently, Freeman, Champion and Warren (2010) explained perceptual estimates during smooth pursuit using a completely different approach than that of using vector algebra: the authors turned to the Bayesian theory of probability. The idea behind the Bayesian theory-based model (Freeman et al., 2010) is that our

perceptions are influenced by our prior experiences and expectations stemming from the experiences. More specifically, during smooth pursuit, one is less certain than during eyes stationary about the motion signals of the stimulus, and the authors suggest that the observer responds based on a probability distribution rather than according to an absolute image motion signal. In Bayesian theory the uncertain sensation is resolved by prior expectation about the stimulus. As Freeman et al. (2010) point out, “for motion perception, a plausible prior is that objects are largely at rest. The prior is therefore centred on [zero] in which case perceived speed decreases as uncertainty rises” (p. 757). Further, this probability distribution about the experienced world influences our perception of a new unknown set of variables collected by our sensory system. Based on this framework Freeman and his colleagues were able to explain perceptual biases, such as the Filehne Illusion and Aubert-Fleischl phenomenon.

In comparison with many previously developed models of motion perception the Bayesian model does not describe the perceived signal as a single vector, but rather as a probability distribution of vectors based on the observer’s prior experience. This type of representation allows the visual system to integrate information from different sensory stimuli across different locations and times without selecting one specific outcome. The Bayesian model also recognizes the importance of relative motion (between the target and background object) and pursuit-target motion. Relative motion had been shown to dominate absolute retinal image of an object during eye movement and pursuit is not always accurate in comparison to the actual target motion (Freeman et al., 2010). Motion perception is therefore viewed as a result of 2 different steps (see Figure II.1). One

is the measurement stage where separate noise sources influence the retinal motion and pursuit target motion signals. The other, the estimation stage, involves two separate estimators for R_m and T_m , depending on the respective probability distributions. The two estimates, R' and T' are added to retrieve H' (observer's estimate of heading). In this regard, the Bayesian model of motion perception during eye movement is similar to the linear model, except that the linear model involves vector summation rather than summation of the probability distributions.

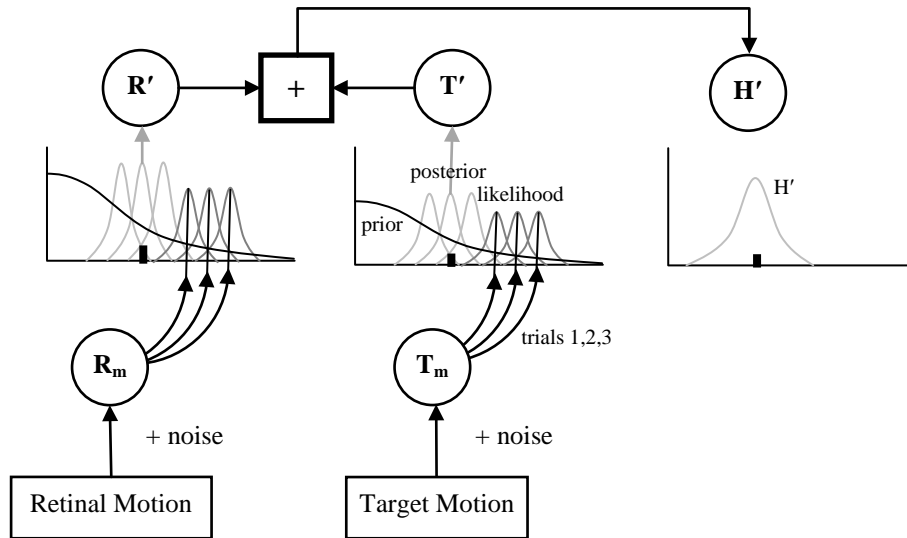


Figure II.1. The Bayesian Model applied to motion perception during eye movements (Freeman et al., 2010). This model was designed to account for perceptual errors such as the Filehne Illusion and Aubert-Fleischl phenomenon. At the measurement stage, measurements by the visual system of the sensory signals coming from retinal image and eye movement velocities are inexact due to noise associated with each source of information. In both the retinal image motion measurement (R_m) and Target motion measurement (T_m) the noise varies as a function of speed and sets the spread of likelihoods. At the estimation stage, R' and T' are the estimated speeds obtained by multiplying the prior with the likelihood. The sum of R' and T' provides an estimate of the head-centered motion (H'). (Adapted from Freeman et al., 2010)

The estimate of motion during eye movement (without body or head movement), which is represented as a combination of R' and T' , is the posterior probability

which is proportional to the likelihood of visual and extra-retinal information. The Bayesian approach assumes that the retinal and extra-retinal signals are independent, so the latter would have a large effect when optic flow is ambiguous and less effect when heading is well specified by optic flow alone. This argument is in agreement with the earlier concept of the reference as a compound signal that is influenced by eye movement as well as visual information (Wertheim, 1994).

Using the Bayesian reasoning to interpret participants' perceptual bias (when estimating a stimulus motion direction during eye movement), the bias is thought to originate in the sensory stage (represented by likelihood functions) and propagated through the visual system in a combination with prior expectation of the world being stationary. According to Freeman et al. (2010), the uncertainty about the world translates itself to noisier signals (with low precision and a wider probability function). Therefore, one can view the estimates as selections from a probability distribution rather than matches to discrete perceptions of the stimulus direction.

2. Non-linear Models

Non-linear models in the context of eye movement cancellation are normally those that do not assume that the retinal image and eye velocity are independent and linearly related to the physical velocities. For example, Turano and Massof (2001) propose that both retinal image and eye movement estimates are non-linearly related to their actual, true velocities, and that the estimated eye velocity \hat{e} is based on an interaction between eye velocity e and retinal velocity r .

According to this model,

$$\hat{r} = R_{max} \left(\frac{1}{1+e^{-\rho r}} - .5 \right) \quad (\text{Equation 7})$$

$$\hat{e} = R'_{max} \left(\frac{1}{1+e^{-\varepsilon e - \alpha r}} - .5 \right) \quad (\text{Equation 8})$$

where ρ , ε and α determine the slopes of the power functions. R_{max} and R'_{max} determine asymptotic values. The variable r represents the retinal image velocity and e represents the eye velocity. The perceived velocity is the sum of the retinal and eye velocity estimates \hat{r} and \hat{e} , respectively (see Figure II.2).

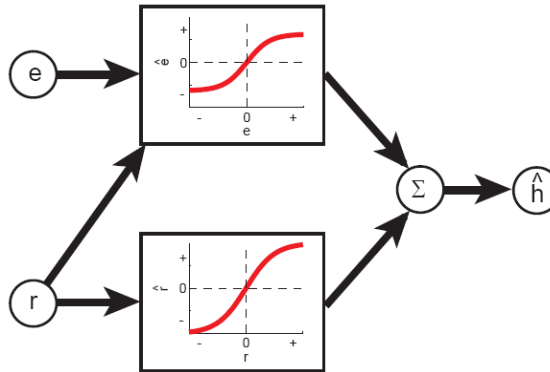


Figure II.2. An illustration of the non-linear model by Turano and Massof (2001). The retinal and eye velocity estimate signals are non-linearly related to the physical velocities. The estimated eye velocity \hat{e} is based on an interaction between eye velocity e and retinal velocity r . (From Souman, 2005)

This non-linear model has four free parameters. Turano and Massof (2001) tested it in a velocity matching task and showed a slightly better fit to the data than the linear model of Freeman and Banks (1998). However, the better fit could have

been due to the doubled number of parameters used compared to the linear model by Freeman and Banks.

In response to Turano and Massof's model, Freeman (2001) proposed and tested an alternative "Transducer model" of head-centered motion perception.

"Transducers" are the input/output functions that convert veridical signals to their estimates. Freeman tested three instances of transducers: (a) linear speed estimation transducers, (b) non-linear speed estimation transducers and (c) hybrid transducers that combined both linear and non-linear components. The model assumed that eye velocity estimation is independent of retinal image velocity.

The non-linear transducers were based on an augmented power law:

$$V_{out} = \text{sgn}(V_{in})[(|V_{in}|+a)^p - a^p] \quad (\text{Equation 9})$$

where V_{in} and V_{out} are the transducers' input and output velocities, and p is the power coefficient. The transducer can change the speed while leaving the direction the same.

The performance of the three transducer versions was compared in three different perceptual tasks: speed-matching, motion nulling and general velocity matching. For the linear transducer model, the free parameter was the ratio of the retinal and eye movement gains, and for the non-linear model it was the ratio of the two powers (retinal and eye movement velocities). Freeman found that the hybrid model is unnecessarily complex and that the improvements of perceptual performance with an increasing number of parameters are only marginal. He also

showed that linear speed transducers adequately describe the Aubert-Fleischl phenomenon (speed matching) and Filehne Illusion (speed nulling) when the ratio of the retinal and eye movement gains is lower than 1. In the general matching task, the linear transducers performed well for some participants, while for others, the non-linear transducers performed better.

3. Other Models of the Compensation Mechanism

So far, previous sections described models that were two-dimensional, with retinal and eye velocity estimations as the two dimensions. Some researchers have considered the compensation process in the context of self-motion estimation, not just eye movements carried out by a static observer (Royden, Banks & Crowell, 1992; Stone & Perrone, 1997; van den Berg, 1993; Warren & Hannon, 1988). It is now generally agreed that an extra-retinal signal contributes to recovering head-centric motion, although sometimes this recovery is not perfect (Crowell & Andersen, 2001; Freeman, Banks & Crowell, 2000), and that the signal corresponding to the cancellation for re-afferent motion is found somewhere in the area MST of primate brain (Bradley, Maxwell, Andersen, Banks & Shenoy, 1996; Page & Duffy, 2000). Compensation-related signals (not necessarily produced by eye movement alone) were also found in areas beyond MST up the visual motion processing pathway (e.g., Zhang, Heuer & Britten, 2004).

Early psychophysical experiments seemed to suggest that the human visual system could solve the rotation problem during self-motion using purely visual means, and so no extra-retinal signal was required (Warren & Hannon, 1988). Therefore a number of models attempted to explain how head-centric motion

perception is retrieved from the retinal image motion, using just the visual signals. For example, Perrone (1992) developed a template model whose computations were tailored to detect patterns of optical flow corresponding to specific movement of the observer. Such a template for detecting forward movement would respond optimally to a pattern of radially expanding velocities on the retina. The uniform retinal motion corresponding to eye movement could also be estimated by rotation detectors picking up the eye and body rotational components from the overall optical flow pattern. The model thus was able to use components that respond to motion similarly to neurons in the primate visual area MT, but did not include eye movement-related signals.

Another model that aimed at explaining how heading is retrieved from the overall retinal image motion was the neural network model by Lappe (1998). Although this model was presented as containing levels of neurons corresponding to areas MT and MST in primate cortex, the actual computation of heading was not based on biological properties of those areas. The heading was extracted mathematically, without using actual eye-movement information. For example, the first layer cells (MT cells) were described as “speed tuned” but it was not clear how they delivered the velocity signal to the second layer (MST area). Although the model is able to differentiate head-centric motion from motion induced by eye rotations, it lacks a realistic input stage preceding area MST.

For a model to be biologically sound, it is important that any eye movement cancellation process at the MST level be based on the properties of neurons from the earlier motion processing stages, such as MT neurons which respond to visual

characteristics such as object contrast and spatial frequency. The latter properties have been shown to affect eye movement compensation (Freeman & Banks, 1998). A few models have emerged that attempt to emulate the characteristics of neurons involved in motion perception, such as MT and MST neurons. For example, a pursuit model developed by Pack, Grossberg and Mingolla (2001) focuses on the interactions between different types of MST cells while also simulating the properties of MT neurons. Although this model captures the key aspects of the visual and extra-retinal signal interactions, it only uses unidirectional laminar motion during horizontal pursuit. In this regard, it may be limited when generalizing to other pursuit directions and to the case where the observer is translating forward.

Similarly, in a template model developed by Beintema and van den Berg (1998), the responses of template cells tuned to retinal flow were multiplied by a rate coded measure of eye velocity, producing a layer of cells that have a preferred flow field that changed dynamically to compensate for eye movements. Using this modulation (called a “gain field” mechanism), the authors suggested that spatial integration of local motion signals precedes the interaction with eye movement signal. Therefore it seems that the eye movement compensation is achieved by the extra-retinal signal after the local motion signals are pooled, at a global stage, rather than at a local level. The model could derive an estimate of eye rotation from the retinal flow but used a mathematical approximation (Taylor series) for the eye rotation distributions.

Vector subtraction model using cosine distributions of neural activity

A new model proposed by Perrone and Krauzlis (2008) addresses the inadequacies of earlier eye movement compensation models in their attempt to describe how re-afferent motion compensation is achieved in the brain. This model can deal with eye movement cancellation for the case where there are multiple motion directions scattered across the visual field while retaining consistency with MST neuron properties. The model uses the output from a number of MT neurons as an input to the MST cells. A single MT cell is tuned to a particular speed at each image location (Maunsell & van Essen, 1983; Perrone & Thiele, 2001; Priebe, Cassanello & Lisberger, 2003), and so the output of individual MT neurons cannot signal the magnitude of combined retinal image velocity created by simultaneous eye rotation and translation. According to Perrone and Krauzlis (2008), such a velocity signal output would be present only later, after the signals from several MT neurons come together, perhaps in area MST. Similarly, pursuit signals occur mainly in MST, not MT (Newsome et al., 1998; Erikson & Thier, 1991; Komatsu & Wurtz, 1988). They use the earlier mentioned concept of vector subtraction to extract the head-centric motion from a composite retinal image velocity. A vector corresponding to the image motion generated by the eye rotation is subtracted from the vector corresponding to the retinal image motion, which produces a vector corresponding to the head-centric recovered motion. Perrone and Krauzlis (2008) demonstrate how this mechanism could be carried out using cosine distributions for the sensory and motor signals, consistent with the physiological neural activity of MT or MST neurons (see Figure II.3).

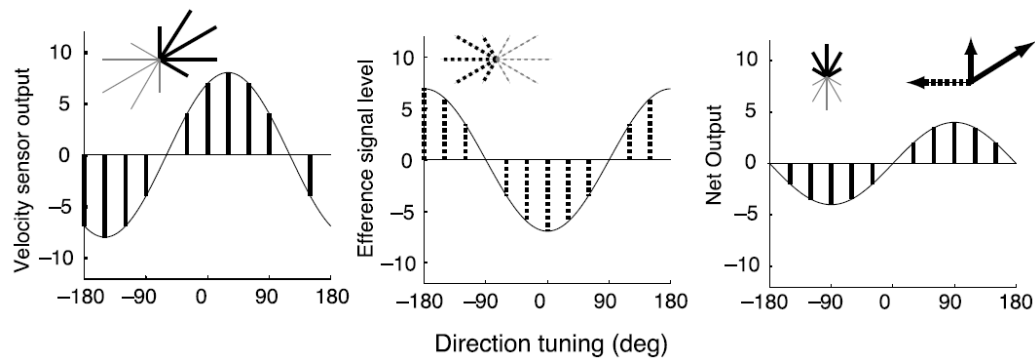


Figure II.3. Vector subtraction using visual motion and extraretinal signals. (a) Cosine distribution representing the output of a set of velocity sensors located at a particular image location. The overall image motion is in a 30° direction with a speed of $8^\circ/\text{s}$. The broad tuning of the motion sensors means that the other directions are activated as well as [it is assumed] that the tuning is cosine. The flower-like insert represents the velocity outputs in polar plot form with the gray lines indicating inhibitory signals. (b) Cosine distribution of activity arising from an extraretinal (pursuit signal) source. The ‘efference copy/corollary discharge’ signal distribution is set to have an amplitude proportional to the speed of the image motion created by the eye movement ($6.9^\circ/\text{s}$) and phase equal to the direction (180°). (c) Sum of the two distributions shown in (a) and (b). It has a peak and phase corresponding to the amplitude and direction of the vector sum of the two motions shown in (a) and (b). (From Perrone & Krauzlis, 2008).

The model assumes that at each location that processes retinal signals there is a set of motion detectors sensitive to motion (tuned to different velocities), resembling MT neurons. When a visual signal is detected, the motion detectors are activated to the level corresponding to its alignment with the velocity of the retinal stimulus. A population code is then used to extract a velocity signal from the distribution of activity across the set of MT neurons. The output of this stage is assumed to be in the form of a cosine distribution that has an amplitude that corresponds to the speed of the stimulus and a phase (shift of peak from its 0° position for cosine) corresponding to its direction. Negative values of the cosine distribution relate to the output of the velocity encoding neurons tuned to opposite directions. The model also assumes that the signals generated by eye rotation have

the form of a cosine distribution. The sum of these cosine distributions represents the perceived velocity. The model essentially shows that the cosine distributions of activity coming from the composite retinal image allow for the possible removal of extra-retinal sources, such as those generated by eye movement.

In summary, when considering eye movements without head or body movements, the optic flow decomposition is believed to occur mainly in the MST area. The question of how the brain is able to disregard the eye-induced retinal image motion has been challenging. The models described above have been formulated and tested alongside various psychophysical studies, which together have shown that an extra-retinal signal is required in the recovery of self-motion information, but that visual information also plays a role in the degree of compensation achieved. The following section reviews some key findings from psychophysical studies that have helped provide more insight into the eye movement compensation mechanism.

Chapter III. Past psychophysical research on perceptual stability during pursuit eye movements

The main question being investigated in this thesis is whether the compensation mechanism in the brain utilizes a form of vector subtraction in recovering heading from the compound retinal image motion. Perrone and Krauzlis (2008) suggested that vector addition or subtraction can actually be carried out if one considers the retinal and extra-retinal outputs to be in the form of cosine distributions. Is this type of vector combination occurring in the brain? Many psychophysical experiments have tested whether vector subtraction is occurring, and many have found support for this type of process. However, the question remains whether this vector subtraction-like compensation process applies to all types of visual and eye movement conditions. Here I will look more closely at the factors that seem to affect the compensation process. The term “stimulus” will be used to refer to a dot or a patch of dots that is to be evaluated by the participant (e.g., its motion direction or speed), and “target” will refer to a dot that is to be tracked with the eyes (generating pursuit eye movement).

The formulation of Freeman’s linear model has ignited new attempts at disentangling the eye movement compensation process. Freeman and Banks (1998) experiments investigating the retinal and extra-retinal inputs included a pursuit-fixate procedure where the stimuli were drifting gratings of various spatial frequencies. Using a staircase method, observers were asked to match the speed of a test grating (varied in spatial frequency) to a standard $1^\circ/\text{s}$ grating viewed for 700 ms during eye movement. Eye movements were monitored and were regarded

as saccadic and unusable when they reached a speed of $10^{\circ}/s$. Freeman and Banks found that the magnitude of perceptual error was dependent on the spatial frequency of the test gratings, not on eye movement gain, which was stable across varying spatial frequencies (around .85).

Similarly, Turano and Heidenreich (1999) also found evidence that supported the hypothesis that retinal and extra-retinal signals are linearly combined to achieve perceptual stability during pursuit. They used a speed matching task and found that when the stimulus moved in the opposite direction to the target, speed perception depended on the stimulus size (an array of random dots). When the stimulus and eyes moved in the same direction, perception followed retinal image motion. The moving stimulus was shown either through a large stationary window (large stimulus) or a small stationary window (small stimulus). When the eyes and stimulus moved in the opposite direction, the speed of a large stimulus was underestimated while the speed of a small stimulus was overestimated compared to the eye stationary interval. The results suggest that the stimulus size affects its perceived speed only when the eyes move in the opposite direction to the stimulus (when the retinal image velocity is increased).

Turano and Massof (2001) showed that a non-linear combination of retinal velocity and extra-retinal signal fits their results better than the linear model with signal gains. Their experiment involved a stimulus consisting of an array of random dots moving horizontally within $24^{\circ} \times 24^{\circ}$ window for 500 ms at 0, 2 or $4^{\circ}/s$ on the retina. The pursuit condition included a target moving horizontally in a gap between the dot arrays at a speed ranging from $.95^{\circ}/s$ to $4.75^{\circ}/s$. Eye

movement gain remained stable for each of the three observers but the average eye movement gain varied between them from .58 to .89. The linear model did well only when the retinal image speed was $0^\circ/\text{s}$. The non-linear contribution of eye velocity to compensation supports Wertheim's idea of a composite reference signal.

The indication of a non-linear relationship between the retinal and extra-retinal signals prompted Freeman (2001) to construct a non-linear "transducer model" (described earlier). The stimuli were not gratings this time, but sparse random dot patterns moving horizontally across the screen and were displayed through an annulus window for 700 ms. The speed of the pursued target was set to 1, 2, 4, 8 or $16^\circ/\text{s}$. Saccades were detected at $40^\circ/\text{s}$ and were not included in the analysis. The non-linearity was based on a power law as opposed to Turano and Massof's (2001) saturating non-linear functions. However, this new non-linear transducer model showed little improvement in explaining the Filehne Illusion and Aubert-Fleischl phenomenon in comparison to Freeman and Bank's linear model (Freeman, 2001).

Souman, Hooge and Wertheim (2005a) examined whether stimuli moving in various directions would have a differential impact on compensation. They used a single stimulus dot moving at 3 or $8^\circ/\text{s}$ in 24 different directions spanning the entire circle. Observers viewed the stimulus while pursuing a target that moved horizontally at a speed of $10^\circ/\text{s}$ and covering 20° of visual angle. Estimates of the stimulus direction were made using a white arrow that could be rotated by moving a computer mouse. Although the measurement method differed from the matching

tasks used in earlier studies, the results fitted the linear model well. The degree of compensation gain was constant across the different stimulus directions as measured by the extra-retinal to retinal signal gain ratio, but was higher for the $3^\circ/\text{s}$ ($e/r = .53$) than the $8^\circ/\text{s}$ stimulus ($e/r = .21$). Souman et al. referred to similar findings by Swanston and Wade (1988) and Wallach (1985) for low stimulus speeds, and suggested that the stimulus speed affects compensation.

In another study by Souman, Hooge and Wertheim (2005b) the degree of compensation was found to vary with stimulus exposure duration during $14^\circ/\text{s}$ pursuit. The pursuit was always horizontal (leftward and rightward) covering 20° of visual angle but moving at 6, 10 or $14^\circ/\text{s}$. The stimulus dot moved vertically (up and down) at $5^\circ/\text{s}$ and was presented for 300, 700 or 1100 ms. Pursuit gain was approximately 1 in all conditions. Increased stimulus exposure time improved compensation only during the fastest pursuit. Compensation did not vary as a function of the moment at which stimulus appeared throughout the pursuit (the varying stimulus presentation times resulted in the stimulus being visible at different stages of pursuit). Instead, Souman et al. concluded that the longer presentation duration increased the extra-retinal signal more than the visual signal. However, there is another possible explanation for their finding. For example, the relative speed of target and stimulus varied substantially during the fastest pursuit. Because the target's travelled distance was kept at 20° of visual angle, but the stimulus' trajectory was not, the increasing stimulus exposure time would result in a longer stimulus path. Therefore, the 1100 ms stimulus exposure would have resulted in a large amount of visual stimulation and this may have helped the compensation signal. In other words, the relative target-stimulus trajectories also

resulted in different retinal stimulus image projections. The constant stimulus speed was relatively low in comparison to the fastest target speed, and it may have produced low retinal stimulation. In this respect, Souman et al.'s finding may not be due to the increased extra-retinal signal but increased visual signal, because increasing the extent of the retinal stimulus trajectory may have helped improve the estimates. It would be useful to further examine the relative target-stimulus speeds and exposure time effect on estimation accuracy.

Souman, Hooge and Wertheim (2006) also examined the perception of stimuli moving at different retinal speeds (head-centric speed was constant), and stimuli moving at different head-centric speeds (retinal image speed was kept constant). The stimulus was a random dot pattern presented for 500 ms during horizontal pursuit. In the first experiment, although the stimulus speed was constant ($8^\circ/\text{s}$) its direction varied, producing different retinal velocities. In the second experiment, stimulus speed was fixed to $7^\circ/\text{s}$ (assuming perfect pursuit). Stimulus directions ranged from 180° to 360° in steps of 20° . The target moved at $10^\circ/\text{s}$ in Experiment 1 and $5^\circ/\text{s}$ in Experiment 2, covering 20° of visual angle. Eye movement gain for all stimulus directions was 1 except for one participant who produced few good trials. A velocity matching method was used in the estimation task which assessed both stimulus speed and direction simultaneously in two dimensions by scrolling a track ball which controlled the stimulus velocity on the screen. The compensation was found to be constant, regardless of head-centric or retino-centric stimulus directions. Results from both experiments provided strong support for the non-linear models (Freeman, 2001; Turano & Massof, 2001),

suggesting that the eye movement signal may be partially determined by visual information.

There are a number of important factors that need to be considered in the study by Souman, Hooge and Wertheim (2006). First, the results were based on 4 participants, only two of whom completed both experiments. It was not noted whether the two groups of participants were matched for pursuit and estimation ability. Further, in their 2nd Experiment the target speed was reduced, but the retinal speed stayed relatively high, producing a strong visual signal. Third, because the retinal speed was kept constant, it was impossible to properly examine how compensation changed with varying retinal image velocities. Compensation was not examined for the different retinal velocities in the first experiment, only for different stimulus directions. They concluded that the compensation mechanism was the same for head-centric and retino-centric motion directions, but acknowledged that more work is needed to specify the effect of retinal image motion characteristics with regard to the eye movement compensation.

Souman and Freeman (2008) explored the temporal characteristics of the eye movement compensation process. They used a somewhat unusual experimental set up that involved a large cylindrical screen of 3.5 m radius and a field of view 240° x 45° horizontally and vertically, respectively. The motion stimulus consisted of two horizontal bands of random dots with a target in the middle strip. The sinusoidally moving stimulus was presented for 2 seconds during horizontal sinusoidal pursuit. Observers compared the stimulus peak velocities in pursuit-fixation intervals. The phase and amplitude of the dot patch varied with respect to

the target motion. A small latency of the extra-retinal signal was found, which had little impact on the compensation. Mainly, the results showed that perceptual errors were due to differences in signal sizes. The signals determine retinal and eye movement velocities in a non-linear, yet independent fashion: the authors did not consider the visual component in the extra-retinal signal in order to explain the data, even though the stimuli spread over a large part of the visual field.

Souman and Freeman (2008) did not find an effect of stimulus-target relative motion direction on compensation. In this respect they supported Souman et al. (2006) finding, but at the same time were in disagreement with other previous studies (e.g., Brenner & van den Berg, 1994; Turano & Heidenreich, 1999). In an attempt to resolve the issue of relative motion, Morvan and Wexler (2009) used residual smooth pursuit after eliminating the target, focusing on the retinal velocity effect. The target dot moved horizontally at $20^\circ/\text{s}$ to a certain position at which point it became the stimulus dot, by becoming brighter and changing motion. The stimulus dot moved at speeds between 5 and $72^\circ/\text{s}$ and directions between 5 and 175° . Estimates of stimulus directions were achieved by rotating a line in the perceived stimulus direction. It was revealed that a stimulus moving in the opposite direction to pursuit was more compensated for than stimulus moving in the same direction as the eyes, and that the compensation was best when the stimulus speed was the largest. They also demonstrated that eye movement may not be the only determinant in the degree of compensation. They hypothesized that when the retinal slip between the stimulus and target is slower than expected when the stimulus was stationary, the visual system could be treating it as a slower eye movement, and thus decreasing the amount of compensation. Their

results indicate that the compensation for eye movement is higher for stimuli that move *against* rather than *with* the eye movement. Overall, the results confirmed earlier observations that retinal information plays a role in the compensation process and that the compensation does not increase on the basis of the pursuit speed alone, but on the relative target and stimulus retinal image motion.

Freeman, Champion, Sumnall and Snowden (2009) also showed that observers rely on the relative motion between pursued target and background and do not need a direct access to retinal motion. They varied the correlation between screen and retinal motion in a speed discrimination experiment and identified two types of relative motion: in one the difference in speed was shown simultaneously, and in the other it was shown sequentially. In the latter case the results revealed that observers were good at making their speed discrimination judgments. This strategy implies that people do not need a direct access to retinal image velocity and can combine motion estimates across time. They seem to use the objective relative motion between target and stimulus incorporating extra-retinal information from eye movement as well as retinal motion information. This finding provides additional insight into how the relative motion between eye movement and external objects can affect perception.

The majority of studies examining the extra-retinal signal used velocity matching tasks and stimuli moving either against or with the target, usually moving in horizontal directions. Even when different stimulus directions were used in the experiments, pursuit direction was always horizontal. Using this limited number of stimulus and pursuit velocities makes it difficult to generalize the results from

these experiments to other conditions, because in reality, eyes move in various directions and so do objects in the visual scene. The question is whether objective motion can be retrieved from retinal image motion using a vector subtraction process. Based on the findings to date it seems that perceived motion can be predicted by a vector subtraction mechanism, but these findings stem from experiments that used only a limited combination of velocities (vectors). To determine whether the linear combination of vectors representing retinal and extra-retinal signals model can sufficiently explain the perception of motion, more experiments using a variety of object and eye velocities are needed. In addition, using a method to measure perception other than velocity matching would also show whether the resulting compensation mechanism can be affected by the measurement method.

1. Summary and rationale for the present research

Neurophysiological research involving primates has systematically characterized a distinct motion processing system in area MST, which integrates eye movement signals and retinal motion signals (e.g., Ilg & Thier, 2003; Newsome, Wurtz & Komatsu, 1988; Bradley, Maxwell, Andersen, Banks & Shenoy, 1996; Erikson & Thier, 1991; Page & Duffy, 1999; Shenoy, Bradley & Andersen, 1999). It has been shown that the ability to perceive the world as stationary during eye movement is a result of an integration mechanism located in the higher cortical areas of the motion processing pathway. Specifically, a significant number of neurons in the posterior area MST were found to differentiate between two types of retinal image motion, responding selectively to externally induced motion or to self-induced image slip. When we move our eyes, we are usually not aware of the

retinal image motion created by our own eye movement. Generally, when tracking an object, the retinal signal encodes the retinal motion velocity and the eye movement signal encodes the extra-retinal signal. Presumably, perceptual stability during eye movement is the outcome of the two signals being compared. If these two signals differ, motion is perceived, even when the background is stationary with respect to the head.

Earlier studies investigated the degree of compensation for the effect of eye movement by examining the strength of the Filehne Illusion and Aubert-Fleischl phenomenon. The strength of the Filehne Illusion has been mainly explored using stimuli that were stationary (Mack & Herman, 1973; Wertheim, 1981; Ehrenstein, Mateeff & Hohnsbein, 1986; Haarmeier & Thier, 1996) or moving collinearly with the target (e.g., Wallach, 1985; de Graaf & Wertheim, 1988; Freeman & Banks, 1998; Turano & Heidenreich, 1999; Morvan & Wexler, 2005). They reported that compensation varied, depending on the visual display characteristics, such as the size (Turano & Heidenreich, 1999), stimulus presentation duration during eye movement (Ehrenstein, Mateeff & Hohnsbein, 1987; de Graaf and Wertheim, 1988), spatial frequency (Freeman & Banks, 1998; Haarmeier & Their, 1996) or relative motion between the stimulus and the target (Brenner & van den Berg, 1994; Turano & Heidenreich, 1999). Similarly, the Aubert Fleisch phenomenon is thought to be a result of the extra-retinal signal carrying an underestimate of the true eye velocity and the strength of the extra retinal signal also depends on the spatial frequency content of the stimulus (Freeman & Banks, 1998). These studies show that the process of compensation for the reafferent motion is not straightforward and is affected by many factors.

The linear model proposed by Freeman and Banks (1998) holds that perceived motion is the sum of two velocity estimates that are linearly related. However, it has been shown over the last decade that perception is not only a result of an inaccurate retinal signal itself but also a result of inaccurate estimation of the retinal signal by the visual system. Although this model explained many examples of motion perception during pursuit, it was less able to account for other experimental data (e.g., Souman, Hooze & Wertheim, 2005; Turano & Massof, 2001). These and other findings led to the conclusion that the recovery of stimulus objective motion is a result of a non-linear combination of the estimated retinal and eye movement velocities. Some authors suggested that retinal and extra-retinal signals are not mutually exclusive and interact in a non-linear manner to produce a composite estimate of eye velocity (Brenner & van den Berg, 1994; Crowell & Andersen, 2001; Wertheim, 1994). The visual system's estimate of eye velocity is partially determined from retinal information. The question remains, how are the retinal and extra-retinal signals combined during eye movement and how is the head-centric motion recovered?

The nature of the non-linear relationship between the retinal and eye movement signals has been addressed by several models on the eye rotation compensation. The development of early computational models based on the physiological and psychophysical findings has led to additional insights into the dynamics of motion processing. For example, the initial belief that lack of compensation, as evidenced by the Filehne Illusion or Aubert-Fleischl phenomenon, is due to under-registration of eye movement signal implied that the retinal image motion signal is more accurate (Mack, 1986). Although the retinal signal may be

veridical, there is no evidence showing this is the case. The mismatch of the retinal and extra-retinal signals being compared simultaneously is often expressed as the ratio (e/r), indicating an “under-registration” of eye velocity. A stationary background stimulus would appear stationary if both signals were equal.

One of the problems in making any firm conclusions about the compensation process regarding retinal and extra-retinal signals is that each study uses different display conditions. Different stimulus characteristics such as shape, size, luminance, contrast, spatial frequency, target and stimulus speed, motion direction, the length of the trajectory path, duration of exposure, stimulus onset during pursuit, as well as different target characteristics are used across different studies. Very few researchers have used stimuli moving non-collinearly with the target. To my knowledge there has been no study to date using pursuits other than horizontal or vertical during which another moving stimulus was to be judged. In the natural environment, our eyes do not just move in horizontal or vertical directions.

Evidence exists that changing the visual characteristics in the display yields to different perceptual experiences. This shows that visual information has an effect on how the retinal and extra-retinal signals are combined, and ultimately has an effect on the compensation process. But what is it in the visual information that makes the compensation vary? Do we use vector subtraction to achieve perceptual stability? What exactly influences the strength of the compensatory signal?

Although current literature generally points to the fact that the extra-retinal signal is affected by visual information to some extent, it is difficult to identify the

factors affecting it because it is difficult to systematically compare the results of the studies. Specifying the factors affecting the strength of the eye movement signal will provide more information on how the retinal and extra-retinal signals interact. At this time, more insight is needed on how the eye velocity signal is combined with the retinal image motion signal in order to resolve the eye rotation problem. One possibility is to examine the compensation signal across different stimulus and target velocities and sizes, while maintaining the same display conditions and stimulus characteristics.

Another problem that arises when comparing the outcomes of different studies is when the perceptual performance was measured using different measurement methodologies. Most studies that examined the eye rotation compensation process used velocity matching tasks where the perceived speed of a stimulus during eye movement was compared to that during eyes stationary. However, the estimation task itself may have an impact on the results as it is possible that the comparison stimulus may affect the extra-retinal signal or even eye movement characteristics which are not detected by an eye tracker (or cannot be manually excluded, such as abnormal pursuit gains). It would be helpful to be able to compare eye movement data and compensation output results across experiments that use an identical display but a different perceptual task.

In summary, investigations into perception of motion during eye movement have shown that the combination of retinal and extra-retinal signals may not be as simple as once thought. Although some findings support the view that the compensation mechanism uses a vector subtraction-like computation, some

studies show that the compensation may vary depending on different stimulus conditions, suggesting a non-linear combination of the retinal and extra-retinal signals. However, it is not well known under which conditions human estimates of object motion during eye movement follow or fail to follow the laws of vector algebra. Existing studies used different types of stimuli, which make it difficult to make comparisons across different studies. For example, gratings of various spatial and temporal frequency (Freeman & Banks, 1998; Turano & Heidenreich, 1999), a patch of dots (Turano & Heidenreich, 1999; Turano & Massof, 2001; Freeman 2001; Souman, Hooge & Wertheim, 2006), single stimulus dots (Souman, Hooge & Wertheim, 2005) or even a dot serving as both pursuit and stimulus (Morvan & Wexler, 2009) have been used. These stimuli varied in size and speed in absolute terms, but also in relation to the eye movement speed. Different relative stimulus-eye movement speeds generate different retinal velocities which can affect perceptual stability by altering the retinal or extra-retinal signal or both. In addition, these studies used eye movements in horizontal directions only and thus the findings may not generalize to other pursuit directions. Some of these studies focused on estimation of stimulus speed using velocity matching task and some assessed the direction of stimulus motion using a line matching task. The lack of comparability across studies due to different perceptual tasks, stimulus types, sizes and velocities and the limited number eye movement directions motivated the experiments in the current thesis.

The current thesis is exploratory and therefore presents a set of experiments that adopt a programmatic approach to investigation. Initial experiments use a single dot as a stimulus to tap into the effects of relative stimulus-eye movement

velocities, while subsequent experiments test the effect of additional background on eye movement characteristics, perception and the compensatory signal. These experiments are designed systematically to focus on identifying factors that affect the perception of object motion during smooth pursuit eye movement, while addressing the gaps of previous research and the lack of comparability across experiments. In particular, the aim is to test people's ability to estimate the direction and speed of object motion using a range of eye movement and object velocities. In addition, the background conditions will be varied to assess their impact on compensation and the eye movement signal. I will examine what features of the retinal image motion affect the strength of the extra-retinal signal. Because an eye tracker will provide information about the eye movement characteristics, it will be possible to measure whether perceptual errors are related to pursuit gain or the strength of the extra-retinal signal. Using different stimulus and eye movement velocities and different backgrounds will help disentangle the relationship between retinal and extra-retinal signal and the nature of their combination in order to achieve perceptual stability of the world.

Chapter IV. Experiment 1: Estimating motion direction of a stimulus during eye movement

The first experiment is derived largely from existing research on perceptual stability during eye movements and presents conditions that produce varying head-centric as well as retino-centric velocities. For example, different stimulus and eye movement velocities will be used to assess how well perceived motion is predicted by the vector subtraction mechanism. A number of eye movement directions will be used to extend previous research that included primarily horizontal pursuit. In addition eye movement speed will reflect a natural scenario, such as tracking a moving object in one's visual field. Stimulus directions will be randomly selected in 45° steps to sample from the entire 360° range in order to ensure that each experiment lasts no longer than an hour to prevent possible fatigue and loss of motivation by the participants. The goal of the initial experiment is to investigate situations where the mechanism appears to break down. The initial findings will prompt the design of the following experiments that can tease out factors or situations which strongly affect the magnitude of the eye-movement signal.

1. Methods

1.1 Participants

Participants for Experiment 1 were recruited through an advertisement on bulletin boards in the Psychology department and the University website accessible to first year Psychology students. Each potential participant was given information about the project, was explained the purpose of the study and given detailed instructions

for the actual task during the experiment. A signed consent form was provided by each person before taking part in the experiment. All had corrected-to-normal vision and to their knowledge had no oculomotor abnormalities. Participants had an opportunity to familiarize themselves with the stimulus display and the response task by completing several practice trials. This practice also provided information about the participants' quality of smooth pursuit eye movement, which was important for generating useable data. Participants were not included in the experiment if their eye positions (measured by the eye tracker) revealed that they produced too many saccades or blinks, if they could not follow the moving target on the screen, or the eye tracker could not properly register their eye movements due to glasses or from an abnormal shape of their cornea. Strict selection criteria regarding the speed and quality of the eye movements were used to ensure that eye movement compensation was measured at its best.

Data for Experiment 1 were collected from 4 males and 2 females whose age was in the range between 24 and 55 years. Out of the 6 participants, 5 were naïve (had no previous experience with similar psychophysical tasks and were unaware of the aims of the experiment) and 1 was an experienced psychophysical observer.

1.2 Eye movement recording

Eye movement was recorded by an Eyelink 1000 desktop mount eye tracker with the illuminator on the right, sampling at a rate of 1000 Hz and producing sample data for x and y eye position. Eye velocity was computed off line using the first derivative of the eye position values. Eye movement data were collected only during a period of time when the target dot (TD) was moving (part of that time the

stimulus was present as well), and eye movement velocity was computed only during the stimulus dot (ST) exposure period. The tracking mode for data recording was monocular (right eye).

Calibration of the eye tracker

A calibration and validation of the Eyelink 1000 eye tracker was performed before each eye movement recording to remove set-up effects, such as the relative position of a participant's eye, the eye-tracker and display. Calibration also standardizes the condition for each participant, accounting for between-subject differences to achieve accurate gaze measurement for all participants and conditions. A standard calibration procedure supplied by the Eyelink was utilized, where the participant was to fixate at a certain number of predetermined and serially presented target points. The difference between the raw gaze position and the actual eye-tracker output values was adjusted automatically by the computer. The calibration lasted approximately 15 seconds. Immediately following calibration, validation of the measured eye position data was performed, also using the Eyelink inbuilt procedure. Validation informs about the accuracy of calibration process, and reflects an error between the gaze accuracy. All participants had to reach valid calibration and validation measures before proceeding to doing the experiment.

1.3 Procedure

The actual experiments took place in the Human Visual Navigation laboratory in the School of Psychology (Faculty of Arts and Social Sciences, University of Waikato). Participants had their head placed on a chinrest to minimize head

movements. Each participant first completed a number of sessions with eyes stationary (control trials) followed by sessions with eye movement. In eye movement trials, participants had to track the target dot (TD) with their eyes while the stimulus dot (ST) moved in the background. The task was to indicate the motion direction or speed (only in speed estimation experiment) of the ST. Each experimental session required the participant to complete at least 10 blocks of trials that generated sufficient eye movement data with no blinks or saccades for a meaningful analysis. Each block of trials included between 20 and 36 combinations (trials) of eye movement and ST velocities, and took about 3 to 4 minutes to complete. After each block, the light in the experimental room was switched on for a few minutes to minimize dark adaptation. The goal was to make the edges of the screen not noticeable to the participants, thus preventing their use as an external frame of reference when viewing the ST. Once the participants were seated with their head fixed in front of the monitor, the edges of the screen display were well in the peripheral area of their visual field of view and were not visible. With the short breaks in between the blocks, one experimental session lasted about an hour. Each experimental session was run on a separate day in order to minimize the effect of tired eyes and lack of concentration.

Stimulus Display

Stimuli were displayed on a 19 inch Dell Trinitron CRT monitor (35.5 cm x 27 cm) with an integrated Intel Graphics Media Accelerator 4500 and a horizontal scan rate of 85 Hz. The display was viewed binocularly from 57 cm distance in a dimly illuminated room. The resolution of the display monitor was 1600 x 1200

pixels, spanning 33° horizontally of visual angle. This equates to approximately 46 pixels per degree of visual angle and 0.022 degrees per pixel.

The experiment was generated using custom software written in Matlab (MathWorks) using Open GL which included elements of the Psychtoolbox (Brainard, 1997; Pelli, 1997). The stimuli included one “target” dot (TD) and one “stimulus” dot (ST). The size of the target dot was 0.22 degrees in diameter and the size of the stimulus dot was 0.20 degrees in diameter. The dots were grey; their luminance was approximately 8.5 cd/m^2 and 4.7 cd/m^2 , respectively (measured by a Chroma Meter CS-100). The ST was of lower luminance in order to lower the visibility of the motion trace which could provide a cue about its trajectory angle. Both dots were shown on a soft black background (average luminance was 0.18 cd/m^2). The background of the arrow that appeared at the end of the trial and was to be rotated, was lighter than the background of the dots in order to minimize dark adaptation during the trials (average luminance was 2.5 cd/m^2) and minimize the ability of the participants to see the monitor frame.

Sequence of events in a direction estimation trial

Timing of the stimulus presentation was controlled by the experimental program (programmed in Matlab). Figure IV.1 shows the sequence of events in the experiments. Each trial consisted of four events. The following is the sequence of events during the trial:

1. A bright (luminance 25.5 cd/m²) fixation cross of 0.20° radius appears in the middle of the screen, stays on for 1 second to allow participants to fixate it and then disappears.
2. Target dot (TD) appears. The TD starting position in relation to the centre of the screen depends on its subsequent direction and speed, so that it passes through the centre of the display midway through the trial. The TD's starting position therefore varied: for example, when its trajectory was horizontal (0°), the TD's starting position was to the left of the center, and when its trajectory was vertical (270°), its starting position was above the center. The TD remains in its initial position for 500 ms and then starts to move at a fixed speed. The participant starts pursuing the target.
3. The stimulus dot (ST) appears after 500 ms of the target motion to capture the closed loop stage of the smooth pursuit eye movement. The ST immediately starts moving in a particular direction and at a particular speed, and continues moving for 750 ms. Both the TD and ST dots disappear at the same time. Each TD-ST combination (trial) was displayed in a random order. In total, the TD moved for 1250 ms while the ST appeared after 500 ms of TD's onset and moved for 750 ms.
4. As soon as the dots disappear, a light grey screen with a white arrow (measuring 100 pixels, covering 2.2° of visual angle) appears which can be rotated using a computer mouse. The trial ends with a click of the mouse by the participant after rotating the arrow in the direction in which they thought the ST was moving. Upon the mouse click a new trial starts.

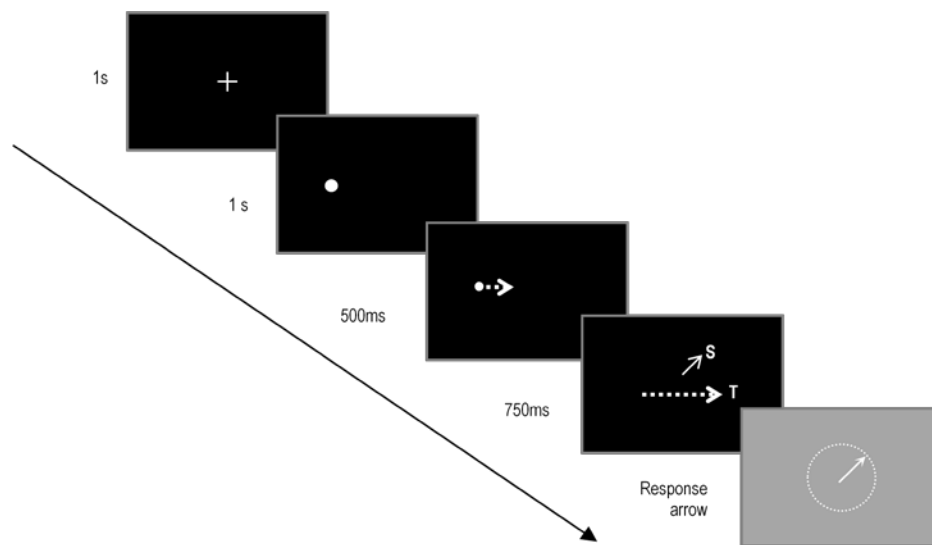


Figure IV.1. Stimulus display in Experiment 1. Each pursuit interval included a single stimulus dot (ST) moving in a particular direction for 750 ms and disappearing simultaneously with the target dot (TD). Observers then indicated in which direction the ST moved by rotating a pointing arrow on the screen.

The TD's trajectory was always centered on the screen. The ST's trajectory originated 80 pixels away (1.76 degrees of visual angle) from the pursuit path. This constant offset was to prevent an overlap with the TD's path in trials where the dots moved in the same direction. In order for the trials to be equivalent, the ST's originating point relative to the centre was determined by its motion direction as if the entire display has been rotated. The separation also helps minimize optokinetic influences that are relevant in later experiments where additional background elements are included in the design and would interfere with the pursuit target dot, i.e. a global motion signal from a background patch covering the TD's trajectory may mask the local motion signal from the TD (Van Die & Colewijn, 1986). If the ST's direction of motion was between 0° and 180° , it started 80 pixels (1.76 degrees of visual angle) on the y-axis above the centre, and if its trajectory was in a direction greater than 180° , then it started 80 pixels (1.76 degrees of visual angle) on the vertical axis below the centre.

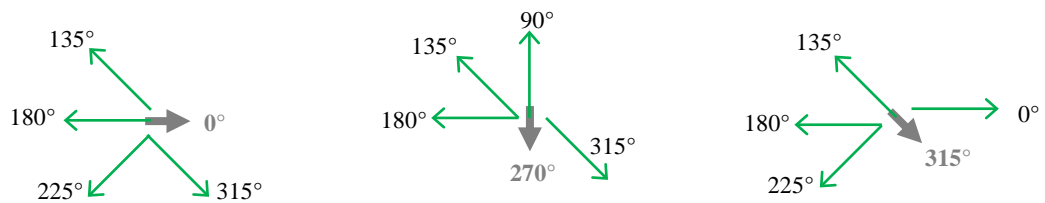
1.4 Target-Stimulus motion combinations

The TD moved in 3 different directions (producing 3 eye movement directions).

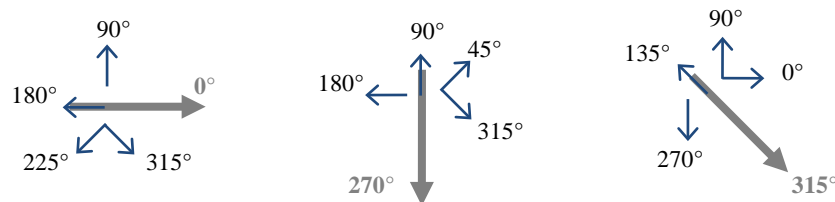
Figure IV.2 shows the TD and ST velocities that were used in Experiment 1.

Experiment 1: A total of 36 combinations (conditions or trials) were included in one block of trials (see Figure IV.2). The aim was to maximize the number of directions tested, while, at the same time, minimizing the number of trials the participants were subjected to, thus keeping the time for completing one block of trials short. This was also another way to prevent dark adaptation during the block of trials.

a) Target moving at $2^\circ/\text{s}$ and stimulus moving at $4^\circ/\text{s}$



b) Target moving at $6^\circ/\text{s}$ and stimulus moving at $2^\circ/\text{s}$



c) Target moving at $6^\circ/\text{s}$ and stimulus moving at $8^\circ/\text{s}$

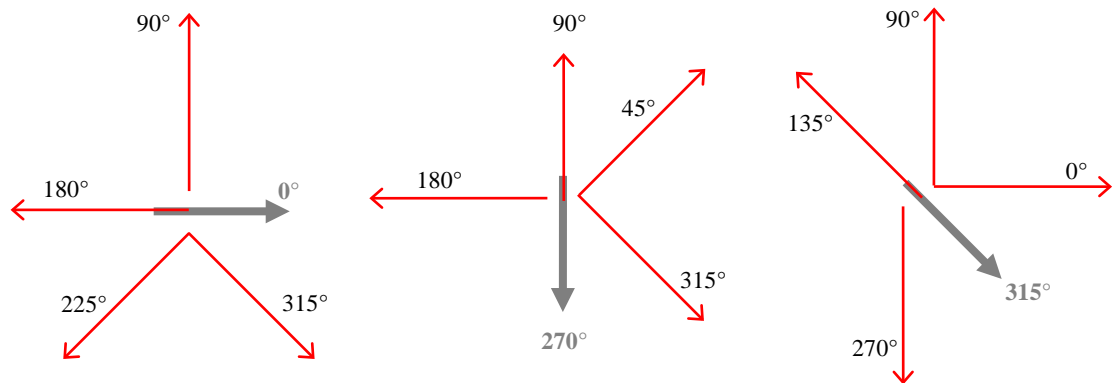


Figure IV.2. Combinations of target and stimulus velocities in Experiment 1. Each target velocity (gray arrow) was displayed with only one stimulus velocity per trial. They are shown on the same plot for compactness. Stimulus velocities are drawn in green (moving at $4^\circ/\text{s}$, associated with $2^\circ/\text{s}$ pursuit), in blue (moving at $2^\circ/\text{s}$, associated with $6^\circ/\text{s}$ pursuit) and in red (moving at $8^\circ/\text{s}$, associated with $6^\circ/\text{s}$ pursuit).

The grey arrow represents the TD velocity. The ST speeds are shown by arrows of different colours and lengths: the green, blue and red arrows represent an ST moving at $4^\circ/\text{s}$, $2^\circ/\text{s}$ and $8^\circ/\text{s}$, respectively. The ST directions associated with each pursuit direction were selected randomly from the entire range of directions in steps of 45° . The ST speed was determined so that it was either slower or faster than the TD speed to explore effects of the TD-ST relative speeds.

The ST motion duration was intentionally held constant across trials because varying stimulus speed leads to varying visual (and in some cases retinal) stimulation. For example, faster stimulus will produce longer trajectory on the screen than slowly moving stimuli. Slow and fast stimulus dots travelling various distances during the same exposure time would allow us to examine their retinal

image motion in more detail. In some instances the ST would move slowly on the screen but on the retina, in combination with the eye movement, it would move much faster. Including a number of different ST and eye movement velocities, one could compare the head-centric perception (the participant's direction estimates) of the stimulus motion to the retino-centric stimulus motion image. The size of the ST retinal image motion was considered as the amount of "retinal stimulation" that resulted from the combination of the ST motion and the eye movement.

1.5 Eyes stationary trials as control experiments

It has been shown that in some situations estimates of motion direction are biased (e.g., Wallach, Becken & Nitzberg, 1985; Mack & Herman, 1978 ; Freeman & Banks, 1998; Souman, Hooge & Wertheim, 2005; Post & Chaderjian, 1988). In order to examine participants' responses for any such bias, a control experiment with eyes stationary was completed by all participants. The stimulus parameters and display were similar to those of the main direction experiments, but without smooth pursuit: instead of following the moving TD, participants fixated on a TD that was stationary at the center of the screen. The ST had the same range of velocities and directions as well as exposure time duration on the monitor as in the main experiments with eye movements. During the response phase, participants had to indicate the direction of the ST.

1.6 Eye movement data analysis

Eye movements were analyzed only during the ST dot exposure, i.e., 750 ms in Experiment 1, 3, 4 and 5, and 125 ms in Experiment 2. The cut off velocity for saccades was 30°/second. In other words eyes moving at 30°/s or more were

recognized as saccadic. Saccadic trials or trials with blinks were identified by the Eyelink 1000 during stimulus exposure. Each block of trials in the experiments produced a separate data file.

Data smoothing procedure

Because the main goal was to measure the velocity of smooth pursuit as well as smooth pursuit gain to target movement, the data were processed using a smoothing filter and saccade removal algorithm in order to reduce noise and complexity. Smoothing of the data was performed using a convolution technique with a Gaussian filter ($sd = 20$ pixels). Saccades were detected using a velocity threshold of $30^\circ/s$. If a saccade occurred before the ST onset, it was removed and smoothed together with the rest of the data for plotting purposes. This did not alter the results of the eye movement data because only data during the stimulus exposure were taken into account for the analysis. A trial was discarded from the data analysis if a saccade or blink occurred in the interval during the time of smooth pursuit when the stimulus dot was visible. The same time-frame during pursuit was used to calculate pursuit velocity, including its standard deviation and gain (mean eye velocity divided by target speed).

1.7 The Linear model

In order to analyze the perceptual data and assess the cancellation signal that helped observers to perceive the ST direction veridically, a model was constructed that was largely based on the linear model (Freeman & Banks, 1998) but was expanded to take into account non-collinear motion and to incorporate vector subtraction. According to the theory by von Holst & Mittelstaedt, (1950), the

compensating signal must be subtracted from the overall retinal image motion (generated by a combination of the external object motion and the eye movement). The compensation signal, along with the retinal image motion can be represented in the form of vectors. Figure IV.3 shows the individual vectors corresponding to the stimulus motion on the screen (ST) and its retinal image motion (r'). In order for the model to be validated, a vector corresponding to the efference copy or the extra-retinal signal (e'), must be subtracted from the combined retinal image motion (r'). The perceived stimulus direction in each trial is given by the participant's estimate (h'). If the estimate is not perfect, it can be assumed that the cancellation signal is insufficient, resulting in an illusory shift in the perceived motion (Filehne Illusion) identified as the *estimate error*.

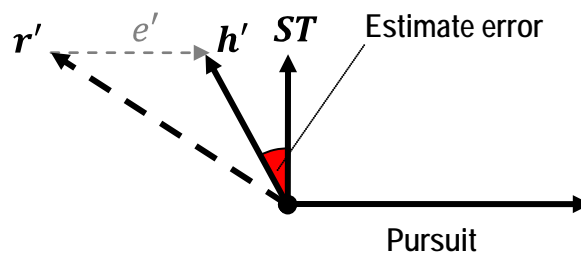


Figure IV.3. Pursuit and stimulus dot velocity components in a vector form. Perceived stimulus direction h' is represented as the sum of the retinal (r') and compensation (e') signals. In this case the retinal signal is assumed to be 1 ($r' = r$). The retinal image velocity is equal to the stimulus velocity plus the reversed eye movement velocity.

Wertheim (1994) replaced the term “eye movement” signal with a “reference signal”, noting that the retinal image velocity may also be in error. This idea led to the introduction of a second, independent gain term for the retinal signal (Freeman & Banks, 1998). Freeman and Banks pointed out that only the ratio of the two

gains (not the individual gains) could be determined from matching task experiments.

Wertheim (1994) also suggested that the compensating reference signal itself includes a visual component so it is not purely extra-retinal. In addition to the efference copy (coming from the eye's velocity in its orbit) the reference signal also includes optokinetic visual information which (in combination with eye movement) produces an estimate of the objective velocity in space. In other words, the reference signal can be modulated by changing the visual information present during eye movements. According to Wertheim (1994) the basic linear model is therefore modified from $h' = r' + e'$ (Equation 2) to:

$$h' = \rho r + (\epsilon e + \gamma r) \quad (\text{Equation 6})$$

where h' is the perceptual estimate, ρr is the retinal signal and e' is the reference (compensation) signal which is further divided into an eye-movement related signal component (ϵe) and a visual signal component (γr).

The fitting procedure in the present experiment

In the present experiment, the eye movement related compensation signal gain was estimated by fitting a modified linear model function (see Equation 6 above) to the perceptual data. The retinal signal gain was assumed to be 1 ($\rho=1$) because preliminary testing that also varied ρ produced problems with the fits and did not result in realistic values of ρ and ϵ . Keeping ρ equal to 1 was also consistent with the linear model used by Freeman and Banks (1998) and thus it allowed us to

determine the ratio of ϵ to ρ . Trials with eyes stationary produced perfect perception of the moving ST which also justified this assumption. The visual component of the compensation signal was assumed to be close to zero ($\gamma=0$) because our initial experiment had no visual information in the display other than the single TD and ST dots. This suggests that the efference copy is only insignificantly affected by these two small visual elements. Therefore the only free parameter in the model was the eye movement-related component gain (ϵ). The model focused on quantifying the effect of pursuit direction on compensation, and included a two-step process. First, an estimate error was determined which referred to the difference between a participants' estimate of the ST direction and the actual ST direction on the screen. Then, using the sum of least squares method a 'function curve' was fitted to the estimation errors for each TD direction. This fitted function curve represented the modeled estimation errors derived from the actual retinal velocities determined from eye movement gains. The following equations were used to determine the vectors representing eye movement and retinal velocities:

$$\mathbf{P} = \text{EM}_{\text{gain}} * \mathbf{T} \quad (\text{Equation 10})$$

where \mathbf{P} is the pursuit velocity, EM_{gain} is the eye movement gain and \mathbf{T} is the target speed

$$\mathbf{R} = -\mathbf{P} + \mathbf{S} \quad (\text{Equation 11})$$

where \mathbf{R} is the retinal velocity, $-\mathbf{P}$ is the reversed pursuit velocity and \mathbf{S} is the stimulus velocity (\mathbf{R} is a vector sum of $-\mathbf{P}$ and \mathbf{S}). Retinal direction was then

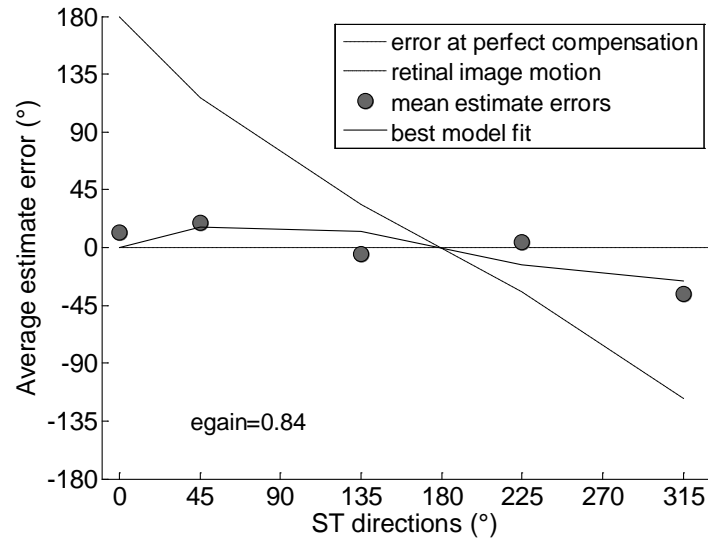
determined using the function $\arctan(Y_r, X_r)$, where X_r and Y_r are the X and Y axis components of the retinal velocity (\mathbf{R}).

Because each TD direction was associated with several ST directions, the fitted curve minimized the differences between the measured and modeled estimation errors across this set of ST directions. The assumption is that the extra-retinal signal encodes a particular pursuit direction irrespective of the external object directions. Our objective was to find one value that represents the strength of the compensating vector. This fitting procedure is similar to the one used by Souman et al. (2005), but the current model was fitted to the direction errors rather than to the direction estimates directly. It turned out that the fit to the direction errors was more linear than to the direction estimates.

This fitting strategy was preferred over averaging the best fit for each of the ST directions that were shown with the particular TD directions separately, because it minimized the effect of outliers (some estimate errors were too large and may have skewed the ‘average’ fit). The outcome of this fitting procedure was a single value representing the extra-retinal signal gain. This gain referred to the overall magnitude of the fitted vector (for each pursuit direction) that had to be subtracted from the retinal velocity to match the participant’s perception (across a range of ST velocities). The value of this fitted compensation vector will be termed the “egain”, and will be identified as $\tilde{\epsilon}$. Figure IV.4 shows the magnitude of the compensation vector (relative to 1) for pursuits at 0° and 315° for two different participants. A small egain indicates a large perceptual error (i.e. an error between

retinal and actual object velocities) for that pursuit condition. On the other hand, a large egain indicates a low estimation error.

(a) Target direction = 0°



(b) Target direction = 315°

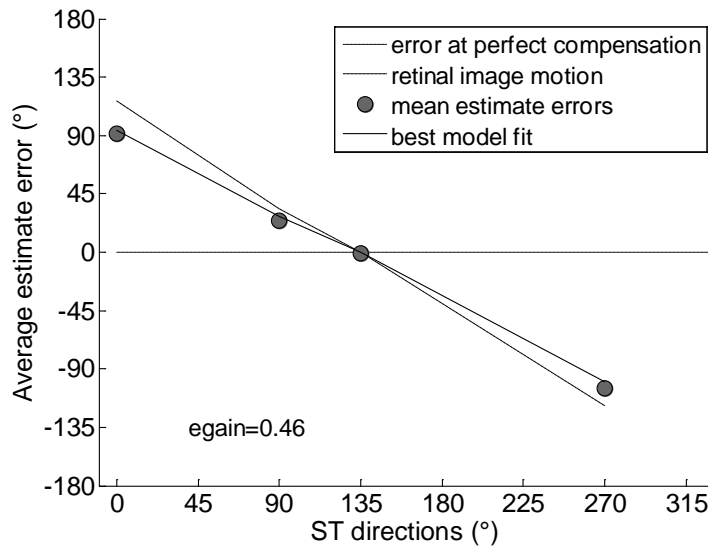


Figure IV.4. Best model fit for pursuit at 0° (a) and 315° (b). The modelled function curve goes through a set of stimulus directions that are presented with the target. The curve minimizes the differences between the actual and modelled estimation errors. The output of the fitting procedure is the egain ($\tilde{\epsilon}$). If the line was fitted to individual estimates rather than the estimate errors during a particular pursuit direction, it would yield as many egain values as there were stimulus directions. However, in the current procedure, the egain

represents the magnitude of the compensating signal for each pursuit direction across a number of stimulus directions. The uneven broken line represent average retinal image directions (no compensation) determined from the actual pursuit velocity of the given participant. The dark circles (mean estimate errors) represent the average estimate errors made by the given participant. The horizontal dashed line represents no errors in estimates (perfect compensation).

The function providing the best fit to the data and its associated again is the main summary statistic that will be used to compare perceptual performance (and eye movement compensation) across a range of target directions and backgrounds. This statistic is unique because it allows for comparisons of perceptual performance across a variety of pursuit and ST velocities.

1.8 Methods of statistical analysis

Circular statistics for directional data

Direction estimation data were analyzed using circular statistics software, specifically, the CircStat toolbox for Matlab (Berens, 2009) which provides methods for descriptive as well as inferential statistics. Directional data cannot be analyzed with commonly used linear statistical software because of their circular nature. The circular scale spans between 0° and 359° where 360° is the same as 0° . If one needs to know the preferred orientation angle (the vector mean) of a sample of different orientations, one needs to add the different orientations to form a combined vector, as shown in Figure IV.5. If one was to use linear statistics to compute, for example, the average of two vector orientations, such as 15° and 345° , the result would be 180° . However, the circular average of these two vectors is 0° . With directional observations, the vector sum represents the average direction orientation.

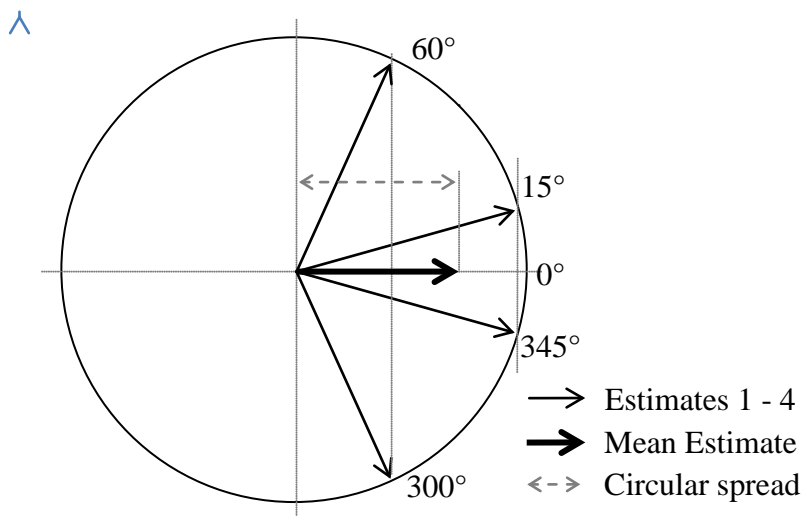


Figure IV.5. Four direction estimates and their circular average and spread

In the same way that the angle of the average resultant vector represents the average direction, the length (magnitude) of the average resultant vector represents the circular spread of the directional data and ranges between 0 and 1. If the vectors point in the same direction, the magnitude of the resultant vector will be close to 1 and variance will be small, because circular spread (cR) is inversely associated with circular variance (cV= 1- cR). Circular variance is related to standard deviation by $s = \sqrt{2cV}$. Therefore, a larger magnitude of the resultant vector indicates higher concentration of data around the mean estimate of stimulus direction (Berens, 2009). In contrast, if the orientations are pointing in various directions, the resultant vector's magnitude will be close to 0 and the variance will be large.

Inferential statistics regarding circular data are commonly based on the von Mises distribution (e.g., Mardia & Jupp, 2000), which is usually unimodal and the preferred direction is the direction of its mode. The CircStat toolbox in Matlab

provides several programs that supply methods for testing different hypotheses about circular data, including analyses similar to t-test and ANOVA for linear data. For example, m-test is equivalent to a linear one sample t-test, and the significance of the result is expressed as $h = 1$ (significant) or $h = 0$ (not significant), instead of a t-value accompanied by a p-value. One way ANOVA is performed using the Watson-Williams test, while two-way ANOVA is performed by a Harrison-Kanji test which is the highest-level available analysis in the Circular Statistics Toolbox for Matlab (Berens & Velasco, 2009).

Linear statistics for analyzing eye movement gain

Linear descriptive and inferential statistics were used in evaluating eye movement and extra-retinal signal gains across different conditions.

2. Results

2.1 Direction estimation during eyes stationary

The direction of the ST motion was first estimated in an experiment with eyes stationary, as a means of response method validation and as a control to see how well participants were able to estimate the stimulus dot angle. Each participant completed 3 blocks of trials, where each trial included 8 ST directions (from 0° to 315° in steps of 45°), moving at 3 different speeds ($2^\circ/\text{s}$, $4^\circ/\text{s}$ and $8^\circ/\text{s}$), appearing on the display for 750 ms. On average, 10.5% of trials had to be discarded because of saccades or blinks (aka saccadic trials). Perceptual results from eyes stationary trials are presented in Figure IV.6.

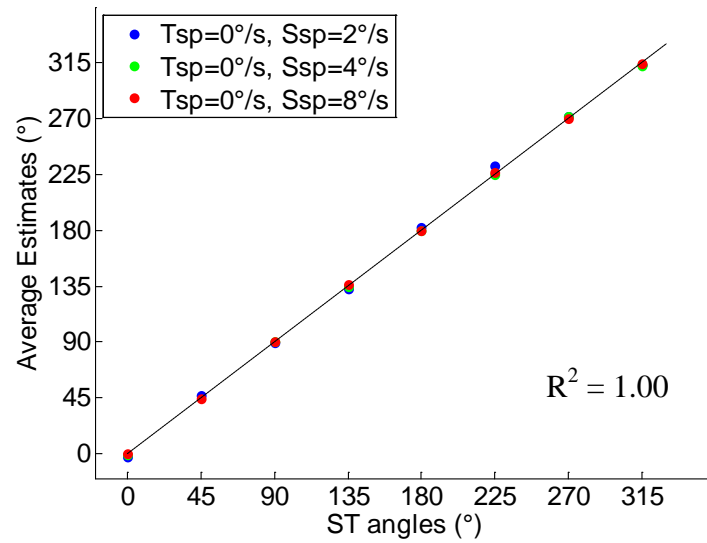


Figure IV.6. Estimation performance during eyes stationary in Experiment 1. R^2 refers to the variance of the data explained by a zero error model where estimate = stimulus direction.

From Figure IV.6 it is evident that participants made almost perfect estimates of the ST directions, regardless of its speed ($R^2 = 1.00$). On average, the greatest error was 2.8° for an ST angle of 225° , regardless of ST speed, but this error was not significant. The high degree of estimation accuracy indicated that using the method of adjustment (by rotating an arrow on the screen) proved to be an accurate measurement technique, and that ST direction estimation ability with eyes stationary is excellent under these experimental conditions.

2.2 Direction estimation during eye movement

Eye movement analysis

Frequency of saccadic trials: Eye movements were analyzed off-line by a custom Matlab program to identify trials with inaccurate pursuit. Some participants produced too many saccades and blinks during stimulus exposure, and as a result they completed additional blocks of trials. Only trials where no saccades or blinks occurred during ST exposure, or where the eye movement gain was between 0.5 and 1.5, were included and used in the analysis. Figure IV.7 shows the percentage of trials that were excluded from the analysis for the different conditions. From all measured trials, 28.35% were saccadic. The most saccades and blinks occurred when TD moved at 270° and TD speed was $6^\circ/\text{s}$. In contrast, the percentage of saccadic trials was lowest when the TD moved at 315° at a speed of $2^\circ/\text{second}$.

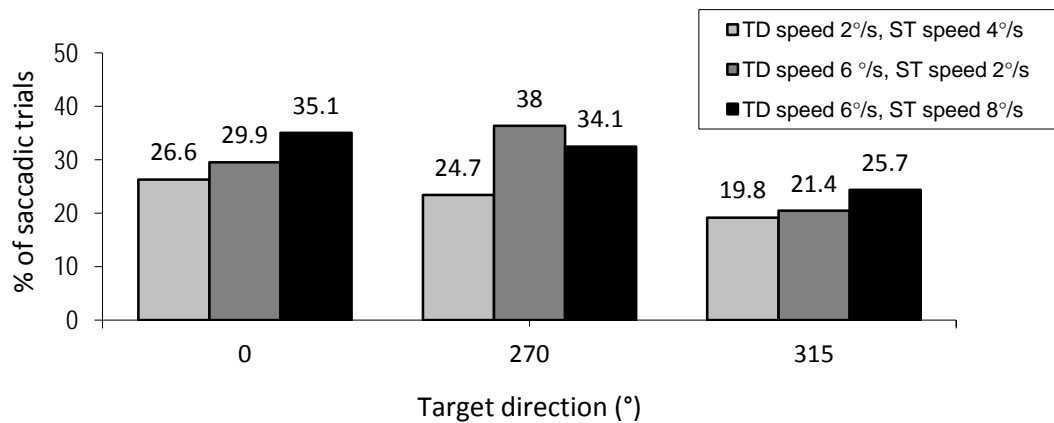


Figure IV.7. Percentage of saccadic trials in Experiment 1.

The overall percentage of saccadic trials is higher than reported previously. For example, Souman, Hooge and Wertheim (2005) had to discard 7% of trials, but they used a threshold of eye velocity of $50^\circ/\text{s}$. Morvan and Wexler (2009) eliminated 16% of trials but their ST exposure time was only 100 ms. In the current experiment the strict criteria for saccades involved not only a careful examination of eye velocity, but also detection of blinks. The ST exposure time of 750 ms as opposed to 100 ms also increases the probability of blinks. Trials with eye movements that did not conform to the established strict criteria resulted in a high rejection rate. On the other hand, there are studies that report a trial exclusion rate as low as 1% (Freeman, Champion, Sumnall & Snowden, 2009) and as high as 50 % (Souman & Freeman, 2008), so our saccadic trial frequencies are within this reported range.

Eye movement velocity: Eye movement direction was calculated off-line using the recorded x and y eye position data. The measured eye positions were smoothened using a low pass Gaussian space filter ($\text{sd} = 20$), and subsequently were utilized to compute eye movement velocity using the first derivative of the eye position change over the ST exposure time. Figure IV.8 presents a plot of a participant's eye x and y position, respectively, during pursuit of a target moving at 0° at a speed of $6^\circ/\text{s}$.

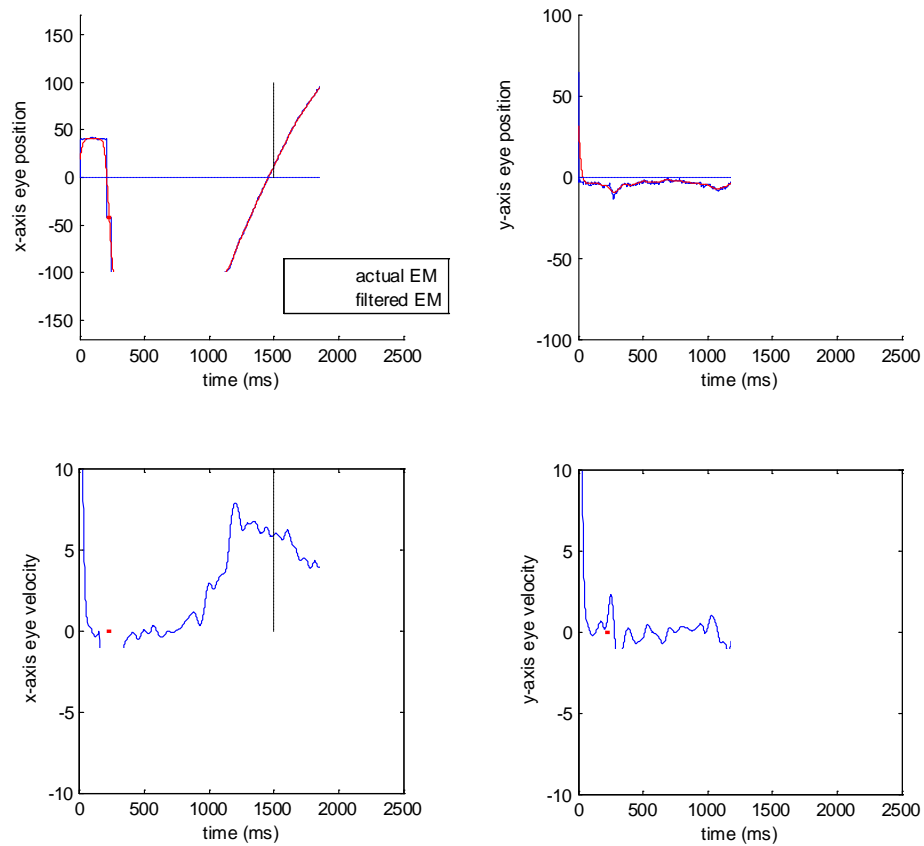


Figure IV.8. Plots showing filtered and non-filtered x and y-axis eye positions and eye velocities. Actual and filtered eye movements (EM) are shown in blue and red, respectively. The vertical dashed lines denote the onset and disappearance (exposure duration) of the stimulus during pursuit.

On average, participants' pursuit directions were close to TD direction although small differences appeared across the three different pursuit angles. Eye movement angle deviations were more evident when the TD moved at $2^\circ/\text{second}$ (the average error was 2.92°) than when it moved at $6^\circ/\text{sec}$ (the average error was -1.45°), but these had little effect on the ST's retinal image motion speed. For example, the 2.92° eye movement angle deviation produced only a minimal error along the horizontal velocity axis ($V \cos 2.92^\circ = 0.998V$ °/s). Figure IV.9 shows the divergence of eye movements from the TD direction for each condition.

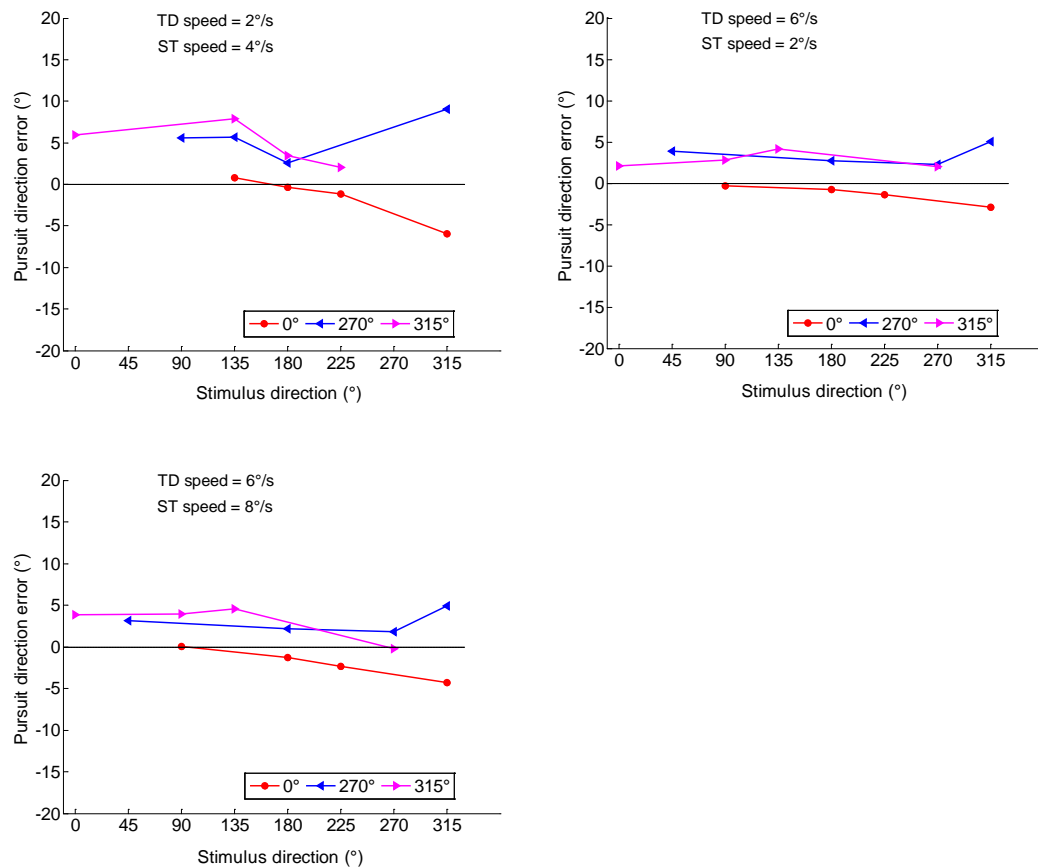


Figure IV.9. Average eye movement deviations from the moving target in Experiment 1. Average errors are plotted for each TD direction (0°, 270° and 315° represented by red, blue and purple lines, respectively) and each screen ST direction associated with a given TD direction. Error bars are not shown because of their small size.

Pursuit gain was determined by a ratio of the measured eye movement and TD speeds for each condition. Figure IV.10 presents pursuit gains for each pursuit condition. In trials where the TD moved at 2°/s, the average gain was exactly 1.0 although it varied slightly across ST directions. Table IV.1 further lists the pursuit gain values for each TD-ST velocity combination in Experiment 1.

According to an ANOVA, when the TD moved at 6°/s, average eye movement gain was lower ($\bar{X} = 0.91$, $sd = 0.14$), than when it moved at 2°/sec ($\bar{X} = 1.00$,

sd = 0.17), $F(1, 1933) = 61.31$, $p < .05$. In addition, eye movement gain differed significantly across the three pursuit directions, $F(2, 1933) = 42.95$, $p < .05$. The lowest pursuit gain was for TD moving at 270° ($\bar{X} = 0.89$, sd = 0.18), compared to TD moving at 0° ($\bar{X} = 0.98$, sd = 0.14) and 315° ($\bar{X} = 0.97$, sd = 0.14). There was also an interaction effect between TD direction and ST speed, $F(4, 1933) = 4.32$, $p < .05$, suggesting the gain varied across pursuit direction depending on the ST speed. ST speed alone had no effect on pursuit gain. The lowest gain (.84) was for the TD moving at 270° and at $6^\circ/s$, when the ST speed was $2^\circ/s$.

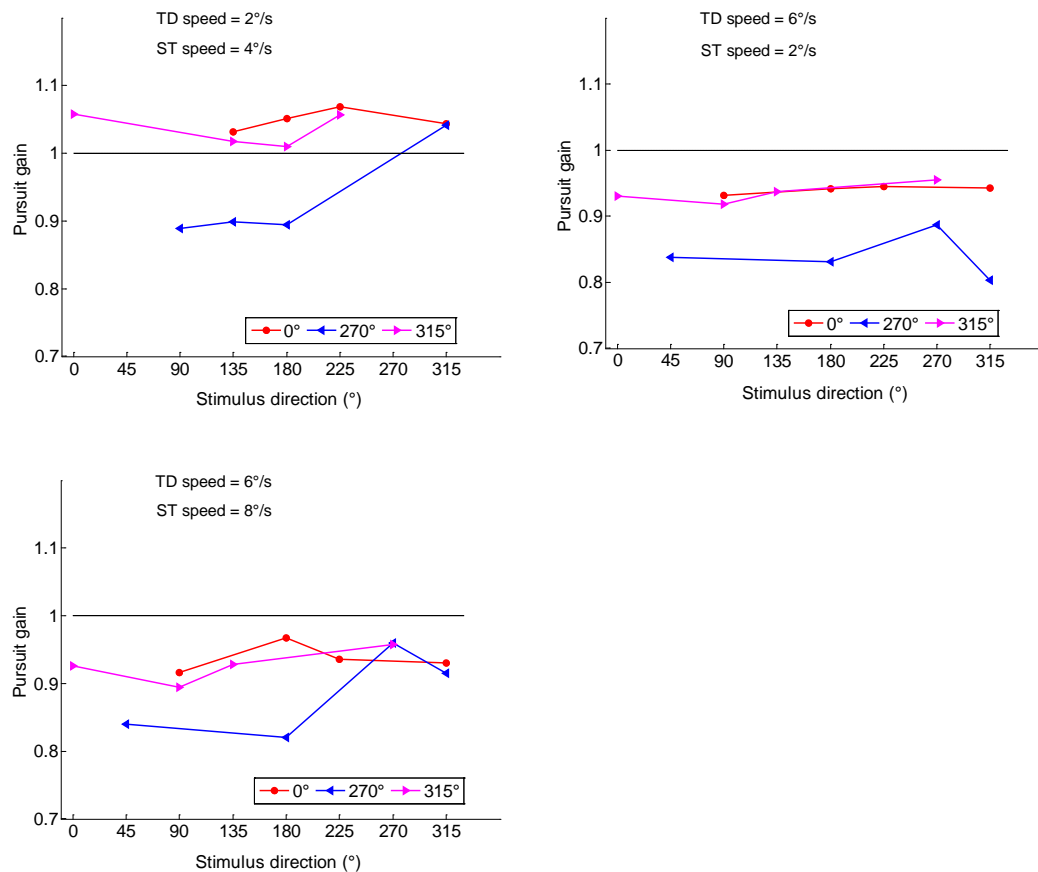


Figure IV.10. Average pursuit gains in Experiment 1. Average gains are plotted for each TD direction (0° , 270° and 315° represented by red, blue and purple lines, respectively) and each screen ST direction associated with a given TD direction.

Table IV.1. *Average pursuit gains in Experiment 1*

	TD speed 2°/s	TD speed 6°/s	TD speed 6°/s	Overall average
	ST speed 4°/s	ST speed 2°/s	ST speed 8°/s	
TD 0°	1.05	0.94	0.94	0.98
<i>90°</i>	-	0.93	0.92	<i>0.92</i>
<i>135°</i>	1.03	-	-	<i>1.03</i>
<i>180°</i>	1.05	0.94	0.97	<i>0.99</i>
<i>225°</i>	1.07	0.94	0.94	<i>0.99</i>
<i>315°</i>	1.04	0.94	0.93	<i>0.97</i>
TD 270°	0.93	0.84	0.89	0.89
<i>45°</i>	-	0.84	0.84	<i>0.84</i>
<i>90°</i>	0.89	-	-	<i>0.89</i>
<i>135°</i>	0.90	-	-	<i>0.90</i>
<i>180°</i>	0.89	0.83	0.82	<i>0.85</i>
<i>270°</i>	-	0.89	0.96	<i>0.93</i>
<i>315°</i>	1.04	0.80	0.92	<i>0.92</i>
TD 315°	1.04	0.94	0.93	0.97
<i>0°</i>	1.06	0.93	0.93	<i>0.97</i>
<i>90°</i>	-	0.92	0.89	<i>0.91</i>
<i>135°</i>	1.02	0.94	0.93	<i>0.96</i>
<i>180°</i>	1.01	-	-	<i>1.01</i>
<i>225°</i>	1.06	-	-	<i>1.06</i>
<i>270°</i>	-	0.95	0.96	<i>0.96</i>
Overall average	1.00	0.91	0.92	0.95

Note. Average pursuit gains are listed for each TD-ST condition (ST directions are in italics, first column). The dashes in the table are for conditions that were not selected during the random selection of ST directions for each TD velocity.

The obtained pursuit gains are higher than those reported by Freeman and Banks (1998), who found that the average gain was 0.85 regardless of pursuit speed or stimulus spatial frequency. The stimuli in their experiment were vertical sinusoidal gratings between 0.125 and 1 c/deg and the target speeds were 3.1, 6.2 and 9.2°/s. The amplitude criterion in their study for saccadic trials was 10°/s. However, it was not noted whether trials with very low gain were discarded, as was done in the current analysis. Including trials with very low gain in their analysis may have reduced the gain averages.

Direction estimates and estimation errors

Target speed 2°/s: In general, participants were able to estimate ST direction well when the TD moved at 2°/s (ST always moved at 4°/s). The estimate errors were small and insignificant, regardless of pursuit direction. The largest discrepancy was in a combination of downward pursuit and ST moving at 315°, where the average ST estimate was 323.5° (standard error = 4.54). In general, estimates were accurate, suggesting a high level of eye movement compensation. As an example, Figure IV.11 on the next page shows a participant's estimates in the form of vectors for an ST moving at 135° during rightward horizontal pursuit.

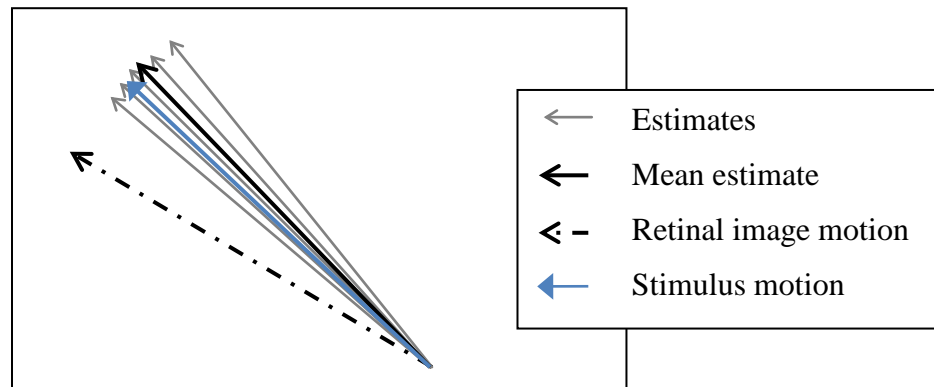


Figure IV.11. Stimulus direction estimation example. The figure shows ST motion direction of 135° (blue), a participant's individual estimates (grey) and their average estimate (black), as well as the average retinal image motion of the ST (broken) that was computed based on the actual pursuit gains across trials for that particular condition.

The vector subtraction mechanism seems to work well when the pursuit speed is $2^\circ/\text{s}$. For example, a participant's estimates were concentrated around the screen ST direction, implying high reliability and low variance of the estimates.

Estimates averaged across participants are shown in Figure IV.12, all of which are close to the predicted line (head-centric ST direction), indicating accurate estimation of the ST direction. However, it should be noted that the retinal image direction predictions for an ST moving at $4^\circ/\text{s}$ during a $2^\circ/\text{s}$ pursuit (if there is no compensation for eye-movement) is quite close to the screen, or head-centric ST directions, particularly in this 135° case. Therefore, even if one was not compensating for their eye movement at all, and estimated the ST direction according to retino-centric direction, their estimate would still be close to the actual direction as it appeared on the screen (head-centric direction). It would be hard to distinguish whether their estimate is closer to the retinal than to the head-centric ST direction. This means that one needs to be careful when interpreting results from previous studies on eye movement compensation. Figure IV.12

shows how the retinal image differs from the screen stimulus angles across the range of conditions.

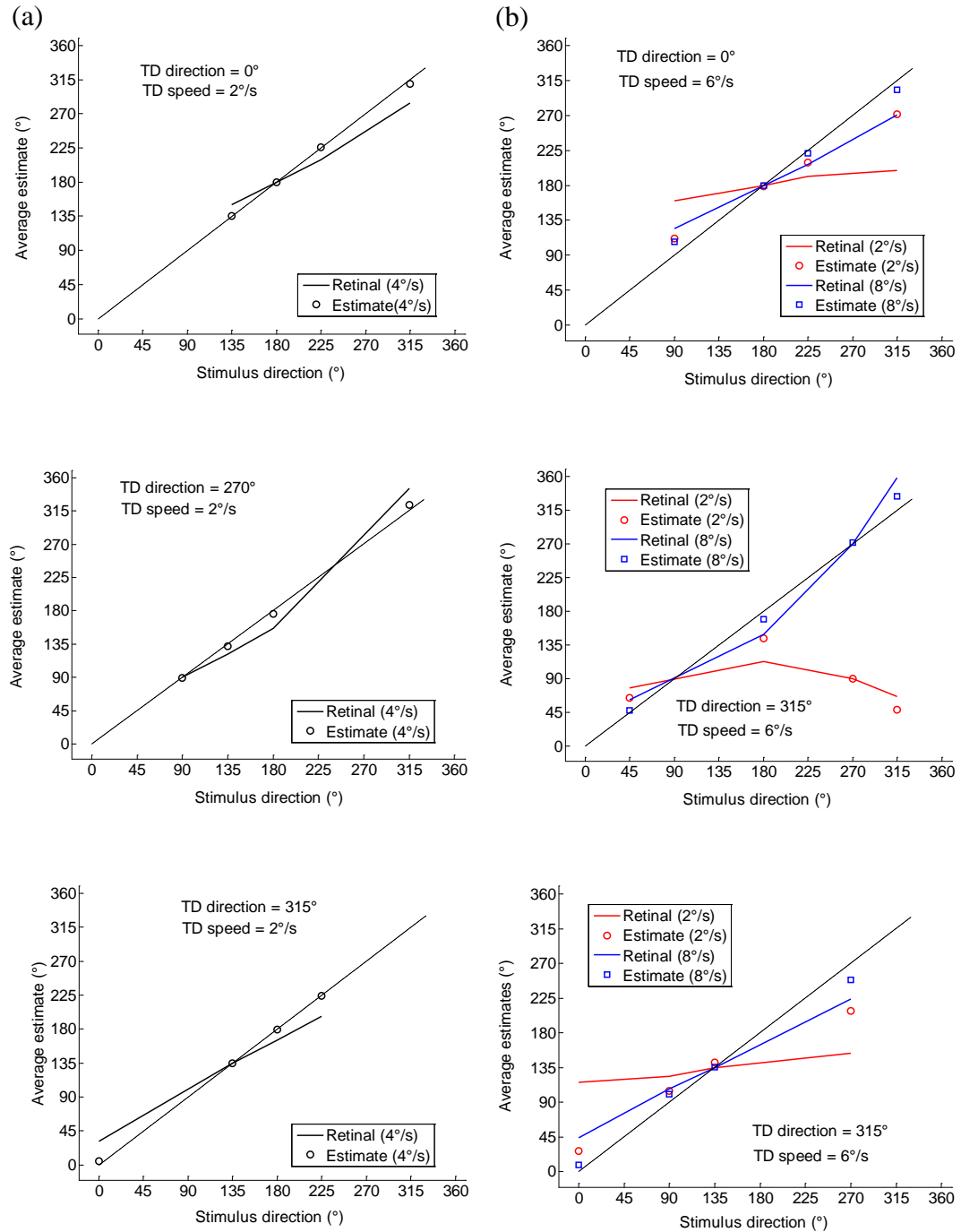


Figure IV.12. Screen and retinal stimulus directions in different ST speed conditions and average direction estimates. The figure shows how different TD and ST speeds lead to different retinal image motions. Plotted are average ST direction estimates (o), ST screen direction (broken line) and retinal image direction (full line) for a given TD–ST velocity combination. When the TD

moves at $2^\circ/\text{s}$ and the ST moves at $4^\circ/\text{s}$, the difference between actual ST screen and retinal image directions is minimal (see column a). For example, in the case of a TD moving at 315° , the retinal image motion of an ST moving at 135° would be exactly the same as the screen ST direction of 135° . When the TD moves at $6^\circ/\text{s}$, the retinal image motion of the ST differs, depending on ST velocity (see column b). If the ST speed is $2^\circ/\text{s}$, the difference between screen and retinal image directions is quite large, as indicated by the red line in relation to the broken line.

Target speed $6^\circ/\text{s}$: During $6^\circ/\text{s}$ TD pursuit the overall average estimates were significantly different than the actual screen ST directions (based on m-test, $h = 1$). Estimation errors varied significantly across pursuit directions, but only when the ST speed was $2^\circ/\text{s}$, $F(2, 1240) = 27.16$, $p < .05$. At this ST speed, the largest average estimate error was -43° when pursuit was 270° , while the smallest estimate error (1°) was at a pursuit of 315° .

Circular spread and the 180° “flip” effect

The variability of estimates is described in terms of circular spread and standard deviation. In general, the circular spread was small, indicating consistent, reliable responding. The largest circular spread ($cR = 0.52$), was in a combination of TD moving at 270° and ST moving at 270° where the TD and ST speeds were $6^\circ/\text{s}$ and $2^\circ/\text{s}$, respectively. The reason for the inconsistent responding, and a large average estimate error was a 180° “flip” effect where the ST was sometimes perceived as going against, as opposed to going with the TD. Although both the TD and ST moved in the same direction on the screen (due to their different speeds) on the retina the ST moved in the opposite direction to the TD. Reduced eye movement compensation would result in retino-centric perception of the ST. Specifically, 35 out of 46 trials had the “flip” effect: two participants perceived the ST retino-centrally 100% of the time, one 85% of the time and one 38% of

the time. The two remaining participants who perceived the ST veridically had only two trials without saccades so their average estimates were based on two values only. After removing the “flips“, the average estimate error during downward pursuit was reduced from -43° to -29° , which was still significantly larger than average estimate errors during 0° and 315° pursuits.

It is interesting that the 180° “flip” effect occurred only when the ST moved in the same direction as the TD. When the slow ST moved in the opposite direction to the TD on the screen, the “flip” did not happen. These cases included TD/ST moving at $0^\circ/180^\circ$ and $315^\circ/135^\circ$, respectively. This result suggests that eye movement compensation is better when the ST moves in the opposite direction as opposed to in the same direction to the eye movement. In addition, the large perceptual errors during 270° pursuit imply that eye movement compensation is reduced in this condition and perception follows the retinal image motion. It should be noted, however, that this downward pursuit had a significantly lower gain than the horizontal or oblique pursuits, and may have contributed to the flip effect. The reduced gain in the 270° pursuit condition seems to be in line with previous studies showing that eye movement gain was higher for horizontal than for downward pursuit (Rottach, Zivotovsky, Das, Averbuch-Heller, DiScenna, Poonyathalang & Leigh, 1996; Collewyn & Tamminga, 1984).

It is noted that the conditions in which the estimation variability was the greatest (besides the “flip” effect conditions), were those in which the ST moved at a 45° angle relative to the TD. The largest individual differences regarding ST direction estimates were present in downward pursuit, which is partially due to the “flip”

effects, but consistent discrepancies were also evident when the ST moved at a 45° angle to the downward pursuit (i.e., at 315° on the screen).

The results show that participants' estimates in most conditions were closer to the screen ST direction as opposed to the retinal image velocity. However, the estimates seemed to approach the retinal image motion during downward pursuit when the ST moved at $2^\circ/\text{s}$. Figure IV.13 shows estimate errors for the two ST speeds when the TD speed was $6^\circ/\text{s}$.

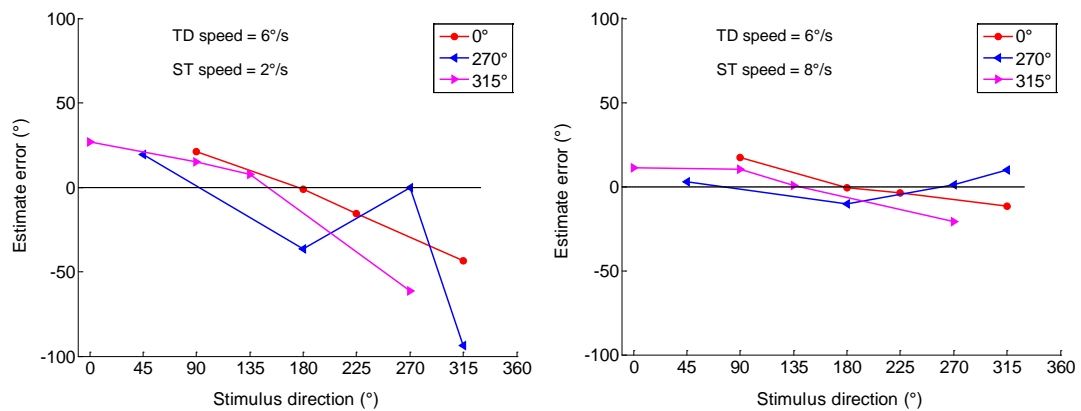


Figure IV.13. Average estimate errors in Experiment 1 for conditions where the target moved at $6^\circ/\text{s}$. Estimate errors are plotted for each ST velocity across the three TD directions.

Using only trials where the TD moved at $6^\circ/\text{s}$, a circular analysis of variance (Harrison-Kanji test) revealed that estimate errors significantly varied across the three TD directions, $F(2, 1275) = 31.82$, $p < .05$, as well as the two ST speeds, $F(1, 1275) = 147.37$, $p < .05$. There was also an interaction effect, $F(2, 1270) = 36.36$, $p < .05$, suggesting that the estimate error varied across the different pursuits as a function of ST speed (errors were higher when ST moved at $2^\circ/\text{s}$ than when it moved at $8^\circ/\text{s}$). This result is consistent with earlier analyses, but is also

predictable from the vector addition model. That is, the retinal image direction is very similar to the head-centric ST direction when the ST speed is high.

2.3 Extra-retinal signal gain (egain)

The strength of the extra-retinal signal was computed using a modified linear model. As stated earlier, estimation error was first determined (the difference between participant's estimate of ST direction and the actual ST direction on the screen). Using the sum of least squares method, a curve was fitted across the estimation errors for each set of ST directions associated with a given pursuit velocity. The curve that gave the best fit to the error terms provided a value that we refer to as the compound strength of the vector, or egain ($\tilde{\epsilon}$), that had to be subtracted from the retinal velocities for a given pursuit to reflect perception.

The goodness of fit was recorded for each participant and each condition, and was expressed by the root of mean squared error (RMSE). This statistic is also known as the fit standard error or the standard error of the regression ($RMSE = \sqrt{(SSE / n)}$, where SSE is the sum of squared error). The lower the RMSE value, the better fit to the data by the model. The fits were evaluated according to the size of RMSE and categorized into 3 groups. The first group included all fits that resulted in $RMSE < 15^\circ$, the second group included fits with RMSE between 15° and 30° and the last group were fits with $RMSE > 30^\circ$. The boundaries for each category were chosen subjectively upon review of the RMSE distributions across all pursuit/ stimulus conditions. The largest spread of fits was in the condition where the ST moved at $2^\circ/s$ ($sd = 18.11$).

Table IV.2 shows average egain values for conditions with TD moving at 6°/s and Table IV.3 shows how well the model accounts for the data, listing the RMSE for each fit. For most participants and pursuit directions the model provided a good fit, although when the ST moved at 8°/s the fit was better than for ST moving at 2°/s.

Table IV.2. *Average egain in Experiment 1*

Direction Experiment 1	Target speed = 6°/s			
	ST speed = 2°/s		ST speed = 8°/s	
	Average egain	sd	Average egain	sd
TD direction 0°	.72	.19	.57	.21
TD direction 270°	.78	.15	.60	.18
TD direction 315°	.70	.17	.53	.16
Overall average	.73	.16	.57	.18

Table IV.3. *Goodness of fit of the model in Experiment 1*

Direction Experiment 1	Target speed = 6°/s			
	ST speed = 2°/s		ST speed = 8°/s	
	Number of fits	% of fits	Number of fits	% of fits
RMSE < 15°	10	56%	18	100%
RMSE 15° - 30°	4	22%	0	0%
RMSE >= 30°	4	22%	0	0%
Total of fits	18	100%	18	100%

Note. The model goodness of fit is expressed as the root of mean squared error (RMSE). The table shows the number of fits for a given range of RMSE.

The above tables do not report on conditions for 2°/s pursuit (in which ST moved at 4°/s) because all the fits were very good, i.e., RMSE was under 15°. In fact, 14 out of all 18 fits resulted in RMSE lower than 5°, and the remainder of fits had

RMSE below 11° . The $2^\circ/\text{s}$ pursuit conditions produced an overall egain value of .89. Specifically, egain values were .96, .75 and .95 for 0° , 270° and 315° pursuits.

The magnitude of the extra-retinal signal (egain) was computed for each pursuit velocity, assuming the retinal signal gain was 1 although it is recognized that retinal signal can also be subject to an error. This assumption has some implications for the interpretations of the results. Specifically, the best fit produced a value that is dependent only on eye-movement-related signal, ignoring any effects coming from the visual signal that has shown to have an impact on overall compensation (Wertheim 1994; Freeman & Banks, 1998). Although the model cannot quantify both the retinal and extra-retinal signal gains, it can provide an indication of the relative size (ratio) of the two gains. Because the retinal signal gain was held constant at 1, this ratio is the value of the best fitted egain to 1. In other words, the model fitting did not compute the actual extra-retinal signal gain but only its relative size to the retinal signal gain.

There was a significant difference in egain between conditions where the TD speed was $2^\circ/\text{s}$ ($\bar{X} = .88$, $\text{sd} = .21$) and $6^\circ/\text{s}$ ($\bar{X} = .65$, $\text{sd} = .20$), $t(52) = 3.81$, $p < .05$. Further, when considering trials where the TD moved at $6^\circ/\text{s}$ only, analysis of variance revealed that egain was consistent for all three pursuit directions, and varied only as a function of ST speed, $F(1, 34) = 9.71$, $p < .05$). When the ST moved at $2^\circ/\text{s}$, the average egain was .75 ($\text{sd} = .18$) compared to .56 ($\text{sd} = .18$) when the ST moved at $8^\circ/\text{s}$.

3. Discussion

One of the observations from Direction Experiment 1 was the difference in results coming from the two pursuit speeds. At $2^\circ/\text{s}$, eye movement gain was almost perfect and estimate errors were minimal. This was not surprising given the fact that the retinal and head-centric directions of the stimulus dot (that moved at $4^\circ/\text{s}$) were very similar. A target speed of $6^\circ/\text{s}$ produced more interesting data. First, eye movement gain varied across pursuit directions and was the lowest for downward pursuit. Second, direction estimates also varied significantly across the three pursuit directions, but only when the ST moved at $2^\circ/\text{s}$: estimates approached retinal velocity during downward pursuit.

ST speeds had diverse effects not only on estimation errors but also on the egain inferred from the model fittings. The low ST speed increased the compensation egain but resulted in high estimation errors. The expectation generally is that high eye movement compensation would mean low estimation errors (veridical perception). The current finding, which is inconsistent with the general expectation, may be related to how the egain (representing the extra-retinal signal for each pursuit direction) is computed. The egain output was based on a modeling technique that assumed retinal signal gain to be 1 and ignored any contribution of visual signal to the eye-movement signal.

Perhaps, when the ST moves very slowly, the retinal (visual) stimulation is reduced (both p_r and γ_r) and therefore the reliance on the extra-retinal sources is greater than when the ST moves fast. Alternatively, larger retinal slip produces larger visual stimulation (also increasing the visual component, γ_r , of the extra-

retinal signal) than stimulation produced by slow ST motion. If the size of the extra-retinal signal is dependent on the amount of retinal stimulation γ_r , then it can be deduced that the compensation process depends more on the eye-movement related component in the extra-retinal signal ($\tilde{\epsilon}$) when there is little retinal stimulation (γ_r is low or insignificant). If the visual stimulation is stronger (in this case when the ST moved faster and further on the screen), but $\tilde{\epsilon}$ is low, it follows that the good compensation is a result of the strong visual component in the extra-retinal signal (γ_r). In other words, in conditions when the ST travels fast and the perception shows high eye movement compensation, but the egain is low, one can presume that the role of the eye-movement signal in the overall compensation signal was reduced. But again it is important to remember that the head-centric direction of the fast ST is very close to its retino-centric direction, and so it is difficult to adequately determine to what degree the visual system depended on the eye movement signal in the compensatory process. This question will need to be addressed in later experiments.

According to early experiments by Mack and Herman (1978), shortened ST exposure results in larger perceptual errors. Based on their findings, they speculated that increasing the exposure increases the extra-retinal signal. However, increasing the ST exposure time causes the ST to travel a longer distance on the screen which may have an effect on the visual signal as well. A fast ST exposed for a very brief period could travel the same distance on the screen as a slow ST exposed for a long time. By manipulating the ST screen trajectory while changing its exposure time and speed, one could determine which of these factors has an effect on the extra-retinal signal.

4. Summary

Experiment 1 included a number of pursuit and stimulus velocities to assess what aspects of the stimuli contribute to the eye-movement related signal. It appeared that a fast ST relative to the target speed was sufficiently compensated for, resulting in low perceptual errors. However, one must consider the retinal image motion in comparison to the head-centric velocity to be able to judge whether estimates really reflected the external object movement. This was very difficult to do in trials with fast stimulus dots because both pursuit speeds (2 and 6°/s) in combination with the fast ST generated retinal image motion that was very similar to the head-centric (screen) motion. It was not clear from the results whether the estimates were closer to the retinal or head-centric ST velocity because they were close to both.

In order to produce a summary statistic that reflected how ‘strong’ the compensation vector needed to be to account for the data across many ST directions a model fitting procedure was used. The fitted egain value in Experiment 1 was the only variable parameter in the model. It was assumed that that retinal signal gain was equal to 1 and the visual component in the compensation signal was 0, given the empty background of the displayed dots. The ST dot itself may have contributed to the visual component, but because it was small and of low luminance, its contribution was likely minimal. Because the relative contribution of the visual component to the overall compensation signal was ignored, the outputted egain value reflects only the eye-movement related component gain. The egain was found to be reduced when the ST moved faster and farther on the screen (despite high overall compensation and low perceptual

errors). Early studies have indicated that overall compensation improves when the stimulus on the screen remains present longer (when stimulus exposure is long as opposed to short). The question is, what leads to an increased compensation: increasing the stimulus speed or increasing the stimulus exposure? A faster stimulus produces a longer trajectory on the screen than a slow stimulus during the same exposure time period. Analogously, short and long exposure times produce different lengths of trajectories on the screen when the stimulus speed is held constant.

The observations from Experiment 1 generated questions that can be addressed by further experimentation. One of the new experiments could answer the question of whether it is the stimulus exposure time or the stimulus speed that helps the compensation process. In Experiment 1 the different stimulus speeds produced different perceptions. One can argue, that the faster the stimulus moves, the farther it travels on the screen and therefore increases the visual or retinal stimulation compared to a stimulus that moves slowly. From the findings of Experiment 1 it was not clear whether perception of the fast stimulus was due to its long trajectory, or whether it was due to its retinal image velocity being close to the objective motion on the screen. This question will be examined in more detail by Direction Experiment 2 in Chapter VI. The following Chapter describes the estimation of ST speed rather than direction during eye movement.

Chapter V. Speed experiment: Estimating stimulus speed during eye movement

Before conducting Experiment 2 for direction estimation, an experiment assessing participants' ability to estimate speed during pursuit was conducted. The Speed experiment differed from direction estimation Experiment 1 only in the type of perceptual task. The perceived speed of the stimulus dot during the eye movement was the main variable of interest. In the direction experiment, for the conditions where the target and stimulus dots are collinear, the direction estimates do not reveal whether or not compensation is occurring unless the 'flip' effect occurs. A direct measure of the perceived magnitude of the image velocity was therefore sought. In addition, I explored the use of a magnitude scale for measuring the perceived speed, as an alternative to the matching paradigm used in previous research (e.g., Turano & Heidenreich, 1996; Turano & Heidenreich, 1999; Freeman & Banks, 1998; Freeman & Banks, 2001; Turano & Massof, 2001; Souman & Freeman, 2008). As mentioned in the Introduction, there is a possibility of 'contamination' or 'cross-talk' when a matching stimulus is introduced during the experimental procedure.

The inclusion of the Speed experiment in the thesis was also motivated by an interest in finding out whether the speed estimation task would produce different eye movement and perceptual results from those in the direction estimation task, despite identical display characteristics in both types of experiments.

1. Methods

The same six participants who completed the Experiment 1 also completed the Speed experiment, which took place at least one day after Experiment 1. The experimental setup as well as the stimulus conditions was identical to Experiment 1. The only difference between the Speed estimation experiment and Experiment 1 was related to the perceptual task and the response method. In Experiment 1 a bright white arrow appeared on a light grey background upon the disappearance of the dots. In the Speed experiment the light grey background appeared without the arrow. Participants were required to estimate the speed of the stimulus (ST) using a magnitude scale ranging from 1 to 8 (1 represented a speed of $1^\circ/\text{s}$ and 8 represented a speed of $8^\circ/\text{s}$), and to press a number on the keyboard that most closely matched the ST speed. Once the number was pressed, a new trial began with the fixation cross in the middle of the screen.

First, participants had to learn associating the ST speed with a number. Several learning trials were conducted with eyes stationary. There were two stages of learning trials: the initial stage consisted of trials with a fixation dot and an ST moving in a horizontal direction. The first trial showed an ST moving at $1^\circ/\text{s}$ and in each consequent trial the ST increased in speed by $1^\circ/\text{s}$ up to $8^\circ/\text{s}$ (the ST speed ranged between $1^\circ/\text{s}$ and $8^\circ/\text{s}$ in steps of $1^\circ/\text{s}$). After the ST disappeared, a number (blue in colour) appeared on the screen indicating the ST speed. The second stage of learning trials included a fixation dot and an ST moving in different directions and at different speeds. Specifically, 24 ST velocities were shown in random order: 3 directions (0° , 270° and 315°) and 8 speeds ($1^\circ/\text{s}$ to $8^\circ/\text{s}$ in steps of $1^\circ/\text{s}$). Only three of these ST speeds were used in the eye movement

experiment ($2^{\circ}/s$, $4^{\circ}/s$ and $8^{\circ}/s$), but the goal was to teach participants to distinguish between ST speeds during eyes stationary. Again, after the ST disappeared during this learning trial, a number corresponding to the speed of the ST was shown on the screen. Participants had an opportunity to enter the number key on the keyboard as a practice for entering their estimates in the dark.

Participants completed both training stages and could repeat either of them as many times as they wanted. It turned out that all participants viewed the initial training session once and the second training session twice.

Following the training sessions, participants were tested on their speed estimation ability (during eyes stationary) to ascertain that they were able to match a correct number to the presented stimulus speed. The test trial was identical to the second stage training session except the stimulus velocities were presented in different order, and no feedback was provided. A correlation between the actual ST speed and the participant's estimated speed was computed based on 3 blocks of continuous trials. A participant had to achieve a correlation of .85 between their estimates and the actual stimulus dot speeds in order to continue in the eye movement experiment. This criterion was achieved by all participants during their first testing. This 'test' also served as a control for the eye movement experiments as it provided a base line for the participants' ability to estimate speed without eye movements.

2. Results

Speed perception errors were computed from the collected estimation data and eye movements were monitored and measured by the eye tracker. Similarly to the

direction experiments, the speed estimation data were used to determine the best fit for egain ($\tilde{\epsilon}$). First, an estimation error was calculated which was the difference between the estimated speed and the screen stimulus speed. In addition, a theoretical error term was computed using the sum of least squares method to match the estimation errors for the set of stimuli associated with a particular pursuit direction. The output of the fitted model was a value representing the amplitude of the compensation vector (egain).

2.1 Speed estimation during eyes stationary

Stimulus speed was first estimated with eyes stationary, as part of the response validation stage. Participants completed 3 blocks of trials. Each trial included an ST moving steadily at one of 3 different speeds and in one of 8 directions for 750 ms.

Generally, participants made accurate estimates of the ST speed regardless of its direction. The correlation between average individual estimates and the actual ST speed ranged between .87 and .95. As shown in Figure V.1 the average estimates were very close to the actual ST speed on the screen. Participants tended to slightly underestimate the ST moving at 2°/s and slightly overestimate it when it travelled at 4°/s (average estimates were 1.88°/s and 4.43°/s, respectively). When the ST moved at 8°/s, the speed was slightly underestimated (estimate average was 7.65°/s) but the errors remained small (estimate standard deviations for ST speeds 2°/s, 4°/s and 8°/s were 0.69, 1.08 and 0.66, respectively). Overall, the results suggest that using the magnitude estimation of the stimulus speed is a valid method of measurement, but at the same time it hints at a non-linear relationship

between actual and perceived velocity, as found by Turano and Massof (2001). In the current Speed experiment a linear as opposed to a non-linear model was used. In the eye movement conditions with only two data points (estimates) to fit, the use of a non-linear model with a greater number of parameters would be under-constrained, and therefore was not adopted.

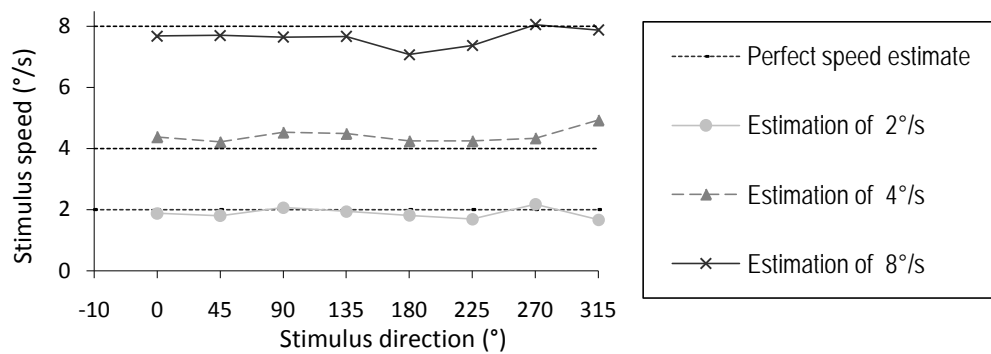


Figure V.1. Speed estimation performance during eyes stationary.

2.2 Speed estimation during eye movement

Eye movement analysis

Frequency of saccadic trials: Figure V.2 shows the percentage of trials that were excluded from the analysis due to saccades or blinks. From all measured trials, 30.5% were saccadic. The most saccades occurred during a 270° pursuit (35.2%), while the fewest saccades occurred when the pursuit direction was 315° (24.6%). The increased percentage of saccades during downward pursuit was not due to trials in which the stimuli were ‘far’ from the target because the stimuli moved in similar angles to target as during other pursuit directions. One possible explanation for the saccades is that downward pursuit may be differently affected by eye muscle control. The saccades occurred primarily when the ST moved very

slowly and mostly appeared above the TD. Perhaps the visual system is not used to registering motion above the horizon line or in the upper periphery of the visual field, and this may have caused participants to make a saccade.

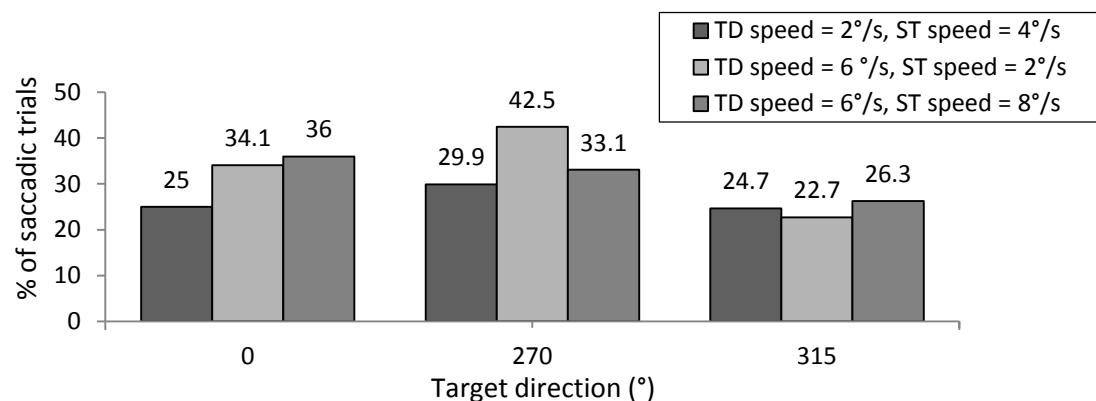


Figure V.2. Percentage of saccadic trials in the Speed experiment

Eye movement velocity: Eye movement velocity was calculated in the same way as in Experiment 1 (off-line using the recorded x and y eye position data). The average eye movement angle was within 4.5° of the target dot direction. The greatest eye divergence occurred during a downward pursuit at $2^\circ/\text{s}$ when the ST moved at 315° (the average error was 12.61°).

The average pursuit gain when the target dot (TD) moved at $2^\circ/\text{s}$ was .97 (averaged across all pursuit directions). However, average pursuit gain was significantly lower when the TD moved at 270° (.91) than when it moved at 0° (1.02) or 315° (.97), $F(2, 718) = 5.46$, $p < .05$.

During target pursuit at $6^\circ/\text{s}$ the overall average eye movement gain was .88.

There were significant differences in pursuit gains across the three pursuit

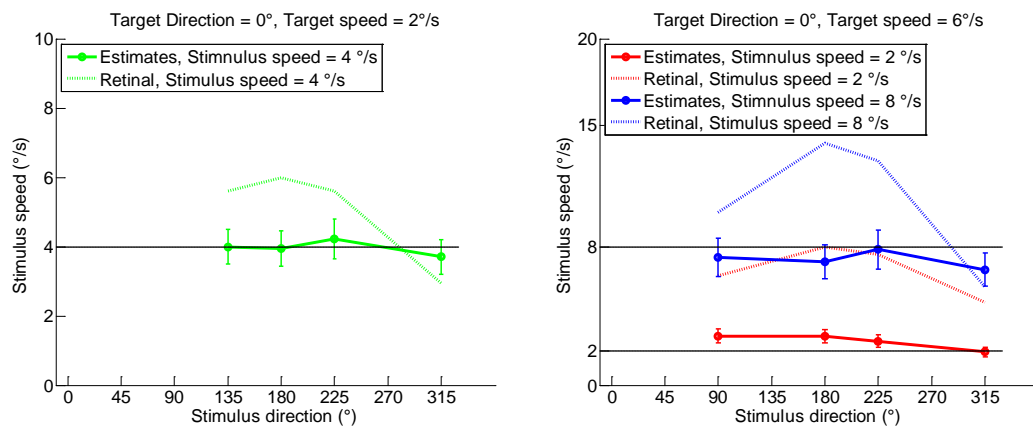
directions, $F(2, 1320) = 17.8$, $p < .05$. The lowest gain was for 270° pursuit (.84), while the highest gain was for 0° pursuit (.91). Gain for 315° pursuit was .88, which was different from the two other gains as indicated by a post-hoc analysis. The ST speed also had an overall effect on pursuit gain, $F(1, 1320) = 13.1$, $p < .05$. Gain in conditions with a slow ST ($2^\circ/\text{s}$) was .86, whereas in conditions with a fast ST ($8^\circ/\text{s}$) it was .89. The main effect of ST speed indicated that pursuit gain was lower when a slow ST was presented. There was an interaction effect of TD direction and ST speed, which indicates that pursuit gain varied across pursuit directions, depending on ST speed, $F(2, 1315) = 4.9$, $p < .05$.

Pursuit gain also significantly varied between the two pursuit speed conditions, $t(2038) = 10.07$, $p < .05$, with a lower gain for TD moving at $6^\circ/\text{s}$ (.88) than for TD moving at $2^\circ/\text{s}$ (.97), regardless of the pursuit direction. Figure V.6 later in the chapter summarizes the eye movement gain results in comparison to direction estimation Experiment 1.

Speed estimates and estimation errors

Target speed $2^\circ/\text{s}$: When the target travelled at $2^\circ/\text{s}$, the ST always moved at $4^\circ/\text{s}$ on the screen, but on the retina it varied depending on the target and ST directions. Figure V.3 shows the retinal stimulus speeds for each target-stimulus velocity combination. Overall, the average ST speed estimate was $3.89^\circ/\text{s}$ (compared to the $4^\circ/\text{s}$ speed on the screen) and there was no significant difference in average estimates across the three pursuit directions.

Target speed 6°/s: When the TD moved at 6°/s, the ST moved either at 2°/s or 8°/s on the screen (see Figure V.3 for retinal speed at each stimulus-target velocity combination). An ANOVA revealed that there was a main effect for pursuit direction, $F(2, 1320) = 4.67$, $p < .05$. According to a post-hoc analysis, the estimate errors significantly varied between 0° pursuit ($\bar{X} = -.09$) and 270° pursuit ($\bar{X} = -.37$) and between 0° and 315° pursuits ($\bar{X} = -.33$). Estimate errors at the 270° and 315° pursuits were similar. There was also a main effect for ST speed, $F(1, 1320) = 531.98$, $p < .05$. Larger errors occurred when judging the 8°/s ($\bar{X} = -1.06$, $sd = 1.04$) than the 2°/s speed ($\bar{X} = .54$, $sd = 1.40$), regardless of pursuit direction. Stimulus speed was slightly overestimated when it moved slowly (2°/s) and underestimated when it moved at 8°/s. However, when the estimate errors were considered in absolute values, the difference in the magnitude of the errors between the two ST speed groups was insignificant.



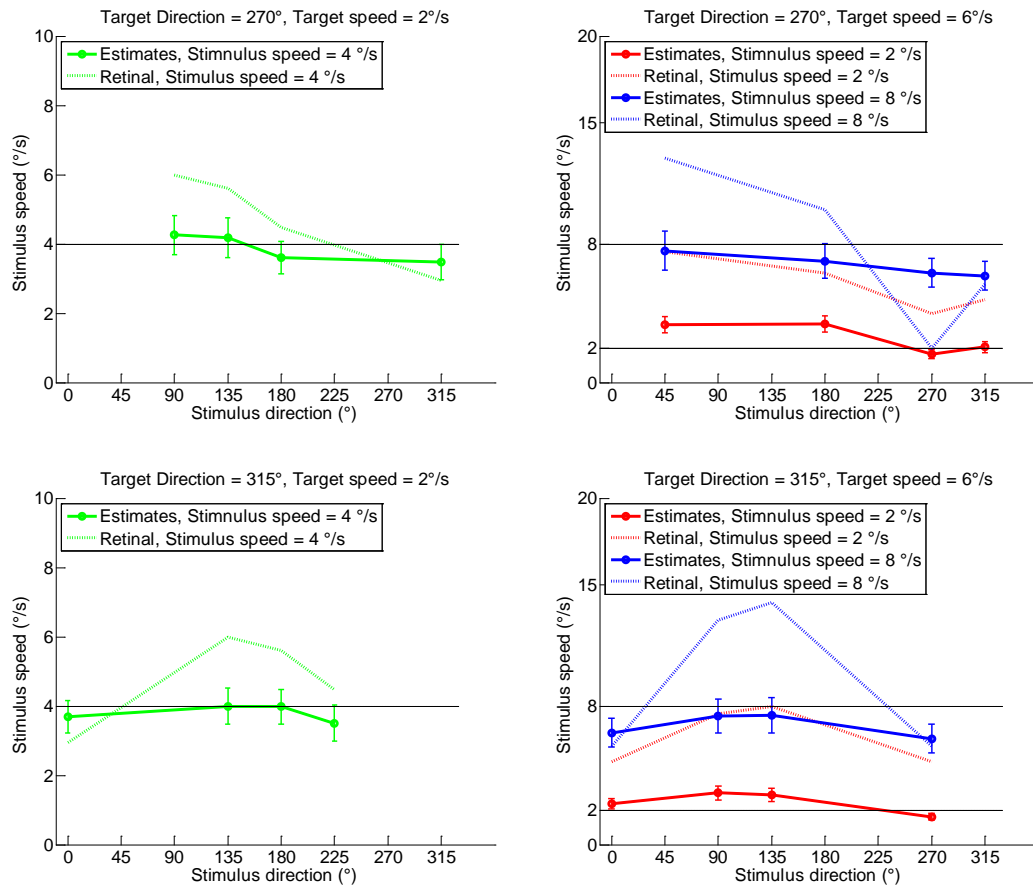


Figure V.3. Stimulus speed estimates. Average speed estimates are shown for the three TD directions when TD moved at 2°/s and ST moved at 4°/s (green solid line), when TD moved at 6°/s and ST moved at 2°/s (red solid line) and 8°/s (blue solid line). Broken black lines indicate screen ST speed, and broken coloured lines indicate the retinal image speeds for each ST speed. Retinal image speeds are calculated from TD and ST velocities (and are the slowest for conditions when the TD and ST move in the same direction). The variation shown for each estimate value is the standard error of the mean.

A significant interaction effect between pursuit direction and ST speed suggests that the magnitude of the errors vary for different target directions, depending on ST speed. For example, the highest speed estimation error occurred during a downward pursuit when estimating an ST travelling at 8°/s, while the smallest error occurred during a pursuit of a TD moving at 315° when estimating a 2°/s speed (see Figure V.3). Overall, speed estimations were closer to the screen ST

speeds than retinal speeds, indicating good eye movement compensation.

Stimulus speeds $2^\circ/\text{s}$ and $4^\circ/\text{s}$ were overestimated, regardless of the eye movement speed, while ST speed $8^\circ/\text{s}$ was underestimated.

Flip effects: It was of interest to assess whether in some cases participants perceived the ST speed retino-centrally. For example, in the direction estimation experiment some people perceived the ST moving in the opposite direction to that on the screen. This happened mainly when the TD and ST moved collinearly in the same direction at $6^\circ/\text{s}$ and $2^\circ/\text{s}$, respectively (when the ST had an opposite direction on the retina compared to screen). Analogically, in the speed experiment, the “flip” effect could occur when the ST moves collinearly with the eyes and is perceived to be moving at the retinal speed. There were 67 non-saccadic trials that could potentially have a “flip” effect where the TD and ST moved at $6^\circ/\text{s}$ and $2^\circ/\text{s}$ respectively. The retinal speed in these cases was $4^\circ/\text{s}$. Table V.1 shows the distribution of estimates for this condition. Only one participant in one trial during downward pursuit made this estimate.

Table V.1. “*Flip*” effect in the Speed experiment when target and stimulus moved in the same directions

Speed Estimates	$1^\circ/\text{s}$	$2^\circ/\text{s}$	$3^\circ/\text{s}$	$4^\circ/\text{s}$	Total
# of non-saccadic trials	21	15	4	1	41
% of non-saccadic trials	51.2%	36.6%	9.8%	2.4%	100%

Note. The data are shown for the condition where “flip” effect occurred: TD speed = $6^\circ/\text{s}$, TD direction = ST direction (270°), head-centric (screen) ST speed = $2^\circ/\text{s}$, retinal speed = $4^\circ/\text{s}$ (TD speed minus ST speed).

Another point of interest is when the slow ($2^\circ/\text{s}$) moving ST is largely overestimated. Specifically, conditions where the retinal speed would be the sum of TD and ST speed were those in which the TD and ST moved in the opposite direction to each other, at $6^\circ/\text{s}$ and $2^\circ/\text{s}$ respectively. There were 111 such trials that were non-saccadic. Out of these, no one estimated the ST as moving at $8^\circ/\text{s}$ (the retinal speed). However, 41 (37%) produced overestimation by at least $2^\circ/\text{s}$. That means that the estimates ranged from $4^\circ/\text{s}$ to $7^\circ/\text{s}$. What was also interesting was that the $2^\circ/\text{s}$ ST were underestimated in 26% of trials. It is important to note that eye movement gain did not influence these results (i.e. low pursuit gain did not result in lower incidence of overestimation). Table V.2 summarizes the results.

Table V.2. *“Flip” effect in the Speed experiment when target and stimulus moved in the opposite directions*

Speed Estimates	$1^\circ/\text{s}$	$2^\circ/\text{s}$	$3^\circ/\text{s}$	$4^\circ/\text{s}$	$5^\circ/\text{s}$	$6^\circ/\text{s}$	$7^\circ/\text{s}$	Total
Number of trials	29	27	14	24	9	6	2	111
Percentage of trials	26.1%	24.3%	12.6%	21.6%	8.1%	5.4%	1.8%	100 %

Note. The table shows the distribution of estimates for the condition where the ST moved in the opposite direction to the TD (180° vs. 0° , respectively) and where the retinal image speed was the sum of TD and ST speeds ($8^\circ/\text{s}$). There were no estimates at $8^\circ/\text{s}$.

Overall, the results of the speed estimation “flip” effect analysis indicate that when the TD and ST move in the opposite direction to each other, the estimation errors are larger and more variable than when the TD and ST move in similar directions. This is in contrast to direction estimation where only TD and ST moving together at the different speeds produce reversal errors (the “flip” effects).

Due to the limited range of ST speeds tested, and the low number of trials where reversal errors were possible, this finding may need to be tested further in future research.

2.3 Extra-retinal signal gain (egain)

The model fitting procedure

In the speed experiment, the egain ($\tilde{\epsilon}$) for each pursuit direction was determined in a similar way as in the direction experiment, using vector algebra in the linear vector model (overall compensation $e' = \epsilon e + \gamma r$, where ϵ and γ are gains of the eye-movement and retinal components in the overall compensation signal, respectively). The measured pursuit gain was used to compute the retinal stimulus velocity. In this case, we needed to find out the magnitude of a vector (a compensation vector) that had to be added to produce the participant's average estimate. This predicted estimate was determined by varying the compensatory egain such that the difference between the predicted magnitude estimation errors and the actual participants' magnitude estimation errors was minimal. In other words, V_m (predicted error) - V_o (observed error) was minimized, using the sum of least squared errors. In summary, in the speed experiment the egain was a value given by the best fitting function curve to the speed estimation errors (not direction estimation errors), for each pursuit and stimulus combination.

The model was fit across speed estimation errors for the two different stimulus speeds associated with 6°/s pursuit. In the 2°/s pursuit condition the model was fit to only one stimulus speed. Similar to the fitting procedure in the direction experiment 1, the retinal gain ρ was assumed to be 1 and the visual component in

the compensation signal was assumed to be 0. This simplified the model to include only one free parameter, egain ($\tilde{\epsilon}$), that represented the ratio of extra-retinal to retinal signal gain. Table V.3 shows the model's goodness of fit, using the root of mean squared errors between the model and the data. The fits were divided into two groups that resulted in RMSE less or equal to $1^\circ/\text{s}$ or in RMSE more than $1^\circ/\text{s}$. Although the $1^\circ/\text{s}$ criterion is much more liberal when the ST speed is $2^\circ/\text{s}$ (50%) than when the speed is $8^\circ/\text{s}$ (12.5%), it was the smallest speed increment used. A constant percentage of actual speed was not used because this would create fractions and the estimates were whole numbers from 1 to 8.

Table V.3. *Goodness of fit of the model in the Speed experiment*

Speed Experiment	TD speed = $2^\circ/\text{s}$	TD speed = $6^\circ/\text{s}$		All fits
	ST speed = $4^\circ/\text{s}$	ST speed = $2^\circ/\text{s}$	ST speed = $8^\circ/\text{s}$	
	Number (percentage) of fits			
RMSE $\leq 1^\circ/\text{s}$	18 (100%)	17 (94%)	12 (67%)	87%
RMSE $> 1^\circ/\text{s}$	0 (0%)	1 (6%)	6 (33%)	13%

Note. The model goodness of fit is expressed as the root of mean squared error (RMSE). The table shows the number of fits for a given range of RMSE.

Target speed $2^\circ/\text{s}$: The overall average modeled egain ($\tilde{\epsilon}$) was .85 (sd = .23) and did not significantly varied as a function of pursuit direction, despite individual differences. Figure V.4 shows the best egain fit for each participant across the three different pursuit direction conditions.

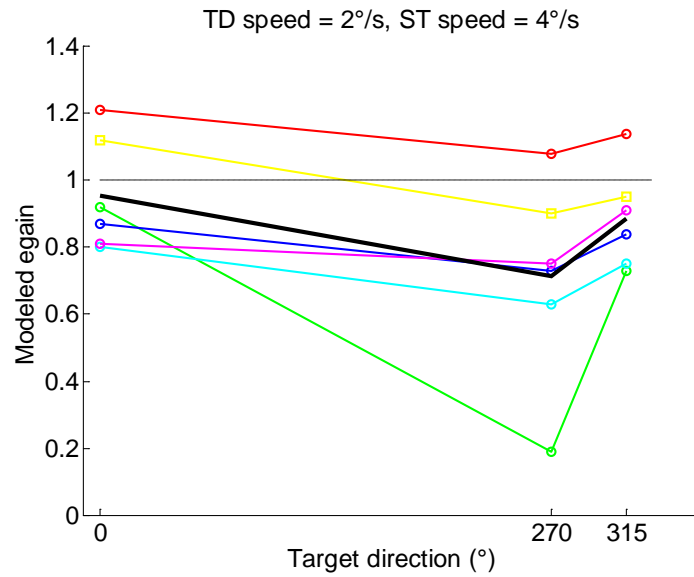


Figure V.4. Extra-retinal signal gain (modeled egain) for 2°/s pursuit in the Speed experiment. The colour lines show the model fitted egain for each participant and the black line represents an average egain across all six participants.

Target speed 6°/s: A two way ANOVA with TD direction and ST speed as the two factors revealed that the egain ($\tilde{\epsilon}$) significantly varied across target directions, $F(2, 33) = 6.0$, $p < .05$. The lowest $\tilde{\epsilon}$ occurred for a downward pursuit ($\bar{X} = .59$, $sd = .23$), but for 0° and 315° pursuits it was .83 ($sd = .16$) and .72 ($sd = .16$), respectively. There was also a main effect for ST speed, $F(1, 34) = 7.2$, $p < .05$. The $\tilde{\epsilon}$ output was higher (compensation best) when the ST speed was 8°/s ($\bar{X} = .79$, $sd = .13$) compared to .63 ($sd = .25$) when the ST speed was 2°/s (see Figure V.5). There was also more inter-participant variability in the egain between the two ST speed conditions. When the ST moved at 8°/s, the inter-participant variability was much lower than when the ST moved at 2°/s. This indicates that the perception of the ST speed varies more among people when the stimulus speed is very slow.

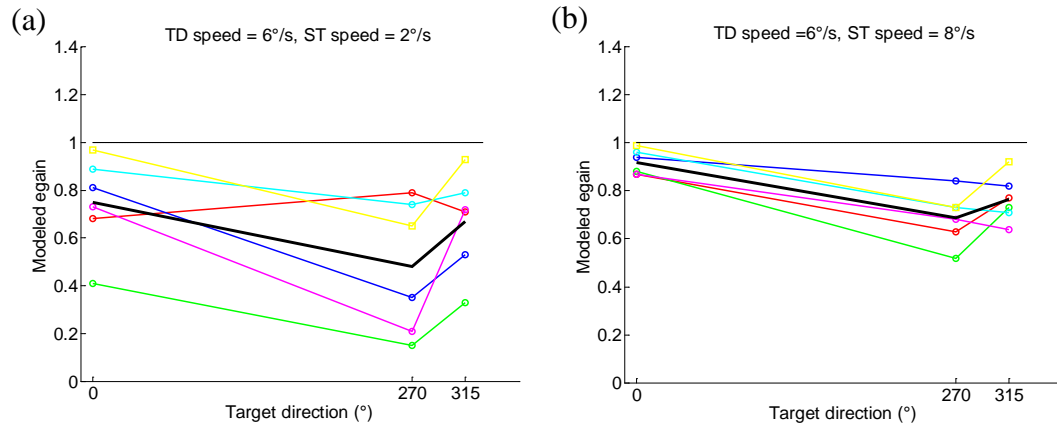


Figure V.5. Extra-retinal signal gain (modeled egain) for $6^{\circ}/s$ pursuit in the Speed experiment. The colour lines show the model fitted egain for each participant and the black line represents an average egain across all six participants. (a) ST speed = $2^{\circ}/s$, (b) ST speed = $8^{\circ}/s$.

3. Discussion

First, using the magnitude scale turned out to be a good response method for estimating ST speed during eyes stationary. Similar to the eye stationary trials, during eye movement participants tended to underestimate fast ST and overestimate slow ones. This trend of under and over-estimation seems to occur regardless of whether the eyes were still or moving. The estimation errors were larger when estimating $8^{\circ}/s$ than $2^{\circ}/s$ ST, but the average absolute values of the errors were similar. The results are consistent with previous findings by Turano and Massof (2001) where the speed of faster ST was underestimated and slow ST were overestimated. Participants also reported that it was much harder to think about a number corresponding to the ST speed than when they used an arrow during the direction estimation task in Experiment 1. The compensatory signal for each pursuit direction across ST speeds which was reflected by the egain ($\tilde{\epsilon}$), was the highest for the $8^{\circ}/s$ ST. This result was inconsistent with the result in the direction estimation Experiment 1 where the outputted egain estimate was the

highest for the slow, 2°/s moving ST. To further look at the differences between the Speed experiment and the direction Experiment 1, additional analyses were conducted, that specifically assessed eye movement gain and the modeled compensatory gain in those two experiments.

3.1 Comparison of direction Experiment 1 and the Speed experiment

Eye movement gain

Eye movement gains from the speed estimation experiment were compared to those from the direction experiment. Although the conditions were the same in both experiments, the response task differed, and this may have had an effect on the eye movement. Figure V.6 shows average pursuit gains for the two experiments.

Target speed 2°/s: When the target moved at 2°/s, there was a significant difference between pursuit gains in the two experiments, $F(1, 1418) = 13.23$, $p < 0.5$, regardless of target directions. Pursuit gain was higher in the direction Experiment 1 ($\bar{X} = 1.0$, $sd = .17$), than in the Speed experiment ($\bar{X} = .97$, $sd = .21$). The gain also varied across the three pursuit directions, $F(2, 1418) = 46.04$, $p < .05$. Pursuits of targets moving at 0° and 315° produced perfect gain but for 270° pursuit the gain was 0.91 ($sd = .21$).

Target speed 6°/s: When the target speed was 6°/s an ANOVA was conducted using Experiment type and ST speed as factors. The analysis revealed that there was a significant difference between pursuit gains in the two experiments, $F(1, 2517) = 39.51$, $p < .05$. On average, pursuit gain was higher in the direction

experiment ($\bar{X} = .91$, $sd = .14$) than in the speed experiment ($\bar{X} = .88$, $sd = .16$). It should be noted here that the same six participants completed these two experiments and that all participants completed the direction experiment first. Thus they had more experience with following the targets on the screen in the speed experiment and the expectation would be that their eye movement gain would be better in this experiment. However, the data show that the speed experiment produced worse eye movement gain values than the direction experiment. Eye movement gain results for both direction and speed experiments showed a main effect of pursuit direction, $F(2, 2517) = 51.53$, $p < .05$, and a main effect of ST speed, $F(1, 2517) = 13.95$, $p < .05$. The results for pursuit gains for Experiment 1 and the Speed experiment are summarized in Figure V.6.

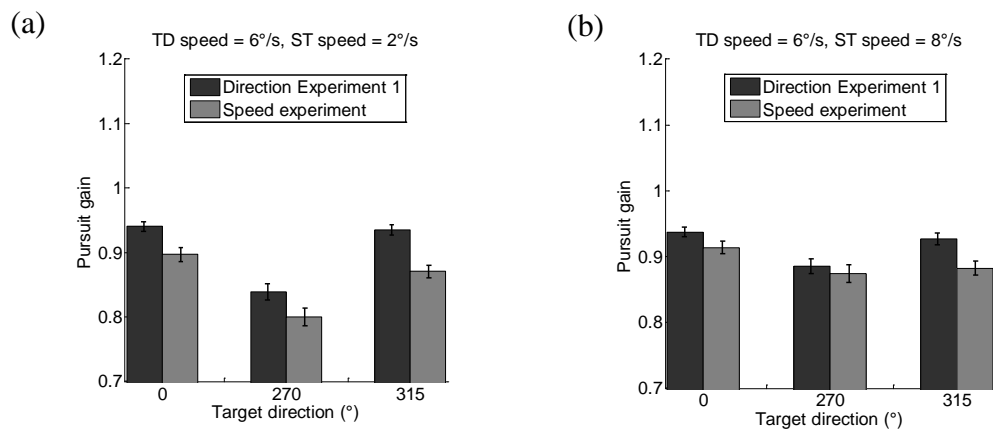


Figure V.6. Average pursuit gains in direction Experiment 1 and the Speed experiment. Results are shown for conditions where the TD moved at 6°/s and the ST moved at (a) 2°/s and (b) 8°/s.

Extra-retinal signal gain (egain)

Target speed in both direction Experiment 1 and the Speed experiment affected the strength of the modeled compensatory signal, or egain ($\tilde{\epsilon}$). Overall, 2°/s

pursuit generated higher egain ($\tilde{\epsilon} = .87$, $sd = .22$) than $6^\circ/s$ pursuit ($\tilde{\epsilon} = .69$, $sd = .20$; $F(1, 104) = 19.39$, $p < .05$), suggesting that eye movement compensation is better for slow eye movements.

The egain was then analyzed only for conditions where TD moved at $6^\circ/s$ to allow for assessing the effect of ST speed. During the $6^\circ/s$ pursuit the egain did not differ between the direction and speed experiments, according to an ANOVA (where Experiment type, TD direction and ST speed were used as independent fixed factors). There was also no main effect for pursuit direction when both experiments were included in the analysis but when analyzed separately the effect of pursuit direction was significant only in the speed experiment, not in the direction experiment. The only significant results were an interaction effect of Experiment type and TD direction, $F(2, 60) = 4.30$, $p < .05$ (egain varied as a function of TD direction, depending on the type of experiment), and an interaction effect of Experiment type and ST speed, $F(1, 60) = 15.38$, $p < .05$ (in the Speed experiment egain was lower for the slow ST but higher for the fast ST in comparison to the Direction experiment). Figure V.7 shows the modeled egain values for both speed conditions and experiment types. Both Target direction and Stimulus speed each had a differential effect on $\tilde{\epsilon}$ in the two experiments. In sum, the cognitive tasks of direction Experiment 1 and the Speed experiment seemed to have different effects on eye movement gain as well as on the extra-retinal signal output ($\tilde{\epsilon}$). However, it should be noted that in the Speed experiment fewer points (speeds) were used for the model fitting, compared to the direction experiment, in which four or five points (directions) were used. Due to the different number of

data points to which the model was fitted, it is important to use caution when viewing the comparison results between the two experiments.

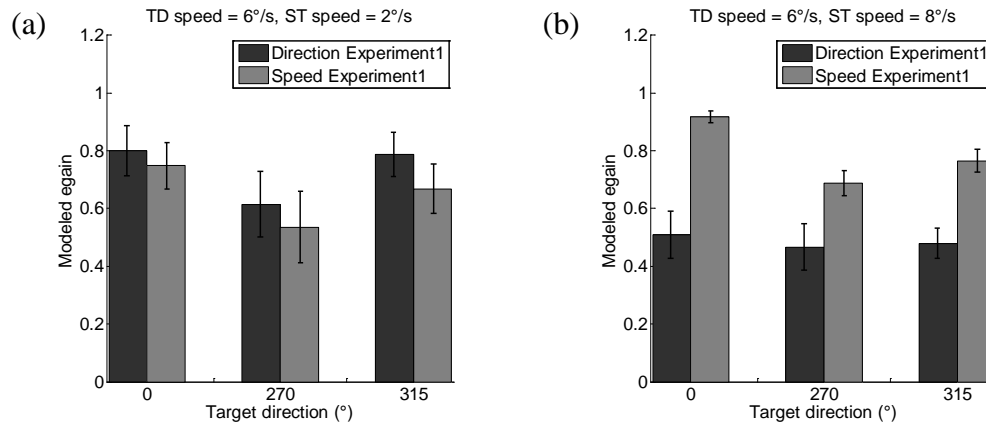


Figure V.7. Comparison of extra-retinal signal between Experiment 1 and the Speed experiment. Average egain values are shown for conditions where the TD speed was 6°/s and the ST speed was (a) 2°/s and (b) 8°/s.

In summary, the Speed experiment was useful in a number of ways. First, eyes stationary trials indicated a non-linear relationship between true and estimated retinal velocities, as higher ST speeds were underestimated and slower ST speeds tended to be slightly overestimated. In contrast, the estimation of the ST direction during eyes stationary was excellent, indicating that true and estimated retinal velocities are linearly related. Second, the method of speed estimation proved to be a good measurement technique because participants were able to learn to associate a number to a particular ST speed. Third, the eye movement results indicated that the perceptual task in the Speed experiment had a different effect on eye movement gain. Similarly, the magnitude of the compensatory signal was different between the Speed and Direction experiments and this difference was not consistent across the slow and fast ST speed conditions (the modeled egain was lower in the Speed experiment only when the ST moved at 2°/s). Overall,

however, the speed estimation was more time consuming and more difficult for participants to do than the direction estimation. As a result, the rest of the thesis will examine direction estimation only, although it is recognized that speed estimation is a topic worth pursuing in future studies.

Chapter VI. Experiment 2: Short stimulus exposure time

Direction Experiment 2 was designed to address the question of stimulus exposure time. Does the eye movement compensation increase as a result of lengthening the stimulus exposure time or as a result of increasing the stimulus speed? As mentioned earlier in the Direction Experiment 1 chapter, longer exposure time of the ST may improve direction estimation ability (increase eye movement compensation), because the ST will travel longer distance on the screen.

Experiment 1 used a stimulus exposure time of 750 ms and ST speeds of $2^\circ/\text{s}$ and $8^\circ/\text{s}$ during a $6^\circ/\text{s}$ pursuit. Perceptual performance was better for the faster ST dot, and it was not clear whether this result could have been affected by the fact that the fast ST traveled further on the screen.

To remove the exposure-related confound of the ST trajectory length, the distance travelled by the fast ST was reduced in Experiment 2: the fast ($8^\circ/\text{s}$) moving ST was exposed for 125 ms, which was six times shorter than 750 ms during which the slow ($2^\circ/\text{s}$) moving ST was presented. Thus, the ST exposure varied for the slow and fast ST such that the fast ST now travelled shorter distance (1.0° of visual angle) than the slow ST (1.5° of visual angle). This experimental design allows for the following hypothesis: If the fast ST exposed for 125 ms is estimated better than the slow ST exposed for 750 ms, one can conclude that it is the ST speed rather than its exposure period (or travelled distance on the screen) that helps compensate for the eye movement. Because direction Experiment 2 produced new data based on a shortened stimulus exposure time, these are reported before any comparison is made to the direction Experiment 1 results.

1. Methods

1.1 Participants, equipment and procedure

The same six participants who completed Experiment 1 also completed Experiment 2. Experiment 2 was completed at least several weeks after Experiment 1, because it was designed only after examining the perceptual data from Experiment 1. The same eye tracker equipment and eye-movement recording procedures were used as in Experiment 1.

1.2 Stimulus display

The sequence of events in Experiment 2 is shown in Figure VI.1. The setting in the main experimental set-up was identical to Experiment 1 except the following:

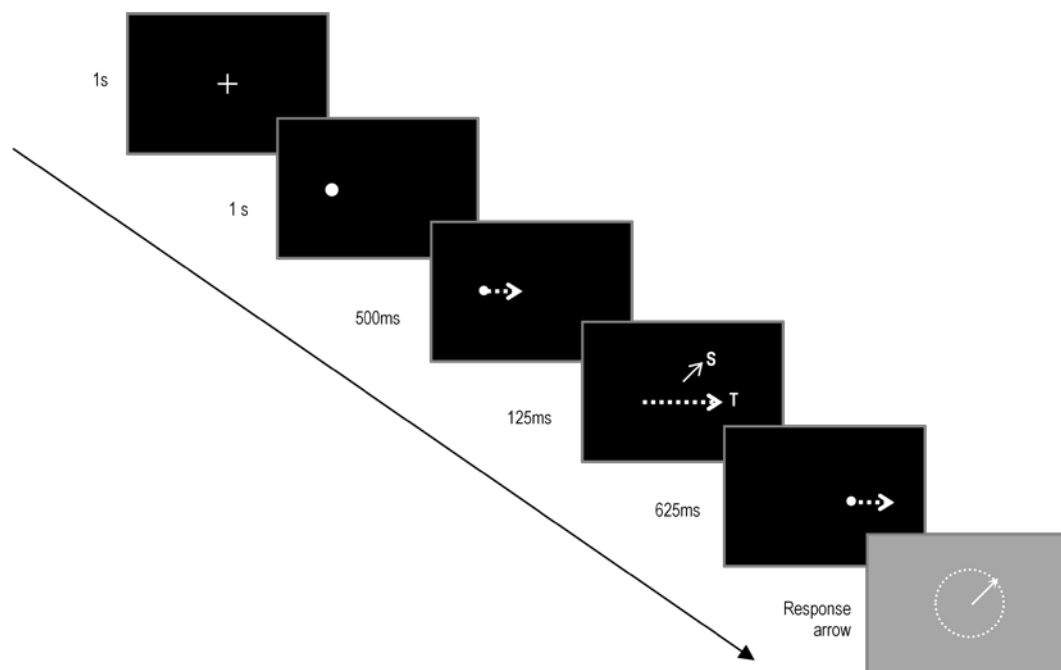


Figure VI.1. Stimulus display for Experiment 2. Each target pursuit interval included a single stimulus dot moving in a particular direction for 125 ms. Observers indicated in which direction the stimulus moved by rotating an arrow on the screen.

- a) In Experiment 2 the stimulus dot was exposed for only 125 ms. This means that the stimulus dot appeared only for a portion of the pursuit time, disappearing 625 ms earlier than the target.
- b) In Experiment 2, conditions with the $2^\circ/\text{s}$ pursuit were removed. One ST direction was added to each pursuit condition in the block of trials. As a result, the total block of trials included 30 conditions, as shown in Figure VI.2 (each of the 3 pursuit directions was combined with one of 5 stimulus directions, where the stimulus moved either at $2^\circ/\text{s}$ or $8^\circ/\text{s}$). There were different ST directions associated with each pursuit direction as they were selected randomly for each pursuit direction.

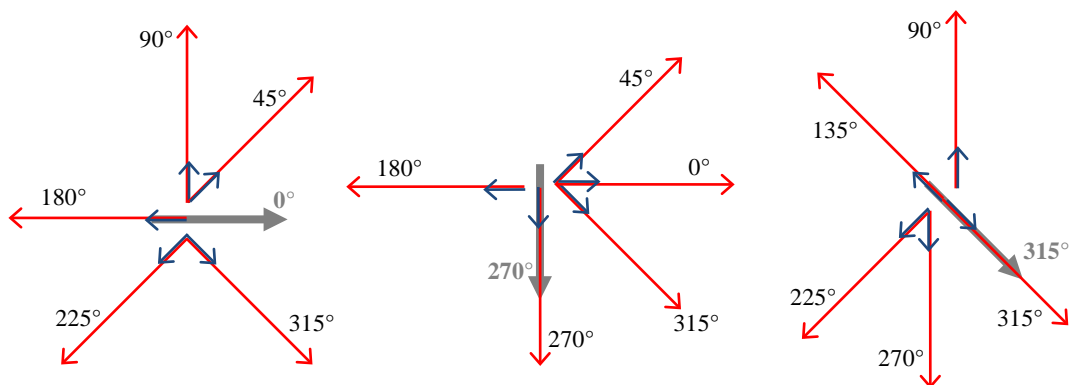


Figure VI.2. Combinations of target-stimulus velocities in Experiment 2. Each TD velocity (grey) was displayed with only one ST velocity per trial. They are shown on the same plot for compactness. The TD always moved at $6^\circ/\text{s}$, while the ST moved either at $2^\circ/\text{s}$ (blue) or $8^\circ/\text{s}$ (red).

2. Results

2.1 Direction estimation during eyes stationary

Similar to Experiment 1, the Experiment 2 participants first estimated the direction of a moving ST in trials with eyes stationary. As mentioned earlier,

Experiment 2 differed from Experiment 1 in that the ST exposure time was reduced from 750 ms to 125 ms, and only pursuit speed of 6°/s and ST speeds of 2°/s and 8°/s were used. Despite the very brief exposure of the ST dot, participants' responses were consistent and varied little from the screen ST direction ($R^2 = 1.00$ for both ST speeds, based on the prediction that the estimate is the same as the screen ST direction).

2.2 Direction estimation during eye movement

The same six participants as in Experiment 1 were tested on a total of 30 different conditions. The condition with TD speed 2°/s and ST speed 4°/s from Experiment 1 was not included in this experiment because it yielded excellent perception and thus was not informative. In addition, this condition produced almost perfect eye movement gain regardless of pursuit direction. I was interested in exploring conditions that resulted in various perceptual errors such as those with 6°/s pursuit, while, at the same time keeping the number of trials to a minimum to prevent dark adaptation of participants. The resulting 30 conditions in a block of trials in Experiment 2 consisted of a combination of 3 pursuit directions, 5 ST directions and 2 ST speeds.

Eye movement analysis

Frequency of saccadic trials: Saccadic trials were calculated in the same way as in Experiment 1. Figure VI.3 shows the percentage of trials in different conditions that were excluded from the analysis. From all measured trials, 7.7% were saccadic (7.6% and 7.8% for ST speed 2°/s and 8°/s, respectively). This percentage is smaller than in Experiment 1, likely due to the brief ST exposure

during which the eye movement was recorded. With shorter stimulus exposure, the chance of producing saccades and blinks is reduced. The most saccades and blinks occurred when the ST moved at $2^\circ/\text{s}$ collinearly with the TD.

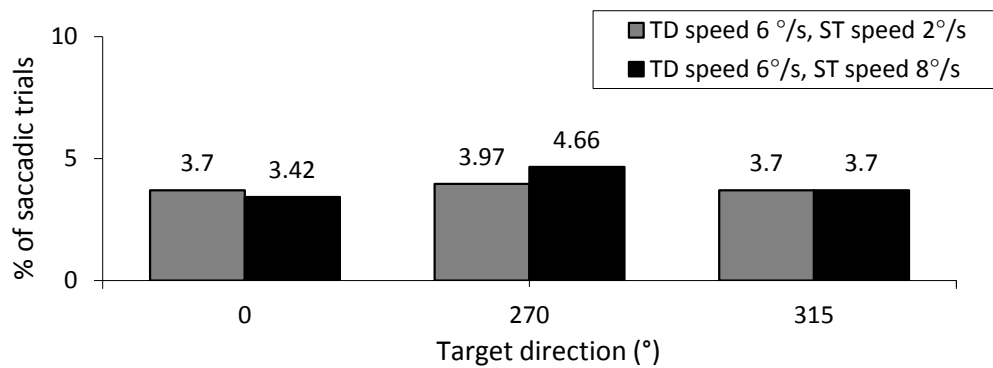


Figure VI.3. The percentage of saccadic trials in Experiment 2

Eye movement direction: eye movement direction was compared to the TD direction to assess how much the eyes deviated from the TD. Figure VI.4 presents pursuit angular errors averaged across the six participants. Pursuit of the TD moving at 315° was the most accurate, regardless of the ST speed.

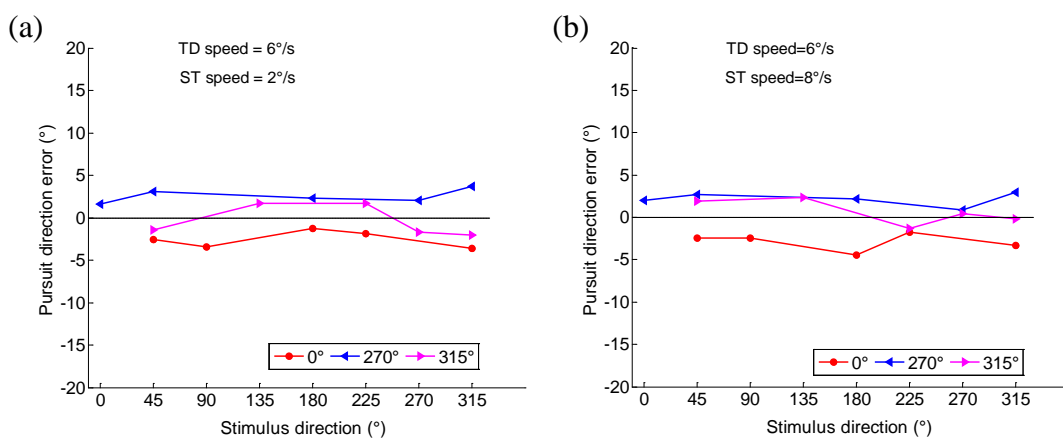


Figure VI.4. Pursuit deviations from the target in Experiment 2. Average eye movement direction errors are presented for the three TD directions and ST speeds of $2^\circ/\text{s}$ (a) and $8^\circ/\text{s}$ (b).

Eye movement gain: Average pursuit gains are presented in Figure VI.5. Overall, pursuit gain was 0.97 (sd = .19), but it significantly varied across TD directions, $F(2, 1947) = 12.12, p < .05$. It was the lowest for TD moving at 270° ($\bar{X} = .92$, sd = .19), while it was similar for the TD moving at 0° ($\bar{X} = .98$, sd = .18) and 315° ($\bar{X} = 1.0$, sd = .18). Stimulus speed had no effect on eye movement gain. The lowest pursuit gain (.88) was for a downward pursuit when the ST directions were 0° and 180° (perpendicular to the TD).

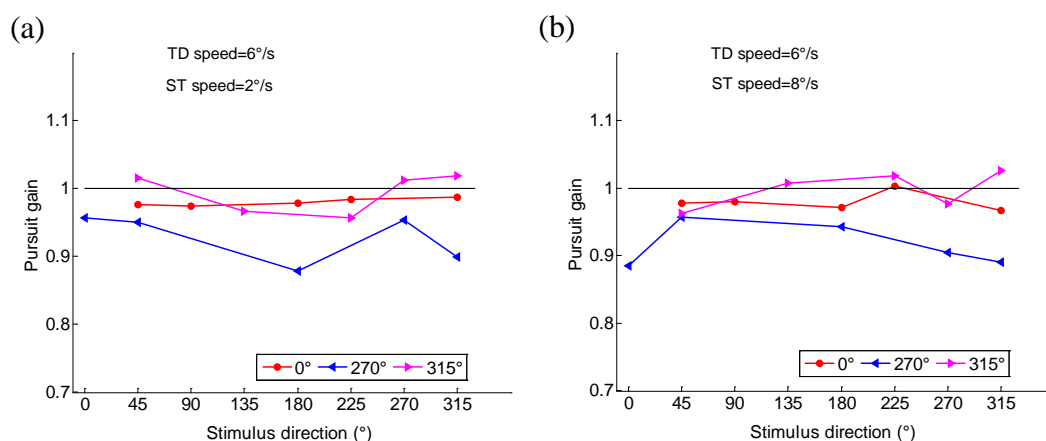


Figure VI.5. Pursuit gains in Experiment 2. Average pursuit gains are plotted for the three TD directions when ST moved at 2°/s (a) and 8°/s (b).

When reviewing the eye movement traces, the brief exposure time became a concern when computing the average eye velocity. Figure VI.6 shows that the fraction of time during which eye movement was measured may not have represented the “average” eye movement velocity at all. The eye velocity fluctuated between about 4.5°/s and 7.0°/s during 125 ms (see Figure VI.6). Therefore, pursuit gain as well as the computed compensatory (extra-retinal) signal averaged during the stimulus exposure time, needs to be taken into account

when interpreting the results. Averaging over a number of trials may alleviate this problem.

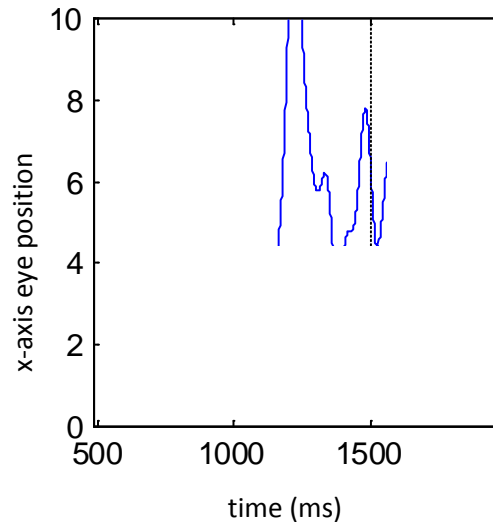


Figure VI.6. Eye velocity trace in Experiment 2. The eye movement velocity was traced when a participant pursued a TD moving at 0° and $6^\circ/\text{s}$. The vertical dashed lines denote the onset and disappearance (exposure duration) of the stimulus during pursuit.

Direction estimates and estimation errors

Reversal errors: In direction Experiment 1 it was found that participants sometimes perceived the ST as moving against the TD when it actually moved in the same direction as TD. This 180° “flip effect” occurred because the slow ST retinal image motion was in the opposite direction to its screen direction. In order to conduct an analysis of variance, it was necessary to remove conditions where the reversal errors occurred. There were 66 out of 259 (25.5%) non-saccadic trials where the ST was perceived as moving in the opposite direction than it actually moved on the screen. After removing the instances with these reversal errors, the estimate averages were still computed across a very large number of trials. The

highest percentage of the reversal errors occurred in conditions where the TD and ST both moved in the same direction on the screen at speeds of 6°/s and 2°/s, respectively (89.7%). Table VI.1 shows the proportion of the reversal errors in the experiment:

Table VI.1. *Proportion of trials with reversal errors in Experiment 2*

Motion Directions	trials with reversal errors	# of trials
TD 270° ST 270°	46 (73%)	63
TD 315° ST 315°	15 (23%)	66
TD 0° ST 180°	5 (8%)	65
TD 315° ST 135°	1 (2%)	66
Total	67 (26%)	260

Note. The number (and proportion) of reversal errors are shown for all non-saccadic trials in the specified condition where TD speed was 6°/s and ST speed was 2°/s.

Table VI.2. *Reversal errors per participant in Experiment 2*

Participant	# of trials with Reversal errors	# of good trials
1.	18	171
2.	13	176
3.	18	161
4.	14	180
5.	5	165
6.	0	159
Total	68	1012

Note. Reversal errors occurred only in conditions where the stimulus moved at 2°/s in the same direction as the target.

The reversal errors were made at some point by five out of the six participants. Reversal errors occurred when participants perceived the ST as moving against the target when it was actually moving in the same direction as the target. Out of a total 1012 non-saccadic trials where the ST moved at $2^\circ/\text{s}$ in the same direction as the TD, only 68 reversal errors were made (6.7%). Table VI.2 shows the amount of reversal errors made by the 5 participants and Figure VI.7 below presents average estimate errors, with the reversal errors removed.

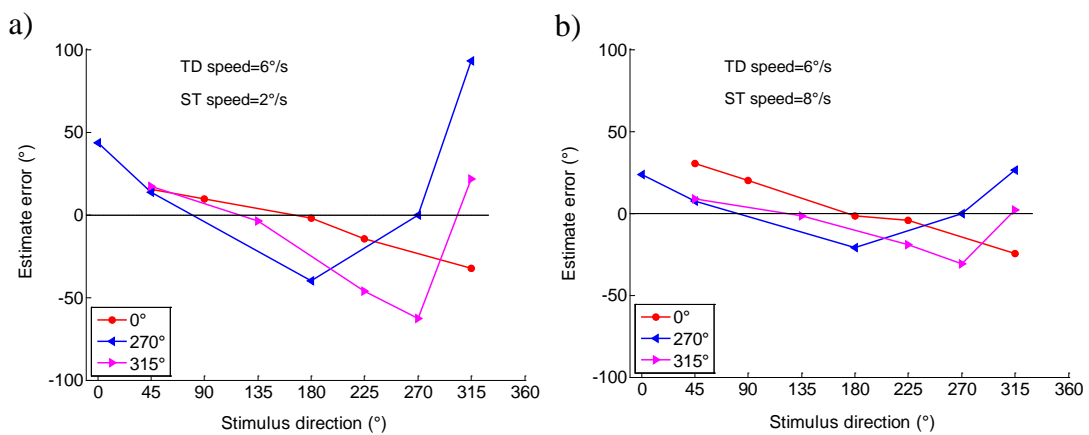


Figure VI.7. Estimation errors in Experiment 2. Average estimation errors are plotted for each pursuit direction when the TD moved at $6^\circ/\text{s}$ and the ST moved at (a) $2^\circ/\text{s}$ and (b) $8^\circ/\text{s}$.

Based on Harrison-Kanji circular analysis of variance, estimation errors significantly varied across the three pursuit directions, $F(2, 1947) = 33.17$, $p < .05$. There was also a main effect of ST speed, $F(1, 1947) = 168.82$, $p < .05$, and an interaction effect of pursuit direction and ST speed, $F(2, 1947) = 9.86$, $p < .05$. Despite removing the reversal errors, the greatest estimate errors occurred when the TD moved at 270° in both ST speed conditions but were larger particularly when the ST moved at $2^\circ/\text{s}$ ($\bar{X} = 20.98$) than when it moved $8^\circ/\text{s}$ ($\bar{X} = 7.52$). The interaction effect can be explained by the finding that the higher ST speed led to

better direction estimations, but only during downward pursuit (the 8°/s ST speed reduced the estimation error from 20.97° to 7.52°). Perceptions of the ST direction were similar during 0° and 315° pursuits for both ST speeds.

When not considering the conditions that produced the reversal errors (TD and ST moving in the same direction on the screen at 6°/s and 2°/s, respectively), the largest estimate errors seemed to occur in conditions where the ST moved a $\pm 45^\circ$ angle to the TD. This trend became apparent for all three pursuits and for both ST speeds, although the errors were larger when the ST moved at 2°/s as opposed to 8°/s (see Figure VI.7a) - during 270° (blue line) and 315° (purple line) pursuits the largest errors occurred when the ST moved at 315° and 270°, respectively.

Extra-retinal signal gain (egain)

The extra-retinal signal gain was determined using the same procedure as in Experiment 1 which is described in detail in Chapter IV. In essence, the egain ($\tilde{\epsilon}$) refers to the compensatory vector that produces the best fit to the given set of ST directions associated with each pursuit direction. An ANOVA revealed that the size of the egain varied as a function of ST speed, $F(1, 30) = 29.59$, $p < .05$, not pursuit direction. For an ST speed of 2°/s the egain was higher ($\bar{X} = .81$, $sd = .39$) than for an ST speed of 8°/s ($\bar{X} = .41$, $sd = .24$). Table VI.3 presents egain values for each ST speed across pursuit directions. Although the estimate errors were larger when the ST moved at 2°/s than when it moved 8°/s, the egain derived from the model fit turned out to be higher for the slow stimulus dot (see Table VI.3).

Table VI.3. *Average egains in Experiment 2*

Direction Experiment 2	Target speed = 6°/s			
	ST speed = 2°/s		ST speed = 8°/s	
	Average egain	sd	Average egain	sd
TD direction 0°	.82	.29	.39	.12
TD direction 270°	.75	.15	.36	.27
TD direction 315°	.87	.26	.49	.31
Overall average	.81	.23	.41	.24

Table VI.4. *Goodness of fit of the model in Experiment 2*

Direction Experiment 2	Target speed = 6°/s			
	ST speed = 2°/s		ST speed = 8°/s	
	Number (percentage) of fits			
RMSE < 15°	4	22%	17	94%
RMSE 15° - 30°	4	22%	1	6%
RMSE >= 30°	10	56%	0	0%

Note. The model goodness of fit is expressed as the Root of mean squared error (RMSE). The table shows the number of fits for a given range of RMSE.

3. Discussion

The main outcome from direction Experiment 2 was the effect of ST speed, not the ST exposure duration on estimation errors. During the brief stimulus exposure in Experiment 2, an ST moving at 8°/s covered shorter trajectory than an ST moving at 2°/s during the long exposure in Experiment 1. This way, a comparison between these two conditions would reflect the role of the stimulus exposure time in the compensation. If direction estimation performance is dependent on the exposure time of the stimulus, then the estimate errors should be worse in this experiment compared to Experiment 1 because the stimulus exposure time was six times shorter. If the direction estimation of the fast ST (8°/s) exposed for a very

short time (125 ms) is better than the estimation of the slow ST ($2^\circ/\text{s}$) exposed for a long time (750 ms), then it can be concluded that direction estimation ability increases with increasing stimulus speed, and not with the greater distance travelled by the ST. This is because the distance travelled by both stimuli was very similar.

3.1 Comparison of direction Experiment 1 and 2

Pursuit gain

Pursuit gain was compared between the long (Experiment 1) and short (Experiment 2) stimulus exposure trials when the TD moved at $6^\circ/\text{s}$. Three-way ANOVA (where the three factors were Experiment type, TD direction and ST speed) revealed a main effect for Experiment type, $F(1, 3187) = 84.68, p < .05$, and a main effect for TD direction, $F(2, 3187) = 58.22, p < .05$. Overall, the long exposure trials generated lower pursuit gain ($\bar{X} = .91, \text{sd} = .14$) than the short exposure trials ($\bar{X} = .97, \text{sd} = .19$). The lowest pursuit gain was for the downward pursuit ($\bar{X} = .90, \text{sd} = .19$) compared to the 0° or 315° pursuits (.96 and .97, respectively). There was also a three-way interaction effect of Experiment type, TD direction and ST speed, $F(2, 3187) = 3.22, p < .05$. This interaction effect implies that pursuit gain variation between the long and short exposure experiments is dependent on TD direction and ST speed.

More specifically, trials with the slow ST exposed for 750 ms (long-slow) were compared to trials with the fast ST exposed for 125 ms (short-fast). A two-way ANOVA with Exposure time and TD direction as the two factors was conducted. Pursuit gain was higher in the short-fast conditions ($\bar{X} = 1.00, \text{sd} = .33$) than in the

long-slow conditions ($\bar{X} = .91$, $sd = .14$), $F(1, 1617) = 49.52$, $p < .05$, although it varied more in the short-fast conditions. In addition, there was a main effect of TD direction, $F(2, 1617) = 19.39$, $p < .05$. Downward pursuit had the lowest gain ($\bar{X} = .91$, $sd = .27$) compared to 0° pursuit ($\bar{X} = .98$, $sd = .29$) or 315° pursuit ($\bar{X} = 1.00$, $sd = .27$).

Direction estimates and estimation errors

A comparison of estimation errors was conducted between the long-slow trials (Experiment 1 trials with ST moving at $2^\circ/s$ for 750 ms) and short-fast trials (Experiment 2 trials with ST moving at $8^\circ/s$ for 125 ms). Perception was more accurate in the short-fast conditions than in the long-slow conditions. A circular inferential analysis, Watson-Williams test revealed a significant difference between these two conditions, $F(1, 1621) = 34.85$, $p < .05$). The slow ST exposed for 750 ms produced larger estimation errors ($\bar{X} = -9.45^\circ$) than the fast ST exposed only for 125 ms ($\bar{X} = .94^\circ$). The fast ST was estimated more accurately than the slow ST despite of the fact it travelled a shorter distance on the screen than the slow ST. In other words, the direction judgments were not made on the basis of the orientation of the ST trajectory when the ST travelled a long distance on the screen, but on the basis of ST speed. However, as discussed earlier, the faster ST also changes its retinal image motion such that it is closer to its screen direction which confounds the perceptual results. In other words, the fast ST may be estimated better simply because its retinal and screen directions are similar, regardless of its exposure time period. Nevertheless, this experiment showed that the direction judgments were based on the ST dot's velocity, regardless of its travelled distance, where higher velocity yields better perception.

Estimation errors in general were compared between Experiment 1 and 2 using circular inferential statistics, particularly the Harrison-Kanji test (equivalent to a two-way ANOVA). In the first analysis, Experiment type and ST speed were used as the 2 factors. There was a significant main effect of Experiment type (long vs. short exposure), $F(1, 1619) = 35.20$, $p < .05$, a main effect of ST speed ($2^\circ/\text{s}$ vs. $8^\circ/\text{s}$), $F(1, 1619) = 239.84$, $p < .05$, as well as an interaction effect, $F(1, 1619) = 16.62$, $p < .05$. Table VI.5 shows the descriptive statistics for the estimation errors in Experiment 1 and Experiment 2, for each ST speed and TD direction conditions.

Table VI.5. *Average estimation errors in direction Experiments 1 and 2*

	Experiment 1			Experiment 2			Experiment 1			Experiment 2		
	<i>ST speed $2^\circ/\text{s}$</i>			<i>ST speed $2^\circ/\text{s}$</i>			<i>ST speed $8^\circ/\text{s}$</i>			<i>ST speed $8^\circ/\text{s}$</i>		
TD	\bar{X}	sd	R	\bar{X}	sd	R	\bar{X}	sd	R	\bar{X}	sd	R
0°	-8.3	34.6	0.81	-5.6	48.0	0.65	0.4	14.8	0.97	3.9	23.5	0.92
270°	-29.3	47.7	0.65	21.0	51.0	0.60	0.2	14.2	0.97	7.5	23.1	0.92
315°	0.7	42.4	0.72	-5.8	58.2	0.48	0.2	17.1	0.96	-8.4	21.2	0.93
Total	-9.5	42.5	0.73	2.8	53.4	0.57	0.3	15.5	0.96	0.94	23.6	0.92

Note. TD is the target direction, R is the circular spread, sd is the standard deviation of estimates and \bar{X} is the average estimate error (in degrees).

Interestingly, the long stimulus exposure duration (and longer ST travelled distance) in Experiment 1 produced larger estimation errors on average than Experiment 2 (short ST exposure). This could be partially explained by the fact that pursuit gain was much lower in Experiment 1 than 2. However, a closer look

at the estimation data for each participant revealed that the magnitude of errors was larger in Experiment 2, but due to the summation of positive and negative signs of the errors, the average error turned out to be small. A more informative statistic regarding the size of errors would be a circular spread or standard deviation, which is substantially larger in Experiment 2 than Experiment 1. Alternatively, computing the average estimation error from *absolute values* of estimate errors (rather than from the actual errors that have both positive and negative values) would provide more information about the error sizes. Average absolute errors revealed that estimates were much worse in the short than the long exposure conditions (see Figure VI.8 b). It is therefore helpful to compute both types of average errors to provide a fuller picture about the estimation data. Pursuit gain in Experiment 2 cannot be used to explain the poor performance in that experiment because it was very close to 1.

Estimate errors differed as a function of ST speed, regardless of the stimulus exposure period: estimate errors were small in both experiments when the ST speed was higher. This difference cannot be attributed to pursuit gain because the average pursuit gain was very similar for both ST speed conditions. In addition, the interaction effect of Experiment type (exposure time) and ST speed indicates that the estimation errors differ between the two ST speeds as a function of the ST exposure time: the difference in the average perceptual errors between ST speeds 2°/s and 8°/s is larger in Experiment 1 than Experiment 2. Thus, the fast ST has a more profound effect on perception in the trials with the longer stimulus exposure. Figure VI.8 presents how estimate errors varied across the three pursuit directions for each experiment and ST speed. The plot reveals how the method of average

error calculation may alter the outcome: a) shows average error sizes based on negative and positive error values, whereas b) shows average estimate errors computed from absolute values of estimate errors. Average estimate errors for Experiment 1 when the ST moved 8°/s were .46, .22 and .21 for 0°, 270° and 315° pursuit, respectively, and line up with the blue horizontal line representing veridical perception (see Figure VI.8 a).

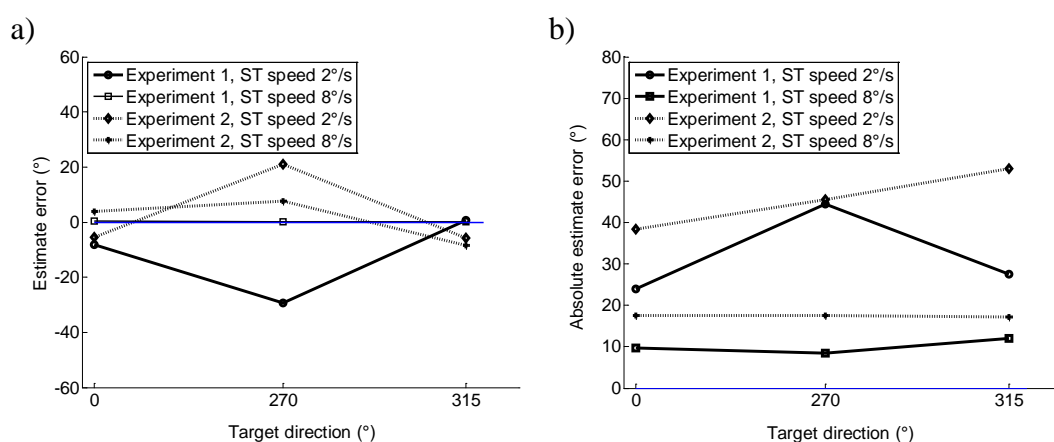


Figure VI.8. Comparison of estimate errors between Experiments 1 and 2. Average estimate errors were computed from actual errors (a), and absolute values of estimate errors (b). The blue abscissa in each plot represents veridical perception. Average estimation errors for ST moving at 8°/s in Experiment 1 are less than .5° and line up with the blue abscissa on graph a).

Extra-retinal signal gain (egain)

Regarding the extra-retinal signal gain (egain $\tilde{\epsilon}$), when TD moved at 6°/s, there was a main effect for ST speed, $F(1, 24) = 38.48$, $p < .05$, and an interaction effect between Experiment type and ST speed, $F(1, 24) = 5.57$, $p < .05$. The interaction effect suggests that differences in egain between ST speed conditions vary in the two experiments, or that the effect of ST speed on egain differs between the 2 experiments. Table IV.2 (page 82) and Table VI.3 (page 117) present the average compensatory egain values for the two ST speeds in Experiment 1 and 2,

respectively. The data show that the short ST exposure time in Experiment 2 has a more pronounced effect on egain. The egain is increased when the ST moves at $2^\circ/\text{s}$ and decreased when the ST moves at $8^\circ/\text{s}$, more so in Experiment 2 than Experiment 1.

In summary, Experiment 2 addressed the exposure duration question in that it implied that it is the ST speed, not the extent of its displacement, which helps in the compensation process. However, changing the ST speed also changes its retinal image motion when pursuit is the same. Thus perceptual performance may be influenced by the pattern occurring on the retina in relation to the movement on the screen. As suggested earlier, the fast moving ST ($8^\circ/\text{s}$) had very similar head-centric and retino-centric velocity during $6^\circ/\text{s}$ pursuit. In contrast, the retinal image motion of the slow ST ($2^\circ/\text{s}$) during $6^\circ/\text{s}$ pursuit was quite different from its head-centric velocity. An ST moving at $2^\circ/\text{s}$ resulted in an overall weaker visual effect than an ST travelling at $8^\circ/\text{s}$. Moreover, it was observed that the slow ST moving at $\pm 45^\circ$ to TD, as opposed to moving away from the TD, resulted in poorer perceptual performance. It became of interest to examine whether different ST directions (and thus different retinal velocities) would have any effect on perception if their speed remained identical on the screen. Additional experiments were designed to answer this question.

3.2 Motivation for Experiments 3, 4 and 5

The main finding from comparing Experiment 1 and 2 was that it is the ST speed rather than the length of ST exposure time or its trajectory that affects perceptual performance. When the fast stimulus dot's exposure time was only 125 ms and its

travelled distance was short, its motion direction was estimated much better than that of the slow stimulus exposed for 750 ms (and travelling a longer distance). Therefore, perception improves as a result of increasing ST speed. However, the proportion of the eye movement-related compensation signal associated with each pursuit direction ($\tilde{\epsilon}$), according to the model computation, was reduced for the faster, more briefly exposed stimulus dot. This implies that the proportions of the eye-movement and visual components in the compensation signal vary as a function of ST speed, and that the visual component is increased by faster moving stimuli.

This inference provides support for models based on velocity signals, such as that by Perrone and Krauzlis (2008). In this model, the authors consider that a cosine distribution representation exists of the visual signal that is produced by a set of velocity sensors located at a given image location. The amplitude of the cosine-like signal produced by the set of velocity sensors is assumed to be proportional to the retinal image speed (the sensor tuned in the direction of the motion is activated the most) and the phase of the signal represents its direction. Under this model, the higher the image speed, the higher the amplitude of the cosine distribution representing the image motion at the level of MST. Therefore, one would expect that the estimation of ST direction would be better when the ST moves faster, which was confirmed by our results. In both experiments the direction estimation errors were lower when the ST moved at 8°/s than when it moved at 2°/s during a pursuit of 6°/s moving TD.

Further, perceptual data were compared between short (125 ms) and long (750 ms) ST presentation conditions. In the short exposure condition the ST moved faster ($8^\circ/\text{s}$) but shorter distance on the screen (1° of visual angle) than in the long exposure condition where the ST moved very slowly ($2^\circ/\text{s}$) but its trajectory on the screen was longer (1.5° of visual angle). According to the findings of Experiments 1 and 2, faster ST dots even during a very brief exposure time produce better perceptual performance than slow ST dots exposed for a long time. The data suggest that it is the ST velocity that is important in the compensation mechanism, not the length of the ST trajectories, and thus support the Perrone & Krauzlis model which uses the image velocity at a particular location and does not rely on the distance covered by the dot.

The observations from Experiments 1 and 2 suggest that when the ST speed is relatively low with regard to the target speed, the estimation accuracy significantly decreases. Specifically, when the ST speed was $2^\circ/\text{s}$ it was more difficult for the participants to judge its direction than when the speed was $8^\circ/\text{s}$. As a result, the combination of a pursuit target moving at $6^\circ/\text{s}$ and stimulus moving at $2^\circ/\text{s}$ was selected for further examination. It was of interest to assess whether additional visual information in these target-stimulus speed conditions would affect ST perception. As mentioned earlier, a single dot stimulus moving slowly across the screen display would produce a relatively weak visual signal. We therefore wanted to increase the global visual signal by adding background elements during eye movement, and test whether this additional retinal flow would affect the magnitude of the motion signal at the MST level, i.e., whether it would alter the degree of compensation. A new experiment was designed that

included background elements in the form of small, randomly positioned static dots during the time when the single stimulus dot was visible on the screen. In addition, stimuli were selected to be moving either at a $\pm 45^\circ$ or $\pm 135^\circ$ angle to the TD. This arrangement allowed the separation of the ST directions into two groups, based on their retinal speeds. For example, an ST would move at $2^\circ/\text{s}$ on the screen, but it would have different speeds on the retina, depending on its screen direction.

Chapter VII. Experiment 3: Introducing stationary background

The aim of Experiment 3 was to uncover what influence the visual component (γ_r) has on the eye-movement related signal as determined by the modeled egain ($\tilde{\epsilon}$).

In Experiments 1 and 2 the visual information contained on the display was minimal. In addition, compensation was very good when the ST moved at $8^\circ/\text{s}$ but worsened when the ST moved at $2^\circ/\text{s}$. It was of interest to inspect the instances with the slow ST, which was perceived with larger errors than the fast ST, and test whether its perception would improve as a result of increasing the strength of the visual input by the addition of features into the background. To increase the visual component of the display, additional elements were introduced to the background during the stimulus dot exposure. These elements were static dots, smaller and dimmer than the ST dot itself to help the ST be seen clearly. The stimulus and background exposure was set to 750 ms to produce a strong visual effect, because it was felt that it would be too hard for participants to judge the direction of a $2^\circ/\text{s}$ moving stimulus presented only for 125 ms.

Considering the results of the slow ST from Experiments 1 and 2, it was of interest to further investigate how its retinal image motion may affect compensation. For example, when the slow ($2^\circ/\text{s}$) ST moves at $\pm 45^\circ$ relative to the TD moving at $6^\circ/\text{s}$, the ST retinal image motion is much smaller than when it moves away from the TD. To assess whether the additional background would decrease the occurrence of reversal errors, a condition where the ST would move in the same direction as the TD was included. However, it was also important to

include other ST directions that would produce varying retinal speeds while keeping the head-centric ST speed at $2^\circ/\text{s}$.

The hypothesis for Experiment 3 was that increasing the visual component in the stimulus display by adding the background stationary dots would improve perceptual performance and reduce estimation errors. Based on Wertheim's model, it was also hypothesized that the visual component in the compensation signal (γ_r) would increase. Because γ_r was not quantified, it could be only assessed from perceptual performance (indicating an overall compensation e') and the modeled egain representing the eye-movement related signal (ϵe), such that $\gamma_r = e' - \epsilon e$. If perception is better in Experiment 3 than in Experiment 1 (in which the ST exposure time was the same) and the ϵe portion of the overall compensation signal stays the same or decreases, we can presume that the γ_r has increased.

1. Methods

1.1 Participants, equipment and procedure

There were a total of 13 participants who completed direction estimation Experiment 3. Out of these, only 3 participants were from the original sample (who completed Experiments 1 and 2). Ten new participants were randomly selected from a pool of first year Psychology students recruited through the same means as participants in previous experiments. The new sample of 13 included 6 males and 7 females with normal vision whose age ranged between 22 and 40 years. The same eye tracker equipment and eye-movement recording procedures were used as in previous experiments.

1.2 Stimulus display

The sequence of the events in the experiment is shown in Figure VII.1. The main experimental set-up was identical to Experiment 1 except the following:

- a) Similarly to Experiment 1, the stimulus dot (ST) was exposed for 750 ms. However, during this exposure time in Experiment 3, the stimulus background was covered by 200 static dots randomly positioned over an area of 800 x 600 pixels (visual angle of $17.30^\circ \times 13^\circ$ horizontally and vertically, respectively). The static background dots were dimmer and half the size of the ST dot.

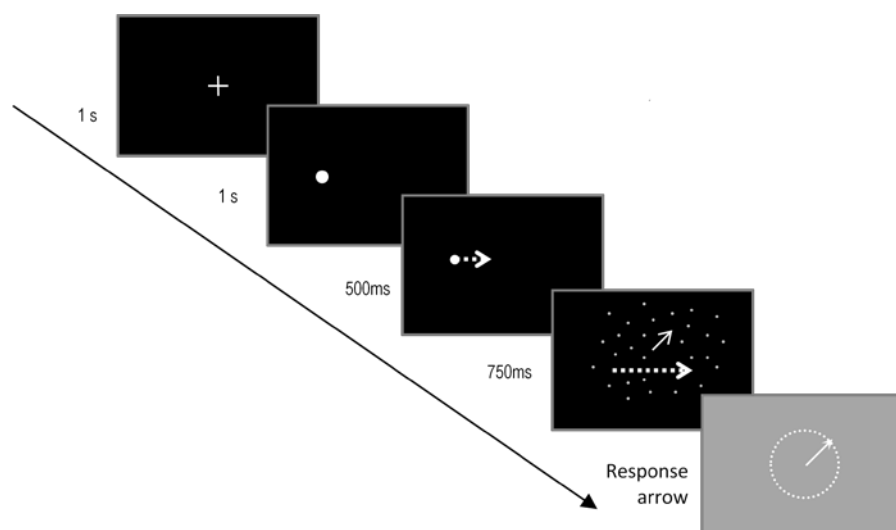


Figure VII.1. Stimulus display in Experiment 3. Each pursuit interval included a stimulus dot moving in a particular direction for 750 ms across a background covered with 200 randomly positioned small stationary grey dots. Observers indicated in which direction the ST moved by rotating an arrow on the screen.

- b) In Experiment 3, two more pursuit directions were added to provide data for pursuits covering other areas of the screen (other than the right lower quadrant). Specifically, targets moving at angles 225° and 180° were

added to provide a more symmetrical sample of eye movements. Each block of trials consisted of 5 target directions, each combined with one of 5 ST directions. The ST directions were chosen to be consistently related to the TD motion: that means the ST moved either at $\pm 45^\circ$ or $\pm 135^\circ$ to the TD. Figure VII.2 shows a diagram with the five TD directions, each associated with the five ST directions. The TD always moved at $6^\circ/\text{s}$ while the ST always moved at $2^\circ/\text{s}$.

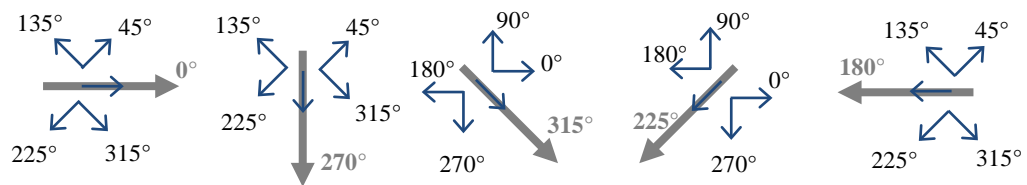


Figure VII.2. Combinations of target-stimulus velocities in Experiment 3. Each TD velocity was displayed with only one ST velocity per trial. They are shown on the same plot for compactness. The TD always moved at $6^\circ/\text{s}$ and the ST always moved at $2^\circ/\text{s}$.

2. Results

2.1 Direction estimation during eyes stationary

Each participant completed ten eyes stationary blocks of trials for direction Experiment 3. Participants' responses were in agreement with the screen ST directions ($R^2 = 1.00$, where R^2 refers to the variance of the data explained by a zero error model where estimate = stimulus direction).

2.2 Direction estimation during eye movement

Frequency of saccadic trials

The percentage of trials excluded from the analysis due to saccades or blinks for each condition is shown in Figure VII.3. The overall percentage of saccadic trials across all 25 conditions was 40.9%. This frequency is high because strict criteria were used to select only good quality eye movement trials for the analysis. The most saccadic trials occurred during 270° pursuit (53.7%) while the fewest saccadic trials occurred during 315° pursuit.

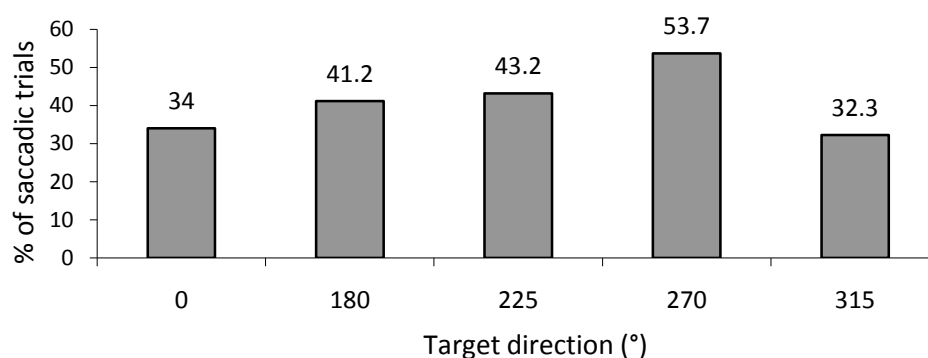


Figure VII.3. Percentage of saccadic trials in Experiment 3.

Eye movement velocity

Pursuit direction: The average eye movement direction, as recorded by the eye-tracker, was compared to the screen TD direction. Figure VII.4 a) shows the pursuit deviation from the moving TD. Pursuit direction was generally good and deviated little from the TD direction (see Table VII.1). There were differences in pursuit direction errors across the five TD direction conditions, $F(4, 1918) = 84.12$, $p < .05$. The largest eye movement error occurred during the diagonal pursuits (225° and 315°). Interestingly, for both pursuits, the eye movement ‘gravitated’ upward.

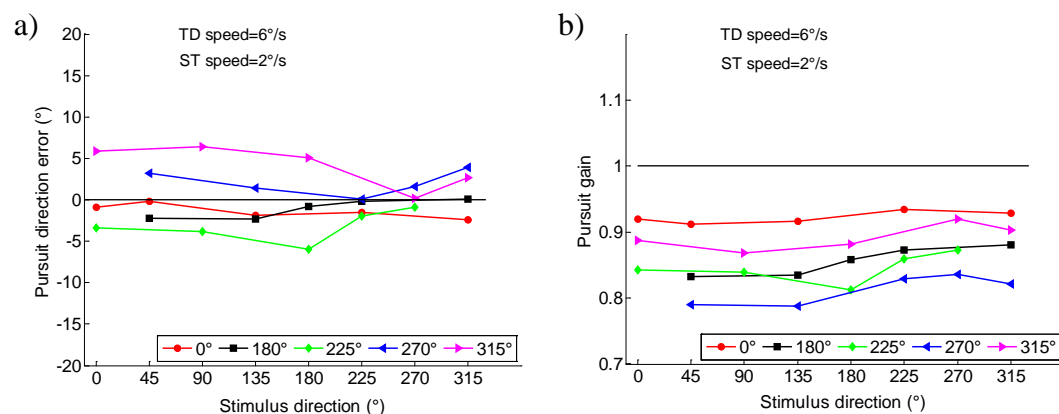


Figure VII.4. Pursuit errors and pursuit gains in Experiment 3. Average pursuit deviations from the TD (a) and average pursuit gains (b) are presented for all five pursuit directions (coloured lines) across the given ST screen directions.

Pursuit gain: Table VII.1 presents average eye movement gains for the five pursuit conditions in Experiment 3, and Figure VII.4 b) further shows average eye movement gains for each TD–ST combination. Overall, eye movement gain ranged between .81 (for TD 270°) to .92 (for TD 0°), and tended to slightly increase when the ST moved at a $\pm 45^\circ$ angle to the TD. Overall, pursuit gain significantly varied across the five TD directions, $F(4, 1918) = 33.98$, $p < .05$.

Table VII.1. *Pursuit gain, pursuit error and estimation error in Experiment 3*

Target direction	n	Average pursuit gain	Average pursuit error	Average absolute pursuit error	Average estimate error	Average absolute estimate error	Estimate sd
0°	429	.92	-1.33°	3.40°	-1.59°	22.52°	34.4°
180°	382	.86	-1.06°	3.93°	2.04°	22.24°	34.2°
225°	369	.84	-3.25°	6.22°	-1.42°	19.05°	29.3°
270°	301	.81	2.03°	4.80°	-2.17°	23.38°	33.9°

Target direction	n	Average pursuit gain	Average pursuit error	Average absolute pursuit error	Average estimate error	Average absolute estimate error	Estimate sd
315°	440	.89	4.20°	6.38°	2.31°	20.01°	30.8°
Overall	1921	.87	0.18°	4.95°	-0.17°	21.44°	

Direction estimates and estimation errors

Reversal errors: A reversal error occurs when the ST is perceived as moving in the opposite direction to the TD when on the screen it actually moves in the same direction as the TD. Direction estimation is based on the retinal image rather than screen ST direction during pursuit. There were 5 conditions where the ST moved in the same direction as the TD (5 different target directions). The total number of completed trials displaying these conditions resulted in 384 non-saccadic trials from all participants. Only 2 reversal errors occurred: one during 225° pursuit and one during 315° pursuit. Both reversal errors were made by the same participant. This result suggests that the background dots virtually eliminated the occurrence of reversal errors.

Estimate Errors: Average estimate errors for each pursuit direction, computed both on actual and absolute error values (excluding trials with the reversal errors), are listed above in Table VII.1. The largest estimate error occurred for downward pursuit while the lowest estimate errors were associated with the diagonal pursuits. However, according to the Watson Williams test (circular equivalent to one-way analysis of variance), the average estimate errors did not differ significantly across the five different pursuit directions. The error curves in

Figure VII.5 indicate larger errors for trials when the ST moved at a $\pm 45^\circ$ angle to the TD than when it moved at a $\pm 135^\circ$ away from the TD.

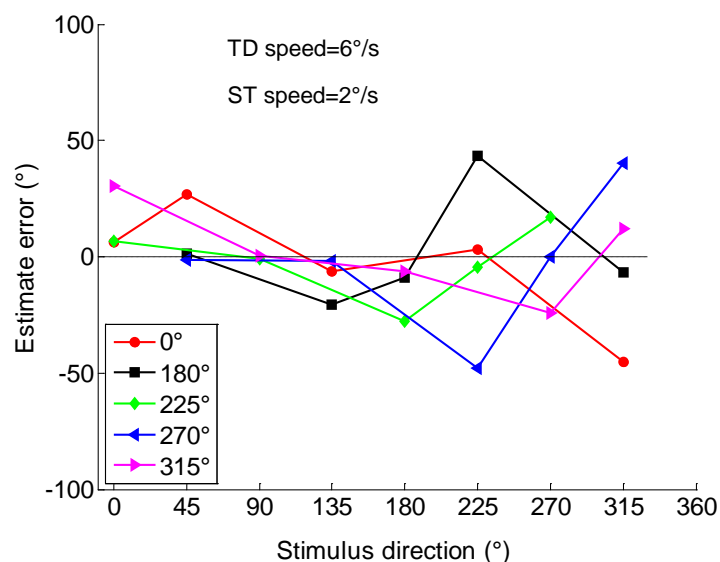


Figure VII.5. Average estimate errors in Experiment 3. The coloured lines represent the five pursuit direction conditions. Estimate errors are plotted for the given screen ST directions, relative to veridical perception (represented by the zero error horizontal dashed line). The standard error of the mean was very small in all conditions and is not visible on the graph.

In Experiment 3 significant correlations were noted between pursuit errors (eye movement deflection angle from the TD) and estimate errors, and between eye movement gain and estimate errors. Unlike in Experiment 1 and 2 in which these correlations were insignificant, in some conditions of Experiment 3 they were weak but significant. A correlation analysis was performed between the actual estimation errors and pursuit gain (r_1) and between the actual estimation errors and pursuit direction errors (r_2). Table VII.2 shows that generally, correlations were low, and were significant only for some pursuit directions. The strongest

significant correlation (.27) was found between eye movement gain and estimation errors for downward pursuit.

Table VII.2. *Relationship between eye movement characteristics and perception in Experiment 3*

TD direction	r₁	r_{1(abs)}	r₂	r_{2(abs)}
0°	n.s.	n.s.	0.09*	n.s.
180°	.19*	0.19*	n.s.	-0.11*
225°	n.s.	n.s.	n.s.	0.19*
270°	0.27*	0.28*	0.13*	n.s.
315°	0.12*	0.14*	n.s.	0.24*

Note. Correlations are presented between pursuit gain and estimate error (r_1), and between pursuit direction error and estimate error (r_2). Correlations computed using absolute values of the errors are presented as $r_{1(abs)}$ and $r_{2(abs)}$.

* Significant correlation, $p < .05$

Extra-retinal signal gain (egain)

Extra-retinal signal gain or egain refers to the eye movement-related compensatory gain based on the best fit of the linear vector model to the estimation errors for a set of ST directions associated with a particular pursuit direction. The model's best fit is represented by an egain value (\tilde{e}) for each pursuit direction. The model's goodness of fit is expressed as the root of mean squared error (RMSE), and is reported in Table VII.3. RMSE rather than R^2 was used because the fitted curves were in some cases non-linear and R^2 turned out to be negative.

Table VII.3. *Goodness of fit of the model in Experiment 3*

Direction Experiment 3	Target speed = 6°/s	
	ST speed = 2°/s	
	Number (percentage) of fits	
RMSE < 15°	31	48%
RMSE 15° - 30°	27	42%
RMSE >= 30°	7	11%
Total of fits	65	100%

Note. The model goodness of fit is expressed as the Root of mean squared error (RMSE). The table shows the number of fits for a given range of RMSE.

The overall average compensatory egain ($\tilde{\epsilon}$) in Experiment 3 was .73. An analysis of variance revealed that the egain did not vary much across pursuit directions: the average $\tilde{\epsilon}$ was .78, .74, .73, .65 and .76 for 0°, 180°, 225°, 270° and 315° pursuits, respectively. The egain was very similar for all pursuit directions except for downward pursuit when it was insignificantly the lowest (see Figure VII.6). The average egain did not seem to change in accordance with estimation errors; for example, egain was not increased when the estimate errors were low (e.g., during the diagonal pursuits).

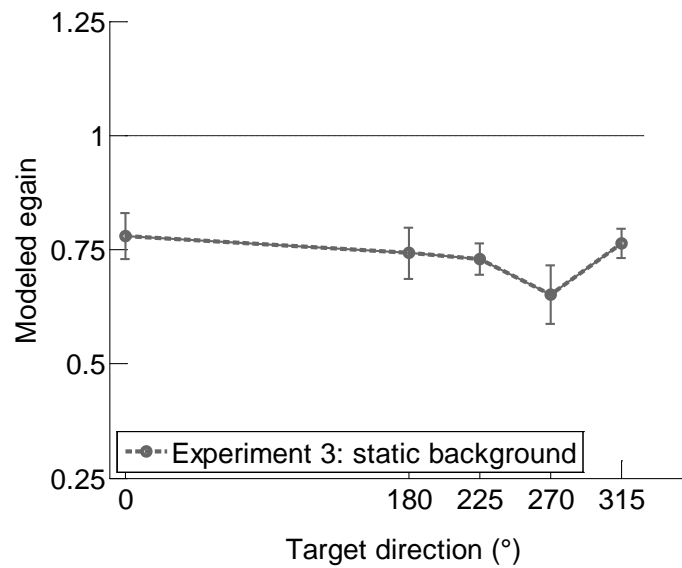


Figure VII.6. Modeled extra-retinal signal gain (egain) in Experiment 3. The egain value represents the best model fit to a set of estimation errors for a given pursuit direction. The variation shown for each egain value is the standard error of the mean.

3. Discussion

The total amount of saccadic trials in direction Experiment 3 was 40.9%. These were excluded from statistical analyses. The most saccades and blinks occurred during downward pursuit (53.7%) which was much higher than in Experiment 1 (36.4%). It may be that the additional dots in the background increased the number of saccades and blinks, in comparison to the no background conditions. The results of Experiment 3 also revealed that pursuit gain was dependent on target direction. Eye movement gain was the lowest for downward pursuit (.81) and the highest for horizontal pursuit (.92). Pursuit direction was generally good and was very close to the target dot trajectory.

There were only two occasions in Experiment 3 in which a reversal error was made (out of possible 384 good trials), and these were made by one participant only. This result differs from Experiment 1. In Experiment 1 reversal errors were quite frequent in situations where the slow ST moved in the same direction as the TD, and were made by most participants. It seems that the stationary dots in the background had a positive effect on perception, as they “helped” participants perceive the ST motion correctly. It was possible that the stationary dots provided position cues to the participants, in that they could judge the ST dot’s direction in relation to the background.

Estimation errors in Experiment 3 were very similar across all five pursuit directions. This consistent ability to judge the ST direction across pursuit conditions may have also been the result of the static dots in the background. Participants could have used the relative motion between the ST and static dots to make their direction estimates, especially during downward pursuit (when estimate errors were large in Experiment 1). The role of the additional background in Experiment 3 will need to be examined further. Looking at the estimation errors for downward pursuit in Experiment 1 and 3 revealed that in Experiment 3 the average error was much lower (see Figure VII.7). Using both real and absolute error values, the average estimate error was -29.33° and 44.40° in Experiment 1, and -9.98° and 29.96° in Experiment 3, respectively. However, it should be noted that comparing the results of these experiments may be confounded by the differences in the stimulus display setup (ST and TD direction combinations were different in the two experiments). In addition, Experiment 1 was completed by a much smaller and different sample of people than Experiment 3. To control for

the experimental differences, it would be useful to repeat the Experiment 1 using the same participants and target-stimulus velocities as Experiment 3.

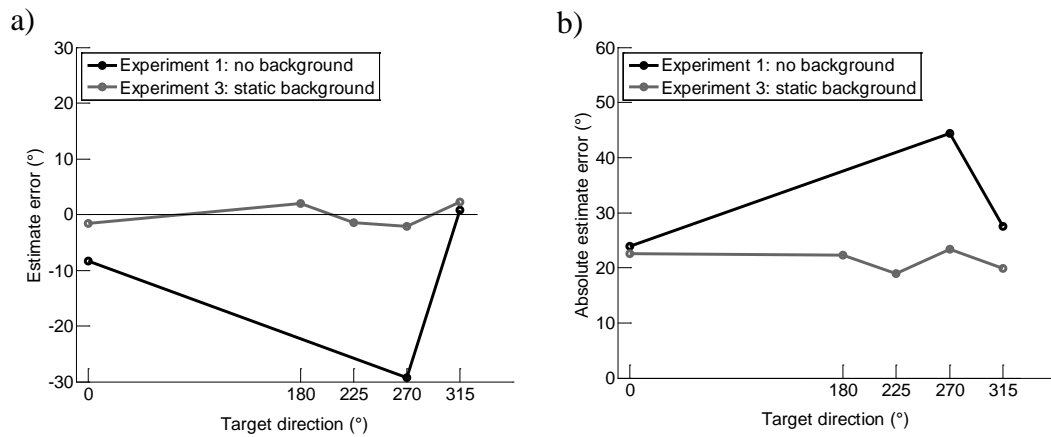


Figure VII.7. Comparison of estimation errors between Experiments 1 and 3. Average estimate errors were computed for each pursuit direction, both from actual estimate errors (a) and absolute error values (b).

The estimate of the extra-retinal signal gain ($\tilde{\epsilon}$), as derived from the linear vector model fit, turned out to be relatively similar across all pursuit directions, except for the downward pursuit when it was quite low (.65). Because the estimate errors during this pursuit direction were similar in comparison to the other pursuit directions, it was expected that $\tilde{\epsilon}$ would be also similar. For the other pursuit directions, again values ranged between .73 and .78. One possible explanation for the low egain during downward pursuit is that the background dots increased the visual component (γr) in the extra-retinal signal. As discussed earlier, the overall compensation is thought to be composed of the eye movement related extra-retinal signal and a visual component ($e' = \tilde{\epsilon} + \gamma r$). The results may imply that the compensation was relatively good due to an increased visual component. The lowered egain for downward pursuit could also be related to the reduced eye

movement gain during this pursuit as e_{gain} is based on eye movement gain, and the correlation between downward pursuit gain and estimate errors was significant.

To summarize, the background dots in direction Experiment 3 lead to a high frequency of saccadic eye movements, however, when these were removed, pursuits were of high quality regarding both eye movement gain and eye movement deviation from the moving target dot. The direction estimation errors were similar and relatively low across all pursuit directions. The extra-retinal signal gain estimate was also consistent across the pursuit directions, except for downward (270°) pursuit when $\tilde{\epsilon}$ was significantly reduced.

The results from Experiment 3 indicate that the relationship between the extra-retinal gain estimate $\tilde{\epsilon}$ and perception is more complex than thought. The expectation was that $\tilde{\epsilon}$ would decrease as a result of the additional background dots, as these would increase the visual component (γ_r) in the overall compensatory signal. This happened, as $\tilde{\epsilon}$ was higher in Experiment 1 (no background dots) than in Experiment 3 (with background dots). However, the downward pursuit condition produced very low e_{gain} although perception was comparable to that in other pursuit conditions. Overall, the static dots in the background may have served as a visual reference cue for judging the ST direction. Therefore, another experiment was necessary which would use different background properties and which eliminated the static visual cue.

Chapter VIII. Experiment 4: Introducing a moving background

Direction Experiment 4 was designed so that relative position of the ST to the background dots could not be used as a reference when judging its direction. This was addressed by making the background dots move at the same velocity as the ST. Even the moving background, however, may aid perception because it increases visual stimulation. The patch of moving background dots spans a large area of the visual field, plus it moves alongside the ST, so in this regard it presents a greater amount of visual motion than the stationary background dots. The question again, is whether the increased global visual signal helps in the compensation when the background moves with the ST. The impact of the static dots in Experiment 3 was evident because estimate errors were low for all pursuit directions. Only in the case of 270° pursuit was the compensatory $\tilde{\epsilon}$ quite low, but it was likely due to the decreased eye movement gain during this pursuit direction, which is taken into account when computing the $\tilde{\epsilon}$. In relation to Experiment 1, overall perceptual performance in Experiment 3 was much better and yet, $\tilde{\epsilon}$ was lower. Because our model is based on $e' = \epsilon e + \gamma r$, the finding from Experiment 3 suggests that if ϵ is low, the γ must have increased to produce a good overall e' , or that the additional background pattern caused the visual system to rely more on the increased visual component of the compensation signal than on the eye-movement-related signal ϵe .

1. Methods

The methodology of direction Experiment 4 was identical to Experiment 3 except the patch of background dots was not stationary and moved at the same velocity and for the same length of time as the ST. The ST/background exposure duration was also set to 750 ms to produce a strong visual effect, because it would be very hard for participants to judge the direction of a $2^\circ/\text{s}$ moving ST for only 125 ms.

Figure VIII.1 shows the sequence of events on the display in Experiment 4.

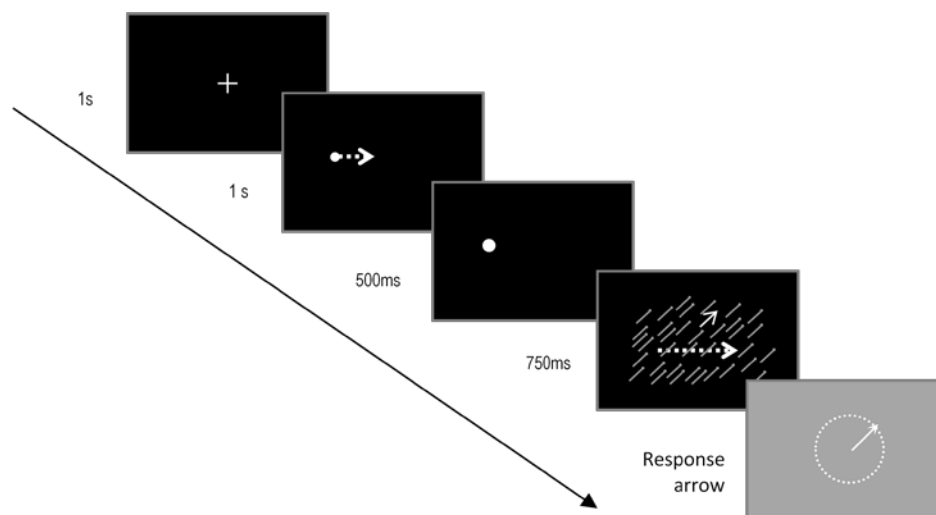


Figure VIII.1. Stimulus display for Experiment 4. Each pursuit interval included a single ST, along with a patch of background dots all moving in a particular direction for 750 ms. Observers indicated in which direction the ST moved by rotating an arrow on the screen.

In pursuit experiments such as these there is always the danger that the participants judge the velocity of the ST using the display frame as a reference. In the earlier experiments with a single ST, this was unlikely because the ST was well away from the display edges. In Experiment 4 the background dots were closer to the edges but it is unlikely that this cue was usable because the dots

appeared and disappeared at random times and locations. In addition, the edges of the computer screen were blacked out and their visibility was minimized by controlling the participants' dark adaptation between blocks of trials and by the use of a brighter screen during the arrow setting phase. Finally, the frame was unlikely to be noticed due to the fact it was in the participants' visual periphery, blending with the black wall behind the computer. The same participants who completed Experiment 3 also completed Experiment 4.

2. Results

2.1 Direction estimation during eyes stationary

Each participant completed ten eyes stationary blocks of trials in Experiment 4. In fact, participants judged not only the ST direction, but the direction of the moving background, while fixating on the stationary TD in the middle of the screen.

Participants' responses were generally in agreement with the screen ST directions, except for one participant who misjudged ST moving at 0° and 180° angles. The R^2 was 1.00 (essentially 100% of the total variance in the estimates is explained by the ST screen directions).

2.2 Direction estimation during eye movement

Frequency of saccadic trials

The percentage of saccadic trials during eye movement is shown in Figure VIII.2. The most saccadic trials occurred in leftward (45.1%) and downward (42.3%) pursuits while 315° pursuit generated the least saccadic trials (27.1%). Overall, 36.5% of completed trials in Experiment 4 were removed from the analysis as a result of saccades and blinks.

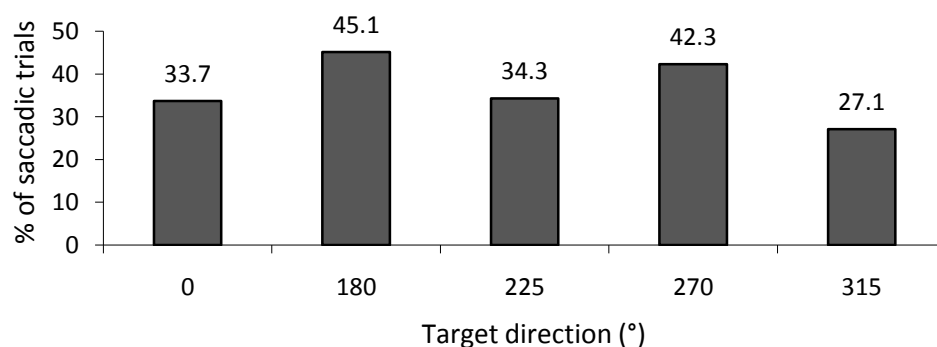


Figure VIII.2. Percentage of saccadic trials in Experiment 4

Eye movement velocity

Pursuit direction: The accuracy of eye movement direction was examined in each pursuit direction condition. Deviations of eyes from the TD, or pursuit direction errors, varied depending on TD direction (shown in Figure VIII.3 a). Based on Watson-Williams circular analysis of variance, there was a significant main effect of TD direction, $F(4, 2008) = 59.75$, $p < .05$. The oblique pursuits deviated more from the TD than pursuits in cardinal directions.

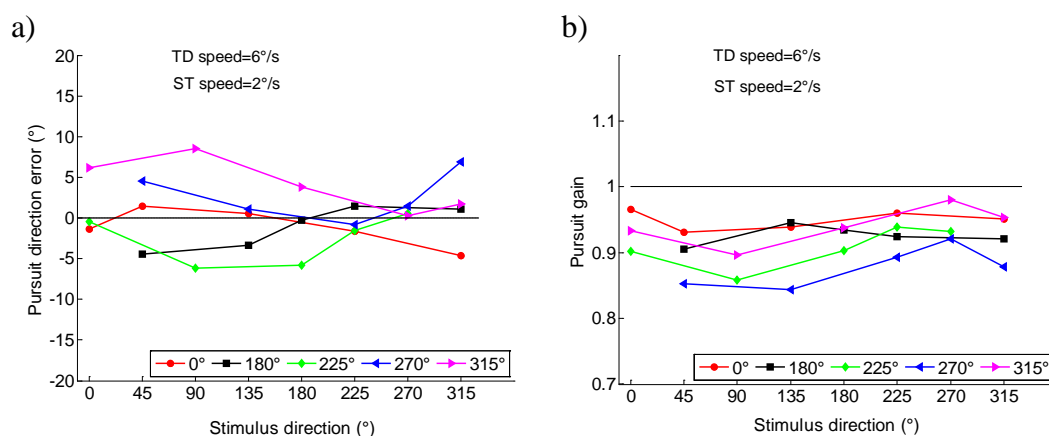


Figure VIII.3. Pursuit errors and pursuit gains in Experiment 4. Average eye movement deviations from the TD (a) and average pursuit gains (b) are presented for all five TD direction conditions.

Pursuit gain: Table VIII.1 presents average eye movement gains for the five pursuit conditions in Experiment 4, and Figure VIII.3 b) further shows average eye movement gain for each TD-ST combination. Overall, eye movement gain ranged between .88 (for 270° pursuit) and .95 (for 0° pursuit), and appeared to slightly decrease when the ST moved away from the TD (at a $\pm 135^\circ$ angle to the TD). Pursuit direction had a significant effect on pursuit gain, $F(4, 2008) = 33.98$, $p < .05$.

Table VIII.1. *Average pursuit gains, pursuit errors and estimate errors in Experiment 4*

Target direction	n	Average pursuit gain	Average pursuit error	Average absolute pursuit error	Average estimate error	Average absolute estimate error	Estimate sd
0°	431	.95	-1.01°	3.66°	-1.93°	23.49°	9.7°
180°	357	.92	-1.27°	4.51°	3.11°	22.37°	38.5°
225°	427	.91	-2.56°	6.32°	1.35°	21.41°	38.6°
270°	375	.88	2.65°	5.49°	-2.57°	25.77°	5.8°
315°	474	.94	4.04°	6.39°	1.44°	22.50°	38.4°
Overall	2064	.92	0.37°	5.27°	0.28°	23.11°	

Direction estimates and estimation errors

Reversal errors: There were no reversal errors (where the perceived ST direction was opposite to the screen ST direction) in the non-saccadic trials.

Estimate Errors: Average estimate errors for each pursuit direction, computed from both actual and absolute values are shown above in Table VIII.1. The largest

estimate error occurred during leftward pursuit when computed from the actual error values, but based on the absolute values, the largest error occurred during the 270° pursuit. Overall, varying TD direction had no effect on estimation errors (no main effect of TD direction). Upon a closer look, the estimate error curves from Figure VIII.4 suggest that larger estimation errors occurred when the ST moved at a $\pm 45^\circ$ angle to the TD than when it moved away from the TD (at a $\pm 135^\circ$ angle to the TD). For example, the largest misperceptions were evident in 180° pursuit (black line) and an ST moving at 225°, in 270° pursuit (blue line) and an ST moving at 225°, or in 0° pursuit (red line) and an ST moving at 315°. The estimation data in Experiment 4 as shown in Figure VIII.4 are very similar to those in Experiment 3 as shown in Figure VII.5 (page 135).

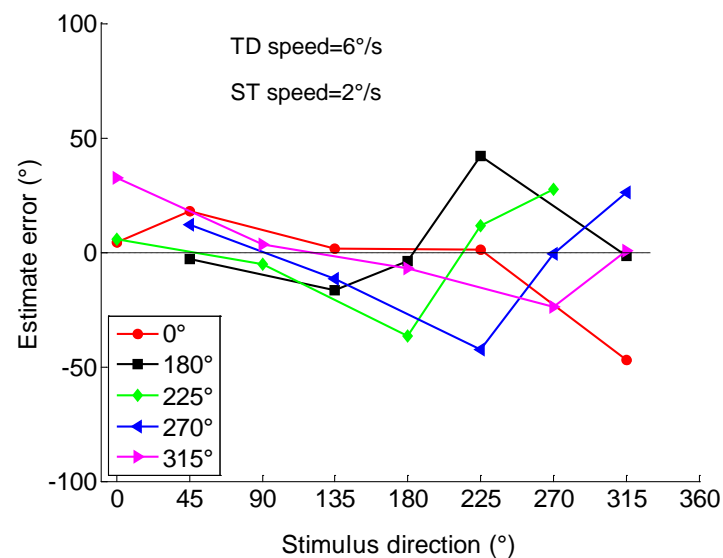


Figure VIII.4. Average estimate errors in Experiment 4. The coloured lines represent the five pursuit direction conditions. Estimate errors are plotted for the given screen ST directions, relative to veridical perception (represented by the zero error horizontal dashed line). The standard error of the mean was very small in all conditions and is not visible on the graph.

Correlations were computed between estimate errors and pursuit gain, and between estimate errors and pursuit direction errors. Table VIII.2 below shows the correlation coefficients for each target direction. The results suggest that a weak relationship exists between estimation errors and eye movement characteristics (eye movement deflection from the TD and pursuit gain).

Table VIII.2. *Relationship between eye movement characteristics and perception in Experiment 4*

Target direction	r_1	$r_{1(abs)}$	r_2	$r_{2(abs)}$
0°	0.21*	0.23*	0.27*	n.s.
180°	0.18 *	0.18*	0.16*	n.s.
225°	0.19 *	0.19*	0.13*	n.s.
270°	0.07	0.13*	0.16*	n.s.
315°	0.10	n.s.	0.16*	0.09*

Note. Correlations are presented between pursuit gain and estimate error (r_1), and between pursuit direction error and estimate error (r_2). Correlations computed using absolute values of the errors are presented as $r_{1(abs)}$ and $r_{2(abs)}$.

* Significant correlation, $p < .05$

Extra-retinal signal gain (egain)

The eye movement-related gain ($\tilde{\epsilon}$) was determined in the same way as in previous experiments, by finding the best compensatory vector for a set of direction estimation errors for the ST associated with each TD direction. The model's goodness of fit is expressed as the root of mean squared error (RMSE) and is shown in Table VIII.3. As stated earlier, RMSE was a preferred goodness of fit measure, rather than R^2 , because the fitted curves in some cases were non-linear.

Table VIII.3. *Goodness of fit of the model in Experiment 4*

Direction Experiment 4	Target speed = 6°/s	
	ST speed = 2°/s	
	Number of fits	% of fits
RMSE < 15°	37	57%
RMSE 15° - 30°	19	29%
RMSE >= 30°	9	14%

Note. The model goodness of fit is expressed as the root of mean squared error (RMSE). The table shows the number of fits for a given range of RMSE.

Overall egain in Experiment 4 was .76, which is very similar to Experiment 3 (.73). The egain also varied across participants but did not vary as a function of TD direction, which is consistent to Experiment 3 results. The egain was .79, .81, .75, .72 and .77 for a TD moving at 0°, 180°, 225°, 270° and 315°, respectively (see Figure VIII.5).

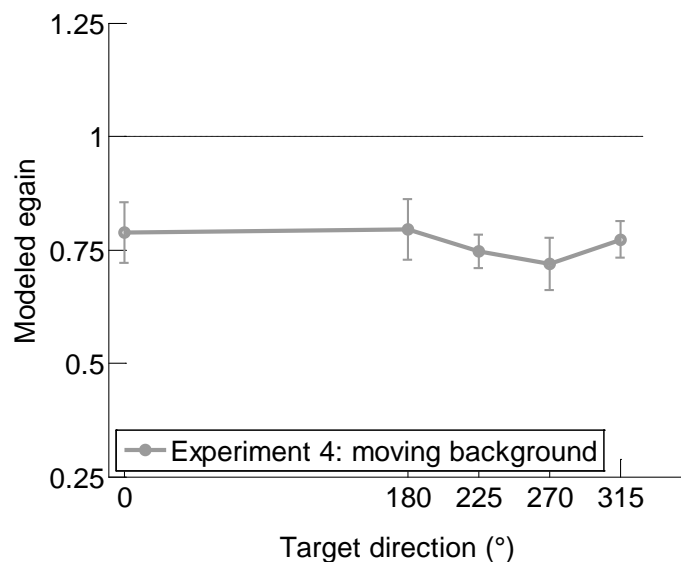


Figure VIII.5. Modeled extra-retinal signal gain (egain) for each target direction in Experiment 4. The egain value represents the best model fit to a set of estimation errors for a given pursuit direction. The variation shown for each egain value is the standard error of the mean.

3. Discussion

Experiment 4 produced 73.5% of non-saccadic trials that were analyzed for eye movement characteristics, estimation performance as well as the modeled egain. The average eye movement gain in Experiment 4 was .92 but varied as a function of TD direction. Similarly to Experiment 3, the lowest pursuit gain occurred during downward pursuit, but turned out to be still quite high (.88) compared to that in Experiment 3. The overall average eye movement gain in Experiment 4 (.92) was significantly higher than in Experiment 3 (.87), $t(3960) = -11.74$, $p < .05$. Because the TD and ST directions were exactly the same in these two experiments, it can be concluded that the moving background increased the eye movement gain.

In Experiment 4 eye movement deviations from the TD varied depending on TD direction. The largest pursuit deviations occurred when tracking the oblique targets (225° and 315°), just like in Experiment 3, suggesting that targets moving in these directions were harder to follow in both experiments. The pursuit deviations had a weak relationship with the estimation errors. The magnitude of the estimation errors, however, did not vary across the five TD directions. The estimate errors were constant across all pursuit directions, producing an average error of 0.28° (and an average absolute error of 23.11°). Egain values, as determined by the linear vector model, were also constant across the five TD directions, averaging .76.

In general, eye movement directions as well as perceptions of the ST were similar between Experiment 3 and Experiment 4. Both eye movement direction errors and

estimation errors were compared between the two experiments using the circular Watson-Williams test, and were analyzed based on the actual as well as absolute error values. In all cases, the results were not significant. So although eye movement gains varied between the two experiments (stationary vs. moving background conditions), the estimates did not. The implication is that the characteristics of the additional background only affect eye movement gain, but not the estimates. In addition, eye movement gain had no effect on direction estimates. The similarity of estimation performance between Experiment 3 and 4 is illustrated in Figure VIII.6.

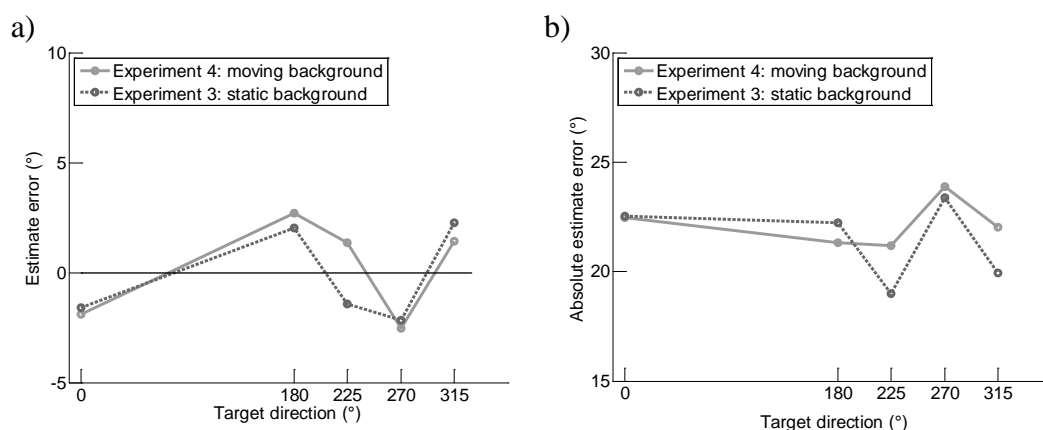


Figure VIII.6. Comparison of estimation errors between Experiments 3 and 4. Average estimate errors were computed for each pursuit direction, both from actual estimate errors (a) and absolute error values (b).

The eye movement-related compensatory gain in Experiment 4 turned out to be constant across different TD directions, and did not significantly differ from Experiment 3. The implication is that the moving vs. stationary background has no differential effect on gain. In sum, the results in Experiment 3 and 4 were very similar, and only differed with regard to eye movement quality: Experiment 4 produced fewer saccadic trials and higher eye movement gain than Experiment 3.

To summarize, introducing a moving (as opposed to stationary) background during ST exposure time did not alter participants' ability to judge the ST motion direction, and did not alter the size of the compensatory saccade. The results suggest that perception and compensation is very similar in conditions with additional background, regardless of whether the background is stationary or in motion. In both background conditions, the visual stimulation was higher than in conditions without additional background elements (Experiment 1). It would be useful to compare these two experiments to one that has no background but includes the same target-stimulus velocities, in order to establish the impact of the background on eye movement, perception and compensation. Experiment 1 cannot be used in the comparison analysis, mainly because the participants and the target-stimulus velocities varied. Moreover, Experiment 1 included longer blocks of trials with a wider variety of TD and ST speed conditions than Experiment 3 and 4. To eliminate these methodological confounds, another experiment was designed that could be analyzed comparatively with Experiment 3 and 4.

Chapter IX. Experiment 5: Direct comparison of background versus no background.

Experiment 5 was essentially a replication of Experiments 3 and 4 except there was no background elements present during the stimulus exposure. In this regard it was similar to Experiment 1, but Experiment 5 included only TD motion of $6^\circ/\text{s}$ and ST motion of $2^\circ/\text{s}$ in all trials. In addition, Experiment 5 included only three TD directions that were used originally in Experiment 1 (i.e., 0° , 270° and 315°). The other two TD directions used in Experiment 3 and 4 (180° and 225°) were excluded. Experiment 5 was therefore much more focused than Experiment 1, and included conditions that were consistent with, and therefore comparable to those in Experiments 3 and 4.

1. Methods

Figure IX.1 presents the sequence of events on the computer image display, which is identical to Experiment 1.

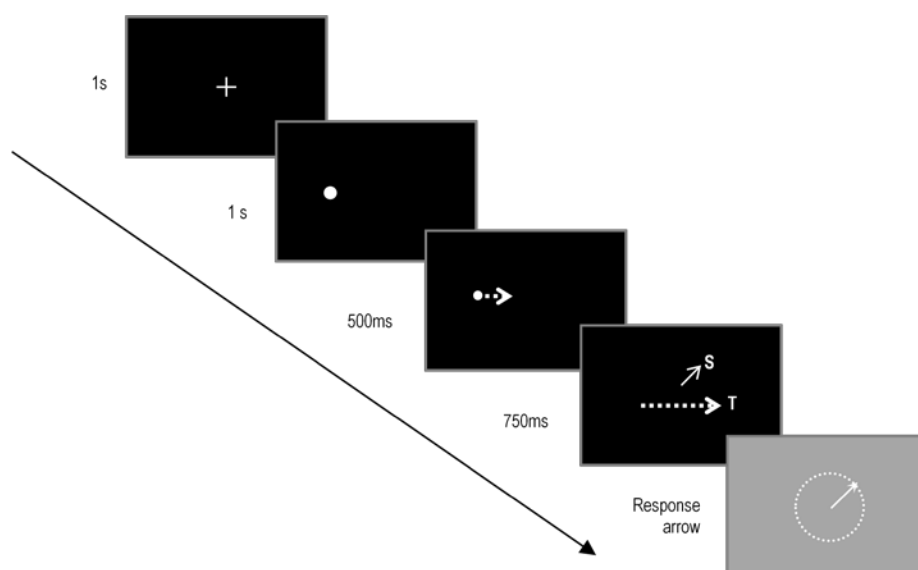


Figure IX.1. Stimulus display for Experiment 5. Each target pursuit interval included a single ST moving in one of 4 possible directions for 750 ms.

Experiment 5 included only 12 conditions (3 TD directions, each combined with one of 4 ST directions). The TD always moved at $6^\circ/\text{s}$ and the ST always moved at $2^\circ/\text{s}$. Because there were only 12 conditions in Experiment 5, and thus each block of trials was going to be much shorter than in Experiment 3 or 4 (25 conditions), the Experiment 5 block of trials was lengthened by presenting each condition twice within the block. The trials were presented randomly, and each block included 24 trials, which took approximately the same amount of time to complete as in Experiment 3 and 4. Figure IX.2 shows the specific ST and ST velocities used in Experiment 5. A total of 24 trials of 12 different conditions were completed by the same participants as in Experiment 3 and 4.

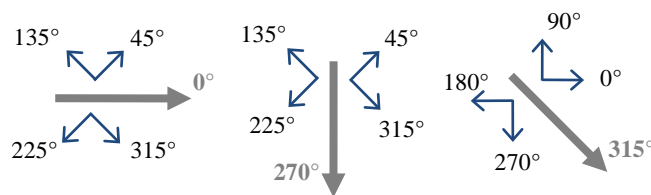


Figure IX.2. Combinations of target-stimulus velocities in Experiment 5. Each TD velocity was displayed with only one ST velocity per trial. They are shown on the same plot for compactness. The TD always moved at $6^\circ/\text{s}$ and the ST always moved at $2^\circ/\text{s}$.

2. Results

2.1 Direction estimation during eyes stationary

Thirteen participants completed at least 5 blocks of trials with eyes stationary.

Each block of trials included two sets of 8 TD-ST velocity combinations.

Participants' perception of the ST motion direction was very good ($R^2 = 1.00$).

2.2 Direction estimation during eye movement

Eye movement analysis

Frequency of saccadic trials: The percentage of saccadic trials during eye movement for each TD direction condition is shown in Figure IX.3. The most saccadic trials occurred during downward pursuit (54.9%) while 0° and 315° pursuits had fewer saccadic trials, 46.1% and 45.4%, respectively. Overall, 48.8% of completed trials were removed from the analysis due to saccades or blinks.

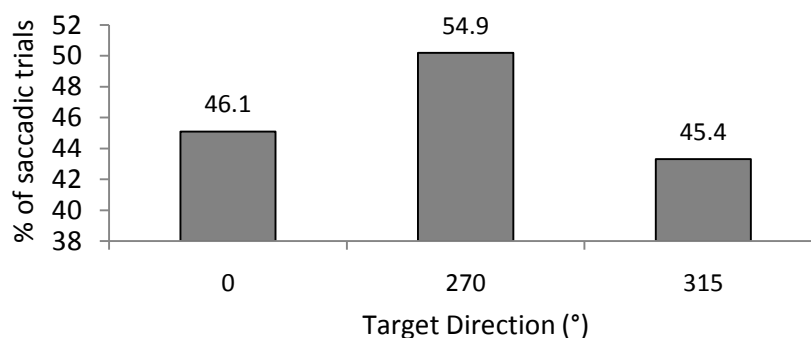


Figure IX.3. Percentage of saccadic trials in Experiment 5

Pursuit direction: Eye movement deviations from the TD (pursuit errors) were computed for each TD direction condition across ST directions and are presented in Figure IX.4 a). Pursuit errors in Experiment 5 were compared to those in Experiments 3 and 4 and are presented in Figure IX.4 b).

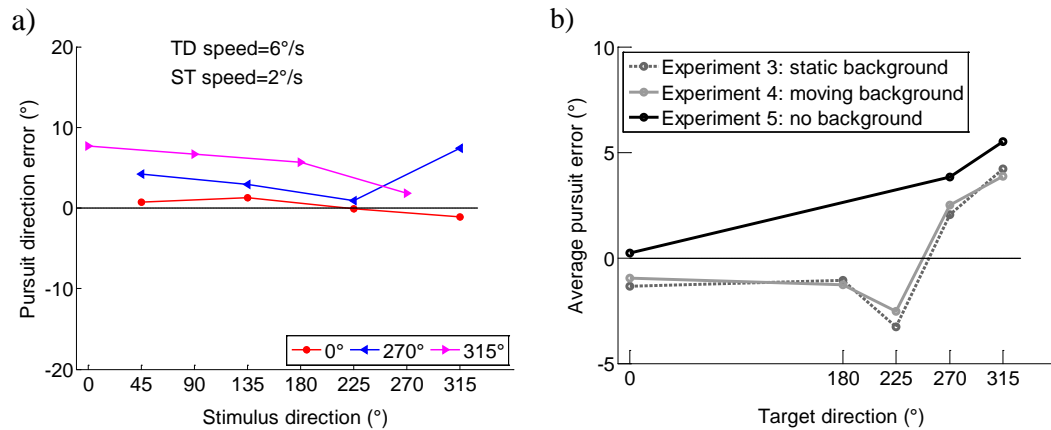


Figure IX.4. Pursuit errors in Experiments 3, 4 and 5. Average eye movement deviations from the TD are presented for each TD direction in Experiment 5 (a), and are compared to Experiments 3 and 4 (b).

Experiment 5 produced higher eye movement errors than Experiments 3 and 4 for the three common target directions (0°, 270° and 315°). Based on the circular Harrison-Kanji analysis of variance, there was a main effect of Experiment type (background vs. no background, $F(2, 3317) = 12.9$, $p < .05$, as well as a main effect of TD direction, $F(2, 3317) = 157.88$, $p < .05$. In other words, Experiment 5 differed from Experiment 3 and 4 in that it produced larger eye movement deviations from the TD. The largest pursuit deviation was when following the obliquely and downward moving TD (see Table XI.1 for average eye movement errors in the three pursuit conditions).

Pursuit gain: Table IX.1 presents average eye movement gains for the three pursuit conditions in Experiment 5, and Figure IX.5 further shows the average eye movement gains for each TD-ST velocity combination. Overall, the average eye movement gain was 1.0 and was constant across the pursuit directions.

Table IX.1. *Average pursuit gains, pursuit errors and estimate errors in Experiment 5*

Target direction	n	Average pursuit gain	Average pursuit error	Average absolute pursuit error	Average estimate error	Average absolute estimate error	Estimate sd
0°	312	1.01	0.23°	3.28°	-5.74°	34.02°	42.1°
270°	283	1.03	3.84°	7.27°	-0.10°	31.54°	39.7°
315°	322	1.01	5.52°	7.03°	15.7°	24.30°	33.8°
Total	917	1.01	3.20°	5.86°	3.27°	30.0°	

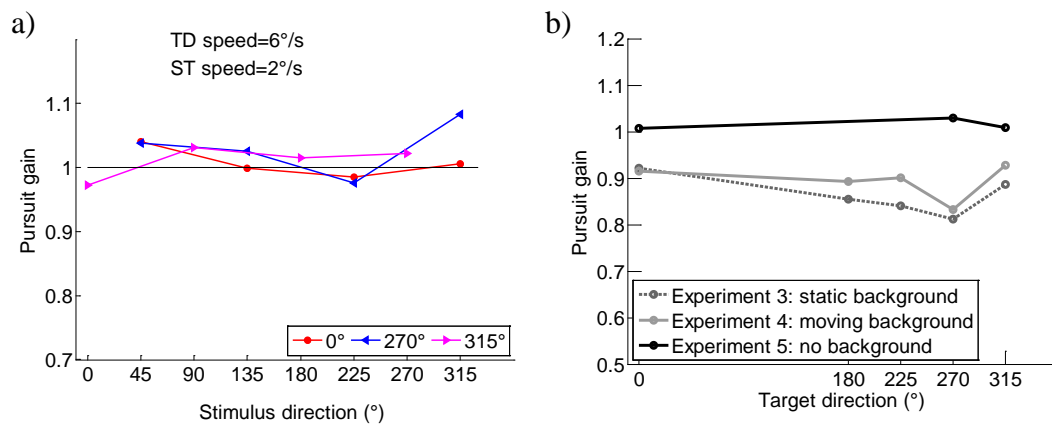


Figure IX.5. Pursuit gains in Experiments 3, 4 and 5. Average pursuit gains are presented for each TD direction in Experiment 5 (a), and are compared to pursuit gains in Experiments 3 and 4 (b).

In order to determine whether eye movement gain in Experiment 5 differed from Experiment 3 and 4, all three experiments were analyzed using only the three target directions common to them (i.e., 0°, 270° and 315°). There was a main effect for Experiment type (significant differences among the experiments, $F(2, 3317) = 170.81$, $p < .05$). The lowest gain occurred in Experiment 3 (.88), and the highest in Experiment 5 (1.02). Pursuit gain in Experiment 4 was .92. There was also a main effect for TD direction, with gain significantly lower for 270° pursuit

($\bar{X} = .90$) than for 0° and 315° pursuits ($\bar{X} = .94$ and $.96$, respectively; $F(2, 3317) = 25.78$, $p < .05$). An interaction between Experiment type and TD direction was also significant, $F(4, 3317) = 13.60$, $p < .05$. Figure IX.5 presents the average pursuit gains for each experiment across TD direction conditions.

Direction estimates and estimation errors

Estimate errors: Average estimate errors for each pursuit direction, computed from both actual and absolute error values are shown in Figure IX.6. Varying the TD direction had no effect on estimation errors in Experiment 5. The error curves from Figure IX.6 indicate that larger errors occurred when the ST moved at a $\pm 45^\circ$ angle to the TD than when it moved at $\pm 135^\circ$ away from the TD. There was no significant correlation between estimate errors and pursuit gain or pursuit error in Experiment 5. This result is consistent with that of Experiment 1 where no ST background was presented, but is not consistent with Experiments 3 and 4 in which additional ST background was introduced.

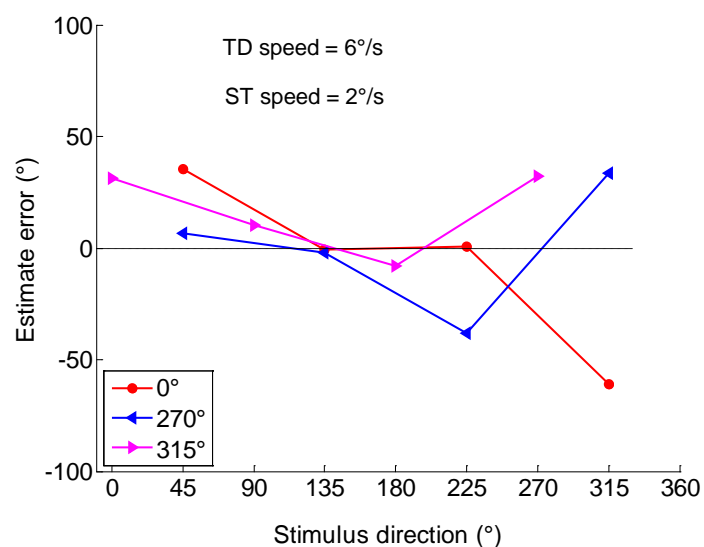


Figure IX.6. Average estimate errors in Experiment 5

Estimation errors were compared across Experiments 5, 4 and 3. There was a main effect of the Experiment type, $F(2, 3317) = 11.55$, $p < .05$, TD direction, $F(2, 3317) = 16.16$, $p < .05$, as well as an interaction effect, $F(4, 3317) = 5.65$, $p < .05$. It was revealed that the inter-experimental differences in the average estimate errors were dependent on target direction: at 315° estimate errors were much higher in Experiment 5 than in the two other experiments. Figure IX.7 illustrates average estimate errors across the three experiments for each TD direction.

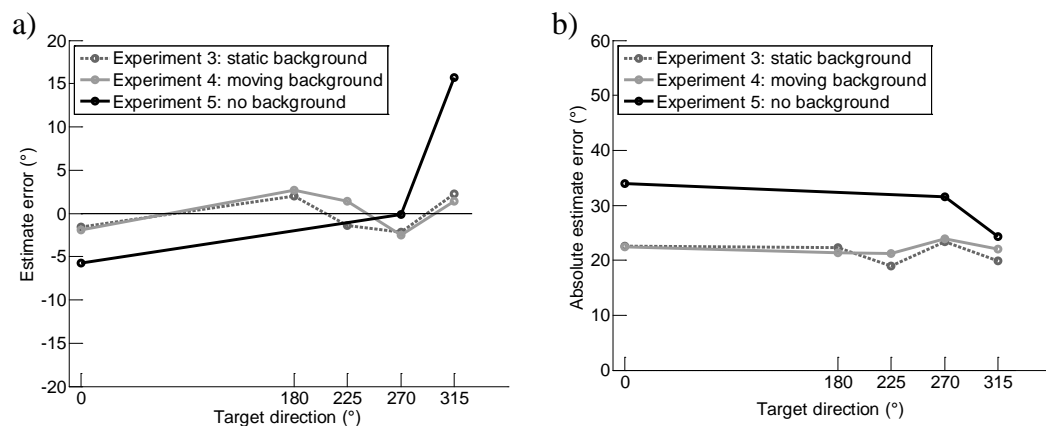


Figure IX.7. Comparison of estimation errors across Experiments 3, 4 and 5. Average estimate errors were computed for each pursuit direction, both from actual estimate errors (a) and absolute error values (b).

Extra-retinal signal gain (egain)

The average extra-retinal signal gain (egain $\tilde{\epsilon}$) turned out to be 0.90 in Experiment 5. The egain represents the strength of a compensatory vector, and was determined by the best fit to a set of estimation errors (the difference between an estimate and ST direction on the screen) associated with each pursuit direction. As in previous experiments, the model's goodness of fit is expressed as the root of mean squared error (RMSE), and is reported in Table IX.2. The goodness of fit was much poorer than in the previous experiments, likely because of the high and

inconsistent estimation errors across different ST directions. This reduced goodness of fit may indicate increased noise in estimation accuracy and may suggest a non-linear estimation of eye movement and retinal signals. This result is similar to the finding by Freeman (2001), that the linear model was not suitable for conditions where the retinal velocities were low. In such conditions the non-linear transducer model showed a better fit to the data.

Table IX.2. *Goodness of fit of the model in Experiment 5*

Direction Experiment 5	Target speed = 6°/s	
	ST speed = 2°/s	
	Number of fits	% of fits
RMSE < 15°	10	26%
RMSE 15° - 30°	11	28%
RMSE ≥ 30°	18	46%

Note. The model goodness of fit is expressed as the root of mean squared error (RMSE). The table shows the number of fits for a given range of RMSE.

The average egain was relatively constant for all three pursuit directions (i.e., TD direction had no effect on egain). There were, however, significant differences among participants, $F(12, 41) = 4.06$, $p < .05$. When compared to Experiments 3 and 4 (using only TD directions of 0°, 270° and 315°), the egain in Experiment 5 was much higher (.90) than in Experiment 3 (.74) or Experiment 4 (.76). The analysis of variance showed only a main effect of Experiment type, $F(2, 45) = 9.35$, $p < .05$, not TD direction. This outcome implies that only the background, not the direction of pursuit, had an effect on $\tilde{\epsilon}$. The values for $\tilde{\epsilon}$ across the three experiments are plotted in Figure IX.8.

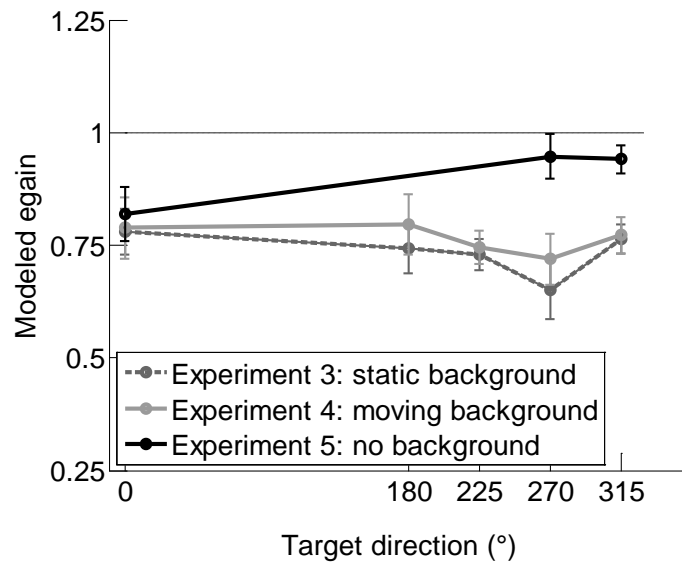


Figure IX.8. Comparison of the modeled extra-retinal signal gain (egain) across Experiments 3, 4 and 5. The egain value represents the best model fit to a set of estimation errors for a given pursuit direction. The variation shown for each egain value is the standard error of the mean.

3. Discussion

Experiment 5 produced perfect eye movement gain (1.0) in all three pursuit directions. The absolute deviations of the eye movements from the moving TD more than doubled when following 270° and 315° moving TD. However, these deviations were still very small and would not have led to a significant drop in pursuit gain size because $\cos(\text{deflection angle})$ is close to 1. Despite the excellent pursuit gain, direction estimate errors were quite high (an average based on absolute values of errors was close to 30°). Estimate errors in Experiment 5 were much higher than in Experiment 3 and 4 although the average eye movement gain was much better than in Experiment 3 and 4. The improved pursuit gain in Experiment 5 may be due to practice effect because participants completed Experiment 5 as last. Perceptual performance, however, was not subject to the practice effect in Experiment 5 because estimation errors were higher in that

experiment than in Experiments 3 and 4. It can be concluded that perception improved as a result of the additional background elements in the two latter experiments.

Average extra-retinal signal gain as estimated from the linear vector model (egain $\tilde{\epsilon}$), was high (.90) in Experiment 5 and did not vary much across the three pursuit conditions. In comparison to Experiment 3 and 4, the egain was much higher in Experiment 5 (see Figure IX.8). This suggests that $\tilde{\epsilon}$ was reduced (less eye movement–related information was needed to correct for the eye-induced retinal image motion) by the additional background during ST exposure in Experiments 3 and 4. The decrease in $\tilde{\epsilon}$ occurred regardless of whether the background elements were stationary or moving. This observation can be explained by Wertheim’s (1994) concept of the “reference” (compensation) signal, described earlier, where the compensation signal $e' = \epsilon e$ (component related purely to eye movement) + γr (component related to visual information during eye movement). The empty background results in a low retinal component (γr) of the reference signal, because it causes minimal visual impact during eye movement. Thus, the empty background must cause an increase in the eye-movement-related component (ϵe) to retain good compensation. In other words, the additional stimulus background provides more visual elements across the visual field and thus increases γr .

In the present model, the calculated egain ($\tilde{\epsilon}$) is purely eye movement related, because the retinal component was not included separately in the model. The analysis revealed that $\tilde{\epsilon}$ was the highest in the empty background conditions (Experiment 5), in which eye movement gains were around 1. The perfect eye

movement gain, however, was not related to the size of egain. The implication is that the additional background in Experiments 3 and 4 caused the visual system to rely less on the pursuit-related component and more on the visual component of the compensation signal. The empty background had minimal visual information and therefore the eye-movement component of the compensation signal was relatively high.

In summary, the findings from Experiment 5 suggest that no background and consistent TD and ST head-centric speeds produce a pursuit eye movement gain close to 1.0, regardless of the TD motion direction. Although the absence of additional background elements improve the eye movement gain, the eye movement direction deviates more from the TD than when the background is present, perhaps because of a lack of a frame of reference for the eye movement in the no background condition. Estimation errors were high in Experiment 5 while the computed extra-retinal signal gain ($\tilde{\epsilon}$) was also very high, in comparison to Experiments 3 and 4. This observation suggests that the perceptual system may use more of the motor information coming from eye movement when the visual information is not available, than when a background is present (and provides additional visual feedback).

It would be interesting to examine how much the retinal image motion contributes to the compensatory signal. In all three experiments (3, 4, and 5), the pursuit speed was the same and the ST moved at the same head-centric speed across direction conditions. However, the retinal image speed of the ST was not equivalent across conditions and varied depending on the ST screen direction. The

ST directions had been selected so that they either moved with or away from the TD and thus produced two different retinal image speeds. These will be examined in the following Chapter.

Chapter X. Exploring the role of retinal image motion in the extra-retinal signal

What role the retinal image motion plays in the extra-retinal signal is an interesting question that became apparent when the results of Experiment 1 were first analyzed. It was noted that stimuli moving closer to the target direction led to less eye movement compensation than stimuli moving away from the target. Similarly, observations from Experiment 3, 4 and 5, provided further evidence that perhaps the stimulus' retinal image speed could be a factor in the level of compensation that occurred. Stimuli with the same screen speed but different retinal speeds produced differing levels of compensation (as measured by the model fit). Therefore, I was interested in exploring the differences between stimuli that moved on the screen at $\pm 45^\circ$ to the target and those that moved at $\pm 135^\circ$ to the target. Stimuli moving in the opposite direction to the target create very different retinal image velocities from those that move in the same direction as the target, even when their screen speed is identical. I therefore went back and re-examined the data from Experiments 3, 4 & 5 to look at the retinal velocities in more detail.

1. Methods

To investigate the retinal image motion more closely, the ST directions from Experiments 3, 4 and 5 were divided into two groups: one group consisted of ST moving “away” from the TD (moving at a $\pm 135^\circ$ angle to the TD) and the other group included ST moving “with” the TD (moving at a $\pm 45^\circ$ angle to the TD). These two ST direction groups were named as AT and WT, respectively, and are shown in Figure X.1. The retinal velocity is larger for the AT than WT stimuli.

Figure X.2 shows the retinal image motions for stimuli that move at $\pm 45^\circ$ (WT) and $\pm 135^\circ$ (AT) to the target.

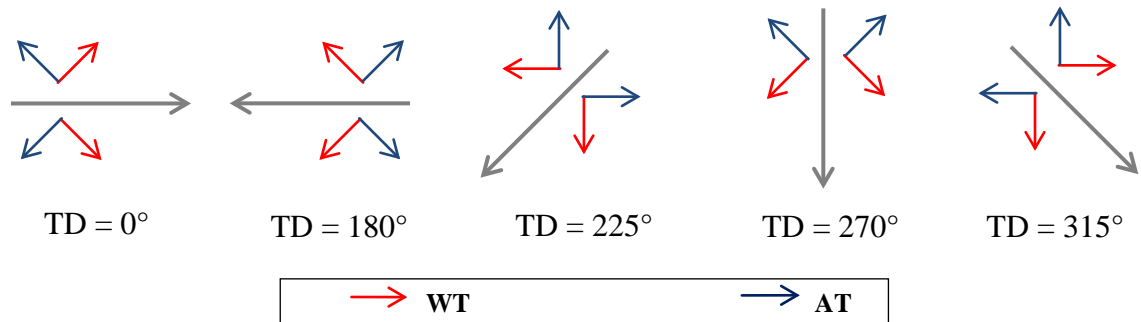


Figure X.1. Stimuli WT and AT. Stimuli moving at a $\pm 45^\circ$ angle to the target are identified as WT (red arrows), and stimuli moving at a $\pm 135^\circ$ angle to the target are identified as AT (blue arrows). Grey arrow indicates pursuit target direction.

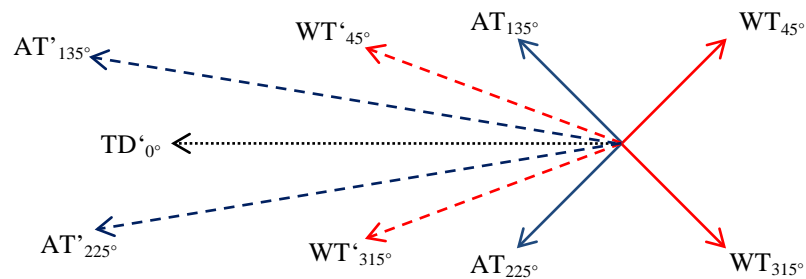


Figure X.2. An example of retinal velocities of WT and AT stimuli for 0° pursuit. The WT and AT stimuli are shown on one plot for compactness. The TD velocity is not shown. TD' (dotted horizontal line) is the stimulus' retinal image motion if the ST remained stationary. The AT' and WT' are the retinal images of AT (moving at 135° or 225° on the screen) and WT (moving at 45° or 315° on the screen) stimuli, respectively.

2. Results

2.1 Eye movement analysis

Frequency of saccadic trials: The percentage of saccadic trials during eye movement was counted for WT and AT stimuli across Experiments 3, 4 and 5, and is shown in Figure X.3. Overall there were 41.23% and 41.55% of saccadic trials for WT and AT stimulus conditions, respectively. The most saccadic trials occurred in AT trials in Experiment 5 (51.1%). The amount of saccadic trials was similar in Experiments 3 and 4, regardless of WT or AT stimuli.

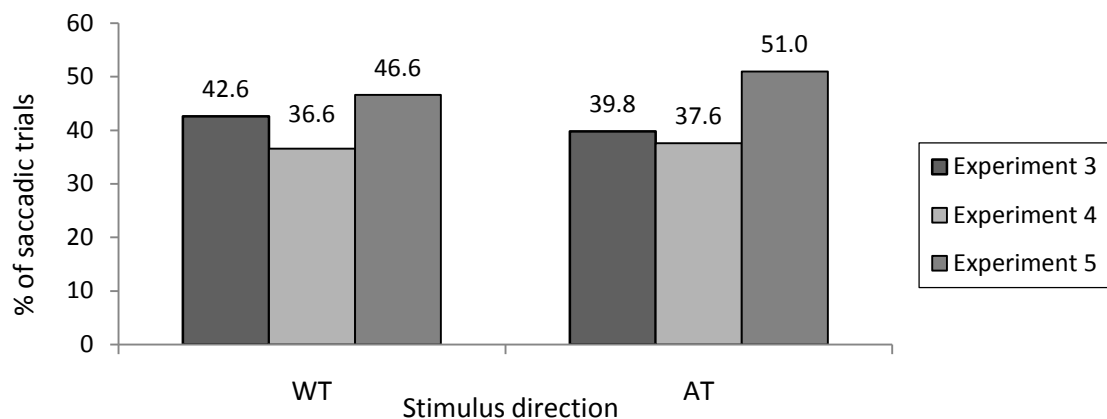


Figure X.3 Percentage of saccadic trials for WT and AT stimuli

Pursuit gain: Pursuit gain was analyzed for WT and AT stimuli groups using ANOVA. There was a difference between the two ST direction groups, $F(1, 2846) = 4.33$, $p < .05$. Pursuit gain was slightly but significantly higher for WT than AT stimuli (see Table X.1). There was a main effect of Experiment type (different background), $F(2, 2846) = 155.39$, $p < .05$. The average pursuit gain was .88, .92 and 1.02 for Experiment 3, 4 and 5, respectively. There was a main effect of TD direction, $F(2, 2846) = 24.69$, $p < .05$. Pursuit gain was .96, .91 and .94 for 0° , 270° and 315° moving TD, respectively. There was also an interaction effect

between Experiment type and TD direction, $F(4, 2846) = 13.15$, $p < .05$, and a 3-way interaction effect for Experiment type, TD direction and ST group, $F(4, 2846) = 2.44$, $p < .05$. The interaction effects suggest that eye movement gain varies as a function of all three factors (background, pursuit direction and whether ST moved along or away from the TD).

Pursuit direction: Eye movement deviations from the moving TD were analyzed using Harrison-Kanji circular test (equivalent to a two-way ANOVA), with Experiments 3, 4 and 5 and AT and WT conditions. There was a main effect of Experiment, $F(2, 2848) = 52.96$, $p < .05$, with Experiment 5 producing the largest pursuit errors (see Table X.1). Eye movement deviations were significantly larger for WT (moving at $\pm 45^\circ$ to the TD) than AT stimuli (moving at $\pm 135^\circ$ to the TD), $F(1, 2848) = 33.76$, $p < .05$, and were the largest in WT conditions with no background.

2.2 Estimation errors analysis

Estimate errors for both AT and WT stimulus groups are shown in Table X.1.

According to the Harrison-Kanji circular analysis, there was a main effect of ST direction, $F(1, 2848) = 114.66$, $p < .05$, as well as Experiment, $F(2, 2848) = 14.81$, $p < .05$. In addition, there was an interaction effect, $F(2, 2848) = 18.12$, $p < .05$, which indicates that the error differences between WT and AT stimuli were not consistent across the 3 experiments. The largest difference in estimation errors between AT and WT was found in Experiment 5, while the difference in estimation errors for Experiments 3 and 4 was similar. These differences are illustrated in Figure X.3.

Table X.1. Pursuit gains, pursuit errors and estimate errors for AT and WT stimuli in Experiments 3, 4 and 5

	Average pursuit gain		Average pursuit errors (°)		Average estimate errors (°)		Average absolute estimate errors (°)	
	AT	WT	AT	WT	AT	WT	AT	WT
Exp 3	.87	.89	0.76	-0.46	-1.82	1.97	17.53	25.35
Exp 4	.91	.93	0.88	0.04	-0.25	1.11	19.04	27.64
Exp 5	1.02	1.02	3.46	2.67	-1.50	17.96	24.85	40.93

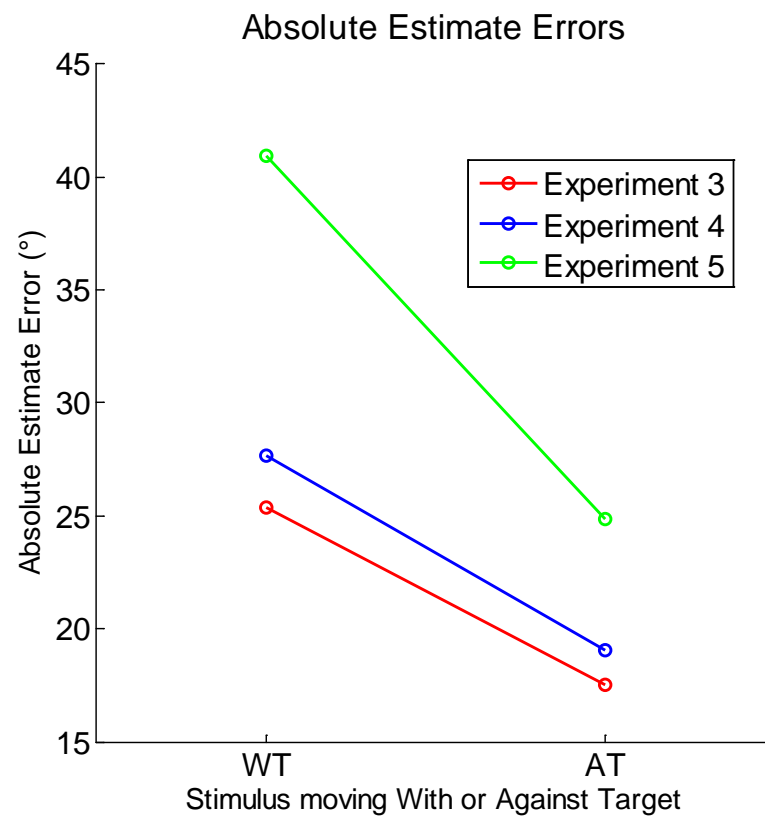


Figure X.4. Average absolute estimate errors for WT and AT stimuli in Experiments 3, 4 and 5.

2.3 Extra-retinal signal (egain)

It was of interest to find out whether ST direction had a differential effect on egain ($\tilde{\epsilon}$), because different ST directions produced different retinal velocities during eye movement. This would allow to further tap into the effect of retinal stimulation on $\tilde{\epsilon}$ and eye movement compensation overall.

Egain ($\tilde{\epsilon}$) was compared between WT and AT trials in each experiment and differed only in Experiment 3, $t(106) = -2.11$, $p < .05$, where the AT stimuli produced higher egain ($\tilde{\epsilon} = .78$, $sd = .22$) than the WT stimuli ($\tilde{\epsilon} = .71$, $sd = .14$). When all three experiments were used, an ANOVA revealed only a main effect of Experiment type, $F(2, 264) = 14.67$, $p < .05$, but not for ST direction group. Figure X.4 shows the changes in egain for the two ST groups at each TD direction. The Tukey's post hoc tests confirmed the earlier finding that Experiment 5 produced higher egain ($\tilde{\epsilon} = .90$) than Experiment 3 and 4 ($\tilde{\epsilon} = .75$ and $\tilde{\epsilon} = .77$, respectively). In sum, the ST direction (AT or WT) had an impact on the extra-retinal gain only in the presence of the stationary dot background.

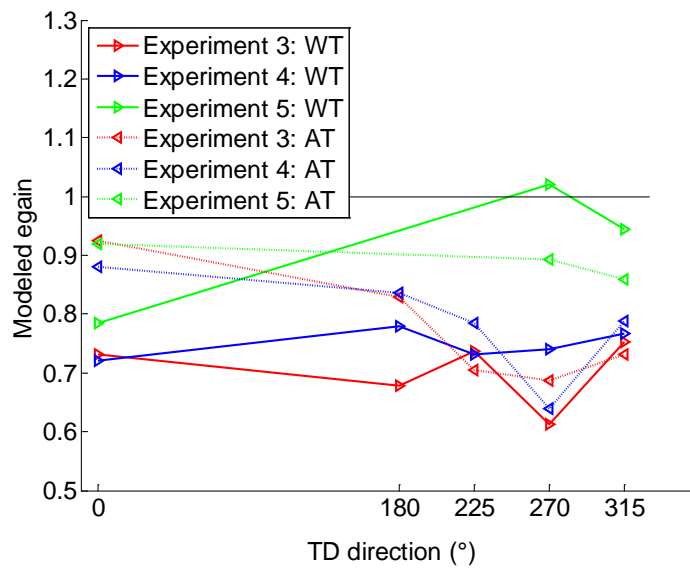


Figure X.5. Egain values for AT and WT stimuli in Experiments 3, 4 and 5.

2.4 “Weak” vs. “Strong” retinal stimulation

To further separate the conditions where the visual stimulation difference was maximized, two subgroups, “Weak” and “Strong”, were identified, relating to the total motion signals feeding into the retinal part of the compensation mechanism. As discussed in the Introduction chapter, neurons in area MST have very large receptive fields and prefer motion of full field stimuli (e.g., Saito et al., 1986; Tanaka et al., 1986). Their properties are consistent with a role in the integration of visual motion signals generated during observer’s movement, including eye movement (Perrone & Stone, 1998; Bradley, Maxwell, Andersen, Banks & Shenoy, 1996). The MST neurons integrate the signals generated by MT neurons distributed over a wide part of the visual field. Therefore, the movement of many elements distributed across the visual field would strongly stimulate these MST cells.

There is also an implication that the AT stimuli producing a higher retinal speed than the WT stimuli would improve the signal output reaching MST. This speculation can be made based on a number of assumptions. First, individual MT neurons are responsive to retinal speed and different neurons have different preferred speeds (Dubner & Zeki, 1971; Maunsell & van Essen, 1983). Second, the signal output by a number of MT neurons arriving at an MST neuron is weighted by its preferred speed tuning (Lisberger & Movshon, 1999). Third, the output of the MT cells is based on the local retinal velocity. If the velocity is low or ambiguous, the MT outputs will be erroneous, but if the local velocity is increased (such as in the conditions when the ST and background moved away from the TD), the outputs will more likely reflect the true velocity and a ‘stronger’ retinal signal will reach the MST level than when the retinal stimulation is weak (as produced by the single WT stimuli). The output from MT cells is produced later, after more signals from MT cells combine, presumably in area MST. The “Strong” retinal signal in our experiment was produced by conditions where the entire background moved with the ST dot at $\pm 135^\circ$ to the target (AT moving background). In this case, the relative speed of the ST (and all the background dots) was high, supplying a strong motion signal into the retinal component of the compensation mechanism. On the other hand, a “Weak” level of stimulation to MST would be produced by conditions where a single ST moved at $2^\circ/\text{s}$ in $\pm 45^\circ$ to the target (WT stimulus dot with no additional background). That means that the relative speed of the single ST dot was low and so the motion signal feeding into the retinal component of the compensation mechanism was weak. In other words, the “Weak” and “Strong” retinal stimulation groups consisted of WT

single stimulus dots from Experiment 5 and AT stimuli from moving background Experiment 4, respectively.

Results

Pursuit direction: Pursuit deviation from the moving TD was analyzed using circular Harrison-Kanji test (equivalent to a two-way ANOVA). One factor was Group (“Strong” vs. “Weak” stimuli) and the other factor was TD direction. There was a main effect of TD direction, $F(2, 960) = 21.33, p < .05$. The average eye deviations from the TD were -1.2° , 3.5° and 1.6° for TD moving at 0° , 270° and 315° , respectively. The size of pursuit errors also differed between the two Groups, $F(1, 960) = 8.72, p < .05$. The “Weak” stimulus group produced larger pursuit errors ($\bar{X} = 2.7^\circ$) than the “Strong” stimulus group ($\bar{X} = 0.9^\circ$).

Pursuit gain: Based on an ANOVA with Group type and TD direction as fixed factors, there was a significant difference between the “Strong” and “Weak” stimuli, $F(1, 960) = 56.52, p < .05$, with higher pursuit gain in the “Weak” retinal stimulation group ($\bar{X} = .99, sd = .24$) than the “Strong” retinal stimulation group ($\bar{X} = .91, sd = .15$). There was also a main effect of TD direction, $F(2, 960) = 14.7, p < .05$. Figure X.5 shows average pursuit gains in the two groups for each TD direction.

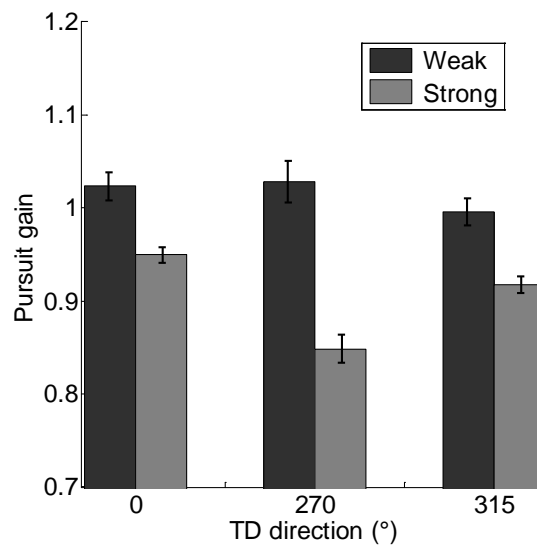


Figure X.6. Pursuit gains for “Weak” and “Strong” retinal stimulation groups

Estimation errors: According to the Harrison-Kanji test, estimation errors significantly differed between the two ST groups, $F(1, 960) = 80.32$, $p < .05$. Higher errors occurred in the “Weak” ($\bar{X} = 4.26^\circ$, $sd = 44.2$) than the “Strong” stimulus group ($\bar{X} = -.13^\circ$, $sd = 21.8$). Figure X.6 shows average estimate errors for each group across pursuit direction conditions. Pursuit direction also had a main effect on perception, $F(2, 960) = 18.75$, $p < .05$. The worst average estimates were during 315° pursuit ($\bar{X} = 14.73^\circ$, $sd = 28.1$). Average estimate errors during 0° and 270° pursuit were -6.77° and -1.45° , respectively. There was also an interaction effect, $F(2, 960) = 26.69$, $p < .05$. Estimation errors increased or decreased between the two ST groups as a function of pursuit direction. When absolute error values were used, only the two main effects remained, but the interaction effect was not significant.

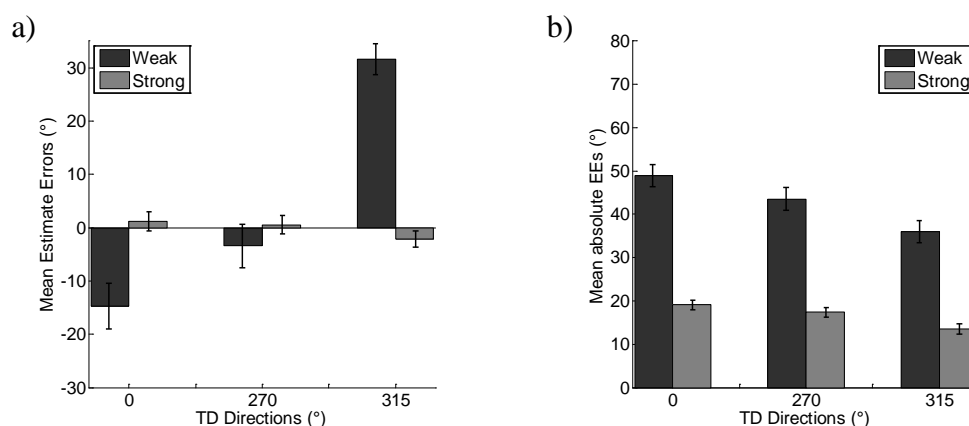


Figure X.7. Average estimate errors for “Weak” and “Strong” retinal stimulation groups. Averages are computed from real estimate errors (a) and absolute values of estimate errors (b). The error bars represent the standard error of the mean.

Extra-retinal signal gain (egain): A two-way ANOVA was performed to analyze the model outputs for egain with Group (“Weak”/”Strong”) and TD direction as the two fixed factors. Egain significantly differed between the “Weak” and “Strong” retinal stimulation groups, $F(1, 102) = 10.84$, $p < .05$ ($\bar{X}_{\text{weak}} = .92$, st. error = .039; $\bar{X}_{\text{strong}} = .74$, st. error = .034). TD direction had no effect on egain. However, there was an interaction effect of TD direction and Group, $F(2, 102) = 5.80$, $p < .05$. This interaction effect suggests that the strong retinal motion signal reduces the egain to a greater or lesser degree, depending on pursuit direction. The difference in egain between “Strong” and “Weak” stimuli was the largest in 270° and 315° pursuit conditions. During 270° pursuit the average egain was 0.60 for “Strong” and 1.02 for “Weak” stimuli, and during 315° pursuit the average egain was 0.79 for “Strong” and 0.95 for “Weak” stimuli.

Although the compensatory egain vector had a lower value for the “Strong” group in comparison to the “Weak” group, the compensation was better for the “Strong” group. This again may be a result of an increased visual component gain (γ) in the

“Strong” stimuli, which was part of the overall compensation signal ($e' = \epsilon e + \gamma r$). However, as stated earlier, γ was not quantified and so it is only assumed it increased since the ($\tilde{\epsilon}$) was low while the compensation (e') was good (estimate errors were low). The overall compensation in the “Strong” retinal conditions was better than the overall compensation in the “Weak” trials. “Weak” conditions produced higher ($\tilde{\epsilon}$) but poorer perception than the “Strong” conditions. The implication of these findings is consistent with previous observations that the magnitude of retinal velocity (global motion signal) affects perception by changing the relative contribution of ϵ and γ in the compensation signal e' . In other words, it seems that the stronger the visual signal, the larger effect γ has on compensation.

3. Discussion

Stimulus directions (AT and WT) showed a significant trend with regard to ϵ again, but only in Experiment 3 (with stationary background dots). The exploration of the retinal image velocity provided additional insight into how the compensation mechanism might work. The head-centric ST speed was relatively low when compared to pursuit, but depending on the ST direction relative to target, it produced varying retinal velocities. For example, the AT stimuli produced higher retinal velocities than the WT stimuli. These ST directions had different effects on $\tilde{\epsilon}$ in Experiment 3. Based on previous results, one would think that the higher the retinal velocity, the lower $\tilde{\epsilon}$ would turn out to be. But according to Experiment 3 results, $\tilde{\epsilon}$ was actually greater in AT than WT trials. One explanation could be that on the retina, WT stimuli are more distinguishable from the background dots than the AT stimuli (the vectors representing WT stimuli during eye movement are at a

larger angle to the vectors representing the background dots than AT stimuli). This can make a less ambiguous visual element for the visual system to process. As a result, the WT stimuli would produce lower egain compared to AT stimuli. In addition, the result is consistent with the notion that the global motion signal is increased as a result of a larger area of the visual field being stimulated.

The difference in the amount of retinal stimulation, with respect to velocity and the area of visual field, was maximized by focusing more on the “Strong” and “Weak” stimulus conditions. The “Weak” retinal stimulation conditions produced perfect gain, but also higher average estimate error than the “Strong” conditions. According to the linear vector model output, the eye movement related signal gain $\tilde{\epsilon}$ was significantly lower in the “Strong” condition, despite good overall compensation. This finding confirms previous observations, which imply reliance of the visual system on the visual characteristics rather than motor signal related to the eye-movement ($e' = \epsilon e + \gamma r$, where e' is the overall compensation signal and ϵ and γ are the gains associated with eye movement and visual components). The “Strong” condition (AT stimulus with moving background dots) significantly lowered the estimated value of the egain ($\tilde{\epsilon}$). It seems therefore that both the overall retinal stimulation (velocity and field size), as well as the degree of ambiguity produced by background elements have an effect on the eye-movement related component of the compensatory signal.

Chapter XI. General Discussion

The aim of the present study was to investigate factors that could contribute to perceptual stability of the world during pursuit eye movements. Because pursuit eye movements add a velocity field to the visual scene on the retina thereby altering the overall pattern of image velocities, the visual system must somehow be able to retrieve the head-centric motion in order to preserve the external objective motion. It has traditionally been hypothesized that the retinal image caused by eye-movements is discounted by an extra-retinal motion signal (von Helmholtz, 1962). The evidence for the presence of this extra-retinal signal has come from perceptual as well as neurophysiological research in primate area MST. Neurons in MST area respond to object motion and are also important for pursuit maintenance. In some instances, however, the extra-retinal signal does not fully cancel the retinal shifts caused by eye movements, and produce Fiehn Illusion and Aubert-Flieschl phenomenon, suggesting a lack of eye movement compensation. In the last few decades research has pointed to various factors possibly affecting the eye movement compensation mechanism, such as the relative movement of the eyes and the stimulus (Wertheim & Van Gelder, 1990; Turano & Heidenreich, 1999; Morvan & Wexler, 2009), preceding motion (Haarmeier & Theier, 1996), stimulus size (Turano & Heidenreich, 1998; Wertheim & Van Gelder, 1999), exposure duration (de Graaf & Wertheim, 1988; Ehrenstein, Mateef, & Hohnsbein, 1987) and spatial frequency (Freeman & Banks, 1998). In other words, the compensation process may rely on many factors that alter the magnitude of the eye movement signal.

The present study extends our existing knowledge of how eye movement compensation occurs by further examining the relative contribution of the retinal image characteristics to the extra-retinal signal. In general, the current experiments have shown that indeed pursuit eye movements alter the perception of a moving stimulus. Results from trials with eye movements, in comparison to the results from eye stationary trials, demonstrate that perceptual errors were caused by the eye movements, particularly during 6°/s pursuit. Eye movements at 2°/s did not alter perception much as the retinal image velocity was very similar to the head-centric stimulus velocity, and therefore this pursuit speed condition was not included in most experiments. Overall, the current experiments revealed that perceptual errors varied as a function of several variables that are likely to play a role in the eye movement compensation process. These variables include relative stimulus speed, pursuit direction, background characteristics and stimulus direction relative to pursuit (retinal velocity).

The amount of retinal stimulation was examined with regard to perceptual performance, as well as the eye-movement compensatory signal. The latter was determined by introducing a model that provided the best fit to a set of estimation errors. This model was derived from the standard linear model (Freeman & Banks, 1998) which uses vector subtraction (Perrone & Krauzlis, 2008). The standard linear model assumes that the extra-retinal signal is linearly combined with retinal velocity to arrive at perception ($h' = r' + e'$), but that the extra-retinal signal itself (e') carries not only an eye-movement related signal (ϵe) but also some retinal component (γr) that pertains to the specifics of the retinal image motion during the eye movement. Here, I quantified the portion of the

compensation signal gain that was purely due to the eye movement (ϵ), namely the strength of the compensatory vector for each pursuit direction over a set of stimulus directions.

The possible mechanisms that underlie the integration of visual elements into the compensatory signal may be related to the MSTd cells that are responsive to large flow fields. These cells may help estimate the parameters of eye rotation thus reducing the need for a motor signal. For example, in a model proposed by Perrone (1992) the eye rotation is first estimated using filters that determine the best common motion vector over the full image flow field. In the model the estimated eye movement is then used to create appropriate templates for various directions of self-motion. Such a mechanism may explain the fact that perception improved in conditions with the additional background elements (producing a large uniform retinal flow field that the MSTd cells respond to) while at the same time the dependence on the motor signal was decreased (as shown by the reduced modeled egain).

The extraction of the eye movement related signal gain allowed us to determine under what conditions it is utilized the most by the visual system. Each unique factor that was found to contribute to the perceptual stability during smooth pursuit is discussed in the context of additional insight into the current knowledge on retinal and extra-retinal signal interaction. It is worth noting that the present study used a model that fitted a function to a set of estimation errors rather than estimations per se. Working with estimation errors, rather than estimates, allowed the comparison of performance across different conditions. If this method is used

in future research, it will potentially be possible to make comparisons across different studies. This has been difficult to do in the past because of differences in the methods and modeling strategies used.

1. The effect of relative stimulus speed

According to the direction estimation results from the first two experiments, which included more than one stimulus (ST) speed when the target dot (TD) moved at $6^\circ/\text{s}$, the ST speed alone had an effect on perceptual performance. In particular, perception was better for an ST moving at $8^\circ/\text{s}$ than at $2^\circ/\text{s}$. This is not surprising because increasing the ST speed in relation to the target speed changes the ST retinal image velocity in such a way that it is closer to the head-centric velocity. This can be seen in plots of the retinal image vs. head-centric velocity in Figure IV.12 on page 78, for both stimulus speeds. This consideration of the change in the retinal image motion with different TD velocities is important because otherwise it could lead to erroneous assumptions about compensation. Because of the little deflection of the retinal velocity from the screen velocity, it is difficult to draw conclusions about perceptual errors when the observer's estimates fall in between these velocities and their angular deviation from the retinal and screen motions is very similar. The retinal information therefore interacts with the compensation process simply because the ST retinal image velocity can sometimes get very close to its head-centric velocity at high stimulus speeds and low target speeds.

The retinal and head-centric stimulus trajectory was very similar at ST speeds of $4^\circ/\text{s}$ and $8^\circ/\text{s}$ during $2^\circ/\text{s}$ and $6^\circ/\text{s}$ pursuit, respectively, and yet, estimations were

much better in the former case (when pursuit was $2^\circ/\text{s}$ and ST speed was $4^\circ/\text{s}$). This suggests that the proximity of the ST screen and retinal trajectories may have not been the only reason for the good performance, and that probably a very slow pursuit speed has little effect on perception. Pursuit at $2^\circ/\text{s}$ does not change the retinal deflection angle by much (see Figure IV.12 on page 85), regardless of ST speed, and the deflection angle is even smaller when the ST speed is increased. It is therefore difficult to determine the degree of compensation in such situations. Moreover, the retinal velocity is disproportionally higher than that of the eyes, resulting in a relatively strong visual signal.

Our results regarding the ST speed effect during $6^\circ/\text{s}$ pursuit differ from those reported by Souman, Hoge & Wertheim (2005). In the present experiment, the accuracy of ST directions judgments varied depending on the ST speed. Souman et al. (2005) observed no difference in perceptual errors when the ST moved at $3^\circ/\text{s}$ or $8^\circ/\text{s}$ during a $10^\circ/\text{s}$ pursuit. One can speculate whether or not faster pursuit would lead to larger perceptual errors than slower pursuit, keeping in mind the good performance during the $2^\circ/\text{s}$ pursuit in Experiment 1. But the relative ST and TD speed is more important than pursuit speed alone. One possible explanation for our results may be that the ST moved either slower or faster than the eyes. The stimuli in Souman et al.'s (2005) experiments were both slower than the eye movements, thus they were more similar in their retinal velocities than the stimuli in our experiments. The reasoning that it is not the ST speed alone that alters the compensation signal, but rather it may sometimes be its speed relative to the eye movement, is in line with suggestions from other researchers (e.g., Wertheim, 1994; Morvan & Wexler, 2009; Freeman, Champion & Warren, 2010).

Another issue related to ST speed is the ST exposure duration. One of the old questions in the psychophysical literature (e.g., Mack & Herman, 1978; de Graaf & Wertheim, 1988) is whether longer ST exposure time improves perception because it covers a longer trajectory on the screen. For example, this increased eye movement compensation during longer stimulus exposure could come about because the motion signals are somehow integrated along the extended path of the moving dots. Experiment 2 addressed this very issue: the fast ST dot's ($8^\circ/\text{s}$) exposure time was shortened from 750 ms to 125 ms which reduced its travelled distance from 6° to 1° of visual angle on the screen. The fast dot's travelled trajectory was now shorter than the 1.5° travelled trajectory of the slow ST ($2^\circ/\text{s}$) exposed for 750 ms. Perception was much worse for the slow ST exposed for 750 ms than for the fast ST exposed for 125 ms. This finding suggests that it is the ST speed that improves compensation – not its trajectory covered during the exposure time. However, it should again be pointed out that the fast moving ST creates different retinal image motion. For some motion directions, fast ST movement produces a smaller deflection angle from the head-centric ST velocity than a slow ST (see above) and so it is difficult to compare the degree of actual eye movement compensation given the two completely different retinal velocities caused by these stimuli.

In relation to previous research, Souman, Hooge and Wertheim (2005) found little difference in perceptual errors across three different exposure periods for a stimulus dot moving at $5^\circ/\text{s}$ and target moving at $6^\circ/\text{s}$. However, when they increased the speed of the TD, the exposure time had a significant effect on direction estimation. They concluded that the presentation duration may increase

the ratio of eye movement signal to retinal signal. They discounted an alternative explanation that the gain ratio gradually increases during pursuit, regardless of presentation duration, because in longer presentation the pursuit lasts longer. In other words, they provided evidence that retinal image velocity (the relative ST and TD velocities) during pursuit is responsible for the increase of the signal gain ratio: the long ST exposure during the fast pursuit ($14^\circ/\text{s}$) decreased perceptual errors. This result suggests that when the ST speed is relatively low in comparison to TD speed, the exposure time must be increased substantially to make up for the low retinal speed. Perhaps the eye movement signal is utilized more (again increases) when retinal image is too ambiguous and cannot provide enough information to the compensation mechanism.

The ambiguity of the motion signal has been considered by Freeman (2010) in his Bayesian model of motion perception during eye movement. According to this model, as the ambiguity of the retinal image motion increases (when the uncertainty of the signal encoding the stimulus motion increases), perception is gradually affected by prior expectations which relate to the real world properties (e.g., world is largely stationary). In other words, the brain must deal with the uncertainty to generate perceptions and does so using a conditional probability function. Freeman stressed that the sensory signals encoding eye rotations and image motion are estimated separately based on their likelihoods that differ in precision (in the spread of the likelihood function), and consequently these two separate likelihoods are added to produce another likelihood function representing the actual perception. If we assume that the slowly moving single dot in

Experiment 5 generates a weaker retinal signal, then we can conclude that the eye movement signal may contribute more to the overall compensation.

2. The effect of pursuit gain

It is worth pointing out that in the current experiments the size of the perceptual errors across the different stimulus directions was not related to pursuit gains. For example, pursuit gains for conditions with an ST speed of 2°/s and 8°/s were very similar in both Experiment 1 and 2, and yet, perception of these stimuli was not similar at all. Even when “Weak” stimulus conditions were separated from “Strong” stimulus conditions depending on the background and stimulus motion direction, the differing pursuit gains had no differential effect on perception. It should be noted that in both cases the gain was quite high (.95 for “Weak” and .93 for “Strong” conditions), but perception was much lower for the “Weak” stimuli. This lack of a relationship between eye movement gain and perception support the view that the same motion signals are utilized differently for smooth pursuit and perception (e.g., Spering & Gegenfurtner, 2007). In Spering and Gegenfurtner’s experiment participants were asked to pursue a target and estimate its speed during a 100 ms perturbation period where the target and context changed speed. They found that perception of target velocity was driven by a relative motion signal and was a result of a target and context motion difference, while pursuit gain was a result of averaging target and context velocities and seemed to follow a motion assimilation process. The authors related the different effects of the context to the different “needs for motion perception and eye movement control” (p. 1360).

The linear vector model developed in this thesis used egain ($\tilde{\epsilon}$) as the only free parameter (retinal signal was fixed to 1) to fit the participants' perceptual errors. It turned out that a higher ST speed ($8^\circ/\text{s}$) produced a lower egain value, representing the pursuit-related component of the overall compensation signal, than the slow ST ($2^\circ/\text{s}$). Despite the large perceptual errors for the slow ST speed, the fitted egain was higher for slow than for the fast ST conditions. One possible explanation could be that when the visual stimulation is weak, such as the case of a slowly moving ST, the information from eye movement is utilized more than when the visual stimulation is strong (such as the case of a fast moving ST). Therefore, an increased extra-retinal signal may still not be sufficient to fully compensate for the eye movement and reach perceptual stability, when the visual signal is minimal. This type of reasoning is in agreement with Wertheim's idea, that the compensation signal is not purely related to eye movement, but also contains a visual component which varies with the varying spatio-temporal structure of the retinal image and is part of the compensation signal. So the eye movement gain itself does not modify perception on its own, but rather it is dependent on visual elements that also contribute to perception.

3. The effect of pursuit direction

In this thesis I varied the direction of pursuit to determine whether pursuit direction alone had any effect on perceptual performance. In general, during the $6^\circ/\text{s}$ target pursuit, the estimation accuracy was similar across different pursuit directions when the ST speed was relatively high ($8^\circ/\text{s}$). Again, this is not surprising since the retinal image vector in this case is very close to the actual screen velocity. In conditions with a slow single stimulus dot (empty background,

stimulus speed $2^\circ/\text{s}$), the perceptual performance varied as a function of pursuit direction. When considering the size of estimation errors in absolute values (regardless of whether the estimates fell below or above the actual ST direction) perception was bad during the cardinal pursuits (and worst during 270° pursuit). However, when the average estimate errors were computed from the actual direction estimates that retained a sign indicating under or over estimation, the oblique pursuit at 315° yielded the largest estimation errors overall.

These inconsistencies regarding perceptual error depending on how it is calculated should be noted: the results may vary depending on the method of data analysis.

Reporting estimate averages based on the absolute values of estimate errors may be a better indication of the error *magnitude* than when the averages are computed from the actual directional estimation errors. On the other hand, directional errors provide a better *directional indication* of the perceptual bias. In order to correctly interpret the compensation results, it is important to calculate the average errors using both actual and absolute values. For example, if an average error computed from actual errors turns out to be very low, one may wrongly conclude that the compensation is high. However, if one uses absolute error values that produce a high average, the conclusion would suddenly change (compensation is low).

Therefore, when reporting outcomes related to perceptual performance it is important to specify how the averages representing perceptual errors were computed. It was shown that the magnitude of errors computed by averaging the absolute values of errors may provide additional information about the data, such as the magnitude of errors as well as an overall indication whether the errors were under or over-estimations of the ST directions (see Figure VI.8 on page 122).

There was a large overall perceptual bias (15.7°) during oblique pursuit in Experiment 5 which cannot be explained by pursuit gain, because the gain during this pursuit was almost the same as in horizontal and vertical pursuits. One could argue that the lower the pursuit gain, the larger the perceptual errors, but the data did not show this pattern, according to the correlation analyses in all experiments. The average direction estimation errors during oblique pursuit were larger compared to the cardinal pursuit directions. A similar effect was noted by Krukowski and Stone (2005) who observed that during oblique pursuit visual-direction discrimination was worse than during pursuit in cardinal directions. Their experiment differed from the ones in this thesis mainly in that their participants judged the direction of the pursued target, not a background stimulus dot. Krukowski and Stone concluded that the increased threshold for perception is due to the oblique direction of eye movement which is in some way under-represented in the visual pathway. In our experiment with no background, when the estimation errors were computed from the absolute values, the errors were the lowest for the oblique pursuit. This suggests that there is a directional bias, not a reduced sensitivity to ST motion, during oblique pursuits. In addition, the oblique effect was noted for both perception and pursuit by Krukowski and Stone, who suggested it is caused by a “suppression” of direction space surrounding oblique directions.

Experiments 3, 4 and 5 revealed an “oblique effect” for eye movement errors – the difference between TD direction and eye movement direction was the largest in 225° and 315° pursuits in all our experiments. These experiments all had the same combination of ST directions for each pursuit direction, eliminating the possibility

of differential influence of the unique combination of ST directions and targets in Experiment 1 and 2. In the additional background experiments (Experiment 3 and 4) target directions at 225° and 315° produced the largest eye movement direction errors. Specifically, on average, eyes deviated upward: toward 180° when pursuing a 225° TD, and toward 0° when pursuing a 315° TD. Similarly, the 315° pursuit led to the largest eye movement angle deviation in the experiment with no additional background.

Perhaps the most surprising observation with regard to pursuit directions was the fact that in Experiment 4 the pursuit errors significantly correlated with perceptual errors for almost all pursuit directions (see Table VIII.2 on page 145). Although the correlations were very small, it is interesting because the deflection of eye movement from the target on the screen was not large (only a few degrees in some cases) and would not change the ST retinal image motion by much. It should be noted that the linear vector model assumes that the extra-retinal compensation vector is aligned with the actual target direction. Only the length of the compensatory vector is adjusted to fit the data. This means that if the pursuit does not perfectly match the target direction, then the model prediction is slightly shifted.

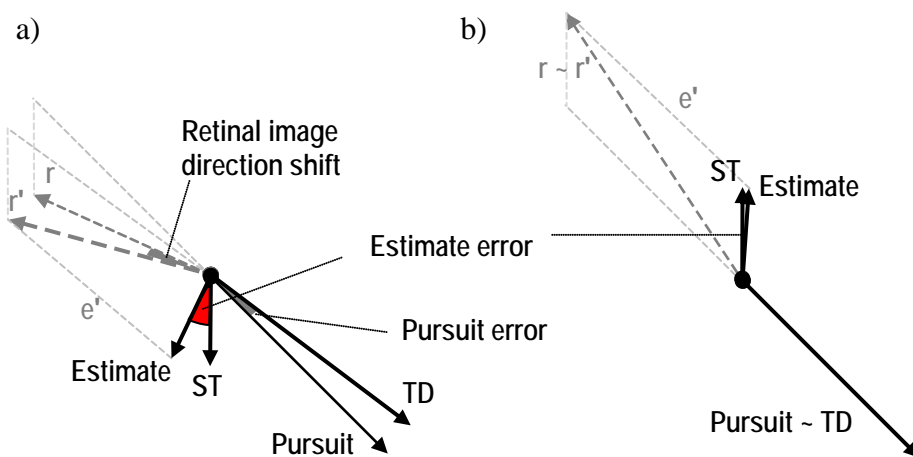


Figure XI.1. Pursuit error and the associated ST retinal image motion shift ($r - r'$) in Experiment 4. In these examples TD moved at 315° and ST moved at 270° (a) or at 90° (b). When the ST moved at 270° , the eye movement was notably different from the TD motion (pursuit error was large) and the average estimate error was also large (-24.7°). When the ST moved at 90° , the eye movement was virtually the same as the TD direction and the average estimate error was also very small (3.3°).

Figure XI.1 presents how imperfect pursuit (eye movement deviation from the target) shifts the ST retinal image motion and its perceived direction. This shift depends on the ST direction relative to TD direction. In Experiment 4 (when the background moved with the ST), the pursuit deflection error was very similar to Experiment 3 (stationary background), and yet the relationship between pursuit direction and perceptual errors was significant mainly in Experiment 4. In other words, similarly imperfect eye movements in both conditions led to different perceptual results. Although the correlations between pursuit and estimate errors were weak in Experiment 4, they were consistent for all pursuit directions. Correlations between pursuit and estimate errors were not significant at all in Experiment 5, likely because of the large spread of the estimates in that experiment. Because different background conditions resulted in varying

correlations between pursuit errors and perception, it would be interesting to explore it further in future research.

This idea of considering directional information in the extra-retinal signal is not novel. Festinger, Sedgwick & Holtzman (1976) also speculated that the visual system estimates the eye movement direction from the extra-retinal signal and it was later supported by other researchers (Krukowski, Pirog, Beutter, Brooks & Stone, 2003; Krukowski & Stone, 2005). However, these authors only used an empty background in their experiments and used the same target for pursuit and perception. What is important is that the oblique effect was found for perceptual responses as well, and was related to the head-centric or screen direction of target, not to the retinal image motion. This suggests that the neural signal associated with the oblique effect occurs after some degree of eye movement compensation, perhaps within area MST. The experiments in this thesis extend current knowledge about pursuit direction effects. First, these experiments involved a number of pursuit directions, where the perceptual judgments were about a stimulus direction (not a target direction) that appeared during pursuit. In addition, different types of background were introduced. Thus the pursuit direction effects were examined in more complex situations than presented in previous studies.

The suggestion that the oblique effect may be evident for both pursuit and perception is related to the discovery that pursuit and perception share the same motion processing signal which encodes motion direction with expanded space around cardinal directions (Krukowski & Stone, 2005). Further, stimulation and lesions in MT & MST affect perception and pursuit simultaneously (e.g., Komatsu

& Wurtz, 1989; Dursteller & Wurtz, 1988; Celebrini & Newsome, 1995). Unlike MT cells, MST neurons are thought to carry extra-retinal signal because they continue to fire during pursuit even when there is no retinal image motion present (Ilg & Theier, 1997; Newsome et al., 1988). The oblique effect is not linked to the retinal image slip but rather to the target motion in head-centred coordinates. Because area MST is likely the earliest area shown to combine the retinal and extra-retinal signals, the oblique effect may be originating in MST (Krukowski & Stone, 2005).

It is worth noting that the present experimental results are based on the information provided by an eye-tracker, which made it possible to capture the eye positions and determine the actual eye movement velocity. The eye tracker was helpful in increasing the validity of this research as it identified saccades and blinks, extreme eye movement gains (less than 0.5 and more than 1.5) and finally, it revealed how participants actually moved their eyes in relation to the pursuit target on the screen. Knowing what the eyes were actually doing was important when investigating the relationship between actual retinal velocities and perception.

4. The effect of background characteristics

The current thesis used three different backgrounds for the single ST dot: clear background, background with stationary random dots and random dot background moving at the same velocity as the ST dot. The largest perceptual errors (including both absolute and directional) occurred in the no background condition (Experiment 5), while perception was good and comparable between the

additional background conditions (Experiments 3 and 4). The moving background had an adverse effect on perceptual judgments but this effect was not large, in comparison to the stationary background results. It appears as if the sensitivity for global motion was reduced in Experiment 4 (when the background moved at the same velocity as the ST) and therefore its direction was misjudged. However, the results show that the estimate errors were actually increased only when the ST moved at a 45° angle to the TD (WT condition). In both experiments, estimation errors were largest for the oblique ST directions.

The type of dot background, whether stationary or moving with the ST, also seemed to have an effect on eye movement. Pursuit gain was reduced when additional background was present (in Experiments 3 and 4) compared to the perfect pursuit gain in the no background Experiment 5. It seems that when there is no background at all the eye is able to follow the target better because it is not interrupted by visual elements in the background, but at the same time the no background situation increases perceptual errors. According to previous research, the additional background provides a global motion signal and a strong visual cue that potentially helps in the compensation process (e.g., Wallach, 1959; Mach & Herman, 1978; Brenner & van den Berg, 1994).

What is puzzling is the similarity of perceptual performance between the stationary and moving additional backgrounds. On one hand, it could be expected that the ST with the moving background would produce smaller errors than the stationary background because it was large and moved in the same direction as the ST, providing strong visual directional information, but the results were to the

contrary. Perception of ST direction in Experiment 4 was slightly worse than in Experiment 3. On the other hand, the stationary background produced smaller errors than the moving background because of the possibility that the static dots provided a reference frame against which the ST dot motion was judged.

Alternatively, the stationary background is a more natural environment (a ‘priori’) and although it reduced pursuit gain, the direction of the single stimulus dot was judged more accurately in comparison to Experiment 4. It may be that the relative motion between the stationary background and the ST dot provided an additional cue to the visual system or that the stationary background had less of a modifying impact on the eye movement signal. This will need to be addressed in future experiments.

Although statistically different, the estimation errors and pursuit gains were still very similar in Experiments 3 and 4 compared to Experiment 5 (when no additional background was present). The influence of background global motion during smooth pursuit has been examined previously (Collewyn & Tamminga, 1984; Lindner & Ilg, 2006; Schwartz & Ilg, 1999; Spering & Gegenfurtner, 2007). In some studies (Lindner & Ilg, 2006; Schwartz & Ilg, 1999; Spering & Gegenfurtner, 2007) briefly exposed background motion in the same direction to pursuit had a greater effect on pursuit than background moving against the eyes which had very little effect. It was suggested that the reduction in sensitivity to background motion in the opposite direction to pursuit was caused by a mechanism that originates from visual reafference associated with pursuit – not from pursuit per se. As stated earlier, the reduced pursuit gains in Experiment 3

and 4 did not worsen perceptual performance in relation to Experiment 5 which had perfect pursuit gain and yet perceptual errors were the largest.

Another important observation from the perceptual results of Experiment 3 and 4 relates to the issue of reference cues. It could be argued that the perceptual results could have been affected if participants could see the frame of the monitor (surrounding the visual display) and thus could use it as a frame of reference when judging the ST direction. However the differences in perception between the 3 different background conditions (no vs. static vs. moving background) would argue against the idea that participants were using the outside frame of the monitor to make their judgments because the monitor frame was the same in all experiments.

Although the additional background improved compensation, the linear vector model fit showed an increased extra-retinal signal (e_{gain}) in conditions with an empty background. Similar finding was reported by Morvan and Wexler (2009). They eliminated relative motion as they did not use simultaneously moving ST and TD and they did not use any additional background either. They concluded that eye velocity estimation came primarily from the eye motor signal. Their findings are similar to the current observation that eye velocity estimation depends on information coming from the eye-movement related signal (e_e) when the relative motion is ambiguous with no additional background present. As suggested earlier, based on the notion that the compensation signal $e' = e_e + \gamma r$, the additional background may provide a stronger visual component (γr) in the compensation signal (e'), and therefore can affect the compensation process by

relying less on the motor command ($\epsilon\epsilon$) coming from the moving eyes and more on the visual cues in the scene. As suggested earlier, MSTd cells may be responsible for increasing the visual component of the compensation signal by estimating the eye rotation parameters based on the global retinal flow (Perrone 1992).

5. The effect of retinal velocity

Stimuli moving at the same speed ($2^\circ/\text{s}$) on the screen were divided into those that moved faster or slower on the retina (stimuli moving backward and forward with respect to the pursued TD, respectively). The $2^\circ/\text{s}$ ST that moved faster on the retina produced a significantly higher model fit value for the extra-retinal signal gain (based on the one parameter linear vector model described earlier), than ST moving slower on the retina, but only in conditions with the stationary background. There was no difference in the model output for $\tilde{\epsilon}$ when the background was blank or when it was moving. A few studies have previously shown that perception can be influenced by background motion by modulating the retinal image motion (Turano & Heidenreich, 1999; Brenner & van den Berg, 1994; Morvan & Wexler, 2009). These studies showed that eye velocity is not estimated from an extra-retinal signal alone but also from the retinal ST velocity (the combined eye and screen ST velocities). This conclusion comes mainly from situations in which the background motion had a uniform velocity. However, in the natural environment, there are often numerous velocities present in the visual field and it is hard to know which of these could be used to control the eye movement signal. Thus the role of the visual signal in the compensation process is not straightforward.

Taking the Bayesian model into consideration, appropriate perception in conditions of ambiguous visual stimulation would likely depend more on information coming from the eye movement. Therefore, one would expect the eye movement signal (represented by *egain*) to increase when the retinal stimulus speed is low. This happened as the highest *egain* was low in the WT stimuli in Experiment 5 (ST retinal velocity low with no background). However, in Experiment 3 (static dot background) *egain* increased for faster retinal stimuli. One possible explanation may be related to the relative motion between the ST dot and the background, because when the whole background is either moving with the ST or when it is absent, there is no relative motion present between the ST and background. This effect of background needs to be assessed further as it is not possible to determine the exact cause of this interesting result.

The target-stimulus combinations were further divided into two condition groups: “Strong” and “Weak”. The first group included conditions that produced “strong” retinal stimulation where the ST and background dots all moved backward in relation to eye movement. The second group included conditions that produced “weak” retinal stimulation where a single ST moved forward in relation to the eye movement. The “strong” group produced lower eye movement gain, lower extra-retinal signal but better perception than the “weak” group. According to previous findings (Masson, Proteau & Mestre, 1995), a background moving in the same direction as the pursuit increased pursuit velocity whereas a background moving in the opposite direction to pursuit decreased eye velocity. Similarly, brief exposure of a background moving in the same direction as the target resulted in an increase of eye velocity (Lindner, Schwartz & Ilg, 2001; Spering & Gegenfurtner,

2007). The asymmetry in background effect on pursuit gain was explained as an asymmetry in the suppression of optokinetic nystagmus (Lindner & Ilg, 2006). The current analysis of pursuit gain when the whole background moved in the opposite direction to the eye movement confirms previous findings, but the average pursuit gain in this condition was still quite high (.91). Overall our results regarding pursuit gain support the idea of spatial averaging of motion signals (“motion assimilation”) in determining pursuit velocity, but the effect is small. This effect on pursuit gain was totally absent in the WT and AT conditions in Experiment 3, 4 and 5. However, it seems that pursuit was prone to larger errors in the WT than AT conditions: in the WT conditions, the eyes were deviating from TD at a larger angle toward the ST dot, whereas eye movements in the AT conditions hardly deviated from TD at all.

Related to the computation of pursuit velocity is the computation of perceived velocity. Spering and Gegenfurtner (2007) proposed that perception follows “motion contrast” (subtracting motion of context from motion of the target). The perceptual results in our experiment are in agreement with this notion, because in general, ST that moved away from the TD and produced a larger angle between ST and TD were estimated more accurately than ST moving at a smaller angle to the TD (AT vs. WT conditions).

The relationship between low compensatory e_{gain} $\tilde{\epsilon}$ and good perception in the “Strong” retinal stimulation trials would make sense, again, if one assumes that the “Strong” retinal stimuli increase the global visual signal and thus increase the overall compensation e' . Results from my current experiments suggest that when

there is a strong retinal signal, the visual system may utilize the eye movement-related signal to a lesser degree. This assumption would explain the low egain output of the linear vector model for the “Strong” retinal stimuli.

6. The effect of perceptual task

Previous research suggested that people’s ability in dual task situations is often reduced because brain resources are competed for by the cognitive tasks, thus limiting the availability of neural resources (e.g., Navon & Gopher, 1979; Ferrera, 2000; Ferrera & Lisberger, 1997). For example, when estimating object motion, one may need to rely on the same central resource to be able to accurately and simultaneously estimate direction and speed of the moving object. This is the reason why the current experiments were designed to test direction estimation and speed estimation ability separately. Therefore, participants could concentrate on one cognitive task at the time.

A separate experiment to assess speed perception was included in the current thesis also in order to test whether using a magnitude scale measurement method proves to be suitable. Most of the research on speed perception to date has used velocity matching or a “nulling” task. These types of tasks may be subject to motion adaptation because the observer views moving stimuli continuously during the matching. Other studies employed a simultaneous task where speed is estimated by length and direction by rotation of an arrow on the screen, but this could also present a potential problem with respect to multitasking. By including a separate speed estimation experiment in the current thesis, I wanted to find out whether the perceptual task itself would have an effect on the eye movement gain,

perception, and compensation. The direction Experiment 1 and the Speed estimation experiment were identical regarding the visual display, and only the method of estimation and task differed.

Overall, ST speed was estimated well, using the magnitude scale, and showed a similar trend to previous findings – that slow speeds are slightly overestimated and high speeds are underestimated during smooth pursuit. This pattern was already present during the eye stationary trials, but was more pronounced during eye movement. One potential methodological flaw in the Speed experiment was in the limited range of the discrete numbers representing speed. This could have been overcome by allowing participants to enter numbers such as 1.3 or 3.7. However, it is uncertain whether this would change the outcome by much. The slight overestimation of low speeds and underestimation of high speeds may have been partially influenced by the speed range used in the training session ($1^\circ/\text{s}$ to $8^\circ/\text{s}$). The lowest ST speed presented in the experiment was $2^\circ/\text{s}$ and the highest was $8^\circ/\text{s}$. Therefore, when viewing an ST moving at $8^\circ/\text{s}$, participants had no option but to select a speed of $8^\circ/\text{s}$ or lower, so their estimates had to be either correct or lower, possibly further contributing to the underestimation result. An ST speed of $2^\circ/\text{s}$, on the other hand, was estimated at 1, 2, 3 or $4^\circ/\text{s}$ (with more choices above $2^\circ/\text{s}$). However, the underestimation of fast ST speeds and overestimation of low ST speeds is consistent with non-linear velocity functions (e.g., Turano & Massof, 2001).

In addition, the speed estimation task could have included a different technique for entering estimates by the participants. The dim light may have caused some

difficulties in pressing the selected number on a keyboard. A more efficient way to enter estimates would be to present a number scale on the screen from which participants could select a number and click on it. Entering estimates in this manner would be more similar to the direction estimation task in that it would involve an illuminated display and mouse clicking rather than searching for a particular key on the keyboard.

According to the eye movement data, the Speed experiment produced much lower eye movement gain than the direction experiment. Participants reported having to “think” about the speed which suggests that the task – having to convert the speed of an ST into a number – may have influenced the oculomotor system (this more complicated perceptual task may “have stolen” from the central resources shared by pursuit). In the Speed experiment, the ST speed had an effect on the model output for egain which increased for the fast ST ($8^\circ/\text{s}$) conditions. In the direction Experiment 1 this did not happen. This finding implies that the cognitive task itself has an effect on perception and the compensation signal. Therefore, when comparing results among studies, it is important to take into account the type of cognitive task and the measurement method used to probe perception. Despite the visual display similarities, the cognitive task of speed estimation was reported as more demanding than direction estimation by participants and therefore direction estimation during pursuit was the primary focus of this thesis. Further investigation into the effects of ST speed on perception and the compensation signal may provide new information in this regard.

In the current experiments, each participant was presented with a given set of moving stimuli that were either in cardinal directions (i.e., 0° , 90° , 180° , 270°) or that were exactly in the middle between these cardinal directions (i.e., 45° , 135° , 225° , 315°). This selection of directions was motivated by the need to include a representative span of directions covering the entire range from 0° to 360° . This selection of discrete directions could have influenced the participants' responses, in that they may have categorized the perceived stimuli and subsequent estimates as moving in a set direction, regardless of their perception. In other words, they could have tried to match the learned category direction rather than the observed direction. In addition, oblique directions were found to produce biases in estimations in eye movement as well as eyes stationary trials, suggesting that the visual system is less sensitive to oblique directions than cardinal ones (Krukowski et al., 2003).

The robustness of the direction estimation results can be improved in future experiments by presenting a moving stimulus whose direction varies slightly in repeat trials. The variation could be constrained to a specified range of directions around the inspected major direction. For example, a stimulus direction of 90° presented in the current study could be randomly varied between 86° and 94° ($90^\circ \pm 4^\circ$). This would provide the participants with uncertainty as to the category direction and encourage them to provide estimates that match their perception of the stimulus in each trial. The estimation errors in this type of experiment would probably be higher because participants would not have the comfort of trying to position the arrow symbol in exactly 0° , 90° , 180° or 270° directions. Future experiments may apply this ST direction selection strategy to the TD as well, to

manipulate the retinal image in a desired manner. However, even though the screen directions were cardinal directions, the retinal velocities had more variation. It is not known whether the ST direction range should ‘equalize’ the retinal velocities or the screen velocities.

7. The effect of other variables

Experiment 5 was very similar to Experiment 1 in that it had no additional background present with the ST, but differed in a number of ways. Besides slightly different ST directions, Experiment 5 did not include the slow pursuit condition (TD moving at $2^\circ/\text{s}$) and the fast moving ST condition (ST moving $8^\circ/\text{s}$). In addition, Experiment 5 was run with many more participants than Experiment 1, and a half of the Experiment 1 participants also completed Experiment 5. It is also important to note that Experiment 5 was the last experiment completed. Participants may have gradually gained experience on Experiments 3 and 4, and particularly found Experiment 5 easier than Experiments 3 and 4 because it presented a single stimulus dot without any additional background. These variations may have contributed to differences in results between Experiment 1 and Experiment 5, despite their main common feature regarding the ST background, and TD and ST speeds.

There was a difference in pursuit gain as well as in the compensatory egain between the two experiments in the trials where the TD moved at $6^\circ/\text{s}$ and the ST moved at $2^\circ/\text{s}$. Lower pursuit gain was observed in Experiment 1 than in Experiment 5, and it also varied across TD directions (downward pursuit had the lowest eye movement gain). Pursuit gain in Experiment 5, on the other hand, was

consistent across all three pursuit directions and was almost perfect (after rounding to the closest decimal it equaled to 1.0). In addition, the model output for the extra-retinal signal was lower in Experiment 1 (.65) compared to .90 in Experiment 5, but this may have been due to the fact that the model was fit to a larger number of points in Experiment 1 (associated with five ST directions) than in Experiment 5 (associated with four ST directions). The fit to a different number of points could have therefore affected the output value for again. Therefore, it is difficult to compare Experiments 1 and 5 (both with empty background) because any differences may be a result of several extraneous factors: higher variability of conditions in Experiment 1, different samples and sample sizes, practice effect in Experiment 5 and model fitting procedure. These issues could be considered in future research.

Chapter XII. Conclusion

The present study supported previous research by showing that the extra-retinal signal incoming to the visual system from the eye movements is important for the perceptual stability of the world. It showed that the human brain may be capable of vector subtraction and that the vector subtraction mechanism works most of the time. Although it did not reveal the mechanisms of how this vector subtraction in the brain works, it did not rule out the approach proposed by Perrone and Krauzlis (2008) that utilizes the cosine distributions of retinal and extra-retinal signals.

Motion perception was examined across different conditions pertaining to stimulus background, stimulus speed, retinal velocity and eye movement velocity. The first experiment revealed that very slow eye movements ($2^\circ/\text{s}$) have a gain close to unity and produce much smaller perceptual errors than faster eye movements ($6^\circ/\text{s}$). Following initial experiments, the goal was to investigate conditions where the vector subtraction process breaks down. The bulk of the experiments therefore systematically focused on conditions with faster eye movements and slower stimulus velocities in order to reveal which factors contribute to veridical perception of motion.

Based on previous psychophysical research, the level of compensation has been tied to the value of the extra-retinal signal. Initially it was thought that the extra-retinal signal was undersized or slower than the retinal signal, as demonstrated by the Filehne Illusion, but later evidence showed that the relationship between the signals is not as simple, suggesting a non-linear interaction between the two signals. However, in most cases the linear model is still a very good

approximation of the compensation mechanism (Freeman 2001). Although the Filehne Illusion often goes unnoticed in everyday life, it has been a subject of investigation for many years because of its relevance with regard to the mechanism underlying it. More insight was needed into the nature of the relationship between the retinal and extra-retinal signals, how they combine and what circumstances produce the best compensation for the reafferent motion.

The present study examined the degree of compensation under different visual conditions, using a linear vector model to find a value for the extra-retinal signal that best fitted the perceptual error data. The linear vector model assumed that the retinal signal was veridical and that any compensation was due to the eye movement signal only, thus separating the extra-retinal and retinal contributions to the overall compensation signal. Most of the experiments used stimulus dots that moved three times slower than the pursuit target so that the retinal velocity did not generate a strong visual signal that could have been contributing to the compensation. It turned out that using such a combination of stimulus-target velocities was successful in identifying factors that influenced perceptual stability. These factors included relative stimulus and target motion, additional background elements and eye movement direction. These factors also revealed that an increased extra-retinal signal does not necessarily mean better compensation. For example, the slowest stimulus velocity led to large perceptual errors (lowest compensation) but at the same time produced the highest value of α that was determined by our linear vector model. A similar trend was observed for the background and retinal velocity factors: conditions with no background and a slow retinal velocity led to poor perceptual performance and a high extra-retinal

signal (egain). In other words, the data showed that the degree of compensation does not necessarily reflect the size of the extra-retinal signal, and that the visual system is likely to use the source of information that is most readily available (sensory or motor) in order to preserve perceptual stability.

Another interesting finding was that the degree of compensation was not dependent on pursuit gain. This was especially clear in results for “Weak” (slow single dot) and “Strong” (fast moving background) retinal velocities. The “Weak” subset of stimuli produced nearly perfect eye movement gain but very large estimation errors. In contrast, the “Strong” stimuli generated a reduced eye movement gain, particularly during downward pursuit, but the perceptual errors were minimal and consistent across pursuit directions. This suggests that the “Strong” stimuli produced higher retinal motion signal which contributed to the overall compensation signal. In this respect, the outcomes support the view that the compensation signal is not composed of purely extra-retinal information, but also includes a visual component stemming from the relative motion between the eye movement and stimulus dot and other visual characteristics.

In conditions where the stimulus motion is slow but its retinal velocity is relatively high, the visual system does not seem to take into account the eye movement gain but rather relies on the retinal information. Generally, however, the extra-retinal signal is sufficient to cancel self-generated retinal motion, and supports the idea that the visual system could be carrying out a form of vector subtraction using the cosine distributions of signals coming from retinal image motion and eye movements (Perrone and Krauzlis, 2008). It appears that the

vector subtraction mechanism starts to fall apart when the retinal velocity is weak, despite almost perfect eye movement gain. In such cases, the visual system cannot depend on the eye movement signal alone to maintain good compensation. Thus a motion signal at a particular retinal location must be represented well in order to produce a retinal signal having an appropriate cosine distribution. If in MST, for example, that motion is estimated poorly (when the retinal velocity is weak and the velocity sensors are not stimulated enough) the cosine distribution of the retinal signal will be distorted.

The current experiments helped reveal the dynamics of the retinal and extra-retinal signals under different visual circumstances. There is no single study that includes a set of conditions that were systematically used to investigate the compensation mechanism in the way it has been done in the present investigation. In the past, different studies focused on different types, speeds or directions of ST, but their results were difficult to compare due to different experimental methodologies and stimulus displays. The present study included a series of experiments that evolved from Experiment 1, which pointed to several aspects that had to be considered in subsequent experiments. These experiments gradually informed how the compensation process works.

First, it was revealed that slow pursuit and fast ST motion could not be used to investigate compensation signal because the retinal and head-centric velocities were too similar and it was difficult to determine whether the estimates were closer to the retinal or head-centric motions. Second, varying the ST exposure during eye movement did not produce major changes in the estimation of the fast

ST and it was concluded that it is the ST speed that is responsible for changes in responses. Both of these findings imply that the relative ST-TD motion is more important than ST speed alone. Third, the compensation for eye movement improves when there is additional background present during ST dot exposure, regardless of whether the background is moving or is stationary. Importantly, estimates differed slightly between moving and stationary background conditions, suggesting that participants did not rely on any other visual cues to make their estimates. Fourth, estimation errors differed depending on pursuit direction. Fifth, retinal velocity as well as the amount of retinal stimulation has been shown to have an impact on perception. Overall, the results show that perception seems to rely on the most salient signal.

Another interesting observation was with respect to the perceptual task. Although there was only one experiment assessing the ability to estimate speed during pursuit, it revealed that the compensation mechanism works differently in that context than during direction estimation. This difference may have been due to the methods used (magnitude estimate for speed vs. line matching for direction), however, it provided evidence that the type of perceptual task is also an important factor affecting perceptual outcomes.

Overall, the results suggest that retinal velocity needs to be represented well at each retinal location in order to produce an adequate retinal signal output and to provide an opportunity for the vector subtraction mechanism to work. Sufficient representation of local velocities on the retina is crucial because the signals reaching MST are based on these ‘local’ estimates; if these local estimates are

incorrect as a result of weak or ambiguous retinal stimulation, the MST signal will also be incorrect and not allow correct compensation. Although the linear vector model used in the current research had only one free parameter (efference copy signal gain represented as a ratio of improve retinal signal gain which was assumed to be 1), it was able to provide a good fit to most of the data (the model fits had a RMSE less than 30° in most experiments). The model explained the data well for the fast ST speed conditions. In the slow ST conditions the model fit deteriorated but still explained more than a half of the data, except for Experiment 5. In Experiment 5 the direction estimates of the single dot (with no additional background present) were not predicted well by the model. The incorrect compensation likely originated in the incorrect estimation of the retinal signal (due to weak retinal stimulation produced by the single ST dot). It should be noted that the model used in the thesis ($h' = pr + (\epsilon\epsilon + \gamma r)$) was not exactly the same as the traditional linear model as it included an additional component ($e' = \epsilon\epsilon + \gamma r$), indicating a visual influence on the compensation signal. Although not quantified, the visual element in the compensation signal (γr) could be deduced based on the relationship between perceptual data (h') and the modeled egain ($\epsilon\epsilon$). The model revealed how much of the extra-retinal (motor) signal was required for the perceptual outcome in each condition, providing new insights into how the retinal and extra-retinal signals may be combined.

The current results are similar to previous findings where the linear model of motion perception during smooth pursuit has been able to account for most of perceptual data (e.g. Freeman & Banks, 1998; Freeman et al., 2000; Souman et al., 2005a). The linear model failed to account for cases where the retinal velocity

was ‘weak’, which is also consistent to the findings from Souman and Freeman (2008) who observed that in conditions with low retinal velocities a non-linear model performed better than the linear one. This suggests that in situations that produce low retinal amplitude the visual system may use non-linear estimates of retinal velocity.

Most importantly, the experiments revealed that different ST directions during pursuit will have a different effect on pursuit error and perception in experiments using different background characteristics. In moving background conditions, for example, one needs to be careful when deciding how well the brain can perform vector subtraction. One combination of ST and TD may produce good perceptual performance but other combinations may not. The current thesis showed that stimuli moving close to the target (WT stimuli) produce much larger estimation errors than stimuli moving away from the target. In addition fast ST will generate retinal image motion that is very similar to the objective motion: if this factor is not taken into account, it is possible to come to the wrong conclusions about eye movement compensation. The current thesis was able to identify the ‘interesting’ combinations of ST – TD velocities, mainly those where the retinal and screen velocities are very different.

The current findings may inform future research in a number of areas where the importance rests in the ability to distinguish external from self-generated motion to preserve perceptual stability, such as robotics, sports, clinical settings and road safety. The results based on the current 2 dimensional experimental setup can be extended to 3 dimensional scenes to provide further insight into the efference

copy signal and the compensation process in general. Visual properties of real world are more complex than lab settings and the current research discoveries can serve as the fundamental baseline for other applications that would include depth and forward motion.

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