

Motion perception in motion

How we perceive object motion during smooth pursuit eye movements

Jan L. Souman

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Motion perception in motion

How we perceive object motion during smooth pursuit eye movements

Bewegingswaarneming in beweging

Hoe we objectbeweging waarnemen tijdens oogvolgbewegingen

(met een samenvatting in het Nederlands)

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1

Introduction

In our daily life, the ability to perceive motion and to discriminate between different velocities and motion directions is of the utmost importance. We need it for such diverse tasks as to participate in traffic, to play sports, to step onto an escalator without falling, to pour coffee into a cup, and many more. The rare cases of patients with cortical lesions that specifically affect the perception of motion vividly illustrate its importance (Zihl, Von Cramon, & Mai, 1983). These patients see the world as a series of sequential snapshots, without a sense of motion. The patient of Zihl et al., for instance, could not cross a street by herself, because she was unable to judge the velocity of oncoming cars. “When I’m looking at the car first, it seems far away. But then, when I want to cross the road, suddenly the car is very near.” (Zihl et al., 1983, p. 315). Even her communication with other people was disturbed, because she could not pick up the subtle movements of the face of the person she was talking to.

Given the fundamental nature of the ability to see motion, it is not surprising that a lot of research has been devoted to how we perceive motion (see e.g. Smith & Snowden, 1994; Watanabe, 1998). Most of this research has studied motion perception during fixation of a stationary fixation target. Methodologically, this makes sense, because eye movements change the retinal image motion, complicating the relationship between the motion stimulus that is presented to the observer and the perceived motion reported by him or her. In daily life, however, we seldom keep our eyes still. We look around all the time, shifting our gaze from one object or part of an object to the other. We also follow moving objects with our eyes and move our heads and our bodies, which also changes the retinal input. It is therefore important to know how these forms of self-motion affect motion perception.

This thesis discusses the perception of motion during one specific type of eye movements, the so-called smooth pursuit eye movements. In this introduction, I will start by describing some of the properties of smooth pursuit eye movements that are relevant to the studies in this thesis. Following that, the

problem that our visual system has to solve in motion perception during smooth pursuit eye movements is outlined and two broad theoretical perspectives on how our brain solves it are discussed in general terms. Also, the relevant physiology will be described briefly. Finally, the contents of this thesis are outlined.

Smooth pursuit eye movements

We make smooth pursuit eye movements in order to follow moving objects with our eyes. In fact, it is very hard to make this type of eye movements without a visual target to track, although they can be made in anticipation of visual targets (Bennett & Barnes, 2003; Kao & Morrow, 1994) or to imagined targets (Gauthier & Hofferer, 1976). The most important function of voluntary smooth pursuit eye movements is to keep the image of moving objects on the fovea, the part of the retina with the highest visual acuity and the highest concentration of colour sensitive receptor cells (the cones). Related to smooth pursuit eye movements are the reflexive eye movements that help stabilize the retinal image when the observer is presented with a large moving visual pattern (the optokinetic reflex) and the fast reflexive eye movements that are made to maintain fixation during vestibular stimulation due to head movements (the vestibulo-ocular reflex; see Leigh & Zee, 1999, pp. 151-152). However, since these two types of eye movements are not voluntary, in contrast to smooth pursuit eye movements, it is debated whether they should be categorized as smooth pursuit (see Krauzlis, 2004, for a review). Smooth pursuit eye movements can be accurate for constant velocities at least up to 30°/s (Meyer, Lasker, & Robinson, 1985). With sinusoidal pursuit, the accuracy depends on the combination of frequency and amplitude (Lisberger, Evinger, Johanson, & Fuchs, 1981). For frequencies above 1 Hz, pursuit gain decreases rapidly, especially for higher amplitudes (15° and more). In the same range the phase lag of the eyes relative to the pursuit target increases markedly.

Several brain areas are involved in the initiation and maintenance of smooth pursuit eye movements (see Leigh & Zee, 1999, pp. 164-174; Krauzlis, 2004). Since ocular pursuit relies on visual input, it is not surprising that the visual motion processing areas MT and MST (in the monkey) are important for both the initiation and maintenance of smooth pursuit eye movements. Lesions in these areas disturb ocular pursuit (Dürsteler & Wurtz, 1988). As these areas are involved in both the generation of smooth pursuit eye movements and the perception of motion, oculomotor behaviour and motion perception during smooth pursuit are often highly correlated (Beutter & Stone, 1998; Stone, Beutter, & Lorenceau, 2000; Stone & Krauzlis, 2003). Opinions vary, however, on whether these correlations indicate a common pathway (Gegenfurtner, Xing, Scott, & Hawken, 2003). In the experiments described in this thesis, I have used smooth pursuit eye movements mainly to create a dissociation between the retinocentric and head-centric motion (see below). Therefore, I will not pay much attention to the eye movements per se, but only in so far as they are

important for the transformation of motion signals from a retinocentric to a head-centric frame of reference.¹

The advantage of smooth pursuit eye movements is that they are relatively easy to induce and to measure. Moreover, we are still able to see motion during smooth pursuit eye movements, contrary to for example saccadic eye movements (the rapid eye movements we use to jump from one position in the visual field to another). With saccades, motion perception is largely suppressed (Burr, Morrone, & Ross, 1994; Diamond, Ross, & Morrone, 2000; Kleiser, Seitz, & Krekelberg, 2004; Thiele, Henning, Kubischik, & Hoffmann, 2002). The study of motion perception during eye movements has a long and venerable tradition, dating back at least to Von Helmholtz (2000) in the nineteenth century and others before him (see Wade, 1978). However, many questions concerning motion perception during smooth pursuit eye movements remain. The central question is how our visual system compensates for the effects that smooth pursuit eye movements have on the retinal image.

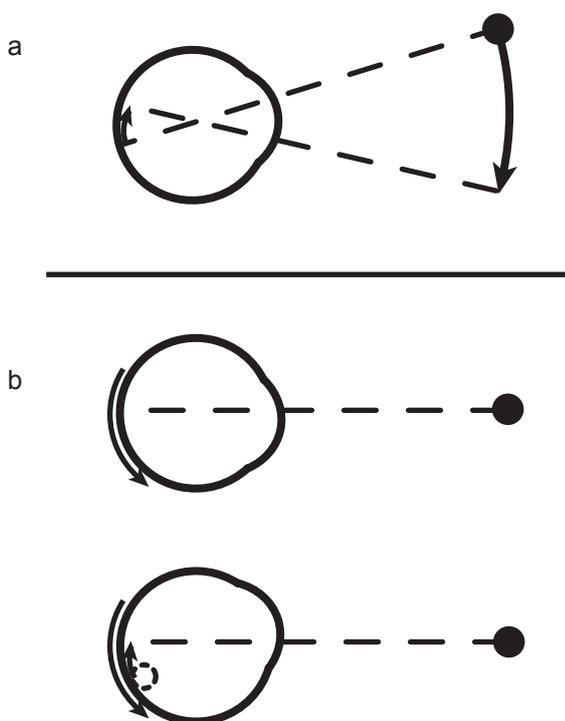


Figure 1. Illustration of the effect of eye movements on retinal image motion. The eye is drawn in horizontal cross-section. (a) A moving object projects a moving image on the stationary retina. (b) The same retinal image motion can be caused by a rotating eye combined with a stationary object.

The effects of smooth pursuit eye movements on retinal image motion

When we see a moving object such as a flying bird or a moving car, the image of the object moves on our retinae if we stand still and don't move our eyes or head. This is schematically depicted in Figure 1a. However, the same retinal image motion can be caused by rotation of the eye (for example, because we follow another moving object with the eyes), combined with a stationary object (Figure 1b). In fact, there are infinitely many possible combinations of eye rotations and object

¹ The terms 'retinocentric' and 'head-centric' are used to indicate the frame of reference in which object motion is judged: with respect to the retinae or to the head. If the head is kept still relative to the world and the eyes don't move in the head, the retinocentric and the head-centric frames of reference coincide (apart from the necessary integration of the motion signals from both eyes). To transform motion signals from a head-centric frame of reference to a geocentric one (relative to the world), self-motion information and the distance to the object that has to be judged should be incorporated (see Swanston, Wade, & Day, 1987; Wade & Swanston, 1996).

movements that will produce the same retinal image motion. Consequently, retinal image motion does not automatically indicate that we see a moving object. Conversely, the absence of retinal image motion may be the consequence of either a stationary object or of an eye velocity that equals that of the moving object, for instance because we follow it with our eyes. Since we normally do not have problems in distinguishing between stationary and moving objects even when we move our eyes, it follows that our visual system somehow must take the eye movements into account when it produces motion percepts. It appears that the visual system uses information about the eye movements to correct the retinal image motion for their consequences. That this is an important function is shown by the case of a patient who, due to cortical lesions, lacked this compensation mechanism (Haarmeier, Thier, Reppow, & Petersen, 1997). Whenever this patient made smooth pursuit eye movements, the world seemed to move, making it difficult for him to perform daily life tasks such as driving or intercepting moving things. Moreover, these eye movements were accompanied by feelings of vertigo and nausea.

Several theories of how our visual system manages to compensate for the effects of smooth pursuit eye movements have been put forward. Generally, they can be divided into two classes (see Wertheim, 1994, for a review). According to direct perception theory (Gibson, 1950, 1966, 1979; Michaels & Carello, 1981), the presence of eye movements can be deduced by the visual system from aspects of the retinal image itself. Eye movements introduce a rotational component into the optic flow, the total array of velocity vectors impinging on the retinae. Theoretically, the visual system could extract this rotational component from the optic flow (Koenderink, 1990; Koenderink & Van Doorn, 1987). Once the rotational component is extracted, it can be used to recover the actual (head-centric, i.e., with respect to the head) motion of objects in the visual field (see Beintema & Van den Berg, 1998; Van den Berg & Beintema, 1997, for an application of this idea in the context of heading perception during smooth pursuit eye movements²). The other class of theories takes the compensation for the effects of eye movements to be an inferential or computational process (Wertheim, 1994; also see Ullman, 1980). According to this account, retinal signals are combined with extraretinal signals that inform the visual system about the eye movements and can be used to correct the retinal image motion. This

tradition dates back to at least Von Helmholtz (2000) in the 19th century. Within the inferential tradition, opinions differed regarding what constitutes the extraretinal signal (see Matin, 1986, for a review). According to the inflow account, the extraretinal signal is based on proprioceptive feedback from the eye muscles and on the proprioceptive information generated by the movement of the eyes relative to the eyelids. When the eye moves, receptors in the eye muscles and the eyelids supposedly signal to the visual system that the eye is moving and these signals can be used to compensate for the effects of the eye movement on the retinal image. The alternative hypothesis, the outflow theory, holds that the extraretinal signal consists of an efference copy of the oculomotor command that drives the eye movement (Sperry, 1950; Von Holst, 1954; Von Holst & Mittelstaedt, 1950). When the motor areas of the brain signal the eyes to move, a copy of this signal is relayed to the visual system and can then be used to correct the retinal image motion.

Nowadays, most researchers in motion perception during smooth pursuit seem to follow the inferential theory. In the related field of heading perception during smooth pursuit eye movements, however, the direct perception theory still is going strong, though often the existence of extraretinal signals is assumed as well (see Lappe, Bremmer, & van den Berg, 1999). Wertheim (1990; 1994) showed that both approaches can be integrated into one framework. According to his theory, the visual system uses both extraretinal and retinal information to estimate the eye velocity. This would mean that the retinal signal and the eye movement signal interact, with retinal image characteristics affecting the estimated eye velocity. In this thesis, I will return to this issue several times (Chapters 3, 6, 7 and 8).

Concerning the issue of inflow versus outflow, it now seems evident that the extraretinal signal mainly consists of an efferent signal, as the outflow theory states. If one presses lightly with a finger against an eye, with the other eye closed or occluded, the world appears to be moving (Bridgeman, 1986; Bridgeman & Delgado, 1984; Bridgeman & Stark, 1991; Mittelstaedt, 1990). Hence, the degree of compensation for the effects of the passive eye movement is minimal in this situation. Because the eye movement is not caused by

² In the model of Beintema and Van den Berg the optic flow analysis may be supplemented by other sources of information, so it is not a 'pure' direct perception model.

an oculomotor command (apart from a small rotational component to maintain fixation, [Bridgeman & Stark, 1991](#)), the efference copy signals to the visual system that the eye is not moving, which explains the perceived motion of the surrounding world. If proprioceptive information would be used, as the inflow theory proposes, we would expect the world to appear more or less stable during eye presses. Another finding that is generally taken to support the outflow theory concerns the case of paralysed eye muscles. In this case, attempts to move the eyes generate an efference copy without accompanying eye movements (or with distorted eye movements in the case of partial paralysis). The outflow theory therefore predicts that the world will appear to move during attempted eye movements, because the visual system uses the efference copy to compensate for the effects of eye movements that haven't been there. However, the results suggest a more complicated explanation. Illusory movement and especially displacement do occur, but only with partial paralysis and when few visual references are present ([Matin et al., 1982](#); [Stevens et al., 1976](#)). With complete paralysis of the eye muscles, observers merely report that they have the feeling that their eyes have been paralysed, without accompanying motion or localization illusions ([Stevens et al., 1976](#)). The crucial factor here appears to be the presence of visual references. If visual stimuli are viewed in a well-lit environment, no illusory motion or mislocalization occurs. In the case of partial paralysis, perception (particularly localization) is distorted only if visual information is restricted. This has not been tested with complete paralysis. Since the amount of proprioceptive feedback is the same with and without visual references, inflow information does not seem to contribute much to the compensation process. The results suggest that this compensation is based on a combination of an efference copy, which forms the main source for eye movement information in the dark, and visual information. This agrees with the theory of [Wertheim \(1990; 1994\)](#).

The importance of visual information for the effects of paralysis of the eye muscles in structured visual environments appears to at least partially support the direct perception account of motion perception during smooth pursuit. However, other results are not easily explained in this framework. If one follows a moving object with the eyes, the image of this object is approximately stationary on the retinae. Still, we perceive objects that we track with the eyes as moving, not as stationary. If the objects move against a textured

background, this compensation might be based on the optic flow alone, as proposed by the direct perception theory. However, if the moving object is the only thing present in the visual field, the velocity of the object cannot be deduced from the retinal image alone. And still, we perceive tracked objects as moving in the dark. Normally, ocular pursuit is never perfect and a small amount of retinal slip will always occur. However, even with stabilized images, for instance afterimages ([Mack & Bachant, 1969](#)) or images that have been stabilized through feedback of the eye movement ([Turano & Massof, 2001](#)), motion is perceived. This can not be explained from just the retinal image motion and suggests that extraretinal information is used to compensate for the effects of the eye movements.

Underlying physiology

Although it is far from clear how our brain exactly combines retinal motion signals and eye movement signals, there is one brain area that seems to be unequivocally implicated in the compensation process. Area MST (the medial superior temporal area) in the monkey cortex and its human homologue (also called area V5a) form part of the major motion processing pathway in the brain, the magnocellular pathway (see [Snowden, 1994](#) for a review). This area is located in the superior temporal sulcus, close to another important motion processing area, the middle temporal area (MT or area V5), from which it gets its major input. Neurons in area MST respond to relative complex motion patterns, such as rotation, expansion and contraction ([Duffy & Wurtz, 1991a, 1991b](#); [Orban, 1995](#); [Tanaka, 1989, 1998](#)). Many neurons in MST also respond during ocular pursuit of a small target in the dark ([Komatsu & Wurtz, 1988a, 1988b](#)). In fact, some MST cells even respond during smooth pursuit when the pursuit target is briefly invisible or stabilized on the retina ([Ilg, Schuman, & Their, 2004](#); [Newsome, Wurtz, & Komatsu, 1988](#)). Taken together, this suggests that area MST receives both retinal and extraretinal input, making it a prime candidate for the integration of these inputs and the transformation of a retinocentric to a head-centric frame of reference (also see [Barton et al., 1996](#)). Recent neural network models based on these properties of MST neurons have successfully simulated the velocity perception of the pursuit target and the concurrent

oculomotor behaviour during smooth pursuit (Furman & Gur, 2003; Pack, Grossberg, & Mingolla, 2001).

Extraretinal signals concerning the rotation of the eyes in the head can only be used to successfully transform motion signals from a retinocentric frame of reference to a head-centric one if the head is stationary relative to the world. If our head or body is moving, these movements have to be taken into account too. Partly, this may also happen in area MST, as the sensitivity of the MST neurons to optic flow components as contraction, expansion and rotation would enable them to signal the speed and direction of self-motion (Ilg et al., 2004). Information about self-motion, however, is also generated by the vestibular system. Not only do the semi-circular canals and the otoliths in the inner ear detect accelerations of the head in space and relay this information to the vestibular nuclei, but these nuclei also receive visual input encoding optic flow (Dichgans & Brandt, 1972, 1978). The visual input to the vestibular nuclei is thought to be the physiological basis forvection, the visually induced sensation of self-motion (e.g., when looking through the window of a stationary train to a slowly moving train; see e.g. Berthoz, Pavard, & Young, 1975). Consequently, even if the head is stationary relative to the world, visual stimulation might still contribute to the estimate of the motion of the head (both translation and rotation) relative to the world and consequently influence the perceived motion of objects in the visual field because it affects the motion of the eyes relative to the world (Wertheim, 1990, 1994).

Outline of the thesis

Two threads run through the contents of this thesis from start to end. The first is the extension of the study of motion perception during smooth pursuit to non-collinear motion. Traditionally, most studies have used collinear motion stimuli, that is, stimuli that move along the line of pursuit (horizontally in most cases). Although some studies had used non-collinear motion (stimuli moving at an angle other than 0° or 180° relative to the pursuit direction) systematic studies were scarce and opinions differed on whether the same compensation mechanisms are at work during collinear and non-collinear motion. In Chapter 2, I address this issue and provide an explanation for the existing differences in the literature. Chapter 3 shows that a

factor which had been shown to affect collinear motion perception during smooth pursuit, the presentation duration of the motion stimulus, similarly affects non-collinear motion perception. More towards the end of the thesis (Chapter 6), the question whether collinear and non-collinear motion perception are based on the same compensation mechanism is addressed again in a more comprehensive framework. Where Chapters 2 and 3 are only concerned with perceived motion direction during smooth pursuit eye movements, the experiments described in Chapter 6 involve judgements of both perceived motion direction and speed at the same time.

Chapter 6 also forms an important part of the second thread, which is the question what model describes motion perception during smooth pursuit best. Traditionally, perceived head-centric velocity has been explained in terms of a simple linear model. This model is extensively described in Chapters 2, 6 and 7. These chapters also provide tests of the linear model; in the latter two chapters the linear model is compared to more recent, non-linear models. Chapter 7 gives a review of the literature on this topic and evaluates the evidence for and against the various models.

As in any interesting carpet, some smaller strands of fibre stand out from the general pattern. Chapter 4 explores possible latency differences between the retinal signals and the eye movement signals supposedly involved in motion perception during smooth pursuit eye movements. It also provides another test of the linear model. Chapter 5 explores the relationship between localization and motion perception during smooth pursuit. Chapter 8, finally, summarizes and discusses the findings of Chapters 2 to 7.

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2

Perceived motion direction during smooth pursuit eye movements

Abstract

Although many studies have been devoted to motion perception during smooth pursuit eye movements, relatively little attention has been paid to the question whether the compensation for the effects of these eye movements is the same across different stimulus directions. The few studies that did address this issue provide conflicting conclusions. We measured the perceived motion direction of a stimulus dot during horizontal ocular pursuit for stimulus directions spanning the entire range of 360°. The stimulus moved at either 3°/s or 8°/s. Constancy of the degree of compensation was assessed by fitting the classical linear model of motion perception during pursuit. According to this model, the perceived velocity is the result of adding an eye movement signal that estimates the eye velocity to the retinal signal that estimates the retinal image velocity for a given stimulus object. The perceived direction depends on the gain ratio of the two signals, which is assumed to be constant across stimulus directions. The model provided a good fit to the data, suggesting that compensation is indeed constant across stimulus direction. Moreover, the gain ratio was lower for the higher stimulus speed, explaining differences in results in the literature.

Jan L. Souman, Ignace Th.C. Hooge, & Alexander H. Wertheim (In Press). *Experimental Brain Research*.

Introduction

When we make smooth pursuit eye movements in order to follow a moving target with our eyes, the retinal image motion of objects in the visual field is affected by these eye movements. For instance, the image of a stationary object sweeps across the retinae during an eye movement. Yet, generally we perceive stationary objects as being stationary and moving objects as moving, even during smooth pursuit eye movements. Apparently, our visual system is capable of compensating for the effects of eye movements on retinal image motion. That this compensation is not always perfect is shown by illusions such as the Filehne illusion (Filehne, 1922; Mack & Herman, 1973), in which a stationary object presented briefly (~500 ms) during smooth pursuit is perceived to move against the pursuit direction. Another instance of incomplete compensation is the Aubert-Fleischl

phenomenon (Aubert, 1886, 1887; Von Fleischl, 1882) that describes the observation that a moving object appears to move slower when followed with the eyes.

As a consequence of the discovery of these two illusions, most research on motion perception during smooth pursuit has focussed on the perception of objects moving along the line of pursuit (horizontally in most cases) or of stationary objects (as in the case of the Filehne illusion). Much less attention has been paid to the perception of objects moving non-collinearly (i.e., at an angle other than 0° or 180°) with the pursuit target. In the latter case the problem presented to the visual system is essentially the same as in that of collinear motion. The eye movement introduces a motion component in the retinal image motion of objects in the visual field, in the direction opposite to that of the eye movement. Both with collinear and non-collinear motion, the visual system has to correct for this effect of

the eye movement in order to arrive at a veridical motion percept of the objects in the visual field.¹ However, the question is whether our visual system performs this task similarly in both cases, or not. This is the question we address in this study.

Earlier studies have investigated whether the degree of compensation for the effects of eye movements is constant for various stimulus motion directions. Wallach, Becklen and Nitzberg (1985) presented observers with a vertically moving stimulus during vertical pursuit and measured the perceived speed of the stimulus. This turned out to be approximately veridical, suggesting complete compensation for the effects of the eye movement. Since they had earlier found a low degree of compensation with vertical stimulus motion during horizontal pursuit (Becklen, Wallach, & Nitzberg, 1984), they concluded that the degree of compensation for the effects of eye movements depends on the stimulus motion direction relative to the pursuit direction. Swanston and Wade (1988), however, measured the perceived motion direction for stimulus directions of 90° to 180° relative to the horizontal pursuit and found for all directions a fairly constant (and high) degree of compensation.

Two factors make these earlier studies hard to compare. First, the pursuit target speed and the stimulus speed varied from study to study. Swanston and Wade (1988) used periodically moving dots with a constant

speed (pursuit target speed was 4.5°/s and stimulus speed ~1.35°/s). In Wallach et al. (1985), sinusoidally moving dots were used with peak velocities of ~3.5°/s and ~4.5°/s (both served as either the pursuit target or the stimulus, depending on the condition). Becklen et al. (1984, Experiment 2) also used sinusoidally moving dots, but with higher peak velocities (~10°/s). Since perceived speed is non-linearly related to actual, physical speed (McKee & Nakayama, 1984), the differences in speed might explain the differences in the degree of compensation found in these studies. A second factor that makes it hard to make definite statements about these studies is the fact that in none of them eye movements were measured. Because of this, neither the exact eye velocities nor the retinal image velocities were known and it is not possible to compute the exact degree of compensation in these studies.

In this study, we take a slightly different approach. We start from the hypothesis that the visual system uses one single compensation mechanism for all stimulus motion directions. This hypothesis is formalized in a simple quantitative model, which essentially is an extension to two dimensions of the classical ‘cancellation theory’ (Von Holst, 1954; Von Holst & Mittelstaedt, 1950). The model is tested against the empirical data from an experiment in which we measured the perceived motion direction during horizontal pursuit, with the physical stimulus motion direction varied between 0 and 360° relative to the pursuit direction. A second hypothesis we tested was that the perceived motion direction would be affected by the physical speed of the stimulus. According to our model, which will be described below, perceived motion direction depends on the ratio of the gain of the signal that encodes the velocity of the eyes as estimated by the visual system to the gain of the retinal motion signal used by the visual system. A gain ratio below unity, due to a retinal signal gain that is higher than the eye movement signal gain, will produce a deviation of the perceived direction from the physical one in the direction of the retinal image motion direction (see Figure 1). Based on the results of McKee

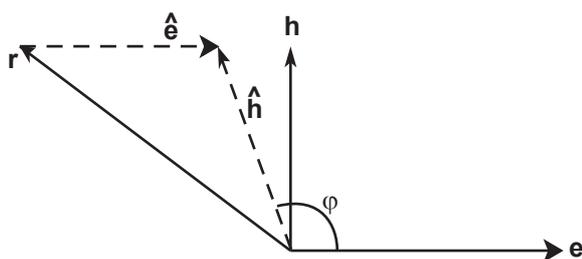


Figure 1. Geometric representation of the linear model. Vector e represents eye velocity, h represents the head-centric stimulus velocity and r the resultant retinal image velocity. Hatted symbols indicate estimates by the visual system. In the case depicted, retinal signal gain $\rho = 1$ (so \hat{h} equals r) and for the eye movement signal gain $0 < \varepsilon < 1$, producing a deviation of the perceived motion direction ϕ from the physical direction towards the retinal motion direction.

¹ In this paper we will restrict ourselves to head-centric motion, assuming that the head of the observer is stationary in space. Also, when we speak of ‘the stimulus’ or ‘stimulus velocity’, we refer to a moving object that is present in the visual field during ocular pursuit of the pursuit target, not to the pursuit target.

and Nakayama (1984) and Tynan and Sekuler (1982) it can be argued that the perceived speed of a stimulus increases progressively with physical speed. Therefore, we expected the retinal signal gain to increase with stimulus speed and, consequently, the gain ratio of eye movement signal gain to retinal signal gain to be lower for higher stimulus speeds. Therefore, the degree of compensation for the effect of the eye movement was expected to be lower for a higher stimulus speed. This might explain the differences between the results of Swanston and Wade (1988) and those of Becklen et al. (1984) and Wallach et al. (1985).

Model

Von Holst and Mittelstaedt (1950; also see Von Holst 1954) were the first to formalize the idea that the visual system might use a copy of efferent oculomotor signals to correct the retinal image motion for the effects of eye movements:

$$\hat{\mathbf{h}} = \mathbf{r} + \mathbf{e} \quad (1)$$

where $\hat{\mathbf{h}}$ is the perceived head-centred stimulus velocity, \mathbf{r} is the retinal image velocity of the stimulus object that is to be judged, and \mathbf{e} is the eye velocity as given by the efference copy (all represent vectors in angular velocity units). To explain errors in motion perception during smooth pursuit like the Filehne illusion and the Aubert-Fleischl phenomenon, a gain term was introduced, linking the estimate of the eye velocity by the visual system to the actual eye velocity (see e.g. Wertheim 1987):

$$\hat{\mathbf{h}} = \mathbf{r} + \varepsilon \mathbf{e} \quad (2)$$

with ε denoting the eye movement signal gain. The Filehne illusion and the Aubert-Fleischl phenomenon might be caused by an underestimation of the eye velocity, that is, a gain $\varepsilon < 1$ (see Wertheim 1994 for a review and for alternative explanations). Wertheim (1994) noted that not only the eye movement signal may err; the retinal image velocity too can be over- or underestimated. This was stated more explicitly by Freeman and Banks (1998) who introduced a second gain term:

$$\hat{\mathbf{h}} = \rho \mathbf{r} + \varepsilon \mathbf{e} \quad (3)$$

where ρ is the retinal signal gain. They also stressed that for matching tasks only the ratio ε/ρ can be estimated from empirical data, not the individual gains ε and ρ .

Generally, the linear model (Eqn. 3) has held up quite well and is able to explain most data on motion perception during smooth pursuit eye movements (see e.g. Freeman 1999; Freeman et al. 2000; Freeman & Banks 1998). Freeman (2001) investigated whether the estimation of retinal image velocity and eye movement velocity indeed happens in a linear fashion (by $\rho \mathbf{r}$ and $\varepsilon \mathbf{e}$, respectively) and found that for some observers the data conformed to the linear model, while for others it did not. Recently, the linearity assumption in equation (3) also has been challenged by some authors (Goltz, DeSouza, Menon, Tweed, & Vilis, 2003; Turano & Massof, 2001), who introduced an interaction term into the equation, but typically the deviations from linearity they found were small. Wertheim (1994) added extra terms to equation (3), which estimate the eye velocity from retinal image characteristics (optic flow) and vestibular inputs, thereby providing an estimate of head-centric eye velocity that also takes head movements into account. We minimized the effects of those potential additional sources of information about the eye movement. Our experiment was performed in total darkness and we used a single small stimulus dot, thereby minimizing the effects of optic flow. Moreover, the experiment was done without head movements, keeping vestibular inputs constant. This allowed us to take the linear model (Eqn. 3) as our starting point.

Since the retinal velocity equals the actual head-centric stimulus velocity \mathbf{h} minus the eye velocity \mathbf{e} , equation (3) can also be written as:

$$\hat{\mathbf{h}} = (\varepsilon - \rho) \mathbf{e} + \rho \mathbf{h} \quad (4)$$

In our experiment, described below, we presented observers with both collinear and non-collinear motion. Therefore, variables \mathbf{h} , $\hat{\mathbf{h}}$ and \mathbf{e} in equation (4) represent 2D vectors, having both a horizontal and a vertical component. As we measured the perceived motion direction in our experiment, we can take the arctangent of the horizontal and vertical components of $\hat{\mathbf{h}}$ to predict the perceived motion direction φ :

$$\varphi = \arctan \left(\frac{(\varepsilon - \rho)e_y + \rho h_y}{(\varepsilon - \rho)e_x + \rho h_x} \right) \quad (5)$$

where x and y denote the horizontal and vertical components, respectively (see Figure 1).² Because in our experiment ocular pursuit was always horizontal, the vertical eye velocity e_y was approximately zero, and formula (5) reduces to:

$$\begin{aligned}\varphi &= \arctan\left(\frac{\rho h_y}{(\varepsilon - \rho)e_x + \rho h_x}\right) \\ &= \arctan\left(\frac{h_y}{(\varepsilon / \rho - 1)e_x + h_x}\right)\end{aligned}\quad (6)$$

This equation shows that the perceived direction φ depends on the value of the gain ratio ε/ρ . When $\varepsilon/\rho = 0$, the eye movement is not compensated for and the perceived motion direction φ will equal the retinal image motion direction. When $\varepsilon/\rho = 1$, compensation is complete and φ equals the actual head-centric stimulus direction. An geometric representation of the case when $0 < \varepsilon/\rho < 1$ is given in Figure 1. The model was tested in the following experiment.

Methods

The experiment was conducted in compliance with the medical-ethical regulations of Utrecht University and with the 1964 Declaration of Helsinki.

Participants

17 Students (6 males, 11 females) from Utrecht University and the first author participated in the experiment. The students were paid for their participation and were naïve with respect to the purpose of the experiment. They all gave their written informed consent before participation. All participants had normal or corrected-to-normal vision. Their age ranged from 18 to 33 years (median age 20.5 years).

Apparatus and stimuli

The stimuli were presented on a 19" computer screen (Iiyama Vision Master Pro 450), with a resolution of 1152×864 pixels and a refresh rate of 100 Hz. Stimulus presentation and response registration were controlled by custom made software running on a Pentium III pc (Dell Dimension 4100; clock speed 933 MHz). The participant's head rested on a chinrest, with the nose kept against a short blunt bar to help minimize head

movements. Viewing was binocular, with a viewing distance of 60 cm. Eye movements were measured from both eyes using an infrared video-based eye tracking device, sampling at 250 Hz (Eyelink system, SMI Sensomotoric Instruments, Teltow, Germany; for a detailed description, see [Van der Geest & Frens, 2002](#)).

Participants were presented with a pursuit target, which they had to follow with their eyes, and a moving stimulus dot, of which they had to indicate the motion direction. Both the pursuit target and the stimulus dot were small grey dots (5×5 pixels $\approx 0.15^\circ \times 0.15^\circ$). The luminance of both dots was kept low (~ 0.04 cd/m²) to minimize afterglowing effects. Both dots were presented against a completely black background (lum. < 0.01 cd/m²). The pursuit target always moved horizontally at eye height, covering an angle of 20° with a speed of $10^\circ/s$ (after initial acceleration, see Procedure). The speed and direction of the stimulus dot depended on the condition tested. After each presentation of the pursuit target and the stimulus dot, participants indicated the perceived motion direction of the stimulus dot by means of an arrow, which appeared at the centre of the screen and could be rotated using the mouse. This arrow was 6 cm long ($\approx 5.7^\circ$). The experiment was performed in total darkness; hence the pursuit target and the stimulus dot or the measurement arrow were the only things the participants could see.

Design and procedure

The experiment consisted of eight blocks, each with 48 trials. In half of the trials (the pursuit trials), the pursuit target appeared at the left or right side of the screen and stayed stationary for 1000 ms. It then accelerated linearly in 500 ms to $10^\circ/s$, moving rightwards or leftwards, respectively. After it reached a speed of $10^\circ/s$, it continued moving at this speed until it had covered 20° of visual angle and then disappeared. Pursuit direction was varied to minimize adaptation to the pursuit eye movement (see e.g. [Van Donkelaar et al. 2000](#)). In the other half of the trials (fixation trials), the pursuit target appeared at the centre of the screen, where it remained

² Equation (5) is equivalent to Equation (11) in [Mateeff et al. \(1991\)](#), with the gain ratio ε/ρ equalling their constancy K . However, they presented their equation as a measure of the degree of compensation. In our form it can be used to fit experimental data and test the linear model.

stationary throughout the trial. These trials served as a control condition, to measure the perceived motion direction during fixation. The stimulus dot moved at a speed of 3°/s in half the trials, and at 8°/s in the other half. 24 Stimulus motion directions were used, sampling the entire range of 0° to 360° (0° to 20°, 160° to 200° and 340° to 355° in steps of 5°, and 55° to 135° and 235° to 315° in steps of 35°). Directions around the horizontal were sampled more densely, because pilot studies indicated that at these directions the largest changes of perceived direction as a function of physical stimulus direction occurred. In the pursuit trials, the stimulus path was centred around a point that lay at the centre of the screen horizontally and 0.5° above or below the pursuit path (which was at the centre of the screen vertically). This vertical offset of the stimulus path served to prevent overlap between pursuit target path and stimulus path in conditions where the stimulus moved (almost) horizontally. Since this vertical offset caused the stimulus to cross the pursuit target path in front of or behind the pursuit target (depending on stimulus direction), the stimulus path in the control (fixation) condition was offset both vertically ($\pm 0.5^\circ$) and horizontally (1.67° in the 3°/s condition and 0.625° in the 8°/s condition) from the centre of the screen. In the pursuit trials, the stimulus arrived at the centre of its path when the pursuit target was at the centre of the screen. All trials were presented in random order. Each block took about 7 minutes. Between blocks, the lights in the experimental room were turned on for approximately 1 minute, to minimize dark adaptation.

Data analysis

The eye movement data were analysed to test for inaccurate pursuit. The measured eye positions were first averaged across both eyes, after which they were low-pass filtered using a seven-point running average. Trials in which saccades were made during stimulus presentation were discarded, because for these trials it is not clear whether the percept resulted from (under)compensation for the smooth pursuit eye movements or from factors related to the presence of saccades (see e.g. Mateeff 1978; Matin, Matin, & Pearce 1969; Matin, Matin, & Pola 1970; Park et al. 2001). A trial was marked as saccadic if the horizontal velocity exceeded 50°/s. Trials with low (< 0.8) or high (> 1.2) pursuit gain were also discarded. To compute the pursuit

gain, the slope of the best fitting linear regression line of the horizontal eye position during stimulus presentation as a function of time was computed and divided by the velocity of the pursuit target. For data in the fixation condition we applied a position criterion. All trials in which the eye position deviated more than 2° from the fixation target were discarded.

Removal of trials with inaccurate pursuit or fixation might (for participants with bad pursuit respectively fixation) cause the loss of most or even all trials in a given condition, making it impossible to fit the model to the data. We therefore removed from further analysis the data from participants for whom not at least half of the trials per combination of stimulus speed and direction remained after the eye movement analysis.

Since pursuit direction and vertical offset did not affect the errors in perceived motion direction, the direction responses were first collapsed across those two factors and then averaged per combination of stimulus speed and direction. This was done separately for all participants, both for the pursuit and the control condition. Since direction is a circular variable, we used the circular mean for averaging the data (Batschelet, 1981). For each participant, the model was fitted to the data from the pursuit condition, separately for the data from the 3°/s condition and those from the 8°/s condition. Fitting was done with MatLab's *nlinfit* function, which uses the Gauss-Newton method of least-squares fitting. The single free parameter that was varied to attain an optimal fit was the gain ratio ϵ/ρ of eye movement signal gain to retinal signal gain. To avoid local minima, the fitting procedure was repeated five times with the initial parameter value varied between 0 and 1. In all cases the same results were produced, so it is unlikely that the fits were the result of local minima. As a measure of how well the model fitted the data, we used the proportion of variance explained by the model, R^2 (the variance of the values predicted by the model divided by the total variance of the data).

Results

After the eye movement analysis, the results of six participants had to be discarded due to inaccurate pursuit. For the remaining twelve subjects, less than 1% of the trials in the control condition and about 7% of the

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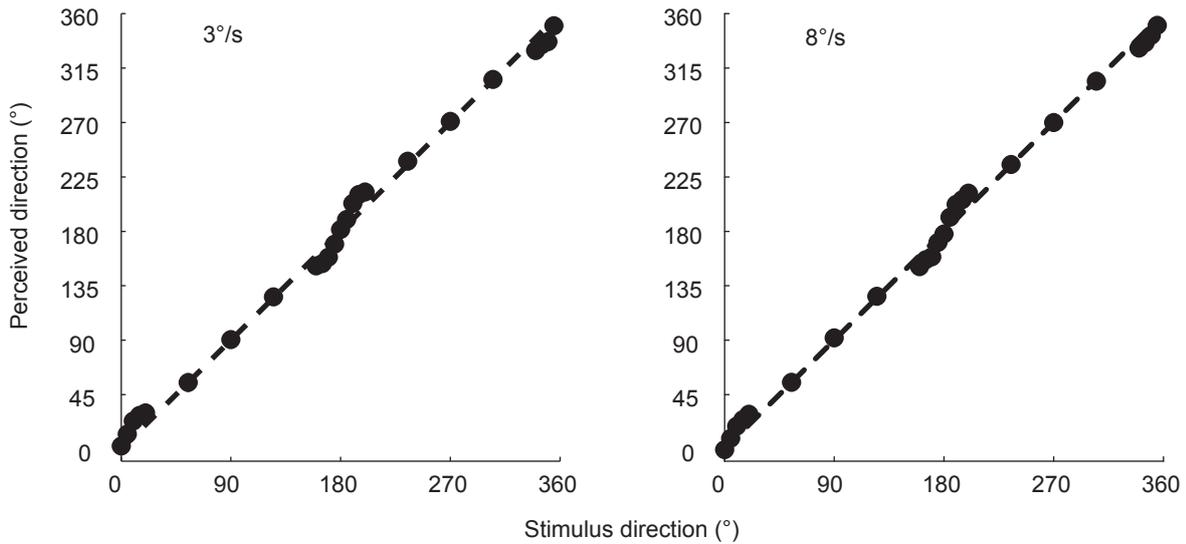


Figure 2. Perceived stimulus motion direction during fixation as a function of the physical motion direction. The stimulus dot moved at 3°/s (left panel) or at 8°/s (right panel). Data points represent the average indicated directions for 12 observers (error bars representing the 95%-confidence intervals across observers are smaller than symbol size).

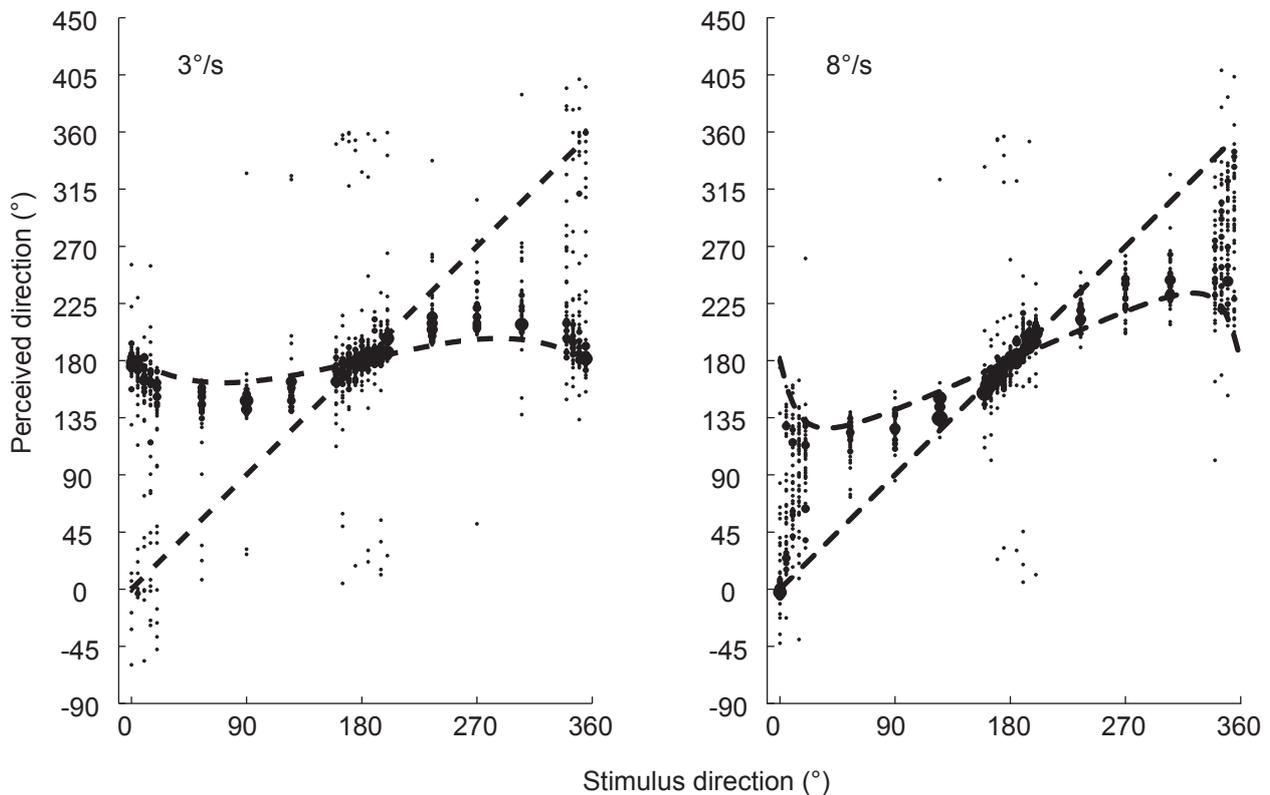


Figure 3. Perceived stimulus motion direction during horizontal pursuit as a function of the physical motion direction. The left panel shows the data from the 3°/s condition, the right panel those from the 8°/s condition. The figures represent the aggregate data of 12 observers, classified in 1° bins, with symbol size proportional to the number of observations in a bin. The diagonal dashed lines represent veridical direction responses (= 100% compensation), the curved lines represent the retinal motion direction (= 0% compensation) of the stimulus dot with perfect pursuit.

trials in the pursuit condition were removed because of inaccurate fixation or pursuit.

The perceived directions from the control condition, in which participants were presented with the moving stimulus dot during fixation, are shown in Figure 2. The results were very similar for both stimulus speeds. Generally, participants indicated the veridical motion direction. Only for directions within a 20° range around the horizontal (0° to 20°, 160° to 200° and 340° to 355°) a systematic deviation of the perceived direction from the physical one of about 10° away from the horizontal was observed. All participants showed the same pattern of data.

The inter-participant variability was much higher in the pursuit condition. The perceived motion directions aggregated across all twelve observers are plotted in Figure 3. The data are presented as if pursuit were to the right (0°). Most of the perceived directions lie between the diagonal (veridical direction perceived) and the curved line that indicates the retinal motion direction, suggesting that the eye movements were compensated for to a certain extent, but not completely. The data points lying outside this region mainly belong to two participants who showed a large unsystematic variability in their data. Because the large inter-participant variability made it meaningless to fit our model to the aggregated data, the model was fitted per participant.

Figure 4 presents the data, averaged per stimulus direction, for four representative participants. As this figure shows, the data from the 3°/s and the 8°/s conditions were generally quite different. In the 3°/s almost all participants (except one of the two very noisy ones) indicated that the stimulus dot moved in the opposite direction to the pursuit target (180°) when it actually was moving in the same direction (0°). This error gradually decreased with stimulus direction and when the stimulus really was moving in the direction opposite to that of the pursuit target (180°), it was correctly perceived as doing so. For stimulus directions from 360° to 180° of course the same pattern occurred, the only difference being that the vertical component of the stimulus motion was downward rather than upward. In the faster stimulus condition (8°/s), however, the perceived direction when the stimulus moved in the same direction as the pursuit target (0°) generally equalled the physical direction (although this was not true for two of the participants, see e.g. Figure 4d). Errors increased with deviation of the stimulus direction from the horizontal and decreased again around the opposite direction (180°).

The linear model (Eqn. 6) was fitted to the perceived direction data. Figure 4 shows the best fitting lines for the four participants displayed and Table 1 gives the resulting gain ratio values (the panels of Figure 4 refer to participants 1, 2, 8 and 11, respectively). Generally,

Table 1. The best fitting values for the model parameter ε/ρ and the proportion of explained variance, R^2 , both before and after outlier removal.

Stimulus velocity	Participant	Before outlier removal				After outlier removal			
		ε/ρ		R^2		ε/ρ		R^2	
		3°/s	8°/s	3°/s	8°/s	3°/s	8°/s	3°/s	8°/s
	1	0.54	0.30	0.22	0.98	0.37	0.30	0.95	0.98
	2	0.39	0.26	0.85	0.97	0.39	0.26	0.85	0.97
	3	0.66	0.25	0.88	0.96	0.66	0.25	0.88	0.96
	4	0.62	0.20	0.81	0.96	0.62	0.20	0.81	0.96
	5	0.44	0.06	0.92	0.81	0.44	0.04	0.92	0.97
	6	0.44	0.20	0.78	0.96	0.42	0.20	0.88	0.96
	7	0.69	0.32	0.40	0.86	0.69	0.32	0.40	0.86
	8	0.54	0.28	0.80	0.94	0.54	0.28	0.80	0.94
	9	0.64	0.16	0.69	0.92	0.58	0.16	0.84	0.92
	10	0.72	0.26	0.58	0.75	0.72	0.26	0.58	0.75
	11	0.42	0.08	0.74	0.49	0.44	0.02	0.82	0.93
	12	0.48	0.20	0.89	0.95	0.48	0.20	0.89	0.95

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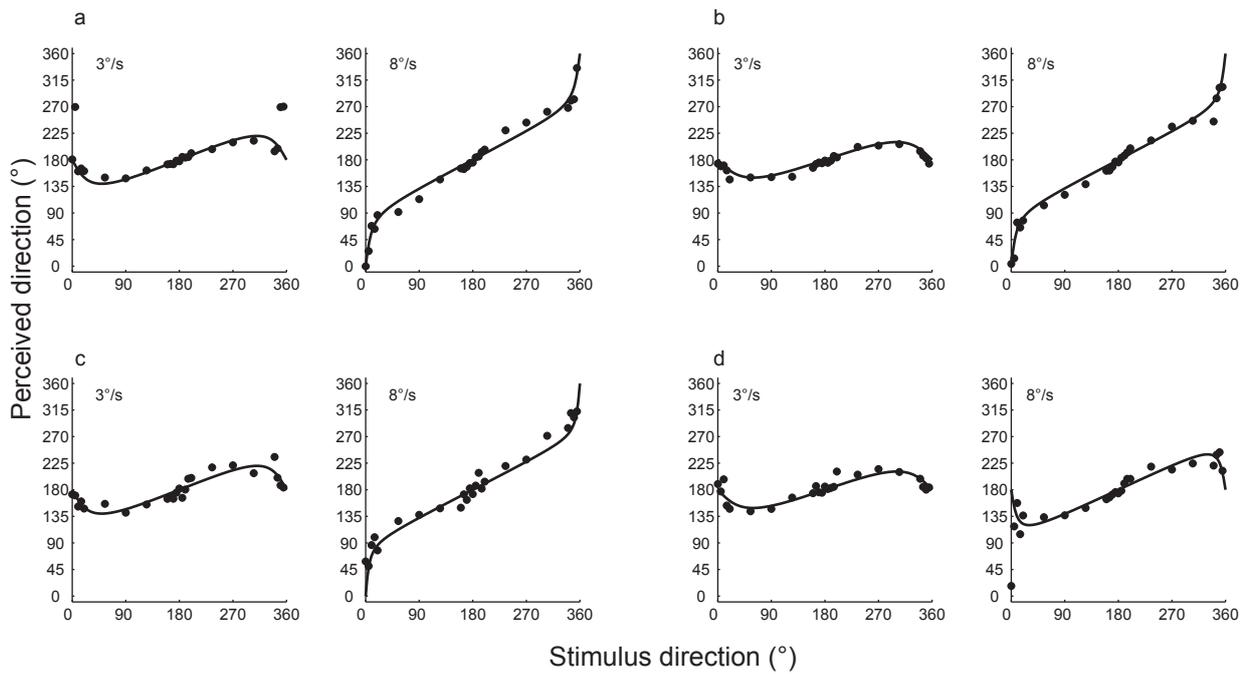


Figure 4. Perceived stimulus motion direction data from four participants (panels a, b, c, d, corresponding to participants 1, 2, 8 and 11 in Table 1). The data points represent the average indicated motion direction per stimulus direction. The lines show the best fitting model curves.

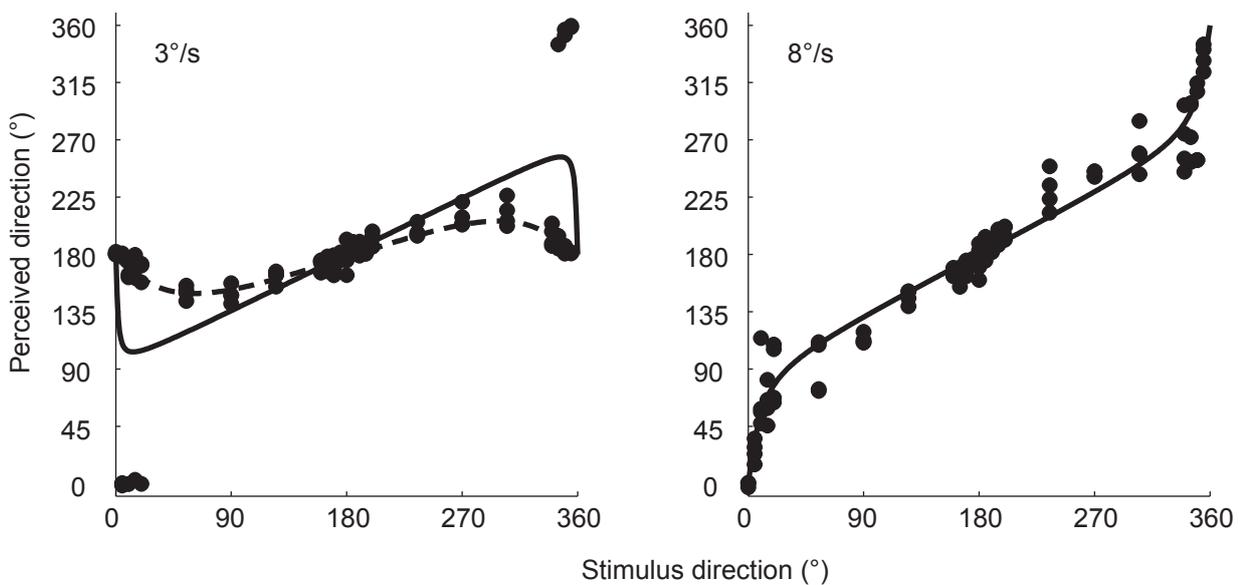


Figure 5. Individual data points of perceived direction from one participant (left panel: 3°/s condition; right panel: 8°/s condition). The continuous line indicates the best fitting model curve with the outliers included; the dashed line that after removal of the outliers (only for the 3°/s condition).

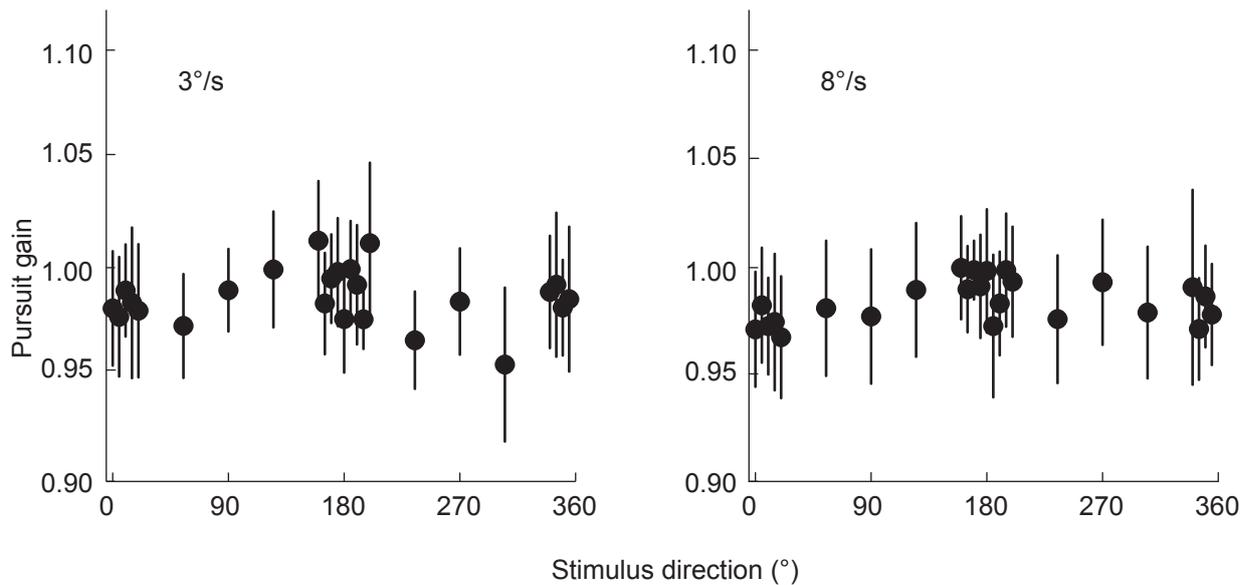


Figure 6. Ocular pursuit gain as a function of stimulus direction for the 3°/s condition (left panel) and the 8°/s condition (right panel). Symbols represent the mean pursuit gain across 12 participants, with the error bars representing the 95%-confidence intervals across participants. removal of the outliers (only for the 3°/s condition).

the model described the data well. In agreement with our second hypothesis, the value of the best fitting gain ratio ε/ρ was higher in the 3°/s condition than in the 8°/s condition for all participants. The degree of fit was expressed in the proportion of explained variance, R^2 (Table 1). For most participants, the fit was quite good (around .80 in the 3°/s condition and .90 in the 8°/s condition). Participants 7 and 10 were the two participants with high variances mentioned before and, consequently, with lower R^2 's. Some of the other participants showed low R^2 's because their perceived direction data were bimodally distributed for stimulus directions around the pursuit direction (0° or 360°). This was the case for participants 1, 6, 9 and 11 in the 3°/s condition and participants 5 and 11 in the 8°/s condition. Figure 5 shows the raw data points from participant 1 as an example. In the 3°/s condition, the indicated directions for the stimulus directions around 0° and 360° fall into two groups. Some of the data points cluster around 180°, others around 0° (or, equivalently, around 360°). Of course, the model fit deteriorates significantly due to this bimodality, as can be seen from the fitted model curve in Figure 5 (continuous line). In these cases, the model was therefore also fitted after removing the outliers. Perceived directions that differed about 180° from the best fitting model curve for stimulus directions between 340° and 20° were removed (33 data points, or less than 4% of the data

points of the above mentioned five participants in the pursuit condition) and the model was refitted (dashed line in Figure 5). The resulting gain ratios and R^2 are presented in Table 1. An explanation for the bimodal distribution will be given in the Discussion, below.

It should be noted that the different magnitudes of the errors in the perceived direction for various stimulus directions cannot be attributed to differences in ocular pursuit gain. As shown in Figure 6, the pursuit gain during stimulus presentation was approximately constant across stimulus direction, for both stimulus speeds. Also, the average vertical eye velocity was close to zero, indicating that the horizontal pursuit was hardly affected by the appearance of the stimulus dot (Figure 7). Moreover, the variability in vertical eye velocity was similar during pursuit and fixation and did not depend on the stimulus direction.

Discussion

The results from the pursuit condition showed that the perceived stimulus motion direction was strongly affected by the pursuit eye movements. In both stimulus speed conditions participants generally made large errors when indicating the perceived motion direction, although the pattern of errors was quite different for the

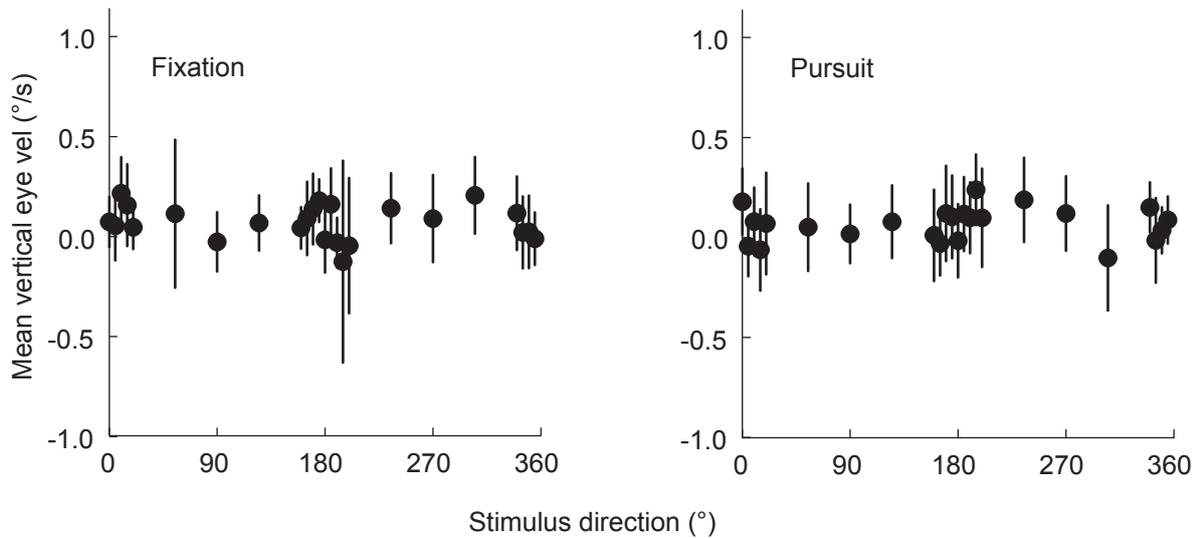


Figure 7. Average vertical eye movement velocity as a function of stimulus direction for the 3°/s condition (left panel) and the 8°/s condition (right panel). Symbols represent the mean vertical eye velocity across 12 participants, with the error bars representing the 95%- confidence intervals across participants.

two speeds we used. Comparison of the results from the pursuit condition with those from the fixation condition shows that the large errors found in the pursuit condition were due to effects of the eye movements, not to a bias in direction perception per se. The data from the fixation condition show that the participants were generally well able to indicate the motion direction by means of the arrow that appeared on the screen after each presentation of pursuit or fixation target and stimulus dot. The small but systematic errors found in the control condition for directions around the horizontal were probably a case of reference repulsion (Grunewald, 2004; Rauber & Treue, 1998, 1999).

The linear model, described by equation (6), fitted the data from the pursuit condition quite well. With only one free parameter the model explained around 90% of the variance for most participants. The good fits suggest that, like we hypothesized, the degree of compensation for the effects of smooth pursuit eye movements is constant across the entire range of stimulus directions in the fronto-parallel plane. Apparently, the same compensation mechanism is at work for different directions. Our results also show a distinct difference in gain ratio between the two stimulus speed conditions (3°/s and 8°/s). The gain ratio was much higher in the lower speed condition. This explains the inconsistencies between results from earlier studies. Swanson and Wade (1988) used a rather low speed for their stimulus and, consequently, found a high degree of compensation.

Wallach et al. (1985) also used a low speed stimulus and they too found a high degree of compensation. In their study participants viewed a vertically moving stimulus during vertical pursuit. Becklen et al. (1984), finally, using a much higher stimulus speed found a low degree of compensation. Rather than an incapability of the visual system to perform vector analysis, as suggested by Wallach et al (1985), the difference in stimulus speeds appears to account for the differences in results. In addition to the low stimulus speed, the continuous (and long) presentation of the stimulus dot in the studies by Wallach et al. (1985) and Swanson and Wade (1988) may also have contributed to the high degree of compensation, since the degree of compensation for the effects of smooth pursuit eye movements is known to increase with stimulus presentation duration (De Graaf & Wertheim, 1988; Ehrenstein, Mateeff, & Hohsbein, 1986; Mack & Herman, 1978).

The effect of noise in the signals

Some participants in our experiment showed bimodally distributed data for stimulus directions around 0° and 360° (see Figure 5 for an example). Figure 8 shows that for these stimulus directions, the linear model predicts that the amplitude of the perceived velocity vector \hat{h} will be quite small for certain combinations of

eye velocity, stimulus speed and gain ratio ε/ρ . Small variations in these entities could cause the perceived stimulus direction \hat{h} to flip its direction from 0° to 180° or vice versa. One possible source of these variations might be the variability in pursuit gain (i.e., in the actual eye velocity) between trials, which would also cause variability in retinal speed. Although the pursuit gain was quite constant (see Figure 6), there were small differences across trials. The effect of differences in pursuit speed would, according to our model, depend on the gain ratio. For gain ratios smaller than unity, as in our data, lower pursuit gains would produce perceived motion directions that are more biased against the pursuit direction (180°) and higher pursuit gains would increase the probability that the stimulus is perceived as moving in the same direction as the pursuit target (0° or 360°). However, the participants with bimodal data did not show a consistent relationship between pursuit gain and perceived motion direction. Some of them had on average slightly higher pursuit gains in trials with a perceived motion direction of around 0° or 360° , but others showed somewhat lower pursuit gains in these trials. Moreover, there was a high degree of overlap between pursuit gains in trials with a perceived direction of 0° or 360° and those of 180° , so differences in pursuit gain do not seem to be the main cause of the bimodality.

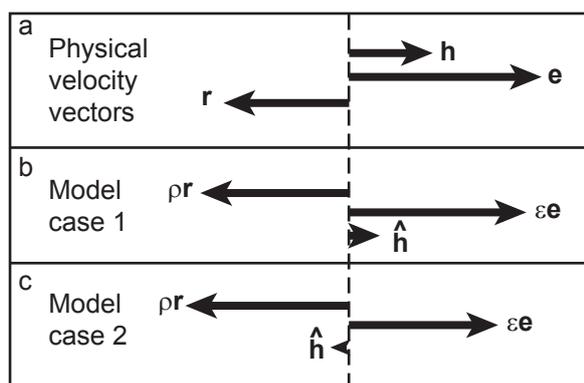


Figure 8. A demonstration of the possible effects of small changes in signal gains on the perceived motion direction. a. Physical velocity vectors for head-centric stimulus velocity (h), eye velocity (e) and retinal image velocity (r). b. Model prediction of the perceived head-centric velocity (\hat{h}) with an overestimated retinal image velocity ($\rho > 1$) and an underestimated eye velocity ($\varepsilon < 1$). c. Idem with ρ slightly higher and ε smaller than in b.

An alternative explanation would be that the gain ratio of eye movement signal gain to retinal signal gain varies across trials. Figure 8 shows a graphical analysis of this possible cause of the bimodality. When the stimulus direction is 0° , the stimulus dot moves in the same direction as the pursuit target (i.e., to the right, since we plotted all our data as if pursuit were to the right). Because the pursuit speed is higher than the stimulus speed, the retinal image motion of the stimulus ($h - e$) will be in the opposite direction. According to the linear model, the perceived head-centric velocity \hat{h} equals the sum of the estimated retinal velocity $\rho(h - e)$ and the estimated eye velocity εe . Since both signals are biological in origin, it seems reasonable to assume that they are noisy ones, their exact amplitude varying from trial to trial. Figure 8b shows the situation that the vector sum of the two signals is just large enough to be positive and produces a perceived motion direction of 0° (i.e., veridical). On a next trial, the retinal signal gain ρ might be slightly higher than in Figure 8b and the eye movement signal gain ε lower (Figure 8c). This change can be just sufficient to produce a perceived motion vector in the opposite direction. Thus, small random variations in signal gains ρ and ε can explain the bimodally distributed data found for some participants. This hypothesis was tested by simulating the effect of noise in both signals on the perceived motion direction as predicted by the linear model (Figure 9). The data of participant 1 in the $3^\circ/s$ condition (plotted in Figure 5, left panel) were simulated. For simplicity we implemented the noise by sampling the gain ratio of eye movement signal to retinal signal from a normal distribution with a mean of 0.37 (which was the best fitting parameter value when leaving out the outliers; see Table 1) and with increasing standard deviations.³ All data points were sampled four times, since all measurements in the experiment had also been replicated four times. As can be seen from Figure 9, the predicted directions at stimulus directions around 0° and 360° show bimodal distributions for standard deviations around 0.30 and closely resemble the actual data of Figure 5. Hence, a

³ Strictly speaking, if we assume that both gains are sampled from normal distributions, the gain ratio would have a Cauchy distribution. Here, however, we just show a possible effect of noise in the signals, without paying too much attention to the shape of the underlying distributions.

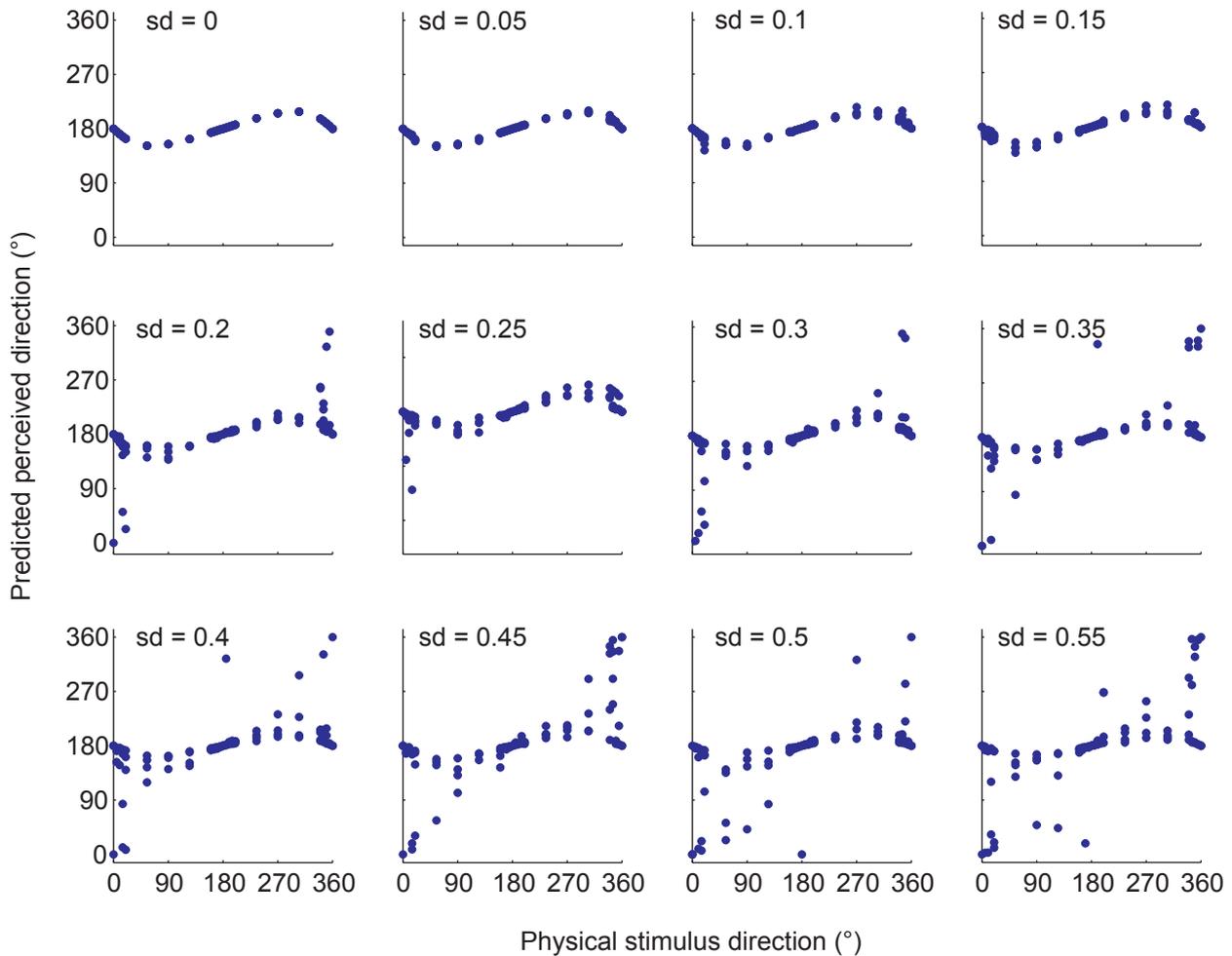


Figure 9. Simulation of the effect of a noisy gain ratio. The gain ratio is sampled from a normal distribution with a mean of 0.37 and an increasing standard deviation (sd). Four replications per stimulus direction were simulated for a stimulus speed of 3°/s and an eye movement velocity of 10°/s.

simple extension of the linear model can easily account for the bimodally distributed data.

Conclusions

The classical linear model (Eqn. 3) well described the data from our experiment, in which we measured perceived motion direction for stimuli moving at various angles relative to the pursuit direction. With only one free parameter, the model adequately captured the various patterns of perceived motion directions exhibited by our participants. This parameter, the gain ratio of eye movement signal to retinal signal, appeared to be constant across stimulus direction, suggesting that the degree of compensation for the effects of smooth

pursuit eye movements is constant across the entire range of stimulus directions in the frontoparallel plane. The gain ratio turned out to be higher for a stimulus speed of 3°/s than for a speed of 8°/s. This (at least partially) explains the differences in results between the studies by Swanston and Wade (1988), who found a constant degree of compensation for the effects of smooth pursuit eye movements across a range of stimulus directions, and those by Becklen et al. (1984) and Wallach et al. (1985), who found much higher degrees of compensation for collinear motion than for non-collinear motion. Finally, we showed that a bimodal distribution of perceived motion directions when the stimulus direction equalled the pursuit direction, occurring in some participants, can be explained by assuming that the eye movement signal and the retinal signal are noisy signals.

Acknowledgements

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3

Vertical object motion during horizontal ocular pursuit: compensation for eye movements increases with presentation duration

Abstract

Smooth pursuit eye movements change the retinal image motion of objects in the visual field. To enable an observer to perceive the motion of these objects veridically, the visual system has to compensate for the effects of the eye movements. The occurrence of the Filehne-illusion (illusory motion of a stationary object during smooth pursuit) shows that this compensation is not always perfect. The amplitude of this illusion appears to decrease with increasing presentation durations of the stationary object. In this study we investigated whether presentation duration has the same effect when an observer views a vertically moving object during horizontal pursuit. In this case, the pursuit eye movements cause the perceived motion path to be oblique instead of vertical; this error in perceived motion direction should decrease with higher presentation durations. In Experiment 1, we found that the error in perceived motion direction indeed decreased with increasing presentation duration, especially for higher pursuit velocities. The results of Experiment 2 showed that the error in perceived motion direction did not depend on the moment during pursuit at which the stimulus was presented, suggesting that the degree of compensation for eye movements is constant throughout pursuit. The results suggest that longer presentation durations cause the amplitude of the eye movement signal that is used by the visual system to increase more than that of the retinal signal.

Jan L. Souman, Ignace Th.C. Hooge, & Alexander H. Wertheim (2005). *Vision Research*, 45, 845-853.

Introduction

In daily life, we encounter many moving objects. The motion of these objects causes their images on our retinæ to move, which is an important source of information for our visual system for producing a motion percept. However, retinal image motion can also be due to movements of our own eyes, of our head, or of our whole body. Since normally we can easily discriminate between motion of the things around us and self-motion, our visual system somehow seems to be capable of taking eye movements, head movements and body movements into account when producing a motion percept. In this study we will focus on motion

perception during smooth pursuit eye movements with a stationary head, as the simplest case of motion perception during self-motion.

During ocular pursuit of a moving target, the retinal image motion of other objects in the visual field is different from when the eyes are stationary. To enable an observer to perceive the motion of these objects veridically, the visual system has to compensate for the retinal image motion component introduced by the pursuit eye movements. This compensation is not always perfect. Stationary objects appear to move in the opposite direction to the eye movement, especially when presented in total darkness (the Filehne-illusion; Filehne, 1922; Freeman, 1999; Freeman & Banks,

1998; Mack & Herman, 1973, 1978; Wertheim, 1987, 1994), indicating that the effect of the eye movement is not completely compensated for. An important factor that affects the amplitude of the Filehne-illusion is the presentation duration of the stationary stimulus. The illusory motion is strongest with short presentation durations (~200 ms) and decreases with longer durations (De Graaf & Wertheim, 1988; Ehrenstein et al., 1986; Mack & Herman, 1978; but see Freeman et al., 2002, for an exception). Generally, the perceived motion during smooth pursuit is explained as the outcome of a comparison of two signals (Freeman & Banks, 1998; Von Holst, 1954; Von Holst & Mittelstaedt, 1950; Wertheim, 1994). For a given object, the retinal signal encodes

the velocity of its retinal image motion, while the eye movement signal encodes the velocity of the eyes as relayed to the visual system (also called efference copy, collary discharge, or extraretinal signal). The Filehne-illusion is thought to be caused by a gain ratio of eye movement signal gain to retinal signal gain that is lower than one (Freeman & Banks, 1998; Wertheim, 1994). An increase of this gain ratio with increasing stimulus presentation durations would explain the decrease in the amplitude of the Filehne-illusion.

Most research on motion perception during smooth pursuit eye movements has been conducted with stationary stimuli (to measure the Filehne-illusion) or with stimuli that move along the same axis as the pursuit target (horizontally in most cases). Very little attention has been paid to the perception of stimuli moving non-collinearly relative to the pursuit target. In this study we investigate whether the presentation duration of the stimulus affects motion perception during smooth pursuit with non-collinear motion in the same way as it does with collinear motion. When a stimulus moves vertically during horizontal pursuit, a perceptual error analogous to the Filehne-illusion occurs. The stimulus path is perceived as oblique, rotated away from the pursuit direction (Becklen, Wallach, & Nitzberg, 1984; Hansen, 1979; Swanston & Wade, 1988). The deviation of the perceived motion direction from the physical one not only occurs with vertically moving stimuli, but also with stimuli moving along an oblique path (Festinger, Sedgwick, & Holtzman, 1976; Swanston & Wade, 1988). The error in the perceived motion direction can be explained by assuming that the horizontal eye movement is not completely compensated for by the visual system, introducing an illusory horizontal component in the perceived motion (as in the Filehne illusion; see Figure 1). If this is the correct explanation, we would expect the errors in perceived motion direction to decrease with longer presentation durations, because this illusory horizontal component should get smaller. In terms of retinal signal and eye movement signal, this would mean that the gain ratio of eye movement signal to retinal signal increases with presentation duration. In Experiment 1, we presented a vertically moving stimulus during horizontal smooth pursuit and tested the hypothesis that increasing the presentation duration of the stimulus would produce smaller deviations of the perceived motion direction from the physical direction. The effect of presentation duration was studied with three different pursuit target velocities. In Experiment

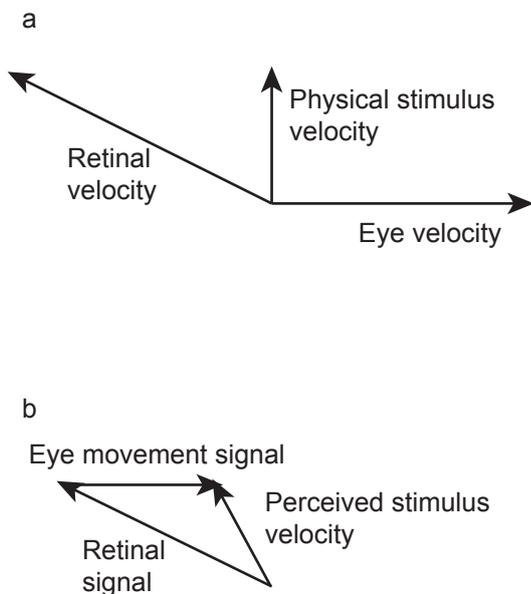


Figure 1. Perceived stimulus velocity as the sum of a retinal signal and an eye movement signal. (a). Physical (angular) velocities. The retinal image velocity equals the stimulus velocity minus the eye movement velocity. (b). Estimated velocities. The perceived velocity equals the estimated retinal velocity plus the estimated eye movement velocity. In this case, both the retinal signal gain and the eye movement signal are smaller than one, underestimating the retinal velocity and the eye movement velocity, respectively. The gain ratio of eye movement signal to retinal signal is also smaller than one, producing a perceived motion direction that lies between the physical (vertical) direction and the retinal image direction.

2, we explored an alternative explanation for the presentation duration effect.

Experiment 1

Methods

Participants

Six staff-members (five male, one female) of the Psychonomics Department of Utrecht University, including the first two authors, participated in the experiment. Their age ranged from 26 to 37 years (median age 27). All had normal or corrected-to-normal vision. Except for the two authors, the participants were naïve with respect to the purpose of the experiment.

Apparatus and stimuli

The stimuli were presented on a 19" computer screen (Iiyama Vision Master Pro 450), with a resolution of 1152×864 pixels and a refresh rate of 100 Hz. Stimulus presentation and response registration were controlled by custom made software running on a Pentium III pc (Dell Dimension 4100), with a clock speed of 933 MHz. The participant's head rested on a chinrest, with the nose kept against a short blunt bar to help minimize head movements. The viewing distance was 60 cm. Participants used both eyes to look at the screen. Eye movements were measured using an infrared video-based eye tracking device, sampling at 250 Hz (Eyelink system, SMI Sensomotoric Instruments, Teltow, Germany; for a detailed description, see [Van der Geest & Frens, 2002](#)).

Participants were presented with a pursuit target, which they had to follow with their eyes, and a moving stimulus dot, of which they had to indicate the motion direction. Both the pursuit target and the stimulus consisted of small grey dots (5×5 pixels $\approx 0.15^\circ \times 0.15^\circ$). The luminance of both dots was about 0.04 cd/m^2 . It was kept low to minimize after glowing effects. The pursuit target and the stimulus dot were presented against a completely black background (lum. $< 0.01 \text{ cd/m}^2$). The pursuit target always moved horizontally at eye height, covering an angular distance of 20° with a constant angular velocity (after initial acceleration,

see Procedure). After each presentation of pursuit target and stimulus dot, participants indicated the perceived motion direction of the stimulus dot by means of an arrow, which appeared at the centre of the screen and could be rotated with the computer mouse. The arrow was 6 cm long ($\approx 5.7^\circ$). The experiment was performed in total darkness, so the participant could only see the pursuit target and the stimulus dot or the arrow.

Procedure

The experiment consisted of four blocks of 36 trials. All four blocks consisted of the same 36 trials, thus replicating them four times. Within a block, the trials consisted of combinations of three stimulus presentation durations (300, 700, and 1100 ms), three pursuit target velocities (6, 10, and $14^\circ/\text{s}$), two pursuit directions (leftwards and rightwards), and two stimulus dot directions (upwards and downwards). The pursuit target velocities we used were well within the range of velocities that humans can track well ([Meyer, Lasker, & Robinson, 1985](#); [Schalen, 1980](#)). The trial order was randomized within each block. Stimulus dot velocity was constant at $5^\circ/\text{s}$ and the stimulus was always presented at the centre of the screen. Each trial started with the presentation of the pursuit target at the left or right side of the screen. The pursuit target first remained stationary for 1000 ms. To facilitate pursuit onset, it then accelerated linearly for 500 ms to the desired velocity (6, 10, or $14^\circ/\text{s}$, depending on the condition), after which it continued to move at that velocity until it had covered 20° of visual angle, at which point it disappeared. The stimulus dot, moving either upwards or downwards, was presented during the constant velocity period of the pursuit target. The pursuit target always crossed the stimulus dot when that was halfway its vertical path. The participants were instructed to follow the pursuit target with their eyes. Immediately after the pursuit target disappeared, an arrow appeared on the screen, which participants could rotate to indicate the perceived motion direction. This arrow was always presented at a random orientation. After the participant had indicated the direction, the next trial was started by pressing one of the mouse buttons.

A block of trials took approximately five minutes. After each block, the lights in the experimental room were switched on for about 1 min, to minimize dark adaptation. Before the experiment started, participants

received a short practice block, to practice ocular pursuit and response production.

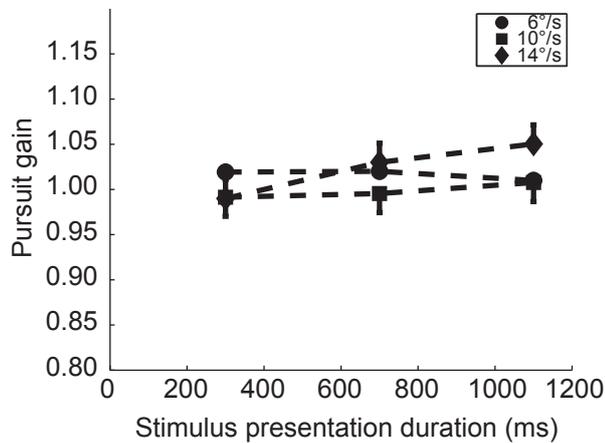


Figure 2. Pursuit gain as a function of stimulus presentation duration and pursuit target velocity (6, 10, or 14°/s), averaged across six participants. The error bars represent the 95% confidence intervals of the means, based on the MS of the interaction terms of participants and the other factors (presentation duration and pursuit target velocity); see Loftus and Masson (1994) and Masson and Loftus (2003).

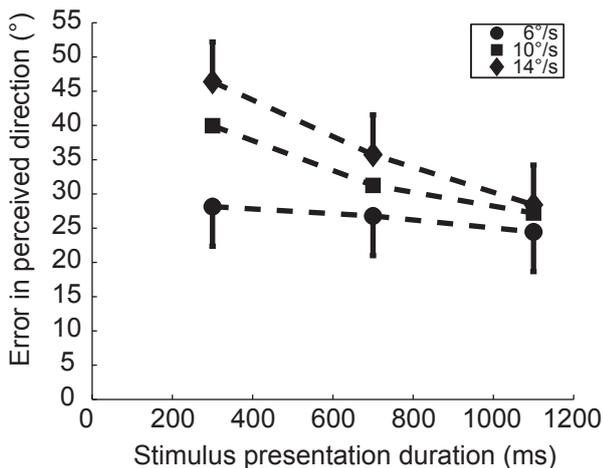


Figure 3. Errors in perceived motion direction as a function of stimulus presentation duration and pursuit target velocity (6, 10, or 14°/s), averaged across six participants. Positive errors indicate perceived motion directions rotated away from the physical direction towards the retinal motion direction. Error bars as in Figure 2.

Analysis

Eye movement data were stored and analysed off-line to compute the pursuit gain and to discard trials with bad pursuit. We discarded saccadic trials, because for these trials it is impossible to say whether the percept resulted from (under)compensation for the smooth pursuit eye movements or from factors related to the presence of saccades (see e.g. Mateeff, 1978; Matin, Matin, & Pearce, 1969; Matin, Matin, & Pola, 1970). Normally, data from both eyes were registered and averaged, but with some participants it was, for technical reasons, difficult to get reliable data from both eyes, so we only recorded from one eye. In the analysis we only used the eye movement data from the part of the trial during which the stimulus was presented.

A trial was discarded when either saccades were present or the pursuit gain was too low or too high. The eye position data were first low-pass filtered using a seven-point running average. Saccades were detected by means of a 60 °/s velocity threshold. The pursuit gain was computed by computing the slope of the best fitting linear regression line and dividing this by the pursuit target velocity. Trials with a pursuit gain lower than 0.8 or higher than 1.2 were discarded.

To test for significance of the observed effects, we used univariate repeated measures analyses (SPSS 10.0). When the sphericity assumption was violated (tested with Mauchly's test), the Greenhouse-Geisser correction was applied. All statistical tests were performed with a significance level of $\alpha = 0.05$.

Results

About 18% of the trials had to be discarded because of inaccurate pursuit. Of the remaining trials, about 1% was discarded because the deviation of the perceived motion direction from the physical direction was more than 90°. Such responses would mean that the vertical component of the perceived motion was opposite to the physical one, which is very unlikely. These cases were probably the result of pressing the mouse button too early, something that was spontaneously reported by the participants a couple of times. The pursuit gain of the remaining trials was computed and averaged across participants. As can be seen from Figure 2, the average pursuit gain was about 1 in all conditions. Neither stimulus presentation duration nor pursuit

target velocity had a significant effect on pursuit gain (univariate repeated measures analysis; both p 's > 0.05). There was a small significant interaction effect ($F(4,20) = 3.131, p = 0.038$), caused by the slight increase in pursuit gain in the 14°/s condition.

Since the pursuit direction (leftwards or rightwards) and the stimulus direction (upwards or downwards) did not have significant effects on the perceived motion direction (p 's > 0.05) and there was only a single small significant interaction effect of these factors with the presentation duration and pursuit target velocity (presentation duration \times pursuit target velocity \times pursuit direction: $F(4,12) = 3.535, p = 0.040$), we collapsed the data across pursuit direction and stimulus direction. The errors in the perceived motion directions relative to the physical (vertical) motion direction of the stimulus dot as a function of presentation duration and pursuit target velocity are shown in Figure 3. The errors in perceived motion direction were quite large and increased with pursuit target velocity. This main effect of pursuit target velocity was significant ($F(2,10) = 10.760, p = 0.018$), as was the interaction between pursuit target velocity and presentation duration ($F(4,20) = 17.658, p < 0.001$). The main effect of presentation duration was not significant ($F(2,10) = 4.213, p = 0.091$). Simple effect tests for the three pursuit target velocities separately showed that only in the 14°/s condition the effect of presentation duration was significant ($F(2,10) = 7.753; p = 0.032$).

Discussion

The results of Experiment 1 show that generally the error in perceived motion direction decreased with higher presentation durations and that this effect was weaker for lower pursuit velocities. This effect of presentation duration corresponds to that found in studies concerning the Filehne illusion that used pursuit velocities in the same range as ours or higher (De Graaf & Wertheim, 1988; Ehrenstein et al., 1986; Wertheim, 1987). Errors in the motion percept get smaller when the stimulus is presented for a longer duration. For the 6°/s and 10°/s conditions in Experiment 1, the effect of presentation duration just failed to reach significance. Mack and Herman (1978) found that with a pursuit velocity between 4 and 5°/s the amplitude of the Filehne-illusion was much higher with a 200 ms presentation duration than with 1200 ms. The presentation duration

effect in their study may have been stronger because they used a larger range in presentation durations. Moreover, the effect of presentation duration appears to be particularly strong below 300 ms (Ehrenstein et al., 1986). In addition, the method we used to measure perceived motion direction was quite noisy, as the large confidence intervals in Figure 3 reflect.

The effect of presentation duration might be explained in terms of an increasing gain ratio of eye movement signal to retinal signal with increasing presentation duration. However, the results of Experiment 1 might also be explained in a different way. Because it was always presented at the same location, the stimulus not only appeared earlier in long duration conditions, but it also disappeared later. An alternative explanation for the lower errors with longer presentation durations might therefore be that the compensation for eye movements gradually builds up during pursuit, or, in other words, that the gain ratio increases during pursuit, irrespective of presentation duration. With longer presentation durations, the pursuit eye movement has lasted longer at the end of the stimulus presentation, and, consequently, the gain ratio might be higher. The results of Experiment 1 do not allow us to discriminate between these two explanations. In Experiment 2 we therefore varied the horizontal location at which the stimulus was presented, which also implied varying the moment during pursuit at which the stimulus was presented. If the alternative explanation were true, errors in perceived motion direction should be larger when the stimulus is presented earlier during the pursuit eye movement.

Experiment 2

Methods

Participants

Twelve volunteering students and staff members (7 male, 5 female) from Utrecht University participated in the experiment. All had normal or corrected-to-normal vision. Their age ranged from 19 to 33 (median age was 24 years). The students were paid for their participation. All participants were naïve with respect to the purpose of the experiment.

Procedure

The general procedure was the same as in Experiment 1. Stimulus presentation duration was now varied in five steps (200, 500, 800, 1100 and 1400 ms). Pursuit target velocity was always 10°/s and the stimulus velocity

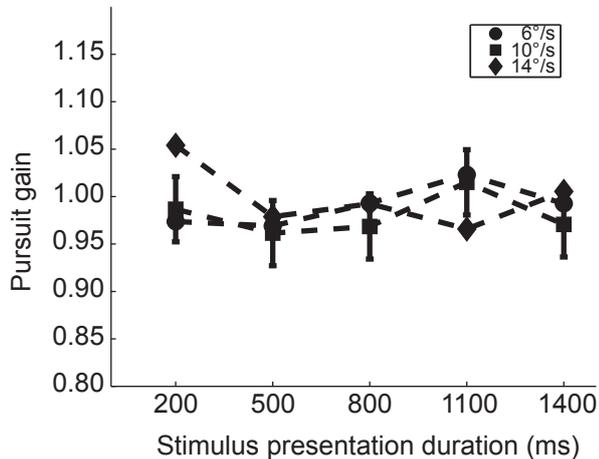


Figure 4. Pursuit gain as a function of stimulus presentation duration and horizontal stimulus path location (-2.5, 0, or 2.5° relative to the centre of the screen), averaged across seven participants. Error bars as in Figure 2.

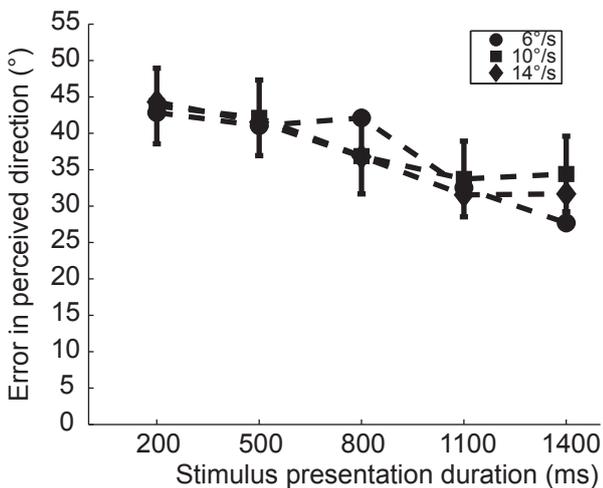


Figure 5. Errors in perceived motion direction as a function of stimulus presentation duration and horizontal stimulus path location (-2.5, 0, or 2.5° relative to the centre of the screen), averaged across seven participants. Positive errors indicate perceived motion directions rotated away from the physical direction towards the retinal motion direction. Error bars as in Figure 2.

was 5°/s. In Experiment 1, the stimulus path was always located at the centre of the screen horizontally. In Experiment 2, this location was varied (centre of the screen, 2.5° to the left, or 2.5° to the right), thereby also varying the moment during pursuit at which the stimulus was presented. The experiment was divided into six blocks of ten trials. Within a block, the trials consisted of the combinations of the five presentation durations and the two pursuit directions (leftwards or rightwards), presented in random order. Stimulus direction (upward or downward) was constant within a block. Stimulus path location was varied randomly across trials.

Instead of an arrow, as in Experiment 1, a line segment (6 cm ≈ 5.7° long) was used to indicate the perceived stimulus motion direction after each stimulus presentation (N.B., Experiment 2 was actually performed before Experiment 1). This line segment could be rotated with the left and right cursor keys of the computer keyboard. Since indicating the perceived motion direction in this way took much more time than with the computer mouse (as in Experiment 1), participants could repeat a trial as often as they wanted. Typically, they repeated trials once or twice. In the eye movement analysis, only the last repetition of each trial was used, since that gave the final estimate of the perceived direction.

In all other respects, stimuli and apparatus were identical to those in Experiment 1.

Results and discussion

Because most participants were untrained observers, pursuit accuracy was worse than in Experiment 1. The data of five of the twelve participants had to be discarded because they didn't have sufficient accurate pursuit trials to analyse the effects of stimulus presentation duration and stimulus path location. Of the remaining seven participants, about 74% of the trials had accurate pursuit. None of these trials had to be discarded because of extreme motion direction responses. The average pursuit gains are shown in Figure 4. Again, pursuit gain was approximately 1 in all conditions. Presentation duration and stimulus location did not have significant effects on the pursuit gain (both p 's > 0.05) and there was a small significant interaction effect ($F(8;48) = 2.521; p = 0.022$).

The errors in perceived motion direction are represented in Figure 5. Just as in Experiment 1, these errors decreased with increasing presentation duration ($F(4;24) = 6.356$; $p = 0.001$). Stimulus path location did not have a significant effect on perceived motion direction, nor was there a significant interaction effect (both p 's > 0.05). Hence, the location of the stimulus path in the pursuit sweep, or, equivalently, the moment during pursuit at which the stimulus was presented, did not have a significant effect on the perceived motion direction.

General discussion

The results of Experiment 2 show that the effect of presentation duration cannot be attributed to a gradual build-up of compensation for the effect of eye movements during pursuit. We found no difference in perceived motion direction between the different stimulus path locations. The results closely replicated those in the 10°/s condition in Experiment 1; only this time the effect of presentation duration was highly significant.

The errors in perceived motion direction in both experiments were quite large, ranging from 25 to 47°, on average. Although the amplitude of the errors may partially depend on the specific stimulus and the response method we used, they do not reflect a mere response bias. In a separate study (Souman, Hooge, & Wertheim, *In Press*) we used the same response method to indicate perceived motion direction during fixation. With a vertically moving stimulus dot, the indicated motion directions deviated only a few degrees from vertical. Hence, the deviation of the indicated motion direction from vertical in our experiments has to be an effect of the pursuit eye movements. The deviations we found are in the same range as those found by Becklen et al. (1984) and Festinger et al. (1976) and somewhat larger than those found by Swanston and Wade (1988).

The only report concerning an effect of presentation duration with non-collinear motion that we found in the literature is that by Mateeff, Eherenstein and Hohnsbein (1986). Their stimulus was a vertically moving vertical bar, which had a different length in different conditions. Since this change in length implied a change in the time that the stimulus was present in a given position, Mateeff et al. interpreted their results in terms of

presentation duration. They found that the deviation of the perceived direction relative to the physical, vertical direction decreased from almost 45° for a presentation duration of 23 ms to 0° for 250 ms and longer, with pursuit target velocities of 5, 10 and 15°/s. Although their stimulus was quite different from ours, their general finding that increasing the presentation duration causes perceptual errors to get smaller corresponds to our results. The effect in their study was much stronger, probably because the stimulus was not a dot, but a bar with a vertical orientation.

How might the effect of presentation duration be explained? As already mentioned in the Introduction, it is generally assumed that the Filehne-illusion is caused by an eye movement signal gain that is lower than the retinal signal gain (Freeman, 2001; Freeman & Banks, 1998; Wertheim, 1994). The stimulus in our experiments, a vertically moving dot, was a 2D stimulus analogous to the stationary stimulus in the Filehne-illusion. The stimulus had no motion component in the eye movement direction, only an orthogonal motion component. Hence, in this case too the deviation of the perceived motion direction from the veridical one can be explained by a gain ratio of eye movement signal to retinal signal that is lower than one. The effect of presentation duration suggests that this gain ratio increases with stimulus presentation duration.

Since the present data do not enable us to pinpoint the effect of presentation duration in one of the two signals (Freeman & Banks, 1998), we can only speculate on possible explanations. Presentation duration might affect the retinal signal, the eye movement signal, or both. Let's first consider possible effects of presentation duration on the retinal signal. Algom and Cohen-Raz (1984) reported that increasing the presentation duration of a single dot presented during fixation produced higher speed estimates (duration range 100 ms to 48 s). Moreover, motion detection thresholds go down with longer presentation durations for single dot stimuli (Brown & Conklin, 1954; Cohen & Bonnet, 1972; Johnson & Leibowitz, 1976; Johnson & Scobey, 1980; Leibowitz, 1955). This contrasts with studies that used random dot kinematogram (RDK) stimuli. For this kind of stimuli motion detection thresholds get higher with longer presentation durations above 133 ms (Watson, Barlow, & Robson, 1983; Watson & Turano, 1995). Similarly, it has been shown that perceived velocity increases with the transience of the stimulus for RDKs (Treue, Snowden, & Andersen, 1993) and apparent

motion displays (Giaschi & Anstis, 1989). Apparently, the effect of temporal factors strongly depends on the type of stimulus used. Based on the results of studies that used a single dot stimulus, like we did in our experiments, the retinal signal gain would be higher for longer presentation durations, which by itself would produce larger errors in perceived direction, contrary to what we found in our experiment.

How about the eye movement signal? Would it be possible that the gain of this signal increased with stimulus presentation duration and that it did so more than the retinal signal gain? If so, that would produce a higher gain ratio of eye movement signal relative to the retinal signal and, consequently, smaller perceptual errors. In Experiment 1, stimulus presentation was always centred around the same moment in time for a given pursuit target velocity, irrespective of presentation duration. This means that for longer durations, the stimulus not only appeared earlier than for shorter durations, but it also disappeared later. If the eye movement signal gain is not constant over time, but builds up gradually, the retinal signal might have been compared to a stronger eye movement signal for longer durations, because there had been more time for the eye movement signal to build up. This would be an alternative explanation for the presentation duration effect. However, this hypothesis can be ruled out on the basis of Experiment 2. In this experiment the location, and consequently, the moment during pursuit at which the stimulus was presented was varied, but did not have a significant effect on the perceived motion direction. Therefore, the degree of compensation for the effect of eye movements does not seem to change during pursuit, at least not on the time scale in our experiments, with the stimulus we used.

Of course, presentation duration might have an effect on the eye movement signal in a different way. According to Wertheim (1987; 1994; Wertheim & Van Gelder, 1990), the eye movement signal is not purely extraretinal, but may also contain a vestibular component (encoding motion of the retinae in space because of head or body movements) and a visually induced component (because optic flow informs the visual system about self-motion: vection; see Berthoz, Pavard, & Young, 1975; Dichgans & Brandt, 1978). The visual system might use this retinal information to estimate the motion of the retinae through space (the eye movement signal). According to Wertheim (1987; 1994), the contribution of this visual component to the

eye movement signal depends on the spatiotemporal characteristics of the retinal image. Based on vection studies, he hypothesized that the visual component gets larger with longer stimulus presentation durations. This might explain the effect of presentation duration in our experiments. Although at first glance it may seem rather unlikely that a single dot can have an optokinetic potential, it is in fact known that one single dot can indeed generate vection (Webb & Griffin, 2003). Hence, the effect of presentation duration might be due to an interaction of the retinal image characteristics and the eye movement signal (see Turano & Massof, 2001, for a similar model).

A single dot stimulus, like we used in our experiments, has the advantage of being simple and relatively easy to judge. However, it also has some drawbacks. Changing the presentation duration with a single dot is confounded with changing the retinal location of stimulation. For longer presentation durations, more peripheral retinal locations are stimulated by the dot at the beginning and the end of the presentation than with shorter durations. Since perceived velocity is lower for peripheral motion (Tynan & Sekuler, 1982), this might explain why we found smaller errors for the longer presentation durations. However, De Graaf and Wertheim (1988) tested this hypothesis by measuring the effect of presentation duration on the amplitude of the Filehne-illusion for foveally and peripherally presented stimuli. They found a similar effect of presentation duration in both conditions. In fact, the Filehne-illusion was stronger in the peripheral condition than in the foveal one. Hence, it is improbable that our results can be explained on the basis of the retinal location confound. The De Graaf and Wertheim (1988) study also falsified another hypothesis that otherwise might have explained our data. Because of the single dot stimulus, varying the presentation duration also changes the adjacency of the stimulus dot to the pursuit target. According to Mack and Herman (1978) this might explain the effect of presentation duration on the Filehne-illusion. However, De Graaf and Wertheim (1988) kept the adjacency constant in their foveal and peripheral conditions, by using a window that moved with the pursuit target, and reported that presentation duration still affected perceived motion.

In conclusion, motion perception in the non-collinear case is affected by stimulus presentation duration in a way that is similar to that in the collinear case. The longer a stimulus is presented, the smaller perceptual

errors get. This effect is probably due to an increase in both retinal signal gain and eye movement signal gain, with the latter increasing more. The effect of presentation duration we found with our single dot stimulus is not necessarily the same with other stimuli, such as RDKs. As noted above, perceived motion strongly depends on the spatiotemporal characteristics of the stimulus used. Apparently, even small differences in experimental set-up can affect the outcome. For instance, contrary to the studies mentioned in the Introduction, Freeman et al. (2002) did not find an effect of presentation duration for the younger participants in their study and the opposite effect for the older participants. This might be due to the fact that their stimulus was a RDK within an annulus that moved with the pursuit target, while the other studies used either a random dot pattern that moved as a whole or a single dot. Hence, other factors than the ratio between eye movement signal gain and retinal signal gain may play a role in the presentation duration effect. In fact, this is illustrated by our finding that the effect of presentation duration was stronger at higher pursuit velocities. Taken together, this seems to imply that motion perception during smooth pursuit eye movements is more complex than a linear combination of eye movement signal and retinal signal (Von Holst, 1954; Von Holst & Mittelstaedt, 1950). Several interactions between retinal image and eye movement signal seem to take place (Goltz, DeSouza, Menon, Tweed, & Vilis, 2003; Turano & Massof, 2001; Wertheim, 1994).

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4

Signal latencies in motion perception during sinusoidal smooth pursuit

Abstract

Smooth pursuit eye movements change the retinal image motion of objects in the visual field. The visual system therefore has to take the eye movements into account to produce a veridical motion percept. According to the classical linear model of motion perception during smooth pursuit the perceived velocity depends on the sum of a retinal motion signal, estimating the retinal image velocity for a given object, and an eye movement signal that estimates the eye velocity. Errors in motion perception during smooth pursuit, such as the Filehne illusion and the Aubert-Fleischl phenomenon, can be explained in terms of the relative size of these signals. However, little attention has been paid to the temporal relationship between the two signals. If the eye velocity is not constant, differences between the latencies of the two signals will also produce perceptual errors. We therefore tested whether the signal latencies differ and what their perceptual consequences are. Participants judged the velocity of a sinusoidally moving random dot pattern, viewed during smooth pursuit of a sinusoidally moving target. In Experiment 1, the phase relationship between the dot pattern and the pursuit target was manipulated and in Experiment 2 we varied the motion amplitude of the dot pattern. In addition we examined whether positional cues affected performance by replicating both experiments with limited lifetime dot stimuli. The relative signal size and phase difference of eye movement signal and retinal motion signal were estimated by fitting the classical linear model to the velocity matches. The model described the data well for most observers. However, the variability of the phase differences estimated from the model made it hard to draw conclusions regarding potential latency differences between the retinal signal and the eye movement signal. Generally, there seems to be a small, but variable, negative phase difference, indicating a phase lag of the eye movement signal relative to the retinal signal. This may suggest that the compensation for the effects of the eye movements is more complicated than just the summation of an extraretinal and a retinal signal.

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Introduction

In order to provide us with a coherent view of the world, our brain has to combine sensory information from several sources. Information has to be combined both across and within modalities and integrated into one percept (see [Ernst & Bühlhoff, 2004](#)). An example of the necessity of sensory combination is that of motion

perception during smooth pursuit eye movements. As eye movements change the retinal image motion, the visual system has to take them into account when it generates a motion percept. Generally, it is thought that this is achieved by combining retinal signals, encoding the retinal image velocities of objects in the visual field, with an eye movement signal that encodes the rotational eye velocity ([Dichgans & Brandt, 1972](#);

Freeman, 2001; Freeman & Banks, 1998; Sperry, 1950; Turano & Massof, 2001; Von Holst, 1954; Von Holst & Mittelstaedt, 1950; Wertheim, 1994). The relative magnitude of these signals determines the perceived head-centric velocity¹ and under- or overestimation of the physical velocities by either signal can produce unveridical motion perception. Illusions such as the Filehne illusion (stationary objects seem to move in the direction opposite to that of a smooth pursuit eye movement; Filehne, 1922; Mack & Herman, 1973) and the Aubert-Fleischl phenomenon (a moving object appears to move slower when tracked with the eyes than during fixation; Aubert, 1886, 1887; Dichgans, Wist, Diener, & Brandt, 1975; Von Fleischl, 1882) can be explained by assuming that the retinal signal gain is higher than the eye movement signal gain (Freeman & Banks, 1998; Wertheim, 1987; for an alternative explanation of the Aubert-Fleischl phenomenon in terms of increasing motion detection thresholds, see Wertheim, 1994 and Wertheim & Van Gelder, 1990). Also, non-unity signal gains are thought to produce perceptual errors in general velocity matching tasks (Freeman, 2001; Turano & Massof, 2001), surface slant judgements (Freeman, 2000) and motion direction judgements during smooth pursuit (Souman, Hooge, & Wertheim, *In press*).

Besides over- or underestimation of the retinal image velocities and the eye velocity, perceptual errors might also be caused by different signal latencies. As most of the abovementioned studies used constant retinal velocities and pursuit target velocities, any latency differences between the retinal signal and the eye movement signal would not have contributed to the perceptual errors found. However, with a non-constant retinal or eye velocity, perceptual errors might be caused both by non-unity signal gains and different signal latencies. The estimate of the eye velocity at time t might be combined with the retinal image velocity of time $t + \Delta t$ and when one of the two velocities is not constant this would produce perceptual errors (unless the latency difference is corrected afterwards). Depending on the size of the latency difference and the velocity profiles of the eye velocity and the retinal image velocity these errors might be quite big and be measured experimentally.

There are good reasons to expect different latencies for the retinal signal and the eye movement signal. Commonly, the retinal signal is thought to be an afferent signal, while the eye movement signal is

mainly conceptualized as an efferent signal (Dichgans & Brandt, 1972; Sperry, 1950; Von Holst, 1954; Von Holst & Mittelstaedt, 1950), although some authors think that it may contain afferent components as well (Goltz, DeSouza, Menon, Tweed, & Vilis, 2003; Harris, 1994; Turano & Massof, 2001; Wertheim, 1994). The eye movement signal is thought to be mainly based on an efference copy of the oculomotor signal. This implies that this signal represents the eye velocity as it is shortly after the signal is sent. It is predictive of the future eye velocity. The retinal signal, on the other hand, encodes the retinal velocity as it is at the moment that the signal is sent. Hence, when these two signals are combined to estimate the head-centric stimulus motion, a correction for the different latencies is necessary, or perceptual errors will result. In fact, such errors have been found in localization during smooth pursuit eye movements, suggesting that at least for localization the difference in latencies is not, or not completely, compensated for (Brenner, Smeets, & Van den Berg, 2001; Mateeff, Yakimoff, & Dimitrov, 1981; Schlag & Schlag-Rey, 2002; Ward, 1976). The latency difference in these studies has been estimated to be about 90 to 100 ms.

Studies on motion perception during smooth pursuit have paid little attention to potential latency differences. The only study that we are aware of is that by Freeman, Banks and Crowell (2000). They presented observers with a simulated ground plane that could both rotate around the vertical axis through the observer and simulate forward translation of the observer. The ground plane was presented while the observer made sinusoidal smooth pursuit eye movements. The task of the observers was to adjust the amplitude and phase of the ground plane rotation in such a way that it appeared to stand still (in the case that simulated forward translation speed was zero) or that it appeared to have only a translational motion component (with non-zero simulated forward translation speeds). The perceptual errors found in their experiments (the Filehne illusion when simulated forward translation speed was zero, a 'slalom' illusion with translation speeds higher than

¹ In this study, we will restrict ourselves to motion perception during smooth pursuit eye movements with the head kept still. Therefore, when we use the term 'perceived motion' this refers to motion as it is perceived with respect to the head of the observer, that is, in a head-centric frame of reference.

zero) indicated that the gain ratio of the eye movement signal to the retinal signal was smaller than one, while the phase difference between the two signals was smaller than 10° (amounting to latency differences less than 8 ms). Freeman et al. concluded that the perceptual errors were mainly caused by the incorrect estimation of the amplitudes of the signals by the visual system, not by different latencies.

The task of the observers in the study by Freeman et al. (2000) was quite complicated. They had to switch between adjusting the phase and the amplitude of the rotation to null its perceived rotation. Moreover, the method of adjustment used in their study made it hard to take the (in)accuracy of the pursuit eye movements into account. Discarding trials with inaccurate pursuit might have resulted in the loss of most of the trials, since trials were quite long. Therefore, we devised a new paradigm, in which observers had to judge only the peak velocity of a sinusoidally moving random dot pattern during sinusoidal smooth pursuit. Their task

was to judge in a 2IFC task whether the peak velocity was higher during the first (pursuit) interval, or during the second (fixation) interval. The gain ratio of the eye movement signal to the retinal signal and the phase difference between both signals were estimated by applying the classical linear model of motion perception during smooth pursuit to the velocity matches. Potential latency differences were studied in two experiments. In Experiment 1, the phase relationship between the motion stimulus and the smooth pursuit eye movement was varied, while keeping the retinal motion amplitude of the stimulus approximately constant. In Experiment 2, the phase relationship was kept constant and retinal motion amplitude was varied. This way, we made two cross-sections of the two-dimensional stimulus space, given the pursuit amplitude and frequency we used.

The linear model

According to the linear model (Freeman & Banks, 1998; Von Holst, 1954; Von Holst & Mittelstaedt, 1950), perceived head-centric velocity $\hat{\mathbf{h}}$ equals the sum of the retinal image velocity and the eye velocity as estimated by the visual system. These estimates are related to the actual velocities by simple gains:

$$\hat{\mathbf{h}} = r\mathbf{r} + e\mathbf{e} \quad (1)$$

where \mathbf{r} and \mathbf{e} are the retinal image velocity and the eye velocity vectors and r and e are the signal gains, respectively. Although deviations from the linear model have been found (Freeman, 2001; Goltz et al., 2003; Turano & Massof, 2001), these are typically quite small. Generally the linear model seems to give a good description of perceived head-centric velocity during smooth pursuit (Freeman, 1999, 2000, 2001; Freeman & Banks, 1998; Souman et al., In press).

With sinusoidal pursuit and sinusoidal stimulus motion, velocity amplitudes R and E of vectors \mathbf{r} and \mathbf{e} , and therefore $\hat{\mathbf{H}}$ too, depend on time t , with potential delays in the signals. The motion vectors can conveniently be represented in polar coordinates, with the angle relative to the positive x-axis representing the phase and the length of the vectors representing the amplitude of the sinusoidal motion (see Figure 1). The physical retinal motion \mathbf{r} equals the head-centric motion \mathbf{h} minus the eye velocity \mathbf{e} . The velocities as estimated

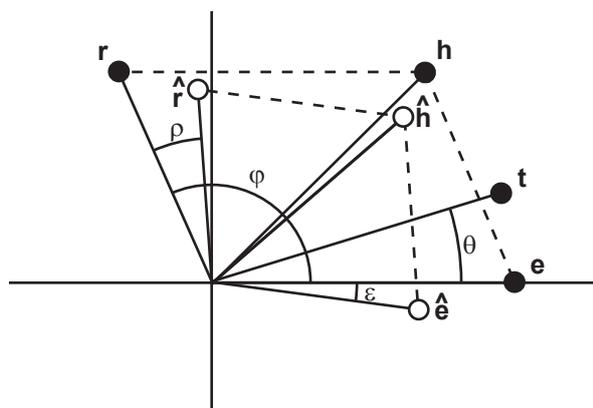


Figure 1. Geometric representation in polar coordinates of the motion vectors involved in judging head-centric motion during sinusoidal pursuit. Closed circles indicate physical velocities, with the radius representing the motion amplitude and the angle relative to the horizontal axis representing the phase relative to that of the eye movement: \mathbf{t} = pursuit target velocity; \mathbf{e} = actual eye velocity; \mathbf{h} = head-centric stimulus velocity; \mathbf{r} = retinal image velocity of the stimulus. Open circles and hatted symbols indicate the corresponding velocities as estimated by the visual system. Greek characters indicate phases: $-\theta$ = eye movement phase relative to the pursuit target; φ = phase of retinal stimulus motion; ε = phase of eye movement signal in the visual system; ρ = phase of retinal signal in the visual system.

by the visual system (indicated by hatted symbols) may not only be scaled in amplitude by the signal gains, but also have a phase lag (or lead). Figure 1 illustrates the case that the retinal signal phase lag ρ is larger than the eye movement signal phase lag ε , with retinal signal gain r higher than eye movement signal gain e . It also shows that the eye velocity \mathbf{e} does not necessarily equal the pursuit target velocity \mathbf{t} , but may show a phase lag (θ). We will return to this point later.

From the geometric relationships in Figure 1, the head-centric velocity as estimated by the visual system according to the linear model can be deduced:

$$\hat{\mathbf{h}}(t) = rR \sin(2\pi ft + \varphi + \rho) + eE \sin(2\pi ft + \varepsilon) \quad (2)$$

where f is the frequency of the pursuit target motion and the retinal image motion (equal in our experiments) and φ represents the actual phase of the retinal image motion relative to the eye movement. Equation 2 can also be written as one single sine wave, with squared amplitude

$$\hat{H}^2 = (rR)^2 + (eE)^2 + 2rReE \cos(\varepsilon - \rho - \varphi) \quad (3)$$

The retinal image motion amplitude R and phase φ can be computed from the identity

$$R \sin(2\pi ft + \varphi) = H \sin(2\pi ft + \eta) - E \sin(2\pi ft) \quad (4)$$

where η is the phase of the stimulus velocity relative to that of the eye movement. In our matching experiments participants had to judge the peak velocity (or, equivalently, the velocity amplitude) of the motion stimulus both during pursuit and during fixation. At the velocity match, the perceived motion amplitude was by definition equal in the pursuit interval and the fixation interval:

$$\hat{H}_f = \hat{H}_p \quad (5)$$

where the subscript f indicates the fixation interval and p the pursuit interval. In the fixation interval, the eye velocity was approximately zero, and therefore, applying equation 3, we get

$$\hat{H}_f^2 = (rR_f)^2 = (rR_p)^2 + (eE)^2 + 2rR_p eE \cos(\varepsilon - \rho - \varphi) \quad (6)$$

Dividing both sides of this equation by r^2 gives

$$R_f^2 = R_p^2 + \left(\frac{e}{r} E\right)^2 + 2\frac{e}{r} R_p E \cos(\varepsilon - \rho - \varphi) \quad (7)$$

Hence, we can estimate the gain ratio e/r and the phase difference $\varepsilon - \rho$ between both signals from the peak velocity estimates in our matching experiments if the linear model fits the data.

From equation 7 it can be seen that if the retinal motion amplitude R_p is kept constant, the linear model predicts that the squared amplitude matches will be a cosine function of the physical retinal image motion phase φ (Experiment 1). If the phase φ is kept constant, the squared amplitude matches will form a second degree polynomial function of retinal image motion amplitude R_p (Experiment 2).

The actual retinal motion amplitude R and phase φ depend on the amplitude and phase of the actual eye movements relative to the pursuit target motion. If the pursuit is not accurate, the actual values of R and φ will deviate from the intended ones, with amplitude R varying as a function of φ . Because the linear model cannot be applied anymore when that is the case, we had to make sure in our experiments that the actual φ equalled the intended φ . In order to do that, we first measured for all participants the actual amplitude and phase of the eye movements relative to the pursuit target motion (the difference between \mathbf{t} and \mathbf{e} in Figure 1) in a series of practice trials. In the experiments described below, we then adjusted the phase and amplitude of the head-centric stimulus motion \mathbf{h} in such a way that the actual eye movement \mathbf{e} would on average produce retinal image motion phase φ and amplitude R . In the analysis, we discarded trials in which the eye movement amplitude or phase differed more than two standard deviations from the assumed ones.

Experiment 1

Methods

Participants

The two authors and two other observers participated in the experiment. The last two participants were not informed of the purpose of the experiment. All participants had normal or corrected-to-normal vision and had extensive experience as participants in psychophysical experiments.

Stimuli and apparatus

To induce ocular pursuit or fixation, a short vertical line segment was presented. In pursuit intervals, this pursuit target followed a sinusoidal velocity profile, with a frequency of 0.5 Hz and an amplitude of 2° (peak velocity $6.28^\circ/\text{s}$), always moving horizontally. Human smooth pursuit performance for this combination of frequency and amplitude is known to be good (Leigh & Zee, 1999, p. 161-162; Lisberger, Evinger, Johanson, & Fuchs, 1981), although the eyes may slightly lag the pursuit target (Freeman et al., 2000). The pursuit target was presented for two periods of the sinusoidal motion, starting at either the left or right extreme of its path. The starting position alternated in consecutive trials. During the second period, the motion stimulus that had to be judged by the participants was presented (duration 2 s). In fixation intervals, the same line segment was presented at the centre of the screen, where it stayed stationary throughout the interval. After 2 s the motion stimulus was displayed, again with a duration of 2 s.

The motion stimulus that had to be judged by the participants was a moving random dot pattern, displayed through a software-generated rectangle ($10^\circ \times 10^\circ$ with 144 dots). The dot pattern consisted of dim dots, presented against a dark background. No dots were displayed in the central strip of the rectangle (height 3°), where the pursuit/fixation target was presented. The dots moved horizontally at the same frequency as the pursuit target (0.5 Hz). In pursuit intervals, their amplitude and phase were determined by the condition tested; in fixation intervals, the phase was chosen at random for each trial, while the staircase measurement drove the amplitude (see below). The position of the dots was defined as the centroid of a 2×2 pixel cluster

and the dots were rendered with sub-pixel accuracy, using standard anti-aliasing techniques (see Georgeson, Freeman, & Scott-Samuel, 1996).

The stimuli were presented on a gamma-corrected computer monitor (Mitsubishi Diamond Pro 20; refresh rate 100 Hz, resolution 800×600), driven by a VSG2/3F graphics card under PC control. The stimuli were viewed binocularly at a viewing distance of 57.3 cm. To minimize head movements, a chinrest and cheek support were used. The experiment was performed in a completely darkened room.

Procedure

Participants had to perform a velocity matching task. Each trial consisted of two consecutive intervals: a pursuit interval and a fixation interval. The task of the participants was to indicate in which of the two intervals the peak velocity of the random dot pattern was perceived to be highest. The responses of the participants drove two randomly interleaved 1-up 1-down staircases, converging on velocity matches between the pursuit interval and the fixation interval. The stimulus velocity amplitude in the pursuit intervals was constant throughout each staircase (the standard velocity), while that in the fixation intervals varied (the test velocity). The two interleaved staircases started at different test velocity amplitudes. After each of the first three reversals of the staircase the step size was halved in log units, until it reached the minimal step size of 0.019 log units (for one of the participants, JHS, the minimal step size was twice this value). The staircase ended after eight reversals at this minimal step size. The velocity match was computed as the mean of the test speeds at those of the last eight reversals that showed accurate pursuit.

The independent variable of the experiment was the phase of the retinal image motion relative to that of the eye movements. The phase and amplitude of the stimulus motion presented on the screen were computed to produce the desired retinal image motion phase and amplitude, given the average pursuit gain and phase of the participant. The retinal image motion amplitude was 1° (velocity amplitude $3.14^\circ/\text{s}$), while the retinal phases tested were 0° , 30° , 60° , 90° , 120° , 150° and 180° . All seven conditions were replicated three times. Within each replication, the order of the conditions was randomized.

Before the actual experiment was performed, participants received at least two practice blocks in which all seven conditions were presented. These practice blocks served to practice the velocity matching task and to measure pursuit performance. The average

pursuit amplitude and phase were used to adjust the stimulus motion, in order to produce the desired retinal image phase and amplitude (see above).

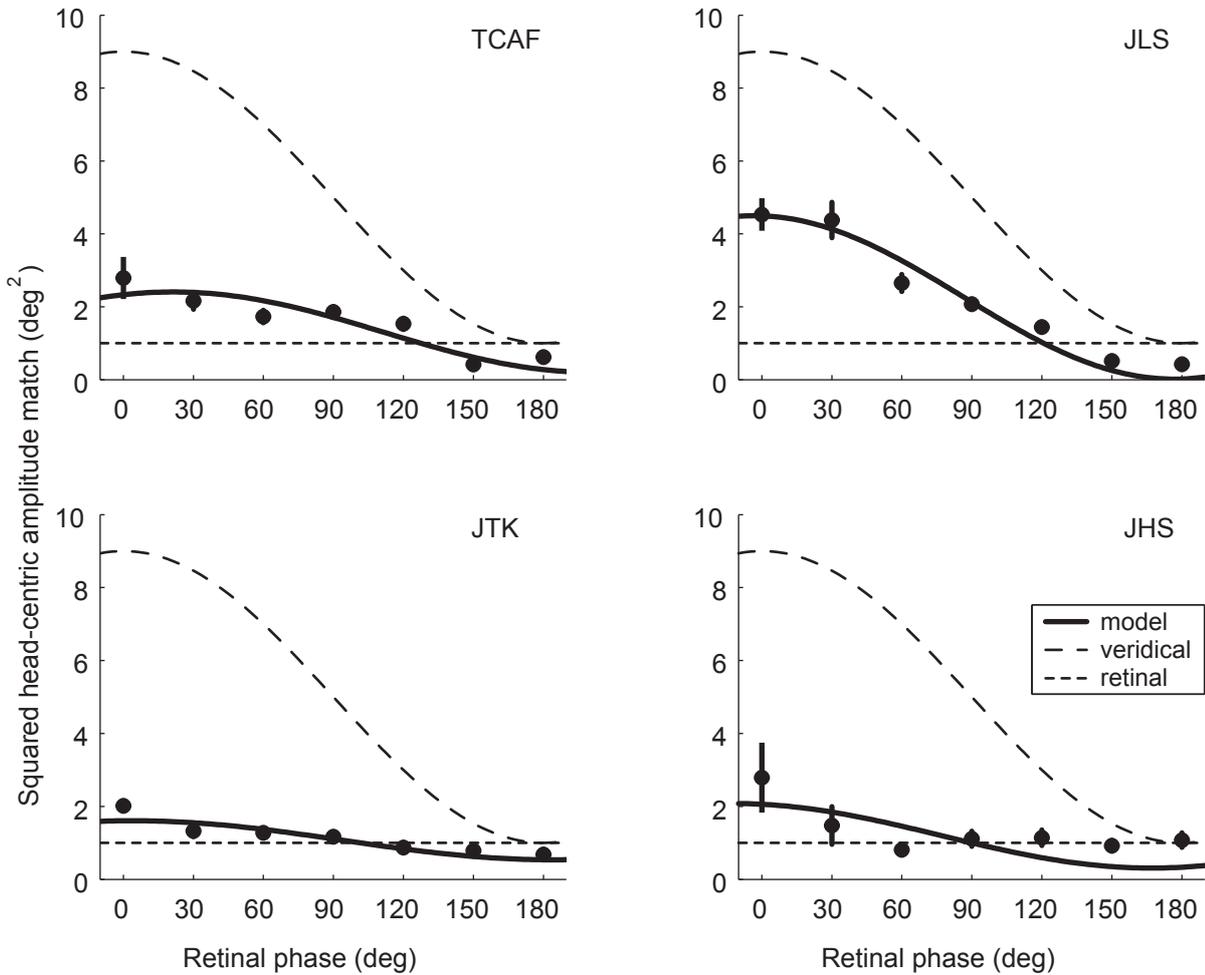


Figure 2. Squared motion amplitude matches for the four participants in Experiment 1 as a function of the phase of the retinal image motion of the stimulus. The thick solid lines give the best fitting curves of the linear model. The thin dashed curved lines represent the actual head-centric stimulus motion amplitude, while the thin dashed horizontal lines show the motion amplitude of the retinal image of the stimulus. Error bars represent the 95%-c.i. of the mean staircase reversal values; they are often smaller than the symbol size.

Table 1. Average pursuit gains and phases in Experiments 1 to 4. Standard deviations are given between parentheses.

Participant	Experiment 1		Experiment 2		Experiment 3		Experiment 4	
	Gain	Phase (°)						
TCAF	1.05 (0.09)	-16.88 (3.28)	1.05 (0.08)	-16.31 (3.15)	1.02 (0.06)	-16.51 (2.68)	0.99 (0.05)	-16.37 (2.53)
JLS	1.01 (0.06)	-15.59 (2.45)	1.00 (0.07)	-15.15 (2.68)	1.01 (0.06)	-15.55 (3.19)	1.02 (0.08)	-15.30 (2.51)
JTK	1.08 (0.10)	-20.24 (5.21)	0.98 (0.07)	-18.87 (4.50)	1.05 (0.11)	-20.59 (4.21)	-	-
JHS	0.98 (0.07)	-24.31 (4.22)	-	-	-	-	-	-

Eye movement registration and analysis

Eye movements were recorded from the left eye, using an ASL Series 4000 video eye-tracker with a sampling frequency of 50 Hz. The eye movement data were analysed offline to check for accurate pursuit. First, the measured eye positions were low-pass filtered and the eye velocity was computed by taking the time

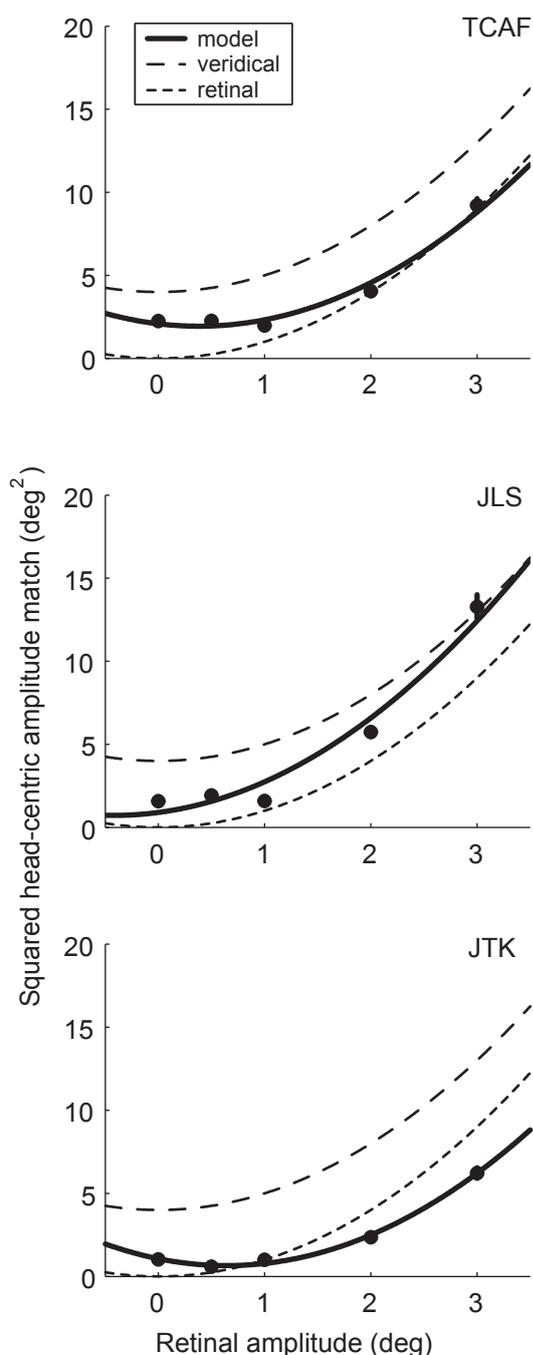


Figure 3. Squared motion amplitude matches for the three participants in Experiment 2 as a function of the amplitude of the retinal image motion of the stimulus. Symbols and error bars as in Figure 2.

derivative. If the eye velocity differed more than 20% from the pursuit target velocity, a trial was discarded from further analysis. The pursuit gain and phase were determined by fitting a sine wave function with fixed frequency (0.5 Hz) to the eye position data. The pursuit gain was computed by dividing the amplitude of this fitted sine wave by the pursuit target amplitude and the phase of the fitted sine wave was taken to be the pursuit phase. Because the fitting of the linear model assumed a certain pursuit gain and phase, all trials in which the pursuit amplitude and phase differed more than two standard deviations from the intended amplitude and phase were removed from further analysis.

Results

On average 27% of the staircase reversals had to be discarded because of saccades or because the pursuit amplitude or phase exceeded two standard deviations from the intended amplitude and phase. The average pursuit gain and phase and the standard deviations in the remaining trials are shown in Table 1. To compute the average phase and the standard deviation of the phases the circular mean and standard deviation were used (Batschelet, 1981). All four participants exhibited a small phase lag, while their pursuit gain was close to unity. This corresponds to earlier findings (Barnes, Barnes, & Chakraborti, 2000; Freeman et al., 2000), although the phase lag in our experiment was slightly larger, possibly because the pursuit target was only presented for two periods. There were no systematic differences in pursuit gain or phase between conditions.

The velocity matches of the four participants are presented in Figure 2. As the linear model (Eqn. 7) is formulated in terms of the squared amplitude, the squared amplitude matches are shown as a function of the phase of the retinal image motion relative to the eye movement. For participants TCAF and JLS, the amplitude matches clearly varied as a function of retinal phase, while those of participants JTK and JHS were more or less constant and almost equal to the retinal image amplitude (indicated by the horizontal dashed line). The linear model (Eqn. 7) was fitted to the amplitude matches by means of the bootstrap method, in order to estimate the parameter values and their standard errors. For each participant, the number of reversals per condition n was determined. Then, a

sample of size n was drawn with replacement from the n reversal values of that participant in a given phase condition. This was done for all seven conditions and the linear model was fitted to the means of these values. This procedure was repeated 100 times and the final estimates of the gain ratio and phase difference were computed by averaging all 100 gain ratios and phase differences found in the bootstrapping procedure. Their standard errors were estimated as the standard deviation of the 100 parameter values.

The model curves computed with the estimated gain ratios and phase differences are shown in Figure 2 (solid curves). For three participants the model provided a good fit. Only the data of participant JHS could not be fitted well by the linear model. The goodness-of-fit was expressed in the proportion of explained variance R^2 (Table 2), computed as

$$R^2 = 1 - \frac{\sum (y - \hat{y})^2}{\sum (y - \bar{y})^2} \quad (8)$$

where y represents the squared amplitude matches and \hat{y} the model predictions. Since according to the linear model the amplitude matches depend in a non-linear fashion on the retinal phase, R^2 may become negative when the fit is bad, as indeed happened for participant JHS.² Note that, due to the bootstrapping procedure, the R^2 are generally slightly lower than those that would

be obtained by fitting the model directly to the average reversal values shown in Figure 2.

The mean gain ratios e/r and phase differences $\epsilon-\rho$ from the bootstrapping procedure with their standard errors are shown in Table 3. Obviously, these parameter values only make sense when the linear model fits well. Specifically, the values for participant JHS are not very meaningful, as the linear model did not fit her data well. The other participants exhibited quite variable values for the gain ratio. In Figure 2 this shows as different amplitudes and offsets of the model curves. Participants JLS and JTK showed a small phase difference, not significantly different from zero (assuming that the distribution of phase differences is approximately normal; hence, a phase difference is significantly different from zero if it is more than 2 standard errors removed from zero). The phase difference for TCAF was much larger and positive, indicating a phase lag of the retinal signal relative to the eye movement signal.

Experiment 2

Methods

In the second experiment, we kept the retinal motion phase constant at 90° relative to the eye movement and

Participant	Experiment			
	1	2	3	4
TCAF	0.71	0.98	0.80	0.96
JLS	0.82	0.93	0.77	0.76
JTK	0.69	0.99	-1.60	-
JHS	-0.88	-	-	-

Table 2. Goodness-of-fit of the linear model in Experiments 1 to 4, expressed in the proportion of explained variance R^2 .

Table 3. Gain ratios e/r and phase differences $\epsilon-\rho$, as the best fitting parameter values for the linear model in Experiments 1 to 4. The standard errors of the parameter values, estimated by means of the bootstrap method, are given between parentheses.

Participant	Experiment							
	1		2		3		4	
	Gain ratio e/r	Phase difference $\epsilon-\rho$ ($^\circ$)	Gain ratio e/r	Phase difference $\epsilon-\rho$ ($^\circ$)	Gain ratio e/r	Phase difference $\epsilon-\rho$ ($^\circ$)	Gain ratio e/r	Phase difference $\epsilon-\rho$ ($^\circ$)
TCAF	0.28 (0.02)	21.47 (3.77)	0.72 (0.02)	-15.27 (1.28)	0.39 (0.01)	-1.72 (1.75)	0.50 (0.01)	-7.40 (2.02)
JLS	0.56 (0.02)	-3.27 (3.37)	0.47 (0.05)	26.44 (7.03)	0.52 (0.02)	-13.93 (2.78)	0.31 (0.02)	90.00 (0.00)
JTK	0.13 (0.01)	3.92 (3.54)	0.52 (0.01)	-38.49 (1.14)	0.24 (0.01)	48.82 (12.65)	-	-
JHS	0.22 (0.16)	-12.81 (25.10)	-	-	-	-	-	-

varied the retinal motion amplitude (0° , 0.5° , 1° , 2° and 3°). The phase of 90° was chosen because the results of the first experiment suggested that this was the phase where small differences in phase had the largest impact on the perceived velocity, as the slope of the fitted model curves was steepest at this phase. Three participants (TCAF, JLS and JTK) served as observers. In all other respects, Experiment 2 was the same as Experiment 1.

Results

After analysis of the eye movements, 19% of the staircase reversals had to be discarded. The number of accurate pursuit trials was about the same as in Experiment 1 for participants TCAF and JLS, while it was somewhat higher for JTK. The average pursuit gains and phases are shown in Table 1. Again, they were very similar to those in Experiment 1.

The amplitude matches in Experiments 2 are shown in Figure 3. Not surprisingly, the amplitude matches increased with the actual retinal amplitude. The linear model was again fitted to the amplitude matches by means of the bootstrap method and the solid curves in Figure 3 show the results. For all three participants, the model fitted the amplitude matches very well, which is reflected in the high R^2 values (Table 2). The mean gain ratios e/r and phase differences $\varepsilon-\rho$ that resulted from the bootstrapping procedure are given in Table 3. While the gain ratio for participant JLS was similar to that in Experiment 1, the gain ratio for participants TCAF and JTK was much higher. The phase difference was significantly negative for participants TCAF and JTK, indicating a phase lead of the retinal signal relative to the eye movement signal, whereas participant JLS exhibited a relatively large phase lag of the retinal signal.

Discussion of Experiments 1 and 2

The linear model (Eqn. 7) generally fitted the velocity matches in our experiments quite well. This simple model with only two parameters was able to describe the behaviour of the participants in a complicated task, both as a function of the phase of the retinal image motion relative to that of the eye movement and of the

retinal motion amplitude. Only the velocity matches of participant JHS in Experiment 1 could not be fitted by the model. From her data (Figure 2), it appears that she judged the retinal image velocity instead of the head-centric velocity of the motion stimulus, as most of her amplitude matches are close to the retinal image amplitude. While observers often already find it hard to judge motion in a head-centric frame of reference during smooth pursuit eye movements of a constant velocity, the sinusoidal motions in our experiments may have exacerbated this problem.

The good fit of the linear model to the amplitude matches allows us to interpret the gain ratios e/r and the phase differences $\varepsilon-\rho$ that we found. The gain ratios can be taken as the degree that the effects of the eye movements on the retinal image velocity were compensated for. A gain ratio of zero indicates that the eye movements are not compensated for at all and that the retinal image motion is reported. With a gain ratio of unity, on the other hand, compensation is complete and the reported velocity is veridical (in the absence of phase differences). Although in Experiment 1 the gain ratios were quite low, this is not uncommon (see e.g. Souman et al., *In press*). Neither is their variability. Gain ratios can be quite different for different observers and also depend on the kind of stimulus and task used. In Experiment 2, participant JLS showed a gain ratio that was comparable to that in Experiment 1, while that for TCAF and JTK was significantly higher. The small standard errors of the mean gain ratios as estimated by the bootstrap procedure indicate that the variability within one experiment was low, even though it was done in three sessions on separate days. However, the large difference in gain ratios between both experiments for participants TCAF and JTK suggest that these standard errors may underestimate the actual variability. In other experiments (e.g., Freeman, 2001) TCAF had gain ratios of about 0.5, which is exactly in the middle of the two values observed here. Possibly, the large difference is caused by the difficulty of the task in our experiments. On the other hand, comparison of the corresponding data points in Experiments 1 and 2 (a retinal motion phase

² Please note that although the linear model (Eqn. 1) describes the perceived head-centric velocity as a linear combination of retinal image velocity and eye velocity, the predicted relationship between the amplitude matches and the retinal phase in Experiment 1 is non-linear.

of 90° and a retinal motion amplitude of 1°) shows that the differences between the amplitude matches are very small (compare the corresponding points in Figures 2 and 3). Hence, in these individual data points the three participants showed highly consistent responses across the two experiments.

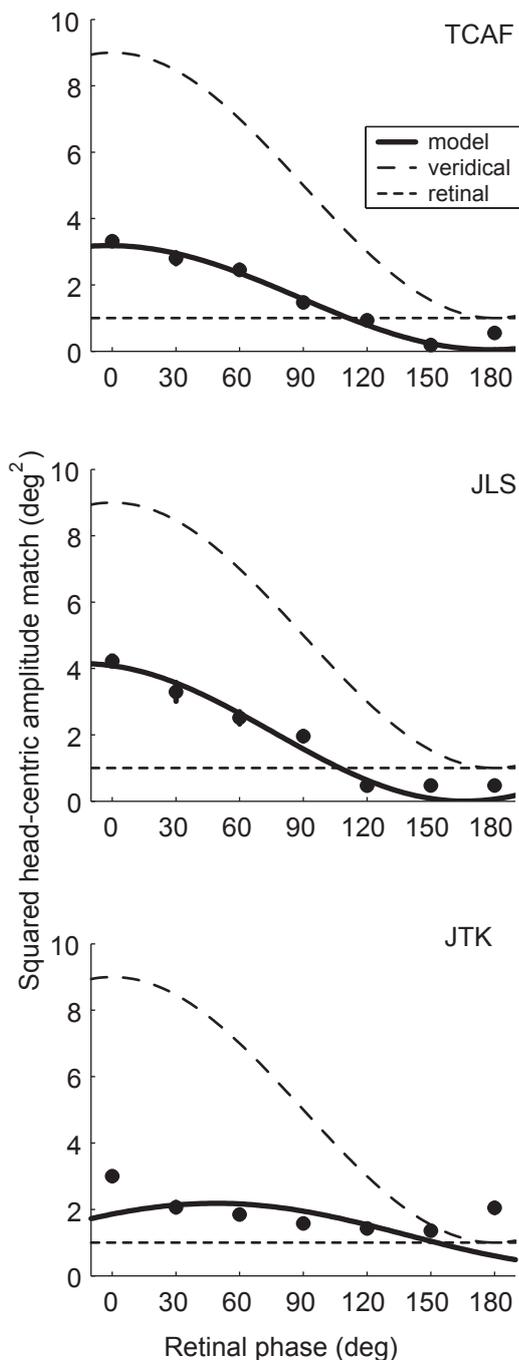


Figure 4. Squared motion amplitude matches for the three participants in Experiment 3 as a function of the retinal image phase. Symbols and error bars as in Figure 2.

The phase differences between the eye movement signal and the retinal signal were quite variable too. In Experiment 1, two participants showed phase differences close to zero, while TCAF showed a large positive phase difference. In Experiment 2, the data of participant JLS showed a similar large phase difference, while TCAF and JTK now had a large negative phase difference. This variability may indicate that the actual phase difference is quite small and that the difficulty of the task caused the estimated phase difference to vary between experiments. This would agree with the results of Freeman et al. (2000), who also found the phase difference to be small.

In our experiments, the velocity amplitude of the motion stimulus was confounded with the displacement amplitude. Since the dots that formed the stimulus were continuously present, a change in peak velocity also implied a change in maximum displacement of the dots. Possibly, the participants in our experiments sometimes used this displacement amplitude to do the task, instead of the velocity amplitude as they were instructed to do. If participants relied on different aspects of the stimulus in different experiments, this might explain the different gain ratios and phase differences found. To check for this possibility, we repeated the two experiments with limited lifetime dots in Experiments 3 and 4.

Experiments 3 and 4

Methods

Experiments 3 and 4 were exact replications of Experiments 1 and 2, respectively, with the only difference that the stimulus dots had a limited lifetime. Each dot appeared at a new, random, location every 200 ms, while the moment at which the dots were repositioned varied randomly across dots. All four participants of Experiment 1 took part in Experiment 3, in which the phase relationship between the retinal image motion and the eye movement was varied, while only participants TCAF and JLS took part in Experiment 4, in which the retinal motion amplitude of the stimulus was varied.

Results

Of the staircase reversals in Experiment 3, 20% had to be removed from further analysis because of inaccurate pursuit. In Experiment 4, this was 14%. The pursuit gains and phases are given in Table 1. The pursuit gains and phases proved very consistent across the experiments

Experiment 3 was a replication of Experiment 1, with the phase relationship between the retinal image motion and the eye movement as the experimental factor. Most participants found the matching task more difficult to perform with limited lifetime dots. For participant JHS, it proved impossible to perform the task consistently with this flickering stimulus. The amplitude matches of the other three participants are shown in Figure 4. As in Experiment 1, the amplitude matches of TCAF and JLS clearly depended on the retinal phase, while those

of JTK showed much less variation. The linear model fitted the amplitude matches of the first two participants well, while it provided a bad fit to the data of JTK (see Table 2 for the R^2 values). The gain ratios and phase differences estimated using the linear model are given in Table 3. Obviously, given the bad fit of the linear model to the amplitude matches of participant JTK, his values are not interpretable. For JLS, the values were similar to those in Experiment 1, but the phase difference for TCAF was now much lower and close to zero.

Figure 5 shows the amplitude matches of the two participants in Experiment 4, which was a replication of Experiment 2. The amplitude matches are shown as a function of the retinal image motion phase. While the amplitude matches of TCAF were quite similar to those in Experiment 2 (see Figure 3), those of JLS were somewhat different. Specifically, the amplitude matches at the lower retinal amplitudes were close to zero. The linear model fitted the amplitude matches very well for TCAF, while the fit was not as good for JLS (Table 2). For TCAF, the gain ratio and phase difference were similar to those in Experiment 2 (Table 3). The phase difference for JLS was 90° , which appears to be mainly the consequence of the low amplitude matches at the lower retinal amplitudes, combined with a relatively high amplitude match at the 3° amplitude.

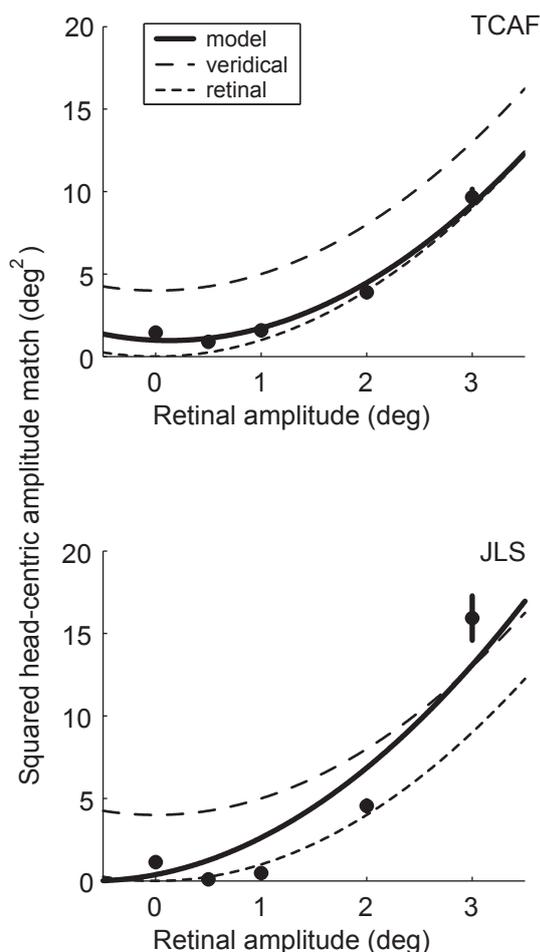


Figure 5. Squared motion amplitude matches for the two participants in Experiment 4 as a function of the retinal image motion amplitude. Symbols and error bars as in Figure 2.

Discussion of Experiments 3 and 4

To what extent do the results of the limited lifetime experiments show that the variability in phase difference was due to reliance on different aspects of the stimulus, specifically maximum displacement versus peak velocity? The phase difference for participant TCAF was slightly negative in both limited lifetime experiments, suggesting that he may have relied on the displacement cue in Experiment 1, where he showed a large positive phase difference. For participant JLS, the results suggest that he may have relied on the displacement cue in Experiment 2. In Experiment 4, where the displacement cue was minimized, his results are not easy interpretable. The same is true for participant JTK, due to the bad fit of the linear model to his amplitude matches.

General discussion

The general picture that emerges from our amplitude matching experiments is that the task was quite complicated for participants, even though they had to judge one single aspect of the stimulus. This caused the gain ratios and especially the phase differences as estimated from the fitted linear model to be quite variable. Partially, this variability may have been due to reliance on different aspects of the stimulus in different experiments, or maybe even in different conditions. In Experiments 1 and 2, the continuous presence of the stimulus dots enabled the participants to do the task on the basis of the maximum displacement of the dots, instead of the peak velocity. This would make the task at least partially dependent on the localization system of the visual system and not just on the motion system. Since motion and position are largely processed in different pathways (see below), this might produce different amplitude matches. In Experiments 3 and 4, the displacement cue was minimized by limiting the lifetime of the stimulus dots. In the three cases that allow interpretation of the gain ratios and phase differences (participant TCAF in Experiments 3 and 4 and JLS in Experiment 3), this resulted in a negative phase difference, suggesting a phase lead of the retinal signal relative to the eye movement signal. The variability of the phase difference makes it difficult, however, to estimate the size of the latency difference.

A negative phase difference indicates a retinal signal that leads the eye movement signal. This was against our expectations. Given the supposedly efferent nature of the eye movement signal, we expected the eye movement signal to lead the retinal signal. This is also what has been found before in localization during smooth pursuit (Brenner et al., 2001; Mateeff et al., 1981; Schlag & Schlag-Rey, 2002; Ward, 1976). Interestingly, Freeman et al. (2000) showed that the small, positive phase difference ϵ - ρ that they found in their path perception experiment turned into a small negative difference when the actual pursuit gain and phase were taken into account. This seems to concur with our present results and begs the question why the latency differences would be different for localization and motion perception during smooth pursuit eye movements. In both cases, the problem that has to be solved by the visual system is the same. Eye movements change both the location and motion of retinal images and in both cases the visual system has to use information about the gaze direction/

motion to compensate for this effect. So, wouldn't we expect localization and motion perception during smooth pursuit to exhibit the same latency differences? The answer is no. Although velocity physically simply is the time derivative of position, their relationship in perceptual terms is much more complex. Our brain doesn't derive motion from position information, but has dedicated motion processing pathways (see e.g. Snowden, 1994). And the integration of retinal signals and eye movements signals also happens in separate, though proximate, brain areas. Area 7a (in monkeys) seems to play an important role in the integration of eye position information with retinal location information (Andersen, Essick, & Siegel, 1985; Andersen & Mountcastle, 1983; Andersen, 1989; Andersen, Essick, & Siegel, 1987), while area MST is important for combining eye movement signals and retinal motion signals (Barton et al., 1996; Bradley, Maxwell, Andersen, Banks, & Shenoy, 1996; Ilg & Thier, 2003; Newsome, Wurtz, & Komatsu, 1988; Pack, Grossberg, & Mingolla, 2001; Shenoy, Bradley, & Andersen, 1999). Consequently, potential latency differences are not necessarily the same for localisation and motion perception during smooth pursuit eye movements.

The question remains, however, why the retinal signal seems to lead the eye movement signal in motion perception during smooth pursuit, instead of a phase lag. Given the large variability in our results, this signal latency may be quite small or even be the effect of random noise. Alternatively, the negative phase difference ϵ - ρ may indicate that the eye movement signal is not a purely efferent signal, derived from the oculomotor command. As suggested by some authors (Goltz et al., 2003; Harris, 1994; Turano & Massof, 2001; Wertheim, 1990, 1994), the eye movement signal might also be partially dependent on retinal image characteristics. This would correspond to physiological evidence that area MST, which is thought to play an important role in the transformation from a retinocentric to a head-centric frame of reference, contains a large population of neurons that preferentially respond to large moving retinal images (Duffy & Wurtz, 1991a, 1991b; Komatsu & Wurtz, 1988a, 1988b). Since smooth pursuit eye movements in everyday life result in a moving retinal image of the stationary background of the pursuit target, these neurons might provide retinal information about the direction and speed of the eye movement (Pack et al., 2001). This would make the relative latencies of retinal signals and eye movement signals much more

complicated, possibly rendering it meaningless to speak of *the* latency difference between retinal signals and the eye movement signal.

Acknowledgments

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5

Localization and motion perception during smooth pursuit eye movements

Abstract

We investigated the relationship between compensation for the effects of smooth pursuit eye movements in localization and motion perception. Participants had to indicate the perceived motion direction, the starting point and the end point of a vertically moving stimulus dot presented during horizontal smooth pursuit. The presentation duration of the stimulus was varied. From the indicated starting and end points, the motion direction was predicted and compared to the actual indicated directions. Both the directions predicted from localization and the indicated directions deviated from the physical directions, but the errors in the predicted directions were larger than those in the indicated directions. The results of a control experiment, in which the same tasks were performed during fixation, suggest that this difference reflects different transformations from a retinocentric to a head-centric frame of reference. This difference appears to be mainly due to an asymmetry in the effect of retinal image motion direction on localization during smooth pursuit.

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Introduction

When we keep our head still with respect to the world, the retinal location where the image of an object in the visual field is projected depends on two factors: the position of the object with respect to the head of the observer and the gaze direction. Similarly, the retinal image motion of an object is affected by eye movements. Therefore, our visual system has to take gaze direction and eye velocity into account in order to perform localization and motion perception tasks, respectively. It has to transform position and motion information from a retinocentric frame of reference into a head-centric one (relative to the head) or even into a geo-centric frame of reference (relative to the surrounding world; see [Swanston, Wade, & Day, 1987](#); [Wade & Swanston, 1996](#); [Wertheim 1994](#)). Put in other words, it has to compensate for the effects of eye movements. That this not always happens perfectly is illustrated by various perceptual errors and illusions. During smooth

pursuit eye movements, flashed objects are mislocalized in the direction of pursuit ([Brenner, Smeets, & Van den Berg, 2001](#); [Hazelhoff & Wiersma, 1924, 1925](#); [Mita, Hironaka, & Koike, 1950](#); [Van Beers, Wolpert, & Haggard, 2001](#); [Ward, 1976](#)). The same is true for the position where a pursuit target suddenly changes its luminance ([Mateeff & Hohnsbein, 1989](#); [Mateeff, Yakimoff, & Dimitrov, 1981](#)). Localization is not only affected by eye movements, but also by gaze direction ([Hill, 1972](#)). Motion perception during smooth pursuit eye movements is distorted too. Stationary objects appear to move slightly against the pursuit direction when presented briefly (the Filehne illusion: [Filehne 1922](#); [Freeman and Banks 1998](#); [Mack and Herman 1973, 1978](#); [Wertheim 1987](#)) and objects appear to move slower when tracked with the eyes than when viewed during fixation of a stationary target (the Aubert-Fleischl phenomenon: [Aubert 1886, 1887](#); [Dichgans et al. 1975](#); [Freeman and Banks 1998](#); [Von Fleischl 1882](#); [Wertheim and Van Gelder 1990](#)). The perceived direction

of objects moving non-collinearly with the pursuit target deviates from the physical motion direction and is biased towards the motion direction of the retinal image (Becklen, Wallach, & Nitzberg, 1984; Festinger, Sedgwick, & Holtzman, 1976; Souman, Hooge, & Wertheim, 2005; Souman, Hooge, & Wertheim, *In press*; Swanston & Wade, 1988). The perceived slant of a surface that moves orthogonally relative to the observer is affected by smooth pursuit eye movements as well (Freeman, 2000). Also, velocity estimates in general velocity matching tasks during smooth pursuit are biased towards the retinal image velocity (Freeman, 2001; Souman, Hooge, & Wertheim, *Submitted*; Turano & Heidenreich, 1999; Turano & Massof, 2001).

In this study we will concern ourselves with localization and motion perception during smooth pursuit eye movements, with the head kept still. Both in localization and in motion perception, the retinal signals have to be combined with gaze direction or eye movement signals in order to transform them from a retinocentric frame of reference into a head-centric one. Since in both cases this transformation is often incomplete, as illustrated by the illusions and perceptual errors mentioned above, we wanted to know whether the degree of compensation for the eye movements is the same for localization and motion perception during smooth pursuit eye movements. Although physically the relationship between location and velocity is simply one of derivation with respect to time, it is much more complex in perceptual terms. Rather than deriving velocity from the successive positions of a moving object, our brain has dedicated motion processing pathways (see e.g. Snowden, 1994, for a review). During smooth pursuit eye movements, perceived position and perceived velocity can be differently affected by for instance background motion (Smeets & Brenner, 1995). Also, the integration of retinal signals and eye movement or gaze direction signals, which constitutes the frame of reference transformation, appears to happen in separate, though proximate, areas of the brain. Area 7a (in monkeys) plays an important role in the integration of gaze direction information with retinal location information (Andersen, Essick, & Siegel, 1985; Andersen & Mountcastle, 1983; Andersen, 1989; Andersen, Essick, & Siegel, 1987), while area MST is involved in combining eye movement signals and retinal motion signals (Barton et al., 1996; Bradley, Maxwell, Andersen, Banks, & Shenoy, 1996; Ilg & Thier, 2003; Newsome, Wurtz, & Komatsu, 1988; Pack, Grossberg,

& Mingolla, 2001; Shenoy, Bradley, & Andersen, 1999). Hence, the frame of reference transformation might be different for localization than for motion perception. On the other hand, in daily life we hardly notice any conflicts between where we see objects and how they appear to move. Apparently, our visual system eventually integrates the two into one coherent percept or at least produces two independent but compatible aspects of the same percept. Consequently, although the frame of reference transformation is not necessarily the same for localization and motion perception during smooth pursuit, the end results might coincide.

We studied the relationship between perceived position and perceived motion during smooth pursuit eye movements in an experiment in which participants judged both the position and motion direction of a moving dot. From the literature, it is known that a vertically moving object is perceived as moving along a slanted path during horizontal smooth pursuit eye movements (Becklen et al., 1984; Hansen, 1979; Souman et al., 2005; Souman et al., *In press*; Swanston & Wade, 1988). This is generally interpreted as the consequence of an incomplete transformation of the retinocentric frame of reference into a head-centric one. If the degree of compensation for the effects of smooth pursuit eye movements is the same for localization and motion perception, one would expect that the starting and end points of the perceived motion trajectory define the same direction as that indicated by participants in a motion direction judgement task. This hypothesis was tested. Moreover, we investigated whether localization and motion perception are similarly affected by a factor that is known to influence the frame of reference transformation in motion perception: the stimulus presentation duration. Generally, the longer a moving object is presented, the higher the degree of compensation is (De Graaf & Wertheim, 1988; Ehrenstein, Mateeff, & Hohnsbein, 1986; Mack & Herman, 1973; Souman et al., 2005). In other words, the deviation of the perceived velocity from the physical one gets smaller. We tested whether this is also true for localization during smooth pursuit eye movements.

Experiment 1

Methods

The experiments described in this study were conducted in compliance with the medical-ethical regulations of Utrecht University and with the 1964 Declaration of Helsinki.

Participants

Seventeen students (12 female, 5 male) from Utrecht University served as participants (ranging from 18 to 24 years of age, mean 21 years). They were paid for their participation. All participants gave their written informed consent before the experiment, but they were not informed of the hypotheses of the experiment. All participants had normal or corrected-to-normal vision.

Apparatus and stimuli

The stimuli were presented on a 19" computer screen (Iiyama Vision Master Pro 450), with a resolution of 1152×864 pixels and a refresh rate of 100 Hz. Stimulus presentation and response registration were controlled by custom made software running on a Pentium III pc (Dell Dimension 4100; clock speed 933 MHz). The participant's head rested on a chinrest, with the nose kept against a short blunt bar to help minimize head movements. Viewing was binocular, with a viewing distance of 60 cm. Eye movements were measured from both eyes using an infrared video-based eye tracking device, sampling at 250 Hz (Eyelink system, SMI Sensomotoric Instruments, Teltow, Germany).

Participants were presented with a horizontally moving dot that they had to follow with their eyes (the pursuit target) and with a second, vertically moving dot (the stimulus), of which they had to judge either the motion direction, the position where it appeared on the screen (starting position), or the position where it disappeared (the end position). Both the pursuit target and the stimulus consisted of a small grey dot (5×5 pixels $\approx 0.15^\circ \times 0.15^\circ$), of which the luminance was kept low (~ 0.04 cd/m²) to minimize after glowing effects. Both dots were presented against a completely black background (lum. < 0.01 cd/m²). The pursuit target always moved horizontally, either leftwards or rightwards, at a speed of 10° /s (after initial acceleration,

see Procedure), covering a visual angle of 20° . The stimulus dot always moved vertically, upwards or downwards, at a speed of 5° /s. After each presentation of pursuit target and stimulus dot, a measurement probe was presented. In trials that measured the perceived motion direction of the stimulus dot, an arrow (6 cm $\approx 5.7^\circ$ long) was presented in the centre of the screen. Participants could rotate the arrow with the computer mouse and indicate in this way the perceived motion direction of the stimulus dot. In localization trials, measuring either the starting point of the stimulus dot or its end point, a cross hair cursor (consisting of two orthogonal line segments, each 2 cm $\approx 1.9^\circ$ long) appeared on the screen. Participants could move the cursor with the mouse to indicate the starting point or end point. The luminance of both measurement probes was kept low (~ 0.01 cd/m²), again to minimize after glowing. The experiment was conducted in a completely darkened room and the pursuit target and stimulus dot or the measurement probe were the only things visible.

Procedure

Stimulus presentation duration (300, 700, or 1100 ms), pursuit direction (leftward or rightward) and stimulus direction (upward or downward) were varied. The twelve resulting conditions were presented twice. They were divided into six blocks, each with twelve trials. In two of the blocks, participants had to judge the motion direction of the stimulus, in two they had to judge the starting point of the stimulus and in two the end point. The order of blocks was randomized for each participant, as was the order of trials within each block.

Each trial started with the appearance of the pursuit target at the left or right side of the screen. It stayed stationary for 1000 ms and then accelerated linearly to 10° /s in 500 ms, after which it kept on moving at this speed until it had covered 20° of visual angle. The vertically moving stimulus dot was presented during the constant velocity phase of the pursuit target. The location of the vertical stimulus path was chosen randomly in each trial between 2.5° to the left of the centre of the screen and 2.5° to the right of it, to make the locations of the starting and end points unpredictable. The pursuit target crossed the stimulus dot when that was at the centre of its vertical path. Immediately after the pursuit target disappeared, the measurement probe appeared. In trials that measured the perceived direction, the arrow

was presented at a random orientation. In localization trials, the cross hair cursor was presented at a random location within a radius of 10° from the centre of the screen. After the participant had indicated either the perceived direction or location, the trial could be repeated by pressing the right mouse button or the next trial could be started by pressing the left button. If a trial was repeated, the measurement probe appeared at the orientation or position where it was last put by the participant. The participants used on average 2.0 repetitions.

Data analysis

The eye movement data were analysed to test for accurate pursuit. The measured eye positions were first averaged across both eyes, after which they were low-pass filtered using a seven-point running average. Trials in which saccades were made during the presentation of the stimulus were discarded, because for these trials it is not clear whether the percept resulted from (under-) compensation for the smooth pursuit eye movements or from factors related to the presence of saccades (see e.g. Mateeff 1978; Matin, Matin, & Pearce 1969; Matin, Matin, & Pola 1970; Park et al. 2001). A trial was marked as saccadic if the horizontal eye velocity exceeded $60^\circ/s$. Trials with low (< 0.8) or high (> 1.2) pursuit gain were also discarded, to prevent large differences in eye

velocity from contaminating the data. To compute the pursuit gain, the slope of the best fitting linear regression line of the horizontal eye position during stimulus presentation as a function of time was computed and divided by the velocity of the pursuit target. Because participants could repeat trials as often as they wanted, they could in principle keep their eyes stationary in one repetition and use this percept to indicate the perceived position or direction in the next repetition. To prevent this from affecting the data, we applied the most stringent criterion possible and removed a trial from further analysis if the abovementioned criteria were not met on all repetitions of that trial.

The localization and direction responses were averaged across pursuit direction and stimulus direction, as we had previously found that these factors did not affect the perceived motion direction during smooth pursuit (Souman et al., 2005; Souman et al., In press). In the present experiment, there were insufficient replications per condition to test for the effects of pursuit direction and stimulus direction. To test the effects of the type of task (localization of starting points and end points and indicating the perceived motion direction) and of the presentation duration of the stimulus for significance, two-factor univariate repeated measures analyses (SPSS 10.1), with a significance level of $\alpha = 0.05$, were used.

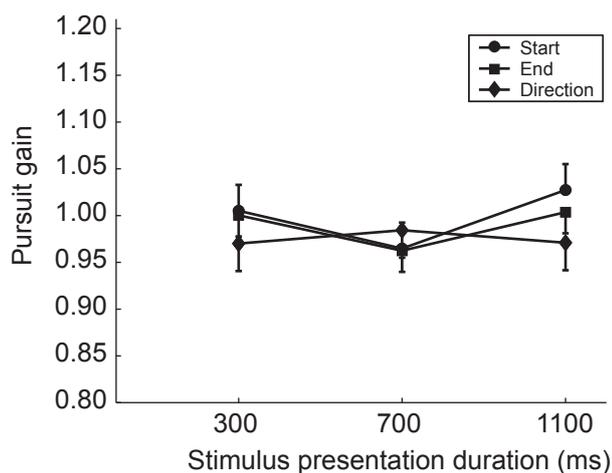


Figure 1. Average pursuit gain versus stimulus presentation duration in Experiment 1 ($n = 11$). The error bars represent the 95% confidence intervals of the means, based on the MS of the interaction terms of participants, task and presentation duration; see Loftus and Masson (1994) and Masson and Loftus (2003).

Results and discussion

For six of the seventeen participants, the removal of trials with inaccurate pursuit had as a consequence that in some combinations of task (starting point, end point, or direction) and presentation duration no valid trials remained. The data of these participants were therefore removed from further analysis. The loss of about a third of the participants due to inaccurate pursuit is not uncommon in this kind of experiments when strict pursuit criteria are used (see Souman et al. 2005; Souman et al. In press). Of the trials of the remaining eleven participants, 32% had to be removed due to inaccurate pursuit. Only the remaining trials with accurate pursuit were used in the further analyses. As can be seen from Figure 1, the average pursuit gain in these trials was close to unity and showed only small, though significant, effects of the presentation duration of the stimulus ($F(2; 20) = 6.35, p = 0.007$) and the type

of task (starting point, end point, or motion direction; $F(2; 20) = 4.43, p = 0.026$). The interaction effect was not significant.

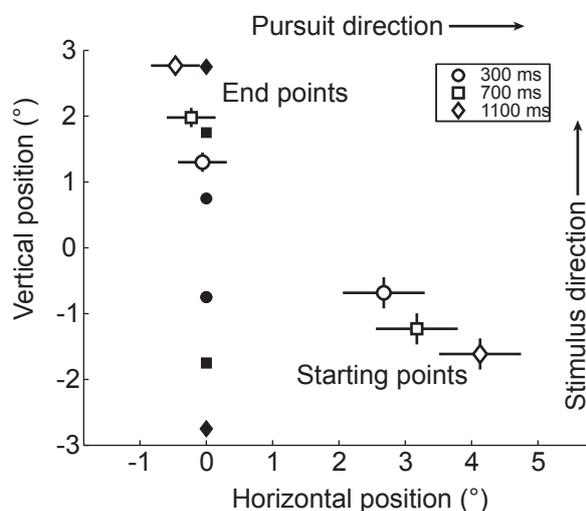


Figure 2. Starting points and end points during smooth pursuit eye movements for three stimulus presentation durations (Experiment 1). The small closed symbols indicate the physical starting and end points, while the bigger open symbols represent the mean settings of 11 participants. Error bars are as in Figure 1. The indicated positions have been plotted as if pursuit were to the right and stimulus motion upward.

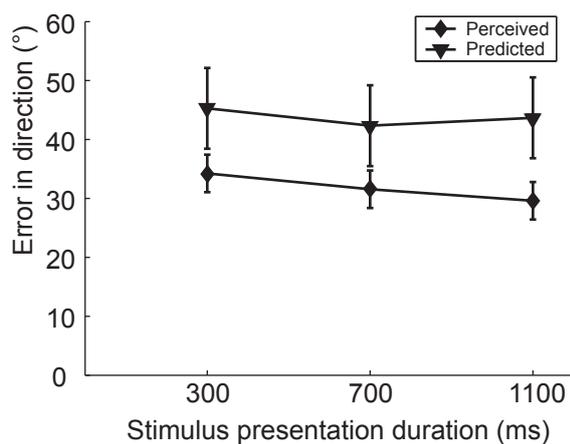


Figure 3. Average errors in indicated motion direction and in the direction predicted from the indicated starting and end points (relative to the physical, vertical motion direction) in Experiment 1. Error bars as in Figure 1. Positive errors indicate a deviation away from the pursuit direction.

Figure 2 shows the indicated starting and end points of the stimulus relative to the physical positions. The positions are plotted as if pursuit were to the right and the stimulus moved upwards. The starting positions were strongly mislocalized in the direction of pursuit and this error was larger with longer presentation durations. This makes sense if one realizes that at the moment that the stimulus dot appeared, the pursuit target moved towards the stimulus dot. With longer presentation durations, the eccentricity of the retinal image of the stimulus was therefore larger, resulting in larger errors. The errors appear to indicate incomplete compensation for the eye movements. The end points of the stimulus were mislocated in the other direction, but the errors were much smaller than those for the starting points. Both starting and end points also exhibited mislocalization in the (vertical) stimulus motion direction at some presentation durations.

The average errors in the indicated motion direction are shown in Figure 3. The average directions indicated by the participants deviated about 30° from the physical (vertical) direction towards the retinal image direction. This error decreased slightly with longer presentation durations. Figure 3 also shows the direction that would be predicted on the basis of the localization data. The orientation of the line that connects the average starting points and end points was computed per participant and the average deviations from the vertical are shown in Figure 3. This predicted direction error was consistently higher than the actual indicated directions. A repeated measures analysis confirmed the reliability of this difference ($F(1, 10) = 16.12, p = 0.002$). Presentation duration did not have a significant effect, nor was there a significant interaction effect. The absence of a significant effect of presentation duration on perceived direction was unexpected. On the other hand, our data do show a slight decrease in the deviation of the indicated direction from the physical one with presentation duration. In an earlier study, we found a significant effect of presentation duration in one experiment (with a larger range of durations: 200 ms to 1400 ms) and an effect that just failed to reach significance in the other experiment (Souman et al., 2005). Apparently, if an effect of presentation duration exists, it is not a very strong one.

The difference between the directions predicted from the localization data and the actual indicated directions suggests that the degree of compensation is not the same in localization and motion perception

during smooth pursuit. However, this conclusion only holds if we assume that the perceived motion direction equals the direction predicted from starting and end points during fixation. Since localization and perceived motion direction were assessed with different tasks, this assumption is not necessarily valid. Therefore, we performed a second experiment, in which the same tasks were carried out during fixation. This would possibly also shed light on the effect of the stimulus presentation duration on localization, particularly of the starting points.

Experiment 2

Methods

Participants

Six staff members (two female, four male) of the Psychonomics Department of Utrecht University, including the first two authors, served as participants. Except for the two authors, the participants were not informed of the hypotheses of the experiment. All had normal or corrected-to-normal vision. Their age ranged from 23 to 38 years (mean 31).

Apparatus and stimuli

The same apparatus and stimuli as in Experiment 1 were used. Instead of a moving pursuit target, participants were now presented with a stationary fixation target. The stimulus dot moved in one out of four directions (63.4°, 116.6°, 243.4°, or 296.6°), which equalled the retinal image directions with accurate pursuit in Experiment 1.

Procedure

The same three stimulus presentation durations as in Experiment 1 (300, 700, and 1100 ms) were combined with four stimulus motion directions. All twelve resulting conditions were replicated three times for all three tasks (starting point, end point, direction). The experiment was divided into three blocks, each with a different task. The order of blocks was randomized

across participants. Within each block, the order of trials was randomized as well.

Each trial started with the presentation of the fixation target. The horizontal position of the fixation target was randomly chosen between 2.5° left of the centre of the screen and 2.5° right of it. After 2100, 1900, or 1700 ms the moving stimulus dot appeared for respectively 300, 700, or 1100 ms. It crossed the fixation target halfway its path. Respectively 850, 650, or 450 ms after stimulus disappearance, the fixation dot disappeared and the measurement probe (arrow or cross hair cursors) was presented. The participants indicated the perceived position or direction in the same way as in Experiment 1.

Data analysis

The eye movement data were checked for accurate fixation. A trial was discarded from further analysis if the eye velocity exceeded 50°/s. For the remaining trials, the direction predicted from the indicated starting and end points was again computed and compared to the actual indicated directions. The indicated starting and end points and the indicated motion directions were averaged across the four stimulus directions.

Results and discussion

Three of the six participants showed accurate fixation in all trials. For the other three participants, on average 10% of the trials was removed from further analysis because of eye movements. The indicated starting and end points are shown in Figure 4. As can be seen from this figure, the localization errors were much smaller than during smooth pursuit (cf. Figure 2). There still was an effect of presentation duration, to the effect that the path of the stimulus defined by the indicated starting and end points was relatively shorter for longer presentation durations. A repeated measures ANOVA with presentation duration and task (starting points vs. end points) as factors showed that this effect of presentation duration was significant ($F(2; 10) = 5.047$; $p = 0.031$). The errors in the localization of the starting points were also slightly bigger than those of the end points ($F(1; 5) = 11.665$; $p = 0.019$).

Figure 5 shows the indicated motion direction and the direction predicted from the indicated starting and

end points as a function of presentation duration. The deviation of the average indicated direction from the physical one was small (about 2.5°) and decreased slightly with presentation duration. This deviation was away from the vertical and may therefore be a case of reference repulsion (Raubert & Treue, 1998). The directions predicted from the localization data deviated slightly more from the physical direction than

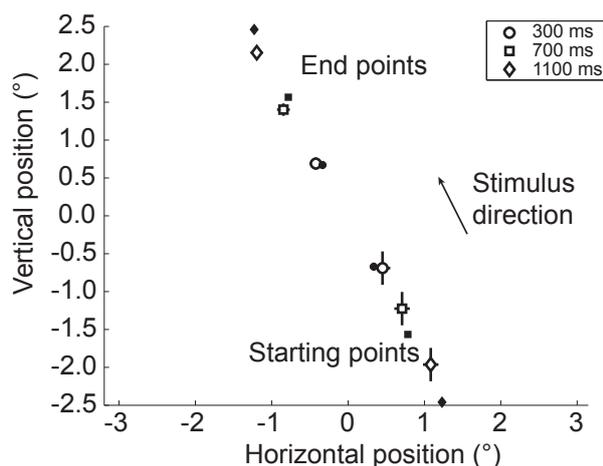


Figure 4. Average indicated starting points and end points during fixation for three stimulus presentation durations (Experiment 2; $n = 6$). Symbols and error bars as in Figure 2. The positions have been plotted as if the stimulus direction was 116.6° .

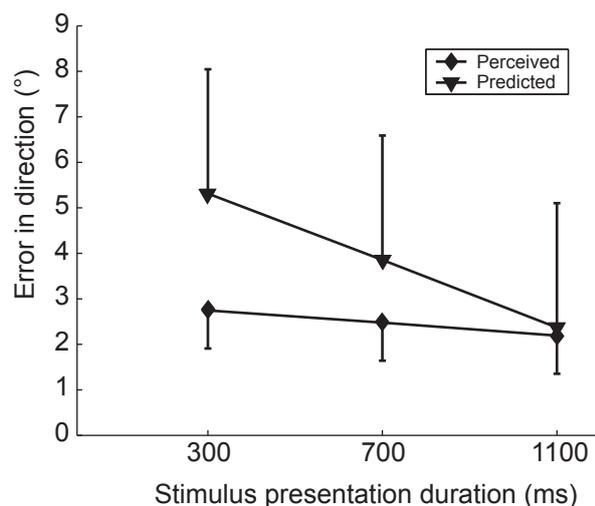


Figure 5. Average errors in indicated motion direction and in the direction predicted from the indicated starting and end points (relative to the physical motion direction) in Experiment 2. Error bars as in Figure 1. Positive errors indicate a deviation towards the horizontal axis.

the indicated directions. However, a two-way repeated measures analysis showed that the difference between the indicated directions and the predicted directions was not significant, nor was the effect of presentation duration or the interaction effect. Hence, localization and perceived motion direction during fixation are consistent with each other, at least for the direction and presentation durations tested. This means that the difference between the indicated motion directions and the direction predicted from localization during smooth pursuit, found in Experiment 1, is not due to a difference between localization and motion perception per se, but to the effect of the smooth pursuit eye movements. Also, the difference between the predicted and the indicated directions in Experiment 1 was not the result of the use of different measurement methods in the localization and the motion direction tasks.

We did not find a difference in the effect of presentation duration on the localization of starting points and end points during fixation (the interaction effect of presentation duration and localization task was not significant). In both cases, the perceived motion path appears to shrink relative to the physical path with longer presentation durations. Consequently, the difference between the mislocalization of the starting points and the end points during smooth pursuit in Experiment 1 cannot be explained from the localization data during fixation.

General discussion

The difference found in Experiment 1 between the motion direction indicated by the participants and the direction predicted from the indicated starting and end points cannot be explained by differences in motion perception and localization per se. During fixation, we found no reliable difference between the two. Our results therefore seem to indicate that the compensation for the effects of the smooth pursuit eye movements produce different results for motion perception and localization. What might be the cause for this difference? First of all, it is important to note that the degree of compensation for the effects of the eye movements are determined by more factors in the case of localization than with motion perception, at least as far as our experiment is concerned. Because both the pursuit target velocity and the stimulus velocity were constant in Experiment 1, the perceived

motion is only determined by the relative magnitude of the retinal motion signal and the eye movement signal (see Freeman and Banks 1998; Souman et al. In press). With localization, however, the perceived positions are not only determined by the estimated retinal position and the gaze direction, but also by the relative timing of both. From several studies it appears that the retinal signal lags the eye position signal by about 100 ms (Brenner et al., 2001; Mita et al., 1950; Schlag & Schlag-Rey, 2002; Ward, 1976). This latency difference, however, would have a different effect on the indicated positions than the error in the estimation of the retinal positions and the gaze direction. The first one would shift the whole path in the direction of pursuit, while the latter would rotate the perceived path, just as in motion perception. These two effects can be seen in Figure 2. The paths defined by starting points and end points are rotated away from the vertical and they are also shifted in the pursuit direction. However, the latency difference does not affect the direction that is predicted from the starting and end points and can therefore not explain the difference between indicated and predicted directions.

From Figure 2, it can also be seen that the degree of rotation for the line through the indicated starting points at the different presentation durations is larger than for the end points. Apparently there is another factor in play, which has different effects on the localization of the starting points than on that of the end points. The difference between the directions predicted from the localization data and the indicated directions seems mainly due to this difference between starting and end points. Possibly, this is due to the different retinal motion directions of the stimulus at the starting and end points. In localization during smooth pursuit, an asymmetry has been found between localization of foveofugal and foveopetal stimuli (Mateeff & Hohnsbein, 1988; Mateeff et al., 1991; Mitrani & Dimitrov, 1982). If the eye moves towards the stimulus (e.g., a flash), the mislocalization in the direction of the eye movement is larger than when it moves away from it. In the latter (foveofugal) case, the mislocalization sometimes even is in the opposite direction (Mateeff & Hohnsbein, 1988). This prompted Van Beers et al. (2001) to suggest that the visual system might use separate eye velocity estimates for the localization of foveopetal and foveofugal stimuli. The difference between foveopetal and foveofugal stimuli might explain the different localization errors we found in Experiment 1. When the stimulus appeared, the pursuit target (and the eye) moved towards the stimulus

dot. Hence, at the starting point it was a foveopetal stimulus and, consequently, large localization errors in the direction of pursuit resulted. When the stimulus disappeared, however, the pursuit target had already crossed the stimulus path and the end point formed a foveofugal stimulus. The end points were therefore mislocated much less than the starting points, and in the opposite direction. This differential effect on starting and end points might explain the difference between the directions predicted from the localization data and the indicated directions.

There is another factor that may have contributed to the difference between the localization errors in starting and end points. The accuracy of localization is affected by the time interval between stimulus presentation and response (Sumi, 1971). Localization errors increase with longer intervals. Naturally, the time interval between stimulus disappearance and response in our experiments was shorter than that between stimulus appearance and response. Would this explain the different localization errors of starting points and end points and, consequently, the difference between the indicated directions and the directions predicted from the localization data? To explore this possibility, we did the following analysis. In Experiment 1, the time interval between stimulus presentation and response was not only determined by the task (indicate starting point vs. end point) and the presentation duration of the stimulus, but also by the location at which the stimulus was presented during the smooth pursuit, which was random. If the path of the stimulus was located early in the pursuit sweep, the time until response was longer (both for starting point and end point) than when the stimulus was located more towards the end of the pursuit sweep. The effect of this time interval can therefore be assessed by studying the localization data as a function of the location of the stimulus path in the pursuit sweep. We regressed both the horizontal and the vertical components of the indicated starting and end points on stimulus path location and used the obtained regression coefficients to adjust the localization data (in effect performing a covariance analysis). These adjusted localization data differed only very slightly from the original data, indicating that the time until response hardly affected the errors in localization. The indicated directions were also hardly affected by the adjustment, which corresponds to our earlier findings (Souman et al., 2005). Hence, the difference in time until response appears to have had only a minor

effect on the localization data and cannot explain the difference found between the indicated directions and the directions predicted from localization.

In conclusion, we have shown that the perceived motion direction of a stimulus viewed during smooth pursuit eye movements cannot directly be predicted from the indicated starting and end points of the stimulus. From the results of Experiment 2, we conclude that this difference reflects a different outcome of the transformation from a retinocentric frame of reference to a head-centric one and not a difference between localization and motion perception per se. The compensation for the effects of the eye movements in localization appears to be more complicated than that in motion perception, at least in our task. While the perceived motion direction is mainly determined by the relative magnitudes of the retinal signal and the eye movement signal, the localization is also affected by the relative latency of the signals and by asymmetries in retinal motion direction.

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6

Frame of reference transformations in motion perception during smooth pursuit eye movements

Abstract

Smooth pursuit eye movements change the retinal image velocity of objects in the visual field. In order to change from a retinocentric frame of reference into a head-centric one, the visual system has to take the eye movements into account. Studies on motion perception during smooth pursuit eye movements have measured either perceived speed or perceived direction during smooth pursuit to investigate this frame of reference transformation, but never both at the same time. We devised a new velocity matching task, in which participants matched both perceived speed and direction during fixation to that during pursuit. In Experiment 1, the velocity matches were determined for a range of stimulus directions, with the head-centric stimulus speed kept constant. In Experiment 2, the retinal stimulus speed was kept approximately constant, with the same range of stimulus directions. In both experiments, the velocity matches for all directions were shifted against the pursuit direction, suggesting an incomplete transformation of the frame of reference. We fitted the classical linear model, the model of Turano and Massof (2001) and that of Freeman (2001) to the velocity matches. The model of Turano and Massof fitted the velocity matches best, but the differences were quite small. Evaluation of the models and comparison to a few alternatives suggests that further specification of the potential effect of retinal image characteristics on the eye movement signal is needed.

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Introduction

Eye movements change the retinal image motion of objects in the visual field. For instance, in the case of smooth pursuit eye movements at a constant angular velocity, a constant velocity is added to the retinal motion. The retinal image of a stationary object will move across the retinae with the velocity at which the eyes are moving and the image of an object that moves at the same velocity as the eyes will be approximately stationary on the retinae. To arrive at a veridical estimate of the motion of the objects in the outside world in a geocentric frame of reference, the visual system has

to apply multiple coordinate system transformations (Swanston, Wade, & Day, 1987; Wade & Swanston, 1996). The images of both eyes have to be combined into a single binocular representation. Moreover, eye movement information has to be incorporated to produce an ego-centric (or head-centric) representation. Finally, a geocentric representation can be produced by taking object-distance information and self-motion information into account.

In this paper we will focus on the second step in the model of Wade and Swanston: the transformation from a retinocentric representation into a head-centric one. We will restrict ourselves to the perception of motion

during smooth pursuit eye movements, with the head kept still. Also, we will concern ourselves with the perception of a single motion stimulus during pursuit, not with the perception of one stimulus relative to others (termed *non-uniform motion* by Wade & Swanston, 1987, and requiring a pattern-centric frame of reference according to Wade & Swanston, 1996). By doing so we limit ourselves to the simplest case of coordinate system transformation, making it easier to specify the characteristics of this transformation.

Most studies on motion perception during smooth pursuit eye movements have only looked at collinear stimulus motion (i.e., with a stimulus moving along the line of pursuit; horizontally in most cases). In these studies perceived speed is used as the dependent variable to quantify the degree to which the transformation from a retinal frame of reference into a head-centric one is complete (see e.g., Freeman & Banks, 1998; Mack & Herman, 1973; Turano & Heidenreich, 1999; Wertheim, 1987). Other studies have focused on the perception of non-collinear motion during smooth pursuit (i.e., moving at an angle other than 0° or 180° relative to the pursuit direction). In these cases the perceived motion direction is used to quantify the degree of compensation for the effects of the eye movements (Becklen, Wallach, & Nitzberg, 1984; Festinger & Easton, 1974; Festinger, Sedgwick, & Holtzman, 1976; Hansen, 1979; Holtzman, Sedgwick, & Festinger, 1978; Souman, Hooge, & Wertheim, 2005; Souman, Hooge, & Wertheim, In press; Swanston & Wade, 1988; Swanston, Wade, Ono, & Shibuta, 1992). Consequently, these two groups of studies have investigated the same process (the transformation of a retinocentric frame of reference into a head-centric one) with different paradigms, which makes them hard to compare. The matter is complicated even more by other differences between the studies, such as the use of a single dot stimulus vs. random dot patterns, constant angular velocity vs. sinusoidal motion and different pursuit and stimulus speeds. It is therefore unclear whether perceived motion direction is affected by smooth pursuit eye movements in the same way as perceived speed is, or whether the effect of smooth pursuit eye movements is the same for different stimulus directions.

It is far from trivial to experimentally measure both perceived speed and perceived direction and know they belong to the same percept. Ideally, perceived direction and perceived speed should be measured at the same time. We developed a new matching task to do exactly

that. Participants were presented with two stimulus intervals. In the first one, they viewed the motion stimulus (a moving random dot pattern) during ocular pursuit of a moving target and in the second interval during fixation of a stationary target. In the second interval, the participant could adjust both the speed and the motion direction of the random dots on-line by means of a track ball. The direction in which the track ball was scrolled determined the motion direction of the dots and their speed was determined by the degree to which it was scrolled. This allowed participants to simultaneously adjust the velocity of the stimulus in two dimensions, in an intuitive way. Their task was to adjust the velocity of the random dot pattern in the fixation interval to match the perceived velocity in the pursuit interval. We conducted two experiments in which the participants were presented with stimulus motion in various directions. Our aim was to study whether smooth pursuit eye movements have the same effects on perceived velocity for stimuli moving in different directions. Furthermore, we tested which of the existing models of motion perception during smooth pursuit eye movements described the velocity matches in our experiments best.

Models of motion perception during smooth pursuit

Historically, the transformation of a retinocentric coordinate system into a head-centric one has been mainly viewed as a simple linear combination of retinal velocity and eye velocity (Freeman & Banks, 1998; Von Holst, 1954; Von Holst & Mittelstaedt, 1950):

$$\hat{\mathbf{h}} = \rho \mathbf{r} + \epsilon \mathbf{e} \quad (1)$$

where $\hat{\mathbf{h}}$ is the perceived head-centric stimulus velocity, \mathbf{r} denotes the retinal velocity vector, \mathbf{e} is the eye velocity vector and ρ and ϵ represent the gains of the retinal and the eye movement signal, respectively. The two terms $\rho \mathbf{r}$ and $\epsilon \mathbf{e}$ describe respectively the retinal image velocity $\hat{\mathbf{r}}$ and the eye velocity $\hat{\mathbf{e}}$ as estimated by the visual system. In the context of this linear model, classical illusions of motion perception during smooth pursuit, such as the Filehne illusion (Filehne, 1922: a stationary object is perceived to move in the opposite direction to the eye movement) and the Aubert-Fleischl

phenomenon (Aubert, 1886, 1887; Von Fleischl, 1882: a moving object appears to move slower when tracked with the eyes than during fixation) are explained by a retinal signal gain that is higher than the eye movement signal gain ($\varepsilon/\rho < 1$). This gain ratio is the single free parameter of the linear model.

More recently, some alternatives to the classical linear model have been proposed. According to Wertheim (1994), the estimate of the eye velocity in the linear model ($\hat{e} = \varepsilon e$) should be extended to include visual and vestibular information. His argument for this extension was that the retinal image velocity of objects in the visual field is not only affected by eye movements, but also by head and body movements. As participants kept their head still in our experiments, we will assume that the contribution of the vestibular signals was minimal. Our stimulus did, however, generate an optic flow pattern, which according to Wertheim (1994) might affect the eye movement signal. As our stimulus had a constant rotational velocity throughout each trial, its optic flow would signal an eye movement in the opposite direction to the retinal image motion. Hence, an implementation of Wertheim's idea specifically targeted at our experiments would be:

$$\hat{\mathbf{h}} = \rho \mathbf{r} + (\varepsilon \mathbf{e} - \gamma \mathbf{r}) \quad (2)$$

where γ denotes the gain of the visual component in the eye movement signal. However, this equation can also be written as:

$$\hat{\mathbf{h}} = (\rho - \gamma) \mathbf{r} + \varepsilon \mathbf{e} \quad (3)$$

implying that, without further specification of how ρ and γ depend on the retinal input, this extended model cannot be discriminated from the classical linear model (Eqn. 1). Consequently, this particular implementation of Wertheim's model makes the same predictions as the classical linear model.

In the model by Turano and Massof (2001) the estimate of the eye velocity is also affected by both retinal and extraretinal input. In their model, however, the relationship between input velocities and the estimated velocities is non-linear. The perceived head-centric velocity equals the sum of this estimated eye velocity

$$\hat{e} = R'_{\max} \left(\frac{1}{1 + e^{-\varepsilon e - \alpha r}} - \frac{1}{2} \right) \quad (4)$$

and the estimated retinal velocity

$$\hat{r} = R_{\max} \left(\frac{1}{1 + e^{-\rho r}} - \frac{1}{2} \right) \quad (5)$$

where R_{\max} and R'_{\max} determine the asymptotic values of the functions, and ε , α and ρ determine the contributions of the eye movement velocity e and the retinal image velocity r . We extended Turano and Massof's model to two dimensions by applying equations (4) and (5) separately to the horizontal and vertical components of the velocities involved in our experiments and then combining those in one velocity vector. The model has four free parameters (ε , ρ , α and $h = R_{\max}/R'_{\max}$).

Freeman (2001) too suggested that the estimates of the retinal image motion and the eye velocity by the visual system might be non-linearly related to the actual velocities. Contrary to Turano and Massof's (2001) model, however, the eye velocity estimate in his model is independent of the retinal image velocity. As in the linear model, the perceived head-centric velocity is the sum of the estimated retinal image velocity \hat{r} and the estimated eye velocity \hat{e} . Although his model was formulated in one-dimensional terms, it is easily extended to more dimensions. The transducers of retinal velocity and eye velocity that provide the visual system with their estimates have the form:

$$\mathbf{v}_{out} = \left[(\|\mathbf{v}_{in}\| + 1)^p - 1 \right] \frac{\mathbf{v}_{in}}{\|\mathbf{v}_{in}\|} \quad (6)$$

where \mathbf{v}_{in} and \mathbf{v}_{out} are the input and output velocities of the transducers and p is the power coefficient. Basically, this transducer changes the speed by applying a power function, but leaves the direction unchanged. The power coefficients for the two inputs (retinal image velocity and eye velocity) are the two free parameters of the model.

The model of Goltz et al. (2003), finally, describes the perceived head-centric velocity in terms of an interaction between local illumination gradients at various retinal locations and the eye velocity:

$$\hat{\mathbf{h}} = \left(\frac{d\mathbf{l}}{d\mathbf{x}} \right)^+ \left(\frac{d\mathbf{l}}{dt} + \frac{d\mathbf{l}}{d\mathbf{x}} \bullet \mathbf{e} \right) \quad (7)$$

where \mathbf{x} denotes retinal position, l is the local retinal illumination and $(\mathbf{v})^+$ is the Moore-Penrose pseudo-inverse of a vector \mathbf{v} . Since their model is primarily directed at stimuli with a certain orientation, such as gratings, it does not seem to be applicable to our data. Moreover, their model does not contain gain terms and

hence cannot describe the partial compensation for the effects of the eye movements in for instance the Filehne illusion and the Aubert-Fleischl phenomenon. It would be easy to extend their model with an eye movement signal gain, by premultiplying the eye velocity vector e with a gain factor, but it does not seem feasible to incorporate a retinal signal gain. For these reasons we did not fit the model of Goltz et al. (2003) to our data.

The mathematical details of the fitting procedures used to fit the linear model, the model of Turano and Massof (2001) and the model of Freeman (2001) to the data of Experiments 1 and 2 are given in the Appendix. The goodness of fit of the models was expressed in the root-mean-squared-error (*rmse*) of the model predictions. As a measure of the errors we used the geometric distance between the empirical velocity matches and the model predictions.

Experiment 1

Methods

Participants

Three students (two male, one female) from Utrecht University and the first author participated in the experiment. The students gave their written informed consent and were paid for their participation. All participants had normal or corrected-to-normal vision. The age of the participants was 19, 20, 23 and 34 years, respectively.

Apparatus and stimuli

The stimuli were presented on a 19" monitor (Iiyama Vision Master Pro 450; resolution 1152 × 864 pixels; refresh rate 100 Hz). Stimulus presentation and response collection were controlled by custom written software, running on a pc with a Pentium III processor (933 MHz). OpenGL was used to display the stimuli. Eye movements were measured from both eyes with an infrared video-based tracking system, sampling at 250 Hz (EyeLink, SMI Sensomotoric Systems, Teltow, Germany). Head movements were minimized by a chinrest and a short blunt bar against which the participants kept the tip

of their nose. Viewing was binocular, with a viewing distance of 60 cm.

A small grey dot (6 × 6 pixels, anti-aliased using OpenGL's anti-aliasing function) served as pursuit target (in pursuit intervals) or fixation target (in fixation intervals). Its luminance was kept low (0.84 cd/m²) to minimize after glowing effects. The motion stimulus that had to be judged by the participants consisted of a moving random dot pattern, presented in a stationary circular aperture (radius 14°). The luminance of dots in the outer 2° of the aperture decreased monotonically to that of the black background (lum. < 0.01 cd/m²) towards the outer edge of the aperture to minimize motion cues from the appearance and disappearance of dots. Similarly, the luminance of dots within a radius of 2° to 3° from the pursuit/fixation target decreased to that of the background in the direction of the pursuit/fixation target. Within a radius of 2° around the pursuit/fixation target the luminance of the stimulus dots equalled that of the background; hence no dots were presented in the area around the pursuit/fixation target. This dark area moved with the pursuit target in pursuit intervals. Dots that moved out of the aperture were wrapped around and entered the aperture at the opposite side. The random dot pattern consisted of dots of 5 × 5 pixels, again anti-aliased, with a luminance of 0.36 cd/m². Its density was about 1 pixel per squared degree of visual field.

The aperture within which the random dot pattern was displayed was stationary on the screen, rather than moving with the pursuit target to prevent the moving contour of the aperture from causing induced motion of the dots. This by itself might affect their perceived velocity. Because the retinal image of a stationary contour moves during smooth pursuit, we made the aperture as large as our screen permitted, thereby ensuring that its contour always was peripheral (at least 11.5° from the pursuit target). Also, this was another reason why we applied a luminance gradient at the edge of the aperture, to diminish the saliency of the edge (see above).

Design and procedure

Perceived velocity of the random dot pattern was measured under two conditions: pursuit and fixation. The pursuit condition was the condition of interest for our research questions, while the fixation condition served as a control, to see how well participants were

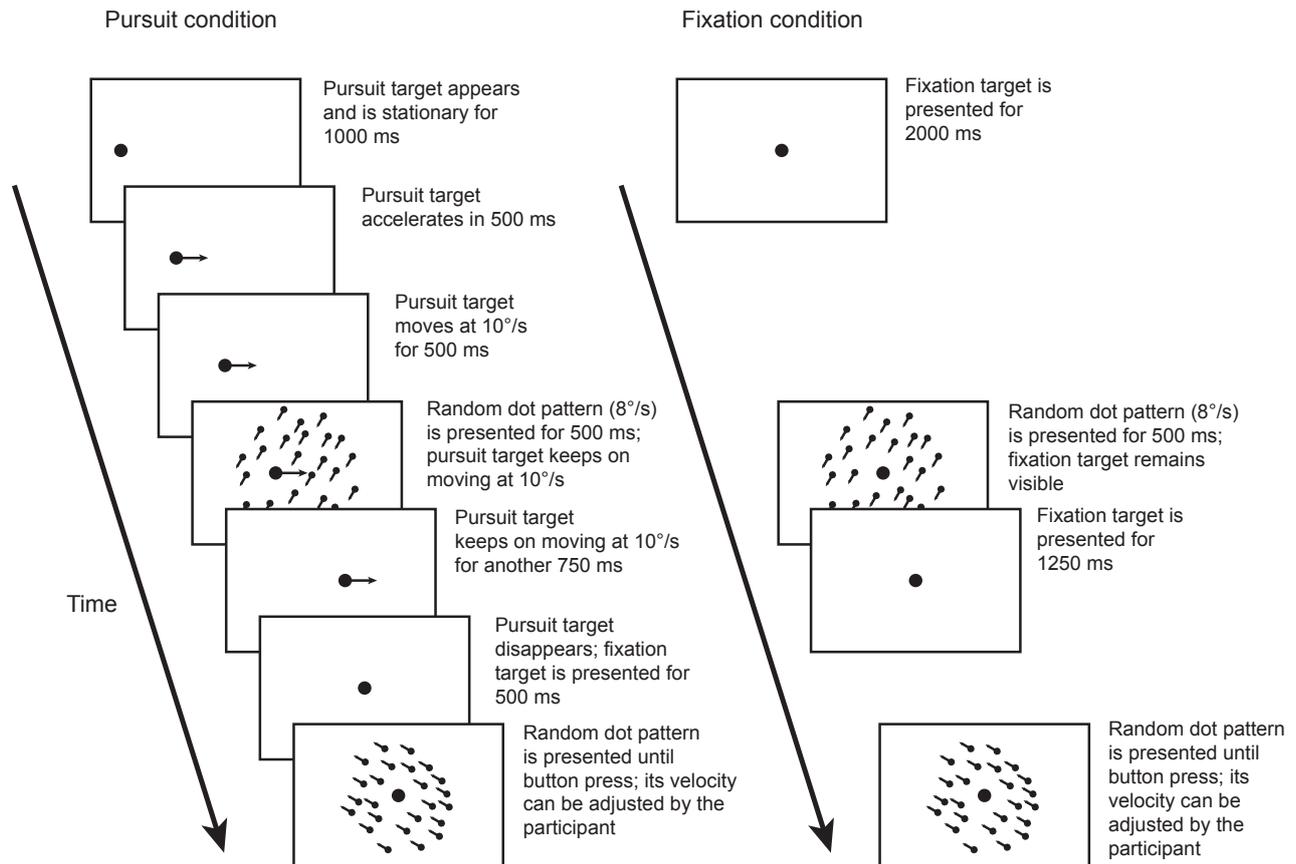


Figure 1. Experimental procedure. The left side shows the procedure in pursuit trials, the right side that in fixation trials.

able to perform the velocity matching task. In both conditions, we had participants match the velocities for 10 different stimulus directions (from 180° , or leftward, to 360° , or rightward, in steps of 20°). Each direction was presented during both leftward and rightward pursuit and replicated 10 times, resulting in 20 trials per direction. The two conditions were measured in two separate sessions, with two participants first doing the fixation condition and the other two first doing the pursuit condition. Within a session, trials were divided into 10 blocks of 20 trials, with the order of trials randomized. Each block took about 8 minutes. The two sessions were performed on different days.

In the first interval of each trial, the random dot pattern moved at a speed of $8^\circ/s$, with its direction depending on the condition tested. In the second interval, the direction and speed of the random dot pattern were determined by the participant. Scrolling the track ball in a certain direction caused the dots to move in that direction and the further the track ball was scrolled in that direction, the faster the dots moved. Each trial

could be repeated as often as the participant wanted, although participants typically used only two or three repetitions. The direction and speed of the random dot pattern in the second interval were randomly chosen in the first presentation of each trial (speed between 0 and $10^\circ/s$), and started at the last setting made by the participant in all subsequent repetitions. To repeat a trial, the participant pressed the right track ball button; to proceed to the next trial the left button was used.

The experimental procedure is illustrated in Figure 1. In pursuit trials, the pursuit target appeared on the left or right side of the screen (10° from the centre), depending on the pursuit direction. It remained stationary for 1000 ms, after which it accelerated linearly in 500 ms to $10^\circ/s$. The pursuit target then moved at this speed, until it had covered 20° of visual angle, after which it disappeared. The pursuit target moved horizontally, at eye height, with its path vertically centred on the screen. The random dot pattern was presented 250 ms before the pursuit target reached the centre of the screen and disappeared 500 ms later. Immediately after the pursuit target disappeared,

the fixation target for the fixation interval appeared at the centre of the screen and 500 ms later the random dot pattern was presented again. The dot pattern remained

visible until the participant pressed one of the track ball buttons. In fixation trials, a stationary fixation target appeared at the center of the screen in the first interval.

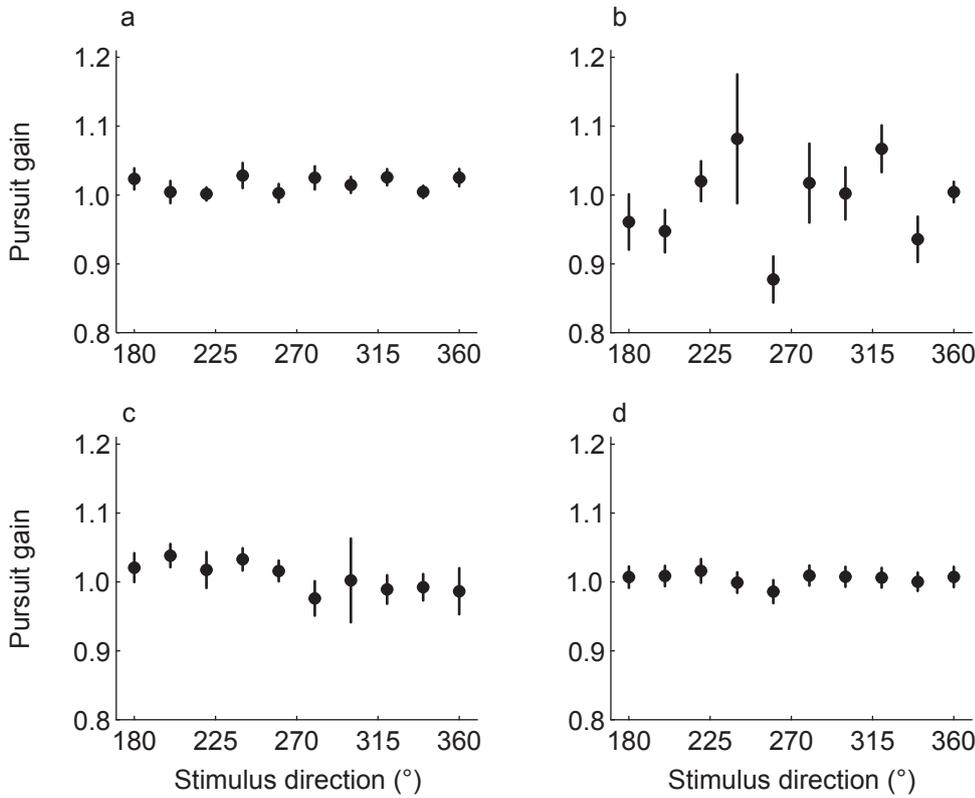


Figure 2. Average pursuit gain for the four participants in Experiment 1. The error bars represent the standard errors of the mean.

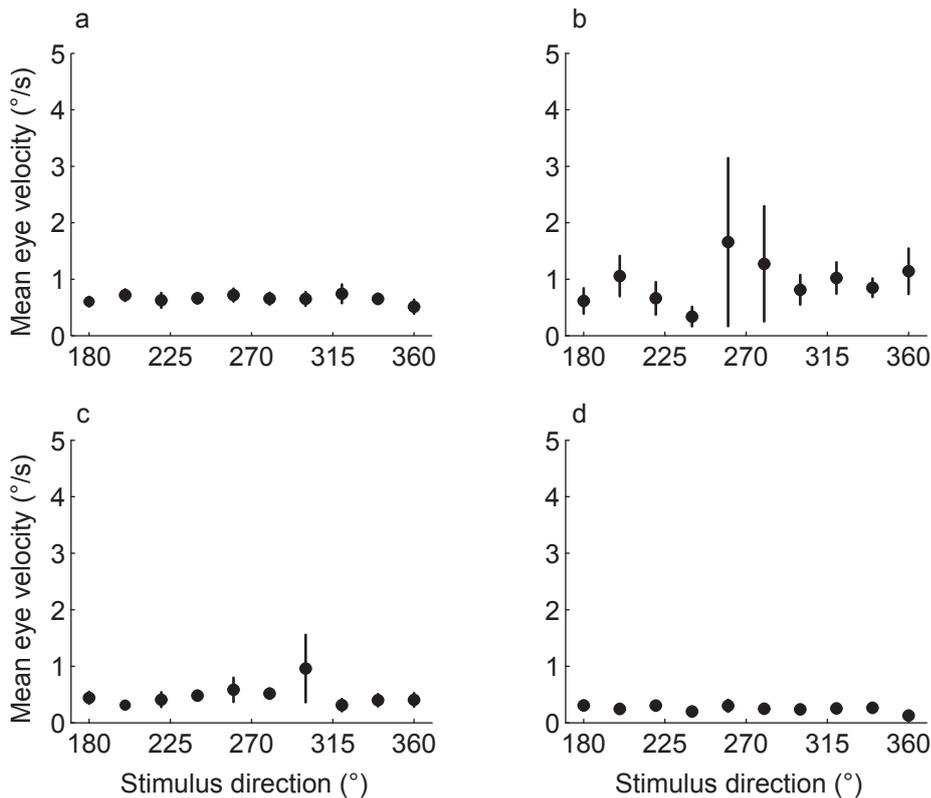


Figure 3. Average eye velocity for the four participants in the fixation interval of the pursuit trials in Experiment 1. The error bars represent the standard errors of the mean.

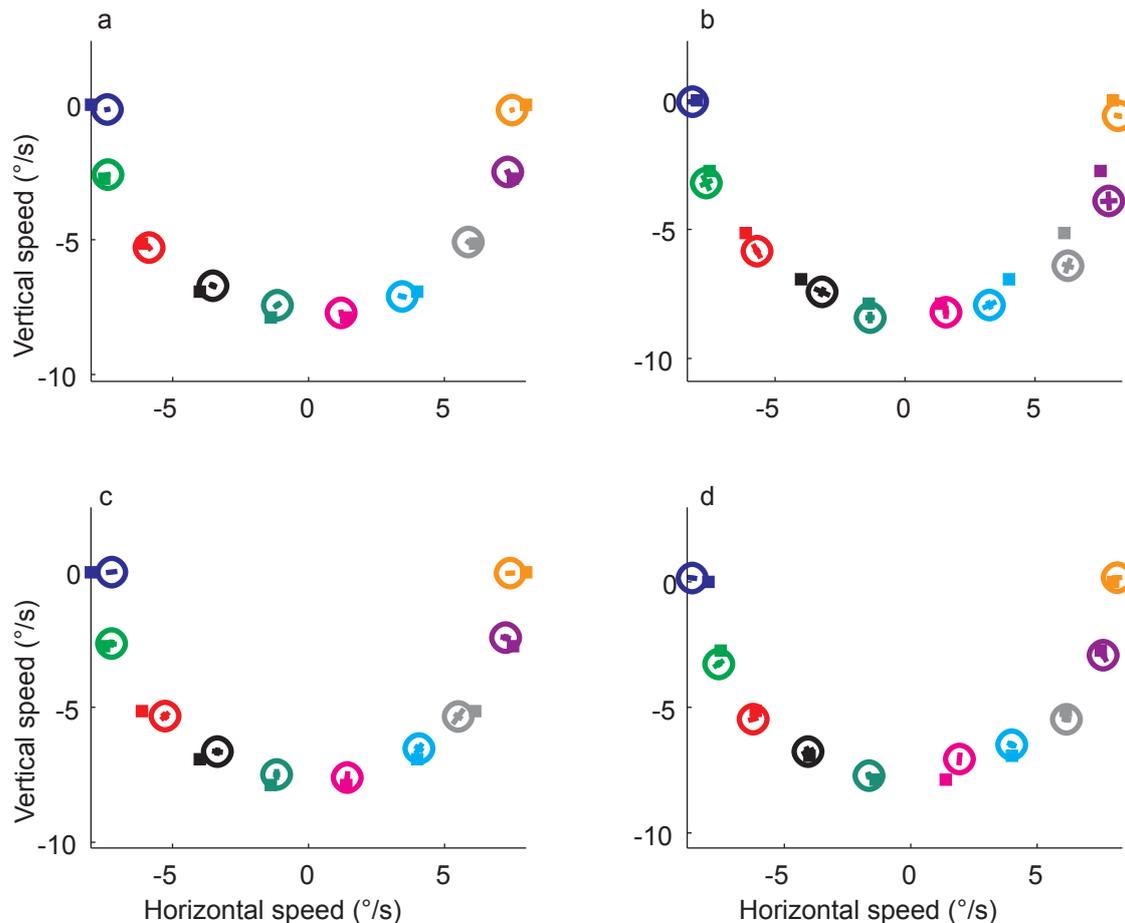


Figure 4. Velocity matches in the fixation condition for the four participants in Experiment 1. Squared symbols represent the physical velocity of the random dot pattern. Open symbols represent the average velocity match set by the participants, with the error bars representing the standard error of the mean in two dimensions (see text for details). Different colours represent different stimulus motion directions (180° to 360°).

After 2000 ms (the same time as in the pursuit intervals) the random dot pattern appeared and was presented for 500 ms. The random dot pattern then disappeared and only the fixation target was visible for 1250 ms; then the dot pattern reappeared and could now be adjusted by the participant. This ensured that the onset times of the random dot pattern in the fixation trials equalled those in the pursuit trials.

The participants first received a training block, to practice ocular pursuit and the matching task. The experiment was performed in a totally dark room, with the pursuit or fixation target and the random dot pattern being the only things visible to the participant. Between blocks the lights in the room were switched on for about 1 min, to minimize dark adaptation.

Eye movement data analysis

The eye movement data were analysed off-line to remove trials with inaccurate pursuit or fixation. First, the measured eye positions were averaged across both eyes, after which they were low-pass filtered using a seven-point running average. A trial was discarded if the eye position data from the pursuit interval contained saccades or showed a very high (> 1.2) or low (< 0.8) pursuit gain. Since saccades are known to affect motion perception and localization (Mateeff, 1978; Matin, Matin, & Pearce, 1969; Matin, Matin, & Pola, 1970; Park, Lee, & Lee, 2001), it would be unclear in saccadic trials whether any potential deviation of the matched velocity from the physical one was caused by incomplete compensation for the effects of the pursuit eye movement or by the presence of saccades. Trials were discarded as saccadic when the eye velocity (horizontal

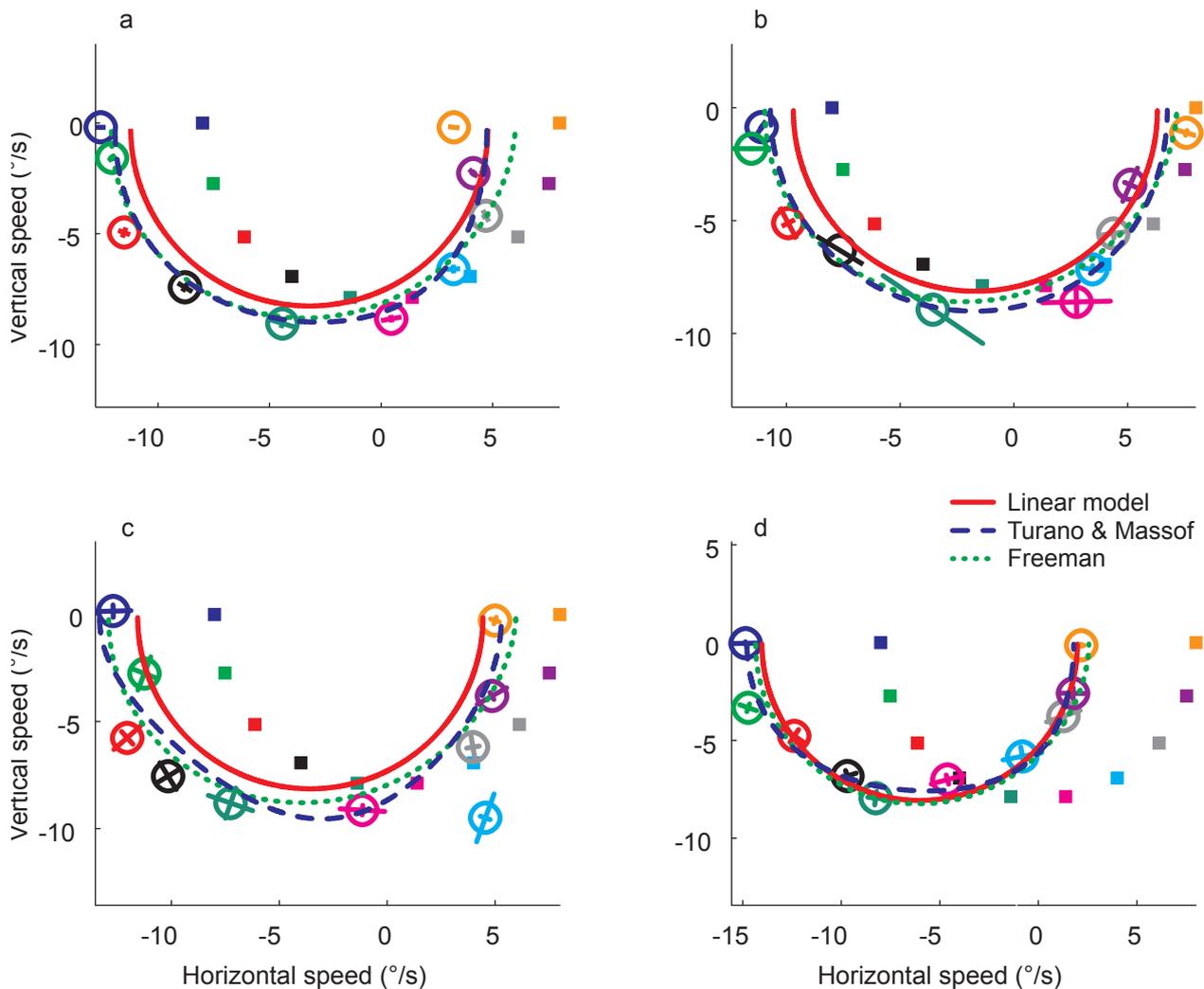


Figure 5. Velocity matches and model fits in the pursuit condition for the four participants in Experiment 1. Symbols and error bars are as in Figure 4. The continuous red lines give the best fitting model curves for the linear model (Eqn. 1), the dashed blue lines represent the non-linear model of Turano and Massof (2001) and the dotted green lines show the predictions of Freeman’s (2001) model.

and vertical components simultaneously) exceeded $50^\circ/\text{s}$. This criterion was applied both to pursuit intervals and fixation intervals. In the second interval of each trial, which was always a fixation interval, eye blinks were allowed, since this interval could last several seconds, depending on the time the participant used for adjusting the velocity of the random dot pattern. The eye movements in the final 500 ms of this interval were not analysed, because participants often started to move their eyes just before pressing the track ball button. Since a trial could be repeated as often as the participant wanted, a trial was discarded if the above mentioned criteria were not met on at least one of the repetitions, making sure only trials with accurate pursuit and fixation in all repetitions remained. The pursuit

gain in pursuit intervals was determined by computing the linear regression coefficient for the horizontal eye positions during stimulus presentation as a function of time and dividing this regression coefficient by the pursuit target speed. The average eye velocity during the fixation intervals was computed by averaging the horizontal and vertical eye speed components separately for each fixation interval, after which the square root of the sum of squares of the mean horizontal and vertical speed was taken.

Results

Because we used rather strict eye movement criteria for inclusion of trials in further analysis, a large percentage of trials was discarded (20% in fixation condition and 42% in pursuit condition). All analyses reported here concern the trials that complied with the criteria. Subsequent analysis showed that the results without discarding trials on the basis of the eye movement analysis were similar.

Figure 2 shows the pursuit gains for the four participants (in Figures 2 to 5, the panels *a* to *d* refer to participants 1 to 4, respectively). For three of them, the pursuit gain was about 1 for all stimulus directions. Participant 2, however, showed much more variability in pursuit gain. As this was also the participant with the largest proportion of discarded trials, this participant probably had difficulty maintaining accurate pursuit. The standard errors of the means were also higher than those for the other participants because they were computed across a smaller number of trials. For none of the participants did there seem to be a systematic effect of stimulus direction on pursuit gain. Figure 3 shows the average eye velocity (horizontal and vertical speed combined) during the fixation interval in the pursuit condition. Here too, participants 1, 3 and 4 showed a constant and low eye velocity that was close to zero for all stimulus directions, while participant 2 showed more variability.

Since the velocity matching task had not been used before, it was important to check whether participants were able to do this task at all. The results from the fixation condition (Figure 4) show that they were. The velocity matches (big open symbols) closely resembled the physical stimulus velocities (closed squares) for

all four participants. Moreover, the variability of the velocity matches was quite small. The error bars in Figure 4 represent the standard errors of the mean, after principal component analysis. Hence, the largest error bar for each data point is in the direction with the largest variance and the other error bar is in the direction orthogonal to that. The results from the fixation condition suggest that the task itself did not introduce any biases in the velocity matches. Therefore, any differences between these results and those of the pursuit condition have to be caused by the eye movements. Figure 5 shows the velocity matches in the pursuit condition. The data were pooled across pursuit direction (leftward and rightward), because this factor did not have an effect on the velocity matches, and are presented as if pursuit were to the right (360°). The velocity matches in the pursuit condition differed strongly from the physical velocities, generally showing a horizontal shift against the pursuit direction. The amplitude of this shift varied across participants, but for all it was smaller than $10^\circ/\text{s}$, which is the shift that one would expect if participants had reported the retinal image velocities. Hence, the effects of the eye movements on the retinal image velocity were compensated for to a certain degree, but not completely.

The linear model (Eqn. 1), Turano and Massof's (2001) model and Freeman's (2001) model were fitted to the velocity matches in the pursuit condition (see the Appendix for the mathematical details of the fitting procedures). The continuous red lines in Figure 5 represent the best fitting model curves for the linear model, the dashed blue lines those for the Turano & Massof model and the dotted green lines show the Freeman model.

Table 1. Root-mean-squared-errors for the linear model, the Turano and Massof (2001) model and the Freeman (2001) model.

Participant	Experiment 1			Experiment 2		
	Linear model	Turano & Massof	Freeman	Linear model	Turano & Massof	Freeman
1	1.85	1.72	1.73	1.43	0.80	1.40
2	1.89	1.59	1.55	-	-	-
3	2.21	1.90	1.72	-	-	-
4	1.06	0.88	1.03	3.90	2.67	3.85
5	-	-	-	2.05	1.03	2.01
6	-	-	-	1.28	1.25	1.21

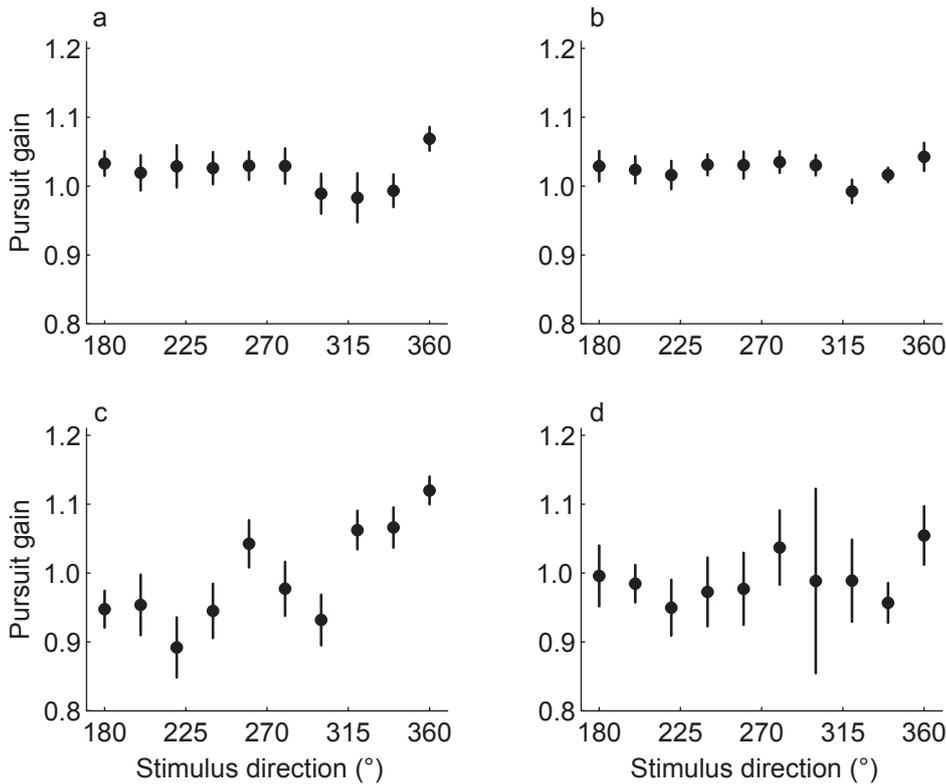


Figure 6. Average pursuit gain for the four participants in Experiment 2. The error bars represent the standard errors of the mean.

All models clearly capture the shift against the pursuit direction. Although both non-linear models provide better fits, the differences between the model fits are quite small. To quantify the goodness of fit of the models, the *rmse*'s of the predictions were computed. These are shown in Table 1. The *rmse* essentially is the standard deviation of the errors in the model predictions. Consequently, lower *rmse*'s indicate a better fit. The errors for both non-linear models were smaller than those for the linear model, but, despite the higher number of free parameters, the Turano and Massof model did not provide a better fit than the Freeman model.

Discussion

The results from the fixation condition show that our new method to measure velocity matches for speed and direction simultaneously did not introduce any biases. Therefore, this task seems very useful to assess the effects of eye movements on perceived speed and direction. The results from the pursuit condition in both experiments show much more variability (both within and between participants) than those from the fixation

condition, but they nevertheless show a consistent pattern.

Generally, the effects of the smooth pursuit eye movements can be described as a shift of the velocity matches against the pursuit direction. This suggests incomplete compensation for the effects of the eye movements on the retinal image motion. The amplitude of the shift varied across participants. It seems to be captured well by the linear model (Eqn. 1), although the speed component of the model predictions (i.e., their radius) was smaller than that of the actual velocity matches for three of the participants (1 to 3). Both non-linear models fitted the data better, but this is not surprising, given their higher number of free parameters. If we use the gain ratio of the linear model as an estimate for the overall degree of transformation from a retinocentric frame of reference into a head-centric one, this gives values of 69, 83, 65, and 40% for participants 1 to 4, respectively. This quantification of the degree of compensation for the effects of the eye movements on motion perception is essentially equivalent to the one proposed by Mateeff, Yakimoff, Hohnsbein and Ehrenstein (1991), except that their measure can only be used with non-collinear motion.

In Experiment 1, the retinal image speed of the stimulus covaried with the stimulus direction from

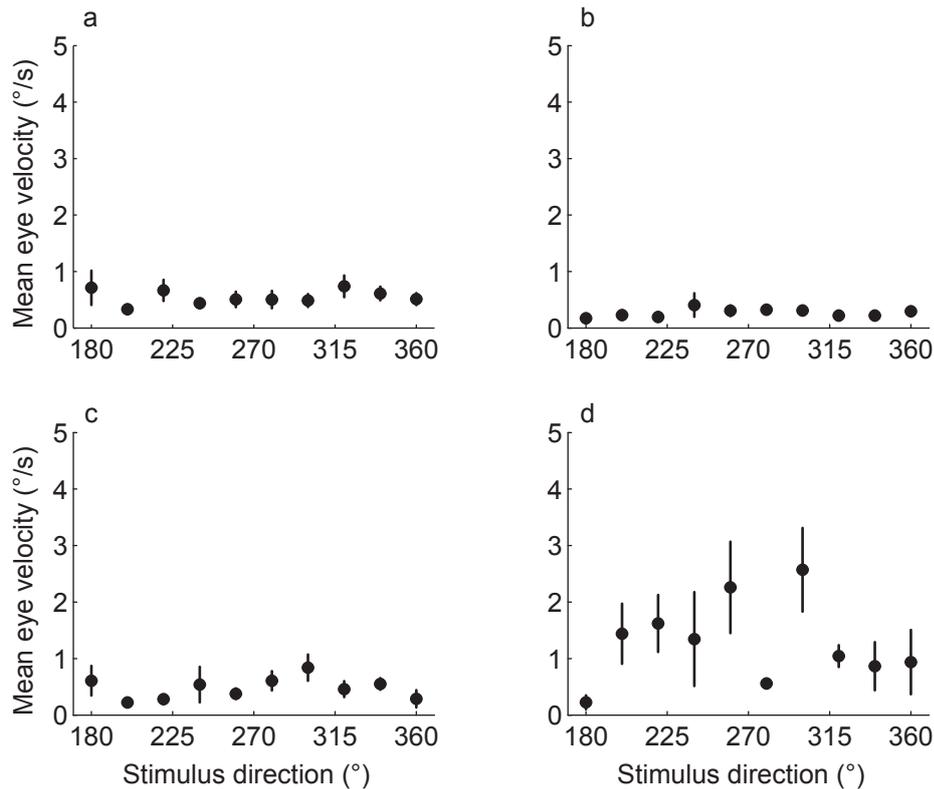


Figure 7. Average eye velocity for the four participants in the fixation interval in Experiment 2. The error bars represent the standard errors of the mean.

$\sim 2^\circ/\text{s}$ (at 360°) to $\sim 18^\circ/\text{s}$ (at 180° , with rightward pursuit). Since both direction discrimination and speed discrimination depend on stimulus velocity (De Bruyn & Orban, 1988) and perceived speed is non-linearly related to physical speed (McKee & Nakayama, 1984), this may have affected the velocity matches in Experiment 1. Moreover, the head-centric stimulus speed in Experiment 1 was lower than the pursuit target speed, producing retinal image speeds with a horizontal component that was always opposite to the pursuit direction. We therefore repeated Experiment 1 with an approximately constant retinal speed that was higher than the pursuit target speed.

Experiment 2

Methods

Participants

Three students (all female) from Utrecht University and the first author participated in the experiment. The students were paid for their participation. They gave

their written informed consent for participation. All participants had normal or corrected-to-normal vision. The age of the participants was 19, 23, 26 and 34 years, respectively. The first author and one of the students had also participated in Experiment 1 (participants 1 and 4 in Tables 1 and 2).

Apparatus and stimuli

Same as in Experiment 1.

Design and procedure

In Experiment 2 only velocity matches in the pursuit condition were measured. This was done in one session. The stimulus direction again varied from 180° to 360° in steps of 20° . The stimulus speed was computed to produce a constant retinal speed of $7^\circ/\text{s}$ with perfect pursuit. Hence, the actual speed of the random dots on the screen varied with stimulus direction. The speed of the pursuit target was reduced from $10^\circ/\text{s}$ in Experiment 1 to $5^\circ/\text{s}$ in Experiment 2, in order to be able to let the retinal image motion span the entire direction range of 180° to 360° , while keeping the head-centric stimulus speed in a range in which participants would be able to match the stimulus velocity reliably for all stimulus

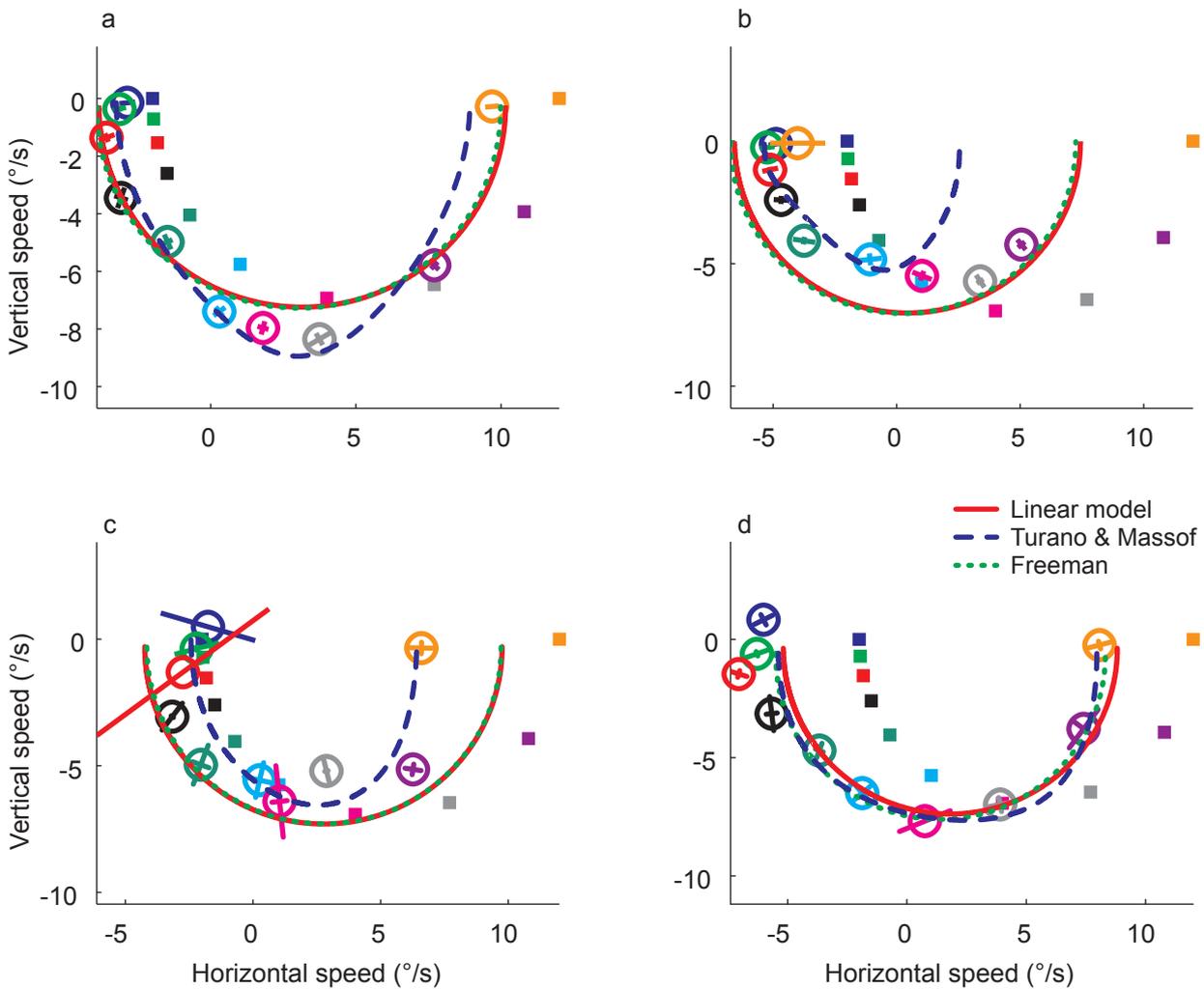


Figure 8. Velocity matches and model fits for the four participants in Experiment 2. Symbols and error bars are as in Figure 4 and the lines as in Figure 5.

directions. In all other respects the procedure in Experiment 2 was the same as in Experiment 1.

Results

An even larger percentage of trials was discarded because of inaccurate pursuit or fixation than in Experiment 1 (52%). But again, this hardly affected the results. Figure 6 shows the average pursuit gain for the four participants (panels *a* to *d* in Figures 6 to 8 refer to participants 1, 4, 5 and 6, respectively). As in Experiment 1, the pursuit gain was about 1 for most participants. Participant 5 showed a large variability in her pursuit gain. This resulted in the loss of a high percentage of trials (72%) and consequently in larger

standard errors of the mean. As can be seen from Figure 7, the average eye velocity in the fixation intervals was low and constant, except for participant 6, who showed much more variability in eye velocity. For this participant too a high percentage of trials was discarded (76%).

Figure 8 shows the velocity matches for all four participants, again with both pursuit directions pooled together and plotted as if pursuit were to the right (360°). As in Experiment 1, the velocity matches were shifted against the pursuit direction relative to the physical velocities for all participants. The data of participant 4 (panel *b*) show a strange velocity match for the 360° stimulus direction (orange point). It has been shifted to the left much more than the other points. Inspection of the individual trials showed that this is because the participant indicated a velocity of $\sim 6^\circ/\text{s}$ in the 360°

direction as the velocity match in 2 of the trials and a velocity of $\sim 6^\circ/\text{s}$ in the opposite direction in the 13 other trials. We don't have an explanation for this behaviour. In Experiment 1, in which she also participated, this participant did not show this (see Figure 5, panel d). Some of the data points of participant 5 have big error bars. This is due to the small number of trials that remained after the eye movement analysis. Her velocity matches are probably noisier than those of the other participants for the same reason.

We fitted the linear model, Turano and Massof's (2001) model and Freeman's (2001) model to the data. The best fitting model curves are shown in Figure 8 (continuous red lines, dashed blue lines and dotted green lines, respectively) and the accompanying *rmse* values are given in Table 1. The fits of the linear model and the Freeman model are virtually indistinguishable, while the Turano and Massof model provided better fits for three of the participants (1, 4 and 5). The model parameter values for the linear model and Freeman's model did not differ much from those found in Experiment 1 for participant 1 (gain ratio's of 0.69 and 0.64, in Experiments 1 and 2 for the linear model; power ratio's of 0.90 and 0.83 for Freeman's model), while those for participant 4 were very different because of the abovementioned strange data point at 360° . Fitting the model without this data point produced parameter values comparable to those in Experiment 1 (gain ratio's 0.40 and 0.34; power ratio's 0.71 and 0.68). The parameter values for the Turano and Massof model deviated much more from those obtained in Experiment 1. The gain ratio's of the linear model for participants 5 and 6 were 0.56 and 0.36, suggesting fairly low degrees of compensation for the effects of the eye movements.

Discussion

As in Experiment 1, the velocity matches were shifted against the pursuit direction, indicating incomplete compensation for the effects of the eye movements. The general pattern of results resembled that in Experiment 1, indicating that the confounding of retinal speed and stimulus direction and the restricted retinal direction range did not affect the results in the first experiment. However, the velocity matches look noisier than those in Experiment 1. Possibly, the varying stimulus speed on the screen confused the participants.

Surprisingly, the linear model and Freeman's (2001) model produced virtually identical fits. Analysis of equation 17 (Appendix) shows that when the retinal speed $\|\mathbf{r}_1\|$ and the eye movement speed $\|\mathbf{e}_1\|$ are constant, this equation describes a semicircle. Hence, by keeping the retinal speed constant in Experiment 2, we effectively limited the degrees of freedom for Freeman's model to fit the data. It could only produce a shift along the line of the eye movement (as the linear model) and a change in the radius of the semicircle on which the velocity matches should lie. This explains why this model produced the same fits to the velocity matches in Experiment 2 as the linear model.

The Turano and Massof model provided better fits to the data for three of the four participants. However, this might be a case of overfitting (see Pitt & Myung, 2002). Possibly, the model picks up random noise in the velocity matches, making the model predictions very specific to the data set at hand. To test for this possibility, we cross-validated all three models by means of the split-half method. For every stimulus direction, the velocity matches were randomly divided into two halves and the average velocity matches were

Table 2. Mean root-mean-squared errors for the linear model, the Turano and Massof (2001) model and the Freeman (2001) model, after 100 split-half cross-validations.

Participant	Experiment 1			Experiment 2		
	Linear model	Turano & Massof	Freeman	Linear model	Turano & Massof	Freeman
1	1.91	1.80	1.79	1.47	1.05	1.49
2	2.27	2.06	1.89	-	-	-
3	2.43	1.98	2.03	-	-	-
4	1.33	1.31	1.34	3.95	2.77	3.85
5	-	-	-	2.68	2.22	2.76
6	-	-	-	1.60	1.36	1.36

computed for both halves. The models were then fitted to the average velocity matches of the first half (the training or calibration set) and the resulting parameter values were used to compute the goodness-of-fit of the models, expressed in the *rmse*, to the second half (the test set) of the velocity matches. If a model overfits the data, the parameter values will be very specific to the training set and provide a much worse fit to the test set. This procedure was repeated 100 times and the average *rmse*-values were computed for all three models. This was done for the results of both Experiment 1 and 2. The resulting *rmse*'s are given in Table 2. In Experiment 1, the differences between the model fits remain small, while the Turano and Massof model still produces the best fit for three of the four participants in Experiment 2. Consequently, this model does not appear to fit the velocity matches better at the cost of generalizability.

An alternative way to assess the importance of the number of free parameters is to try to reduce it and evaluate the impact on the goodness-of-fit of the model. We tried to limit the number of free parameters in the Turano and Massof model. First we assumed that the two asymptotic values in equations (4) and (5), R_{max} and R'_{max} , are equal, setting $h = 1$. This hardly affected the model fits, implying that the asymptotic values for the retinal velocity and the eye movement velocity as estimated by the visual system are equal. Next, instead of assuming $h = 1$, we assumed that the parameter that determines the contribution of the retinal input in the estimate of the eye velocity, α , equals the parameter in the estimate of the retinal image velocity, ρ . This too hardly affected the fits. Setting $\alpha = 0$, however, seriously deteriorated the fits, suggesting that the interaction between retinal and extraretinal information in estimating the eye velocity is essential in this model. Also, combining both reductions (setting $h = 0$ and $\alpha = \rho$) produced very bad fits. Consequently, it appears that, at least as far as our data are concerned, the Turano and Massof model can be reduced to a three parameter model, in either way.

General discussion

The smooth pursuit eye movements generally caused a shift of the velocity matches in the opposite direction to that of the eye movement. Our results show that the effects of smooth pursuit on perceived velocity

are similar for different motion directions relative to the pursuit direction, suggesting one compensation mechanism for both collinear and non-collinear stimulus motion. Earlier, Wallach, Becklen and Nitzberg (1985) suggested that the visual system only compensates for eye movements in the case of collinear stimulus motion, as they found a much higher degree of compensation with collinear motion than with non-collinear motion (Becklen et al., 1984). However, by varying both the speed and direction of the stimulus and measuring perceived direction we have previously shown that this discrepancy was probably due to the difference in stimulus speeds used in their studies (Souman et al., In press). Our results here confirm our earlier conclusion that the visual system applies the same compensation mechanism irrespective of the stimulus direction.

Evaluation of the models

Generally, all three models considered in this paper fitted the data well. The non-linear models of Turano and Massof (2001) and Freeman (2001) provided somewhat better fits than the linear model to the velocity matches of Experiment 1, while the Turano and Massof model fitted the velocity matches of Experiment 2 best. Partly, the differences may be due to the different numbers of free parameters. As the differences in model fits were also quite small, it is hard to choose between these models. In this respect our results are very similar to the general velocity matching experiments of Turano and Massof (2001) and Freeman (2001). In those studies, the differences between the linear model and the respective non-linear models were also quite small. The better fits of the model of Turano and Massof suggest that the eye movement signal that is used by the visual system to estimate the eye velocity may be partly determined by visual information. The retinal signal and the eye movement signal may therefore not be completely independent, as assumed in the linear model and the model of Freeman. The Turano and Massof model does not, however, specify how the effect of the retinal image velocity on the estimated eye velocity arises. In this respect, it might be augmented or combined with alternative models that assume an interaction between visual information and the eye movement signal (see below).

The differences between the fits of the linear and the non-linear models in our experiments cannot be attributed to the fact that we assumed perfect fixation in the fixation interval for the non-linear models, whereas we used the actual eye velocity during the fixation interval when fitting the linear model (see the Appendix). The average eye velocity during the fixation interval was close to zero (Figures 3 and 7). Moreover, refitting the linear model while assuming perfect fixation produced the same results as those reported above, in both Experiments. The maximum difference in the best fitting values for the gain ratio ε/ρ was 0.01.

Alternative models

As stated in the introduction, we were unable to fit the models of Wertheim (1994) and Goltz et al. (2003). Yet, these models contain some interesting properties. They both focus on the importance of retinal image characteristics in the compensation for the effects of smooth pursuit eye movements. In this respect they are reminiscent of the older model of Post and Leibowitz (1985), that emphasized the effect of retinal image characteristics on the activity of a hypothesized reflexive eye movement system. Although that model was falsified by studies that showed that, contrary to its predictions, retinal image motion is required to experience vection (Mergner & Becker, 1990; Mergner, Wertheim & Rumberger, 2000; also see Wertheim, 1990) and that changing the spatial frequency of a stimulus that is tracked with the eyes does not affect its perceived velocity (Sumnall, Freeman, & Snowden, 2003), its emphasis on retinal image characteristics deserves further elaboration. For example, it is presently unclear whether the effect of the spatial frequency of a visual stimulus during smooth pursuit is due to its effects on the retinal image velocity estimate (Freeman & Banks, 1998) or on the eye velocity estimate (Wertheim, 1987). Further specification of the possible interactions between retinal image motion and eye velocity in the abovementioned models might enable them to make more specific, testable, predictions of the spatial frequency effect, making it possible to decide between the models. The same is true for such factors as the size (Turano & Heidenreich, 1999) and presentation duration (De Graaf & Wertheim, 1988; Mack & Herman, 1978; Souman et al., 2005) of the motion stimulus.

Another interesting model of motion perception during smooth pursuit is that by Pack, Grossberg and Mingolla (2001), which describes both oculomotor behaviour and motion perception during smooth pursuit eye movements. Their model is based on neurophysiological evidence that in primates eye movement signals and retinal motion signals are integrated in area MST (Barton et al., 1996; Bradley, Maxwell, Andersen, Banks, & Shenoy, 1996; Ilg & Thier, 2003; Newsome, Wurtz, & Komatsu, 1988; Shenoy, Bradley, & Andersen, 1999). As a neural network model, it describes the combination of retinal motion signals and eye movement signals at a much lower level than the other models discussed in this study. It would be interesting to connect both types of models by showing how the effects of experimental factors on the model parameters of the high-level models (the gain ratio of the linear model, or the power coefficients of Freeman's 2001 and Turano and Massof's 2001 models) derive from the network properties in the model of Pack et al. (2001).

Conclusions

Our new task, in which participants judged both perceived speed and perceived motion direction at the same time, enabled us to make a direct comparison of the perception of collinear and non-collinear during smooth pursuit eye movements. The results of Experiments 1 and 2 show that the effect of smooth pursuit eye movements on the velocity matches can mainly be described as a shift in the opposite direction to the eye movements. This suggests that the compensation mechanism is the same, regardless of the stimulus direction or the retinal image motion direction. Generally, the non-linear model of Turano and Massof (2001) provided better fits to the velocity matches than the linear model and the model of Freeman (2001), though at the cost of a higher number of free parameters. However, any non-linear effects were not very strong, as the difference between the model fits overall was quite small. Evaluation of these models and a few alternatives suggests that further specification of the effect of retinal image motion characteristics on the compensation for eye movements is needed.

Appendix: Mathematical details

A. The linear model

The linear model is described by equation 1, which we repeat here for convenience:

$$\hat{\mathbf{h}} = \rho \mathbf{r} + \varepsilon \mathbf{e} \quad (8)$$

In our experiments, the velocity in the second interval had to be adjusted to match the perceived velocity in the first interval. Hence, at the velocity match the perceived head-centric velocity $\hat{\mathbf{h}}_1$ in interval 1 equalled that in interval 2 ($\hat{\mathbf{h}}_2$). Using equation 8 this gives:

$$\rho \mathbf{r}_1 + \varepsilon \mathbf{e}_1 = \rho \mathbf{r}_2 + \varepsilon \mathbf{e}_2 \quad (9)$$

where the subscripts refer to the interval. Since the retinal velocity \mathbf{r} equals the head-centric stimulus velocity \mathbf{h} minus the eye velocity \mathbf{e} , we can also write:

$$\rho(\mathbf{h}_1 - \mathbf{e}_1) + \varepsilon \mathbf{e}_1 = \rho(\mathbf{h}_2 - \mathbf{e}_2) + \varepsilon \mathbf{e}_2 \quad (10)$$

Rearranging terms and dividing by ρ gives:

$$\left(\frac{\varepsilon}{\rho} - 1\right)(\mathbf{e}_1 - \mathbf{e}_2) = \mathbf{h}_2 - \mathbf{h}_1 \quad (11)$$

The vectors \mathbf{h} and \mathbf{e} have two components, one for horizontal speed and one for vertical speed. Hence, equation 11 equals a system of two equations, one for the horizontal speed components and one for the vertical ones. This equation basically describes a linear regression model with zero intercept. The gain ratio ε/ρ can be estimated by forming the error matrix:

$$\mathbf{D} = \left(\frac{\varepsilon}{\rho} - 1\right)(\mathbf{E}_1 - \mathbf{E}_2) - \mathbf{H}_2 + \mathbf{H}_1 \quad (12)$$

with \mathbf{H} and \mathbf{E} denoting the matrices formed by all observations on the vectors \mathbf{h} and \mathbf{e} , and minimizing the trace of the sum of squares and cross products matrix $\mathbf{D}'\mathbf{D}$. Differentiating the trace of $\mathbf{D}'\mathbf{D}$ with respect

to $\left(\frac{\varepsilon}{\rho} - 1\right)$, setting the derivative equal to zero and solving for ε/ρ gives:

$$\frac{\varepsilon}{\rho} = 1 + \frac{\text{tr}([\mathbf{E}_1 - \mathbf{E}_2]^T [\mathbf{H}_2 - \mathbf{H}_1])}{\text{tr}([\mathbf{E}_1 - \mathbf{E}_2]^T [\mathbf{E}_1 - \mathbf{E}_2])} \quad (13)$$

where $\text{tr}(\mathbf{A})$ is the trace of matrix \mathbf{A} .

B. The Turano and Massof (2001) model

Applying equations 4 and 5 to the velocity matches gives:

$$\frac{h}{1 + e^{-\rho r_1}} + \frac{1}{1 + e^{-\varepsilon e - \alpha r_1}} = \frac{h}{1 + e^{-\rho r_2}} + \frac{1}{1 + e^{-\alpha r_2}} \quad (14)$$

where r_i denotes the retinal image velocity in interval i and h is the ratio R_{max}/R'_{max} . This equation cannot be solved for r_2 algebraically. Turano and Massof approximated the solution by means of a series expansion (Turano & Massof, Personal communication) and we used their result:

$$r_2 = -\frac{1}{\rho} \ln \left(\frac{2h}{\frac{1}{1 + \exp(-\varepsilon e_1 - 0.5\alpha r_1)} - 0.5 + \frac{2h}{1 + \exp(-0.5\rho r_1)}} - 1 \right) \quad (15)$$

To apply this equation to the velocity matches in Experiments 1 and 2, we had to assume accurate fixation ($\mathbf{e}_2 = \mathbf{0}$), which seemed a reasonable assumption (see Figures 3 and 7). We applied the equation separately to the horizontal and the vertical components of the velocity matches, with one set of parameters (ε , ρ , α , and h). The best fitting parameter values were determined by minimizing the trace of the sum of squares and cross products matrix $\mathbf{D}'\mathbf{D}$, with

$$\mathbf{D} = \hat{\mathbf{H}}_2 - \mathbf{H}_2 \quad (16)$$

where $\hat{\mathbf{H}}_2$ is the matrix of velocity matches in the fixation interval as predicted by the model and \mathbf{H}_2 is the matrix of the actual velocity matches. The trace of $\mathbf{D}'\mathbf{D}$ was minimized with MatLab's *fminsearch* function, which implements a unconstrained non-linear optimization procedure.

C. Freeman's (2001) model

To fit Freeman's non-linear model to our data, equation 6 had to be applied to the retinal image velocity and the eye velocity in both intervals. We again assumed that fixation in the fixation interval was accurate ($\mathbf{e}_2 =$

$\mathbf{0}$), which greatly simplified the fitting procedure. At the velocity match ($\hat{\mathbf{h}}_1 = \hat{\mathbf{h}}_2$), the equation becomes:

$$\begin{aligned} & \left[\left(\|\mathbf{h}_1 - \mathbf{e}_1\| + 1 \right)^\rho - 1 \right] \frac{\mathbf{h}_1 - \mathbf{e}_1}{\|\mathbf{h}_1 - \mathbf{e}_1\|} + \left[\left(\|\mathbf{e}_1\| + 1 \right)^\varepsilon - 1 \right] \frac{\mathbf{e}_1}{\|\mathbf{e}_1\|} \\ & = \left[\left(\|\mathbf{h}_2\| + 1 \right)^\rho - 1 \right] \frac{\mathbf{h}_2}{\|\mathbf{h}_2\|} \end{aligned} \quad (17)$$

The direction of the velocity match \mathbf{h}_2 equals that of the left hand side of the equation and can therefore be computed on the basis of the (known) vectors \mathbf{e}_1 and \mathbf{h}_1 . The amplitude of \mathbf{h}_2 equals:

$$\begin{aligned} \|\mathbf{h}_2\| = & \left(1 + \left\| \left[\left(\|\mathbf{h}_1 - \mathbf{e}_1\| + 1 \right)^\rho - 1 \right] \frac{\mathbf{h}_1 - \mathbf{e}_1}{\|\mathbf{h}_1 - \mathbf{e}_1\|} \right. \right. \\ & \left. \left. + \left[\left(\|\mathbf{e}_1\| + 1 \right)^\varepsilon - 1 \right] \frac{\mathbf{e}_1}{\|\mathbf{e}_1\|} - \left[\left(\|\mathbf{e}_2\| + 1 \right)^\varepsilon - 1 \right] \frac{\mathbf{e}_2}{\|\mathbf{e}_2\|} \right\| \right)^{\frac{1}{\rho}} - 1 \end{aligned} \quad (18)$$

The best fitting model parameters, ρ and ε , were found by minimizing the trace of the sum of squares and cross-products matrix $\mathbf{D}'\mathbf{D}$, with \mathbf{D} defined as in equation 16. This was done with MatLab's *fminsearch* function.

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7

It's in the eye of the beholder: models of motion perception during smooth pursuit eye movements

Abstract

The ability to see motion and judge the velocity of moving objects is crucial to our functioning in daily life. This is vividly illustrated by the rare cases of specific brain damage to the motion processing areas (Zihl, Von Cramon, & Mai, 1983). The motion we perceive is not only determined by the retinal image motion caused by moving objects in the world around us. The movements of our eyes, head and body also contribute to the retinal image motion and have therefore to be taken into account. With regard to motion perception during smooth pursuit eye movements, it has commonly been thought that our visual system compensates for the effects of the eye movements by adding an estimate of the rotational eye velocity to the estimated retinal image velocity (Dichgans & Brandt, 1972; Von Holst, 1954; Von Holst & Mittelstaedt, 1950). In this view, the eye movement signal is independent of the retinal signal and the estimate of the eye velocity is supposedly not affected by retinal image characteristics. Recently, however, some doubt has been cast on the independency assumption. Some authors have proposed models that incorporate some form of interaction between both signals (Goltz, DeSouza, Menon, Tweed, & Vilis, 2003; Turano & Massof, 2001; Wertheim, 1994). The existence of such an interaction would be important for the interpretation of motion perception studies. Factors that affect the perceived (head-centric) motion might in fact be having that effect because they influence the estimate of the eye velocity, not of the retinal image velocity. This might be true even in the absence of actual eye movements. Here, I will review the evidence for this interaction and the performance of these newer models compared to the classical linear one. This evaluation suggests that the retinal signal and the eye movement signal do indeed interact. The interaction term is taken to indicate that the eye velocity as estimated by the visual system is not only based on an efference copy of the oculomotor command, but also on retinal image characteristics.

Jan L. Souman (Submitted).

Introduction

Smooth pursuit eye movements change the retinal image motion of objects in the visual field. The image of an object that is tracked with the eyes is approximately stationary on the retina and the images of objects that are stationary with respect to the world move on the retina in the opposite direction to the eye movement. Generally, however, we do not perceive the world around us to move

during smooth pursuit eye movements, so apparently our brain is capable of compensating for their effects on the retinal image motion. Traditionally, the visual system is thought to use an estimate of the rotational eye velocity with respect to the head to transform the retinal image motion from a retinocentric frame of reference into a head-centric one (Swanston, Wade, & Day, 1987; Wade & Swanston, 1996). This estimate is probably in large part based on an efference copy of the oculomotor signal

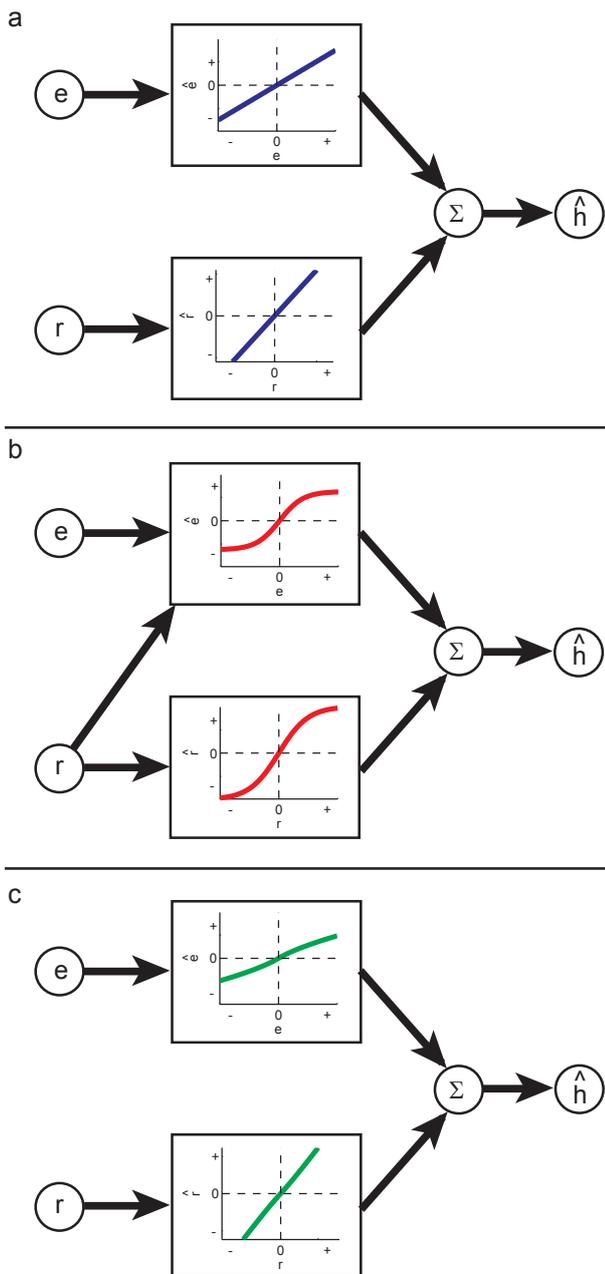


Figure 1. Illustration of the three models tested. In all models the perceived head-centric velocity \hat{h} equals the sum of the estimated retinal velocity \hat{r} and the estimated eye velocity \hat{e} . The models differ in how these estimates are computed. (a) Linear model: both estimates are linearly related to the physical velocities. (b) Turano and Massof (2001) model: both estimates are non-linearly related to the physical velocities and the estimated eye velocity \hat{e} is based on an interaction between eye velocity e and retinal velocity r . (c) Freeman (2001) model: both estimates are non-linearly related to the physical velocities, but independent.

that drives the smooth pursuit eye movements (Sperry, 1950; Von Holst, 1954; Von Holst & Mittelstaedt, 1950). The existence of such an extraretinal signal is supported by a number of facts. Gently pressing with the finger against the eye ball gives the impression that the world is moving (Bridgeman, 1986; Bridgeman & Delgado, 1984; Mittelstaedt, 1990). In this case, the eye movement is not driven by an oculomotor signal and the eye movement is consequently not compensated for. Trying to move the eyes with paralyzed eye muscles, on the other hand, also results in illusory motion or displacement of a visual stimulus viewed in the dark, because the stationary retinal image is erroneously corrected with a non-zero eye movement signal (Matin et al., 1982; Stevens et al., 1976; Von Helmholtz, 2000). Stabilized retinal images are perceived to be moving during smooth pursuit eye movements (Turano & Massof, 2001), even if it concerns an afterimage and nothing else is visible (Mack & Bachant, 1969). Hence, the existence of an extraretinal eye movement signal seems irrefutable, though this not necessarily means that the efference copy always is the only input used by the visual system to estimate the eye velocity.

The importance of the use of eye movement information to compensate for the effects of eye movements on the retinal image motion is illustrated by the case of a patient whose visual system lacked this compensation mechanism due to cortical lesions (Haarmeier, Thier, Reppow, & Petersen, 1997). This patient perceived the world to be moving during smooth pursuit eye movements, hampering him in daily life tasks such as driving and ball games. Moreover, this lack of compensation caused feelings of vertigo and nausea.

In this review, I will evaluate the currently existing models of motion perception during smooth pursuit eye movements. I will restrict myself to quantitatively formulated models and to the results of experiments concerning motion perception during smooth pursuit eye movements with the head kept still. First, the classical linear model will be described and then some more recent non-linear alternatives will be presented. The models will be compared by applying them to the same data sets and the results will be discussed in the context of psychophysical and physiological evidence.

The linear model

Historically (see Freeman & Banks, 1998; Souman, Hooge, & Wertheim, *In press*), motion perception during smooth pursuit has been viewed as the outcome of summation of the retinal image velocity $\hat{\mathbf{r}}$ and the eye velocity $\hat{\mathbf{e}}$ (both angular velocities) as estimated by the visual system, with both estimates linearly related to the physical velocities:

$$\hat{\mathbf{h}} = \hat{\mathbf{r}} + \hat{\mathbf{e}} = \rho \mathbf{r} + \varepsilon \mathbf{e} \quad (1)$$

where $\hat{\mathbf{h}}$ is the perceived head-centric velocity and ρ and ε represent the gains of the retinal signal and the eye movement signal, respectively.¹ I will call this the linear model of head-centric motion perception during smooth pursuit, as the perceived head-centric velocity is defined as a linear combination of retinal velocity \mathbf{r} and eye velocity \mathbf{e} (see Figure 1a). Consequently, the estimated retinal velocity and eye velocity are independent of each other in this model.

In principle, the linear model has two free parameters, ρ and ε . In practice, however, the perceived velocity $\hat{\mathbf{h}}$ has to be measured by means of some kind of matching task, in which an observer has to compare the perceived head-centric velocity during pursuit ($\hat{\mathbf{h}}_1$) with that of another motion stimulus ($\hat{\mathbf{h}}_2$), viewed either during pursuit or fixation. When both perceived velocities match ($\hat{\mathbf{h}}_1 = \hat{\mathbf{h}}_2$) this implies according to the linear model:

$$\rho \mathbf{r}_1 + \varepsilon \mathbf{e}_1 = \rho \mathbf{r}_2 + \varepsilon \mathbf{e}_2 \quad (2)$$

or, equivalently:

$$\frac{\varepsilon}{\rho} (\mathbf{e}_1 - \mathbf{e}_2) = \mathbf{r}_2 - \mathbf{r}_1 \quad (3)$$

(assuming that ε and ρ are the same in both intervals)². This means that only the gain ratio ε/ρ can be estimated from experimental data, not the individual gain parameters. It also implies that the effects of experimental factors on perceived motion during smooth pursuit cannot be uniquely attributed to changes in either the retinal signal or the eye movement signal (Freeman & Banks, 1998).

This simple model has been used to explain several phenomena in motion perception during smooth pursuit eye movements. The two classical illusions of Aubert-Fleischl (objects appear to move slower when tracked

with the eyes than during fixation; Aubert, 1886, 1887; Dichgans, Wist, Diener, & Brandt, 1975; Von Fleischl, 1882) and Filehne (a briefly presented stationary object appears to move opposite to the eye movement direction during smooth pursuit; Filehne, 1922; Mack & Herman, 1973) can be explained by assuming that the gain of the eye movement signal is lower than that of the retinal signal (see Box 1; according to an alternative explanation, the Aubert-Fleischl phenomenon is the consequence of increased motion thresholds during eye movements; Wertheim, 1990, 1994; Wertheim & Van Gelder, 1990). The linear model has also been used to describe the influence of the spatial frequency of the motion stimulus on the perceived velocity during smooth pursuit (Freeman & Banks, 1998). Supposedly, the spatial frequency affects the retinal signal gain, thereby changing the perceived velocity. Alternatively it has been proposed that the spatial frequency affects the estimated eye velocity (Wertheim, 1987). As noted above, at present the data do not allow us to discriminate between both interpretations.

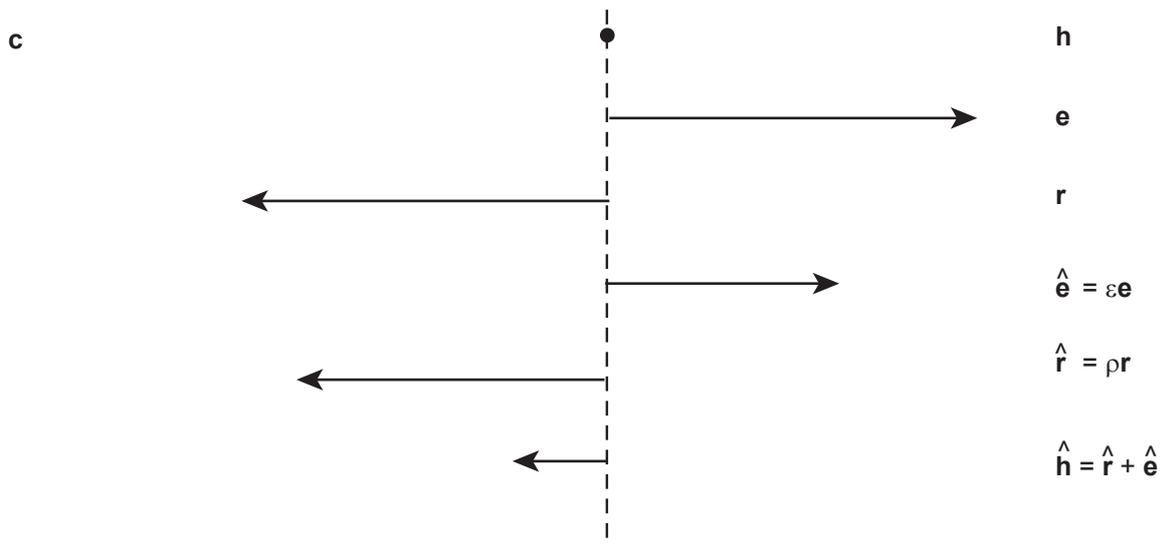
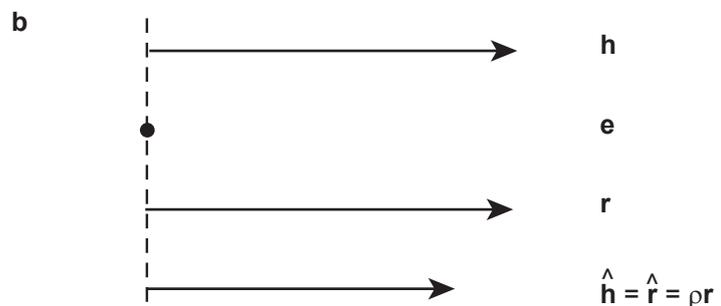
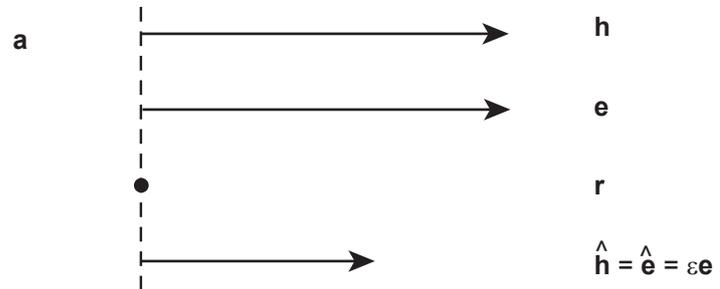
Most research on motion perception during smooth pursuit has been conducted using collinear motion, that is, motion stimuli moving along the same line as the pursuit target (horizontally in most cases). The problem that has to be solved by the visual system is the same, however, with non-collinear motion (stimuli moving at an angle other than 0° or 180° relative to the pursuit target). The eye movements introduce a retinal motion component opposite to the eye movement direction, for which the visual system has to correct in order to produce a veridical motion percept. The linear model has been found to describe the perceived motion direction for stimuli moving in directions ranging from 0° to 360° relative to the pursuit direction quite well (Souman et al., *In press*). Hence, the visual system indeed compensates for the effects of smooth pursuit eye movements with non-collinear motion in the same way as with collinear motion.

¹ Bold lower case characters are used to represent two-dimensional vectors in the frontoparallel plane. Hatted symbols indicate estimated entities.

² If this assumption is not made, four parameters (different ρ and ε for both intervals) have to be estimated, which can be reduced to three ratios. Still, individual parameter values cannot be estimated.

Box 1: the Aubert-Fleischl phenomenon and the Filehne illusion explained in terms of the linear model

Explanation of the Aubert-Fleischl phenomenon in terms of the linear model. During ocular pursuit of a moving target (a), the eye velocity e equals that of the stimulus h , while the retinal image velocity r is zero (with accurate pursuit). Hence, the perceived velocity \hat{h} of the pursuit target is determined by the eye movement signal gain ε . During fixation, the perceived velocity is determined by the retinal signal gain ρ (b). Consequently, the moving target will be perceived to move faster during fixation than during pursuit if $\varepsilon < \rho$.



In the Filehne illusion, a smooth pursuit eye movement e is made across a stationary stimulus h . When $\varepsilon < \rho$, the estimated eye velocity εe will be lower than the estimated retinal image velocity ρr . The result is that the stimulus is perceived to move in the direction opposite to that of the eye movement (\hat{h}).

Non-linear models

More recently, some alternative models of motion perception during smooth pursuit eye movements have been proposed. Contrary to the linear model, these models assume that the retinal image velocity and the eye velocity as estimated by the visual system are not necessarily independent and that they are non-linearly related to the physical velocities. According to the model proposed by Turano and Massof (2001), both the retinal image velocity estimate \hat{r} and the eye velocity estimate \hat{e} are non-linearly related to the actual velocities, with the eye velocity estimate depending on both the physical eye velocity and retinal image velocity:

$$\hat{r} = R_{\max} \left(\frac{1}{1 + \exp(-\rho r)} - 0.5 \right) \quad (4)$$

and

$$\hat{e} = R'_{\max} \left(\frac{1}{1 + \exp(-\varepsilon e - \alpha r)} - 0.5 \right) \quad (5)$$

where ρ , ε and α determine the slopes of the power functions and R_{\max} and R'_{\max} their asymptotic values. The variables e and r represent the eye velocity and the retinal image velocity respectively (both scalars, in one dimension). The perceived velocity \hat{h} is again the sum of both estimates (see Figure 1b). The model has four free parameters (α , ε , ρ and R_{\max} / R'_{\max}), with αr reflecting the input of the retinal image velocity in the estimated eye velocity. This interaction term was mainly motivated by the bad fits provided by a non-linear model with independent estimates of retinal image velocity and eye velocity. Turano and Massof tested their model in a general velocity matching task against the linear model and concluded that their non-linear model provided a better fit to the data. The difference, however, was quite small and difficult to interpret given the higher number of free parameters of the non-linear model.

The crucial issue is whether the interaction term in equation 5 is necessary to describe Turano and Massof's data. Freeman (2001) proposed an alternative non-linear model in which the retinal signal and eye movement signal are independent:

$$\hat{h} = \text{sgn}(r) \times ((r-1)^\rho - 1) + \text{sgn}(e) \times ((e-1)^\varepsilon - 1) \quad (6)$$

where $\text{sgn}(x)$ gives the sign of x . Basically, this model changes the input speeds according to a power function and leaves the direction unchanged (see Figure 1c). In a

series of experiments, this non-linear model described the Aubert-Fleischl phenomenon measured over a range of eye velocities slightly better than the linear model, while the linear model performed better for the Filehne illusion. In a general velocity matching task, similar to that in Turano and Massof's (2001) study, the non-linear model provided a better fit to the data of two observers, while there was little difference between the two models for two other observers.

Recently, Goltz et al. (2003) proposed another non-linear model, based on an interaction between the spatial structure of the retinal image and the eye velocity. According to this model, the perceived head-centric velocity equals:

$$\hat{\mathbf{h}} = \left(\frac{d\mathbf{l}}{d\mathbf{x}} \right)^+ \left(\frac{d\mathbf{l}}{dt} + \frac{d\mathbf{l}}{d\mathbf{x}} \bullet \mathbf{e} \right) \quad (7)$$

where $d\mathbf{l}/d\mathbf{x}$ denotes the spatial illumination gradient at retinal location \mathbf{x} , $d\mathbf{l}/dt$ is the change of local retinal illumination in time and $(\mathbf{v})^+$ is the Moore-Penrose pseudoinverse of vector \mathbf{v} . Goltz et al. showed that the interaction is necessary to explain the empirical finding that the afterimage of a horizontally oriented grating does not seem to move during horizontal eye movements. However, their model seems to be specifically targeted at grating stimuli and not directly applicable to the random dot stimuli that have been used in most studies on motion perception during smooth pursuit. The Moore-Penrose pseudo-inverse serves to solve the aperture problem for individual motion processing neurons with restricted receptive fields: when the end points of a moving line fall outside the receptive field of a neuron, its motion direction is ambiguous because the motion component along the orientation of the line cannot be resolved. When the stimulus is a grating that fills the entire visual field, different neurons have to solve the same problem and the model predicts the same outcome for each of these neurons (ignoring noise). With random dot stimuli, however, integration over both space and time is necessary to produce one coherent motion percept. Moreover, equation 7 cannot account for illusions such as the Filehne illusion and the Aubert-Fleischl phenomenon, because it doesn't contain gains. Although an eye movement signal gain can easily be implemented by premultiplying e with this gain, this is not so easy for the retinal signal. Hence, Goltz et al. make an important point concerning a possible interaction between the retinal signal and the eye movement signal, but their model is in its present

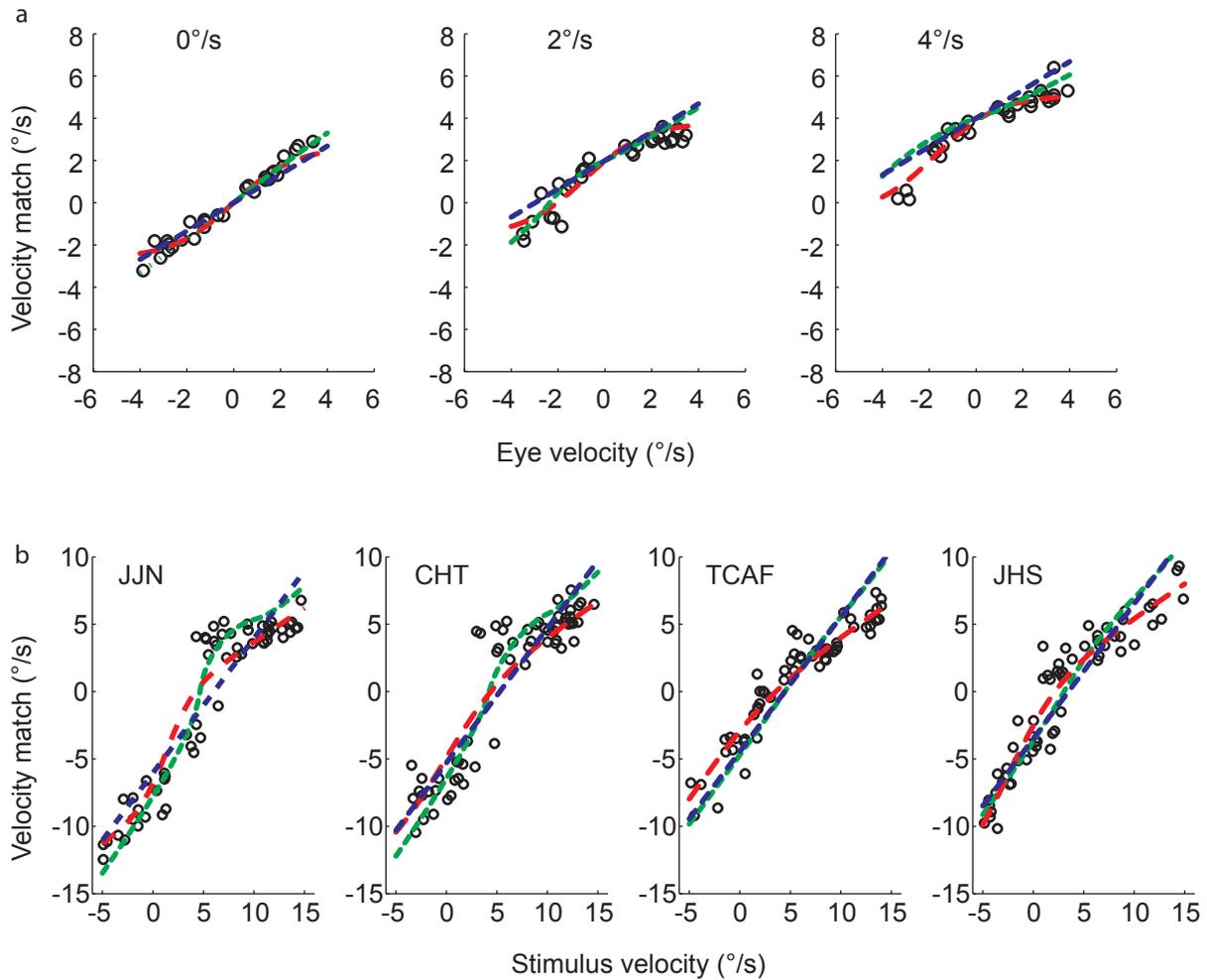


Figure 2. Model fits for two data sets: **a.** data from Turano & Massof (2001): velocity matches for three different retinal base velocities as a function of eye velocity, aggregated across three observers; **b.** data from Freeman (2001): velocity matches for four observers as a function of stimulus velocity. Model of Turano & Massof (2001): red lines; Freeman (2001): green lines; linear model: blue lines.

state not very well applicable to other than their own data.

Evaluation of the models

From the studies of Turano and Massof (2001) and Freeman (2001), the question whether the retinal signal and the eye movement signal are independent is still undecided. Therefore, I compared both non-linear models directly to each other and to the linear model on the same data sets. Figure 2a shows the data from Turano and Massof (2001, their Figure 5), with all three models fitted to the data from three different

conditions (retinal image velocity 0°/s, 2°/s, or 4°/s). In their experiment, observers had to match the speed of a random dot pattern presented during fixation to the perceived speed of a dot pattern viewed during smooth pursuit. As in the original paper, the models were fitted to the data from all three conditions together. The details of the fitting procedure have been described elsewhere (Souman, Hooge, & Wertheim, Accepted). Although the differences between the model curves are quite small, the Turano and Massof model (Eqn. 4-5) fits the data best. This is confirmed by quantification of the model fits in the root-mean-squared errors (*rmse*), presented in Table 1. Since the *rmse* is the standard deviation of the prediction errors, lower values indicate a better fit.

The models were also fitted to the general velocity matching data from Freeman (2001). He had observers perform a velocity matching task at three different pursuit speeds (2.5°/s, 5°/s and 10°/s). Figure 2b shows the results for four individual observers in one condition (10°/s). As in the original paper, the models were fitted to the data from all three pursuit speed conditions together, separately for the four observers (observer JHS only participated in the 10°/s condition). The *rmse*'s, averaged across the observers, are presented in Table 1. Again, the Turano and Massof model provided the best fits. Specifically, it seems to capture the curvature present in the data of observers TCAF and JHS better than the two other models.

Recently, Souman et al. (Accepted) fitted the same three models to data from their velocity matching experiments in which observers had to judge the perceived velocity (both speed and direction) of a random dot pattern moving in one out of several directions during smooth pursuit. They generalized the three models to two dimensions (horizontal and vertical motion in the frontoparallel plane). In their first experiment, the head-centric stimulus velocity was kept constant and stimulus direction was varied. The non-linear models of Turano and Massof (2001) and Freeman (2001) were found to fit the data slightly better than the linear model, with little difference between the two non-linear models. In a second experiment, where the retinal image velocity was approximately constant and the stimulus direction was varied again (as in Experiment 1), the Turano and Massof model fitted the data better, while the model of Freeman produced almost exactly the same model

curves as the linear model. The *rmse*'s found in Souman et al. (Accepted) are shown in Table 1, averaged across the observers in their two experiments.

In order to decide between the three models, two questions have to be answered. First, which model describes the data best? To answer this question, it is not sufficient to look at the goodness-of-fit of the models, as expressed for instance in the *rmse*'s. The goodness-of-fit partly depends on the number of free parameters (Forster, 2000; Pitt & Myung, 2002; Zucchini, 2000). Therefore, it is not surprising that the Turano and Massof model fits the data best, because it has the most degrees of freedom. A higher number of free parameters may make a model fit better to a specific data set, yet decrease its generalizability. To test for this possibility, the models were cross-validated by means of the split-half method. For this purpose the data from Freeman (2001) were used, as these appear to show the largest difference between the models. Half of the data of each observer was randomly selected and all three models were fitted to these data. Then, the best fitting parameter values computed from this training set were used to compute the prediction errors when the models were applied to the other half of the data. Again, the goodness-of-fit was expressed in the *rmse*. This procedure was repeated 100 times and the *rmse*'s obtained were averaged. The results are shown in Table 1. The goodness-of-fit of all three models deteriorated only slightly relative to that based on the entire data set. The Turano and Massof model still produced the best fit. Souman et al. (Accepted) applied the same procedure to their data, with the same results. From this we may

Table 1. Root-mean-squared-errors (*rmse*) for the models of Turano & Massof (2001), Freeman (2001) and the linear model, fitted to the data of three studies (Turano & Massof, 2001; Freeman, 2001; Souman et al., Accepted). Also shown are the results of a cross-validation of the models performed with the data from Freeman (2001). The *rmse*'s for the studies of Freeman and Souman et al. have been averaged across observers.

Study	Model		
	Turano & Massof	Freeman	Linear model
Turano & Massof (2001)	0.45	0.60	0.71
Freeman (2001)	1.48	1.69	1.86
Cross-validation Freeman (2001)	1.53	1.74	1.89
Souman et al. (Accepted)	1.48	1.81	1.96

conclude, therefore, that the Turano and Massof model describes the data from the experiments discussed best.

The second question that has to be answered in order to decide between the models is what they tell us about the underlying mechanisms of motion processing during smooth pursuit. The big advantage of the linear model is its interpretability. Its single parameter, the gain ratio of the eye movement signal gain to the retinal signal gain, reflects the relative contributions of both signals to the perceived head-centric motion. Just as the power coefficients in the non-linear model of Freeman (2001), the two gains in the linear model reflect the transduction of retinal speed and eye movement speed in the visual system. Given its simplicity, the linear model is able to describe an impressive array of phenomena. The Turano and Massof (2001) model, on the other hand, describes these data even better, but its parameters are not as easy to interpret and seem mainly motivated by the goodness-of-fit they provide. Moreover, the model cannot be fitted to experimental data directly. For fitting purposes, it has to be approximated by means of a Taylor series expansion and how good this approximation is depends on the experimental parameters (eye velocity and retinal image velocity). This leaves us in a problematic situation: the better fit of the Turano and Massof model suggests that the retinal signal and the eye movement signal interact, but what does this interaction mean?

Retinal – extraretinal interaction

The interaction term in the Turano and Massof model consists of a retinal input in the eye movement signal (Eqn. 5). Hence, the better fit of this model suggests that the estimated eye velocity partially depends on the retinal image velocity. This possible influence of retinal image characteristics or optic flow on the estimated eye velocity has been proposed earlier in the context of motion perception (Harris, 1994; Wertheim, 1990, 1994), though it has received much less attention in this field than in for instance studies on heading perception during smooth pursuit eye movements (Beintema & Van den Berg, 1998; Bradley, Maxwell, Andersen, Banks, & Shenoy, 1996; Crowell & Andersen, 2001; Lappe, Bremmer, & van den Berg, 1999; Royden, Banks, & Crowell, 1992; Van den Berg & Beintema, 2000). Wertheim (1990, 1994) provided a theoretical rationale for the retinal-extraretinal interaction in motion

perception. He emphasized that retinal image motion is not only affected by rotations of the eyes relative to the head, but also by head movements relative to the world. Therefore, he extended the concept of an eye movement signal to incorporate vestibular and visual components as well (for this reason he called this signal a 'reference signal'). Since retinal optic flow (the visual component) may contribute to activity in the vestibular nuclei (Dichgans & Brandt, 1972, 1978), visual stimulation may signal to the visual system a movement of the head relative to the world, even when the head is stationary with respect to the world (as in the case of visually induced feelings of self-motion orvection, see e.g. Berthoz, Pavard, & Young, 1975). On this account, the visual component of the reference signal may encode both translations and rotations of the head with respect to the world, and, consequently, also of the eyes. The interaction term in the model of Turano and Massof might reflect this visual component.

Additional evidence for the effect of retinal input on the eye velocity as estimated by the visual system is provided by both psychophysical and physiological studies. As mentioned before, paralysis of the eye muscles leads to illusory motion of a stimulus presented in the dark when the observer attempts to move the eyes (Matin et al., 1982; Stevens et al., 1976). However, this does not happen in a normally illuminated environment. In fact, the only thing noticed in this situation by an observer with completely paralyzed eye muscles is that he or she cannot move the eyes (Stevens et al., 1976). Apparently, optic flow information is either combined with extraretinal signals or overrides these and provides a veridical estimate of the eye velocity to the visual system. Also, the afterimage of an horizontal grating is not perceived to move during horizontal smooth pursuit, counter the predictions of the linear model (Goltz et al., 2003). The eye movement or reference signal therefore has to incorporate visual information.

Physiologically, it also makes sense to presume effects of optic flow on the eye velocity estimate in the visual system. One brain area that is thought to be important for combining retinal and extraretinal signals is the medial superior temporal area (MST) in the monkey cortex (Komatsu & Wurtz, 1988a, 1988b; Newsome, Wurtz, & Komatsu, 1988; Pack, Grossberg, & Mingolla, 2001) and its human homologue area V5a (Barton et al., 1996). Besides having extraretinal input, the dorsal part of this brain area also contains many neurons that respond to large moving patterns

(Duffy & Wurtz, 1991a, 1991b; Tanaka, 1989). These neurons might constitute the visual component in the compensation for the effects of smooth pursuit eye movements. The physiological properties of area MST have been successfully used to model both oculomotor behaviour and perceived motion of the pursuit target during smooth pursuit (Furman & Gur, 2003; Pack et al., 2001).

Conclusions

From the evaluation of three quantitative models of motion perception during smooth pursuit the Turano and Massof (2001) model appears to provide the best fits to the data available. Although the better fits are at first sight not surprising giving its higher number of free parameters, cross-validation of the models showed that this does not diminish its generalizability relative to the other models discussed. The presence in this model of a term that represents an interaction between retinal signals and eye movements signals suggests that the estimate of the eye velocity is affected by retinal image characteristics. This agrees with earlier suggestions, according to which optic flow may affect the estimated motion of the head with respect to the world, and consequently also that of the eyes. There is both psychophysical and physiological evidence that this is indeed the case.

The three models that have been discussed in this review do not tell us how the compensation mechanism for the effects of smooth pursuit eye movements is implemented in the visual system. Possibly, compensation arises as a consequence of the combined effect of extraretinal neural signals and the inhibitory activity of MSTd neurons that respond to large moving visual patterns, which may be caused by smooth pursuit eye movements (Pack et al., 2001). In the context of heading perception during smooth pursuit eye movements, it has been proposed that the rotational component of the retinal image motion that is caused by smooth pursuit eye movements is extracted from the visual image by motion templates that are specifically tuned to this optic flow component. The output of these templates may be combined with extraretinal signals to compensate for the effects of the eye movements (Beintema & Van den Berg, 1998; Van den Berg & Beintema, 1997). Empirical evidence suggests that in

heading perception the extraretinal signal interacts with retinal image characteristics as well (Van den Berg & Beintema, 2000).

The presence of such an interaction makes the interpretation of psychophysical results concerning motion perception more complex. Experimental factors such as the spatial frequency of a motion stimulus (Campbell & Maffei, 1981; Diener, Wist, Dichgans, & Brandt, 1976; Smith & Edgar, 1990), its contrast (Blakemore & Snowden, 1999; Campbell & Maffei, 1981; Thompson, 1982), temporal frequency (Giaschi & Anstis, 1989; Treue, Snowden, & Andersen, 1993)

Questions for future research

- How do retinal image characteristics affect the compensation for eye movements? The effects of factors such as spatial frequency, temporal frequency, contrast and presentation duration should be modelled quantitatively.
- What are the temporal dynamics of motion processing during smooth pursuit? Wertheim (1994) suggested different spatiotemporal filters for retinal information used for the estimation of retinal image velocity and for the visual component of the eye movement signal. Supposedly, the latter builds up slower. Recently, Morvan and Wexler (2004) reported that eye movement information is available to the visual system 150 ms after stimulus onset in the case of a search task during smooth pursuit, which is much faster than Wertheim predicted. Does their result reflect just the availability of the efference copy, not of retinal input in the eye movement signal?
- How does the compensation mechanism in motion perception during smooth pursuit relate to that in heading perception during smooth pursuit (Beintema & Van den Berg, 1998; Beintema & van den Berg, 2001; Beintema, Van den Berg, & Lappe, 2004; Crowell & Andersen, 2001; Freeman, 1999; Royden et al., 1992; Royden, Crowell, & Banks, 1994; Van den Berg & Beintema, 1997, 2000; Van den Berg, Beintema, & Frens, 2001)?

and presentation duration (Algom & Cohen-Raz, 1984), to name a few, are known to affect motion perception during fixation. The effect of these factors, however, might be partially due to their role in the compensation mechanism. On the basis of vection studies it has been suggested, for example, that spatial frequency affects the degree of compensation for the effects of smooth pursuit eye movements (Wertheim, 1990, 1994). This would explain the fact that the Filehne illusion has a lower magnitude or even reverses its direction with stimuli that contain lower spatial frequencies (Freeman & Banks, 1998; Wertheim, 1987). Still, it is impossible to disentangle this effect of spatial frequency and assign it to either the retinal signal or the eye movement signal. The present analysis suggests that it may not be appropriate to talk about separate signals and that it would be more productive to pay attention to the factors that influence the compensation mechanism.

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8

Summary and discussion

In this thesis, several aspects of motion perception during smooth pursuit eye movements have been studied. As indicated in the Introduction, the thesis is built around two main topics. The first one concerns the question whether the mechanism of compensation for the effects of smooth pursuit eye movements is the same during collinear and non-collinear motion. The second theme is the evaluation of the classical linear model of motion perception during smooth pursuit. In this chapter, I will summarize the findings on these topics. Also, I will consider some extra arguments concerning potential visual input in the eye movement signal. In addition, some of the remaining problems and questions pertaining to motion perception during smooth pursuit eye movements are discussed. Finally, the relevance of this research project is evaluated.

Collinear and non-collinear motion during smooth pursuit

As outlined in Chapter 2, the literature disagreed on the question whether compensation for the effects of eye movements happens in the same way when observers are presented with non-collinear motion as with collinear motion. Most research on motion perception during smooth pursuit has used collinear motion stimuli: stimuli that move along the line of pursuit (horizontally in most cases). Much less attention has been devoted to the perception of motion stimuli that move at an angle (other than 0° or 180°) relative to the pursuit target (non-collinear motion). According to Wallach, Becklen and Nitzberg (1985), the degree of compensation is much higher for collinear motion than for non-collinear motion (Becklen, Wallach, & Nitzberg, 1984), as shown by smaller deviations of the perceived motion relative to the physical one. Swanston and Wade (1988), on the other hand, found a relatively constant degree of compensation across a range of stimulus motion directions. In Chapter 2, a solution to this apparent discrepancy was offered. The perceived

motion direction across the entire range of directions (0° to 360° relative to the pursuit direction) could be described by the classical linear model with a constant gain ratio of eye movement signal gain to retinal signal gain. Therefore, the degree of compensation seems to be constant across stimulus directions. The difference found earlier between collinear and non-collinear motion was shown to be caused by a difference in stimulus speed. The degree of compensation turned out to be lower for higher stimulus speeds.

If the compensation mechanism is the same in collinear and non-collinear motion perception, one would expect factors that affect the perceived velocity of collinear motion to have a similar effect on perceived non-collinear motion. In Chapter 3, one such factor was studied: the effect of the presentation duration of the motion stimulus. With collinear motion, higher presentation durations generally cause the perceptual errors due to smooth pursuit eye movements to decrease. For instance, the Filehne illusion (illusory motion of a stationary stimulus against the direction of the smooth pursuit eye movement: Filehne, 1992; Mack & Herman, 1973) gets weaker with longer presentation durations (De Graaf & Wertheim, 1988; Ehrenstein, Mateeff, & Hohsbein, 1986; Mack & Herman, 1978). Therefore, we expected the illusory slant of the perceived path of a vertically moving stimulus presented during horizontal smooth pursuit to decrease with the presentation duration of the stimulus as well. This is exactly what we found. The results of a second experiment showed that this effect of presentation duration could not be ascribed to a change in the degree of compensation over time, independent of the presentation duration. Taken together, the results of the two experiments in Chapter 3 suggest that the eye velocity as estimated by the visual system, which is used to compensate for the effects of the eye movements, is affected by the presentation duration of the stimulus.

One of the problems in comparing studies on collinear and non-collinear motion perception during smooth pursuit is that different perceptual measures have been used. In collinear motion studies, the effect of

eye movements is generally deduced from the perceived speed, while the perceived motion direction is used in non-collinear motion studies. This, of course, makes both classes of studies hard to compare. Chapter 6 presented the results of two experiments in which observers judged both the stimulus speed and the motion direction of the stimulus at the same time. For this purpose, a new paradigm was developed. The results showed that, as in the previously mentioned chapters, the effect of the smooth pursuit eye movements was similar for collinear and non-collinear motion. Moreover, our new paradigm turned out to be a useful tool to study motion perception during smooth pursuit eye movements.

Although Chapter 5 was not directly concerned with collinear vs. non-collinear motion perception, the experiment described in that chapter provided in fact the motivation to study the relationship between motion perception with both types of stimuli. We used the same non-collinear motion stimulus as in Chapter 3 (a vertically moving dot) to investigate the relationship between the compensation for eye movements in localization and motion perception during smooth pursuit. From the indicated starting and end points of the stimulus motion the direction of the perceived stimulus path was predicted and compared to the actual indicated direction. While both indicated and predicted directions deviated from the (physical) vertical direction, this error was larger for the direction predicted from localization. Based on the literature, this difference was explained in terms of extra factors that affect localization during smooth pursuit, as compared to motion perception, such as different signal latencies and retinal motion direction asymmetries.

The linear model and alternatives

The second line of research in this thesis concerned the ability of the classical linear model to describe motion perception during smooth pursuit eye movements. This model, described extensively in Chapters 2, 4, 6, and 7, is based on the simple idea that the visual system adds an estimate of the eye velocity to the estimated retinal image velocity in order to produce a motion percept (Freeman & Banks, 1998; also see Von Holst, 1954; Von Holst & Mittelstaedt, 1950; Wertheim, 1990, 1994). Errors and illusions in motion perception during smooth pursuit are explained in terms of the gains of the two

signals. Despite its simplicity, this linear model is able to describe several phenomena during smooth pursuit, such as the earlier mentioned Filehne illusion and the Aubert-Fleischl phenomenon (a moving object appears to move slower when tracked with the eyes than when viewed during fixation: Aubert, 1886, 1887; Dichgans, Wist, Diener, & Brandt, 1975; Von Fleischl, 1882; see Wertheim & Van Gelder, 1990 for an alternative explanation in terms of increased motion detection thresholds during smooth pursuit eye movements). As described in Chapter 2, the linear model was also found to describe the perceived motion direction of stimuli viewed during smooth pursuit very well. In Chapter 4 the linear model was shown to fit the results of a difficult velocity matching task during sinusoidal pursuit. This study was designed to investigate potential latency differences between the retinal signal, encoding retinal image motion, and the eye movement signal, which encodes the rotational eye velocity. Although the linear model fitted the data well for most observers, the latency differences derived from it were quite variable, making it hard to draw quantitative conclusions. It was suggested that the inferred latency differences possibly reflect the influence of a visual component in the eye movement signal. This would mean that the linear model is incorrect or at least incomplete. To further explore this possibility, Chapters 6 and 7 provided explicit tests of the linear model, in which it was compared with two non-linear models. In Chapter 6, these models were applied to the velocity matches of the two experiments in which observers had to judge both the speed and direction of the motion stimulus (as described above). The model of Turano and Massof (2001) provided a slightly better fit to the data than the linear model and the non-linear model of Freeman (2001). Chapter 7 gives a review of these models. Here, they were applied to other existing data sets and the same conclusion was reached. In the Turano and Massof model, the retinal image velocity and the eye velocity as estimated by the visual system are related non-linearly to the physical velocities. Moreover, that model incorporates an interaction between retinal image speed and eye movement speed in the estimate of the eye velocity. The better fits of the Turano and Massof model were therefore taken to imply that the eye movement signal is not only based on extraretinal information (an efference copy of the oculomotor command), but also on retinal image characteristics. This agrees with earlier theoretical ideas (Wertheim, 1990, 1994), with psychophysics (Goltz,

DeSouza, Menon, Tweed, & Vilis, 2003) and with physiologically inspired models (Pack, Grossberg, & Mingolla, 2001). Taken together, the results in Chapters 2, 4, 6 and 7 suggest that the linear model is still useful as a description of experimental data, as the deviations of the velocity matches in the experiments described in these chapters typically are quite small. The advantage of the linear model as a data description tool is that it is a simple model, that can be fitted analytically and has a single parameter that is easily interpretable. As an algorithmic model of how our brain compensates for the effects of smooth pursuit eye movements in motion perception it seems to fall short, as the estimated velocities of the retinal image and the eyes probably are non-linearly related to the physical velocities and seem to interact.

Additional considerations concerning the retinal – extra-retinal interaction

If the extraretinal signal is indeed only a part of the eye movement signal that is used by the visual system to compensate for the effects of smooth pursuit and if it

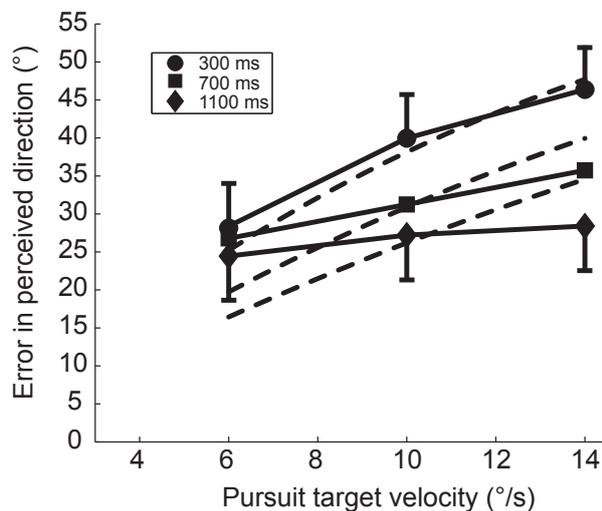


Figure 1. The linear model (dashed lines) fitted to the data of Experiment 1 in Chapter 3. The linear model was fitted in the same way as described in Chapter 2, separately for the three presentation durations. Solid lines connect the average errors in perceived motion direction for the three stimulus presentation duration conditions. Error bars are as in Figure 3 of Chapter 3.

is complemented by a visual component, the question rises why the difference between the goodness-of-fit of the linear model and the interaction model of Turano and Massof (2001) is generally so small. Partly, this may be due to the stimuli used. According to Wertheim (1990; 1994) a visual pattern has to be large, has to contain low spatial frequencies (< 0.1 cpd; see Freeman & Banks, 1998; Wertheim, 1987) and be presented for at least 1000 ms to contribute substantially to the visual component of the eye movement signal. Also, its retinal image speed should not be too high (see De Graaf, Wertheim, Bles, & Kremers, 1990). In this respect, the stimuli used in most experiments on motion perception during smooth pursuit may not have contributed much to the importance of the visual component. Stimuli are typically quite small (covering only a few degrees of visual angle) and are often presented for less than 1 s. Another possible reason for the small differences between linear and non-linear models is that the room for differences may be quite small. If the stimulus motion is perceived veridically during smooth pursuit, the linear model describes the data perfectly with a gain ratio of one. Also, if the retinal image motion is reported as perceived velocity, the linear model gives a perfect description with a zero gain ratio. Only between these two points can any difference between the linear model and non-linear models become evident. Having said that, we should note that in the first experiment in Chapter 3 the linear model fails to fit the indicated motion direction, even when different curves for the different presentation durations are fitted (Figure 1). So, even with a single dot stimulus substantial nonlinearities do occur. Interestingly, from Figure 1 it seems that the non-linear effect is stronger for longer presentation duration, corroborating Wertheim's (1994) theoretical analysis.

The ideal motion stimulus

This brings us to another important topic: what stimulus should be used in psychophysical studies of motion perception during smooth pursuit eye movements? In this thesis, several types of stimuli have been used. In Chapters 2, 3 and 5, observers were presented with a single dot stimulus. In Chapter 5, the use of a single object as stimulus was necessary, because it had to be localizable. It might, however, be questioned whether

a single dot was such a good stimulus in the other two studies (as indeed one of the reviewers of the paper in Chapter 3 did). A single moving dot has a constantly changing retinal position, complicating the motion perception with foveal vs. peripheral differences in motion processing (see e.g. McKee & Nakayama, 1984; Tynan & Sekuler, 1982). Moreover, experimental factors such as presentation duration, stimulus direction and stimulus speed also affect the retinal location of the stimulus. Although it was argued in Chapter 3 that this could not explain the effect of presentation duration, the studies cited there as evidence used random dot patterns as stimuli. There is still the possibility, therefore, that the retinal eccentricity of the single dot stimulus has influenced the results. However, the results of Chapters 2 and 6 can be used to investigate this possibility. In the experiment of Chapter 2, observers indicated the perceived direction of a single dot stimulus viewed during smooth pursuit. In Experiment 1 of Chapter 6, the same experimental parameters (pursuit speed, stimulus speed, overlapping stimulus direction range) were combined with a different stimulus (a random dot pattern moving within an aperture that was stationary on the screen). In Chapter 6, the indicated direction and speed were analyzed together, but we can also look at the separate components. Figure 2 shows the indicated directions from Experiment 1 in Chapter 6 for each of the four observers, together with the best fitting curves

of the linear model. As with the single dot stimulus of Chapter 2, the linear model provides an excellent fit to the direction matches. It seems, therefore, that the difference in stimulus did not affect the validity of the linear model. However, the errors in the indicated directions seem to be larger when the single dot stimulus was used (compare Figure 2 with the 8°/s condition of Figure 3 in Chapter 2). Hence, it is possible that the type of stimulus affects the degree of compensation for the effects of the eye movements, at least with respect to the perception of motion direction.

Theoretically, the ideal motion stimulus for studying motion perception during smooth pursuit should have a constant retinal location and contain minimal position cues (see Freeman & Sumnall, 2002). This would be achieved by using a random dot stimulus that is displayed within an annulus that moves with the pursuit target (see De Graaf & Wertheim, 1988). In this way, the retinal image position remains constant during (accurate) pursuit. Position cues might be minimized by giving the stimulus dots a limited lifetime, reassigning a new, random position within the annulus at the start of each new lifecycle. A potential problem with a moving annulus is that the contours of the annulus may produce induced motion of the stimulus dots by their relative motion (Duncker, 1929). To minimize this induced motion, the luminance of dots that approach the edges of the aperture may be gradually reduced. We tried to use this stimulus in pilot studies for our experiments that measured both direction and speed (Chapter 6). However, most of the observers appeared to have trouble judging the velocity of such a stimulus. Particularly, they often saw the dot pattern move in the direction opposite to its actual direction. The problem seemed to have been caused mainly by the limited lifetime of the dots. This also caused problems in the experiments with sinusoidal pursuit (Chapter 4). Possibly, limited lifetime dots cause some kind of a correspondence problem, in which observers have problems in matching the dots at time t_1 with those at t_2 some time later. Relating appearing and disappearing dots incorrectly may produce apparent motion patterns that conflict with the actual motion of the dots.

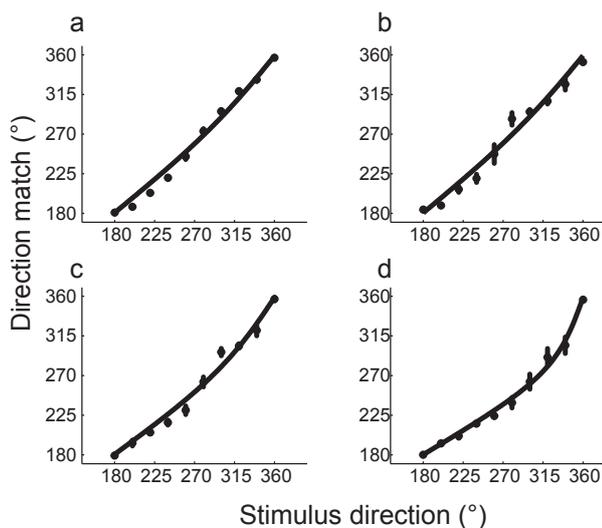


Figure 2. The linear model fitted to the direction components of the velocity matches of the four observers in Experiment 1 of Chapter 6. Error bars indicate the standard errors of the mean.

Motion perception as an active interpretation

Although the compensation for the effects of smooth pursuit eye movements in the literature mainly has been conceptualized as an automatic, unconscious process, introspection suggests that the motion of objects in the world around us is available to our conscious report both in a retinocentric and a head-centric or geocentric frame of reference, at least to a certain extent. For instance, if we cycle along a row of trees, the trees can be seen to move relative to ourselves. The percept that the trees stand still relative to the world and we ourselves are moving may come from a more or less conscious interpretation. In fact, this is the phenomenon as originally described by Filehne (1922). He noticed how the visual background appears to move when we follow our moving finger with our eyes. Apparently, the retinal image motion is to some extent accessible for conscious reports. In this sense, the problem of how our visual system compensates for the effects of eye movements and other forms of self-motion is similar to

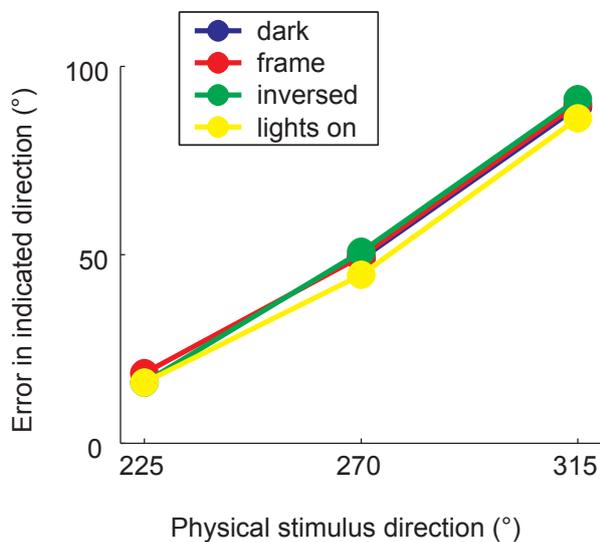


Figure 3. The effect of the presence of visual references on the indicated motion direction of a moving stimulus viewed during smooth pursuit ($n = 6$). The conditions were: dark, only stimulus and pursuit target visible; frame: as dark, but with a grey frame that outlined the edges of the monitor; inversed: white monitor screen with black stimuli and pursuit target; lights on: as dark, but with the lights in the experimental room switched on. The errors in the indicated motion direction are presented as if pursuit were to the right (0°).

other forms of perceptual constancy, such as lightness constancy, colour constancy or size constancy. In size constancy, for example, we perceive identical objects at different distances as equally big. At the same time, however, we often realize that the objects that are farther away appear to be smaller (see e.g. Rock, 1975).

In the experiments described in this thesis, observers were instructed to report the stimulus motion with respect to their head, that is, in a head-centric frame of reference. The extent to which they reported the actual head-centric motion was taken as the outcome of the compensation process. In addition, however, their reports may also reflect the extent to which they were able to direct their *attention* to that head-centric motion and not to the retinocentric motion. In the relatively ‘poor’ visual environments that have been used in the experiments in this thesis, there was little visual information available to make a conscious interpretation of self-motion (smooth pursuit eye movements) and object motion. What is more, observers were instructed to report what they saw, not what they thought that happened. This may actually have biased them towards a more ‘retinal’ report, despite the instruction to report motion with respect to the head. It would be comparable to the instruction to report the size of objects at different distances as they appear to the observer and not the size the observer thinks they have. It would be interesting to see whether the reported percept can be influenced by the instruction to the observer, while keeping the visual stimulus identical. Another way of influencing the interpretation of the visual image may be to vary the amount of relative motion cues in the stimulus display. This might facilitate the judgement in a head-centric frame of reference (see De Graaf, 1990, Ch. 1.2). We studied the effect of visual references on perceived motion direction during smooth pursuit eye movements in a study that has not been presented in this thesis in a separate chapter. Six observers had to judge the motion direction of a random dot pattern, presented in an annulus that moved with the pursuit target. The amount of visual information was varied in four conditions. In the standard condition (‘dark’) that was used in all experiments described in this thesis, there was no other visual information than the pursuit target and the stimulus. A second condition was similar to this standard condition, except for a dark grey frame presented at the edge of the computer monitor. This provided information about the motion of the stimulus relative to the monitor. In a third condition, the background of the

monitor was white and the stimulus and pursuit target were presented in black. A fourth condition resembled the first one, but now the lights in the experimental room were turned on. Figure 3 shows the results, averaged across the observers. As can be seen from this figure, the visual reference conditions had no effect on the reported motion directions. Although this may partly have been due to induced motion because of the moving annulus (see above), it nevertheless creates a problem for both the interpretation that the eye movement signal contains a visual component and for the idea that the reported motion percept partially depends on some kind of conscious interpretation of the visual image. From the theory of Wertheim (1990, 1994), one would expect the errors in the perceived direction to decrease with increasing visual information, because the eye movements create an optic flow of the background across the retinae. This did not happen. Also, the visual references present in all but the first condition were apparently not used by the observers. Clearly, more research is necessary, especially because the presence of more visual references is what is thought to prevent visual illusions during smooth pursuit eye movements, such as the Filehne illusion, from affecting our daily life motion perception (see De Graaf, 1990, Ch. I.2).

Practical and theoretical relevance

Countless times, after I had explained to someone what kind of research I did, I have had to answer the question: “And what can you use this for?”. To pre-empt more critical and difficult questions, I normally answered: “It’s good for absolutely nothing.” Fortunately, I do not think that that is the only possible answer. On the other hand, I do think that the theoretical relevance of this research far outweighs its practical use, and people that asked me the relevance question probably hinted at the latter. The main applications lie in situations with very restricted visual input, such as when flying an airplane or driving a car at night or in foggy conditions. In these situations, severe perceptual errors may occur because the compensation for the effects of self-motion (eye movements, head movements, passive body movements, etc.) is not complete and visual perception may need to be supplemented by other sources of information. The results of this project could also be used in situations where illusions are used to create certain percepts, for

instance in simulated visual environments and computer games.

From the start of this research project, it has been clear that its major importance lay in its theoretical relevance. As outlined in the Introduction of this thesis, the study of motion perception during eye movements has a long and venerable history and still lots of questions remain unanswered. In this thesis, the research has been extended to two dimensions in the frontoparallel plane. To arrive at motion perception in a geocentric frame of reference, however, one should also incorporate the viewing distance to the stimulus and the depth in the visual scene (see Wertheim, 1994, Reply 7). In Chapter 4, we studied the temporal relationship between retinal signals and eye movement signals. It is still an open question, however, how these signals develop in the course of time. Recent research suggests that the eye movement signal may be available to the visual system about 150 ms after stimulus onset (Morvan & Wexler, 2004). Is the estimate of eye velocity provided by this signal constant after this interval, or does it still change? According to Wertheim (1990; 1994), the visual component takes more than 1000 ms to build up. Additionally, we need to know more about the temporal dynamics of the retinal signal and how it interacts with the eye movement signal. Finally, it should be mentioned that a similar problem of compensation for the effects of smooth pursuit eye movements has been studied in the context of heading perception (Beintema & Van den Berg, 1998; Beintema & van den Berg, 2001; Crowell & Andersen, 2001; Royden, Banks, & Crowell, 1992; Royden, Crowell, & Banks, 1994; Van den Berg & Beintema, 1997, 2000; Van den Berg, Beintema, & Frens, 2001). With a few exceptions (Freeman, 1999; Freeman, Banks, & Crowell, 2000), little attention has been paid to the relation between these two fields. As often mathematically more sophisticated models are used in heading perception research, the field of motion perception during smooth pursuit might benefit from integration of the two.

The study of motion perception during smooth pursuit is not just a goal in itself. Besides extending the applicability of our knowledge of how our brain processes motion to circumstances that more resemble our daily life, it is also an instance of a more general problem, namely how our brain integrates information from different sources. In the case of motion perception during smooth pursuit, retinal and extraretinal information need to be combined. This general

problem, however, occurs in many more instances. Our brain has to combine input from different modalities, such as visual, auditory and tactile input, to produce one coherent percept of the world around us (Ernst & Bühlhoff, 2004). And often even within modalities integration is necessary. Our visual system, for example, extracts several features, such as lines, colours, motion, position, etc., from the visual images that are projected on our retinae and to a certain extent it processes those features independently. Yet, we don't see separate lines, colours, and so on, but objects and surfaces. Apparently, our brain is capable of integrating these parts again into one coherent whole. How it achieves that feat (the so-called 'binding problem') may be one of the big challenges of present neuroscience.

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Samenvatting

Oogbewegingen veranderen de retinale beeldbeweging van objecten in het visuele veld. Als we een oogbeweging maken zal het beeld van een stilstaand object over onze retinae bewegen, terwijl het beeld van een object dat we volgen met de ogen juist bij benadering stil staat op de retinae. Om ons in staat te stellen beweging in de buitenwereld veridicaal waar te nemen moet ons visuele systeem dus de oogbewegingen verdisconteren in de verwerking van de retinale beeldbeweging. Met andere woorden, het visuele systeem moet compenseren voor de effecten van oogbewegingen op de retinale beeldbeweging van objecten in het visuele veld. In dit proefschrift zijn verschillende aspecten van bewegingswaarneming tijdens oogvolgbewegingen, een specifieke vorm van oogbewegingen die we maken om bewegende objecten te volgen met de ogen, bestudeerd. Zoals reeds aangegeven in de Inleiding is het proefschrift opgebouwd rondom twee onderwerpen. In de eerste plaats heb ik me beziggehouden met de vraag of het compensatiemechanisme voor de effecten van oogvolgbewegingen op bewegingswaarneming gelijk is voor verschillende bewegingsrichtingen. Het tweede thema van dit proefschrift betreft de evaluatie van het klassieke lineaire model van bewegingswaarneming tijdens oogvolgbewegingen. Hier worden de bevindingen op deze twee punten samengevat.

Collineaire en niet-collineaire stimulusbeweging tijdens oogvolgbewegingen

Zoals uiteengezet in Hoofdstuk 2 verschilde de literatuur van mening over de vraag of de compensatie voor de effecten van oogvolgbewegingen net zo gebeurt als waarnemers niet-collineaire beweging moeten beoordelen als wanneer ze collineaire beweging moeten beoordelen. In de meeste studies naar bewegingswaarneming tijdens oogvolgbewegingen zijn collineaire bewegingsstimuli gebruikt: een punt of een puntenwolk die langs dezelfde lijn beweegt als het doel dat met de ogen gevolgd wordt (volgdoel),

in de meeste gevallen horizontaal. Veel minder aandacht is er besteed aan stimuli die onder een hoek bewegen ten opzichte van het volgdoel (niet-collineaire beweging). Volgens Wallach, Becklen en Nitzberg (1985) is de mate van compensatie veel hoger voor collineaire beweging dan voor niet-collineaire beweging (Becklen, Wallach, & Nitzberg, 1984), wat volgens hen blijkt uit het feit dat het verschil tussen de waargenomen beweging en de werkelijke beweging veel kleiner is bij collineaire beweging. Swanston en Wade (1988), aan de andere kant, vonden een relatief constante mate van compensatie voor een reeks van stimulusbewegingsrichtingen. In Hoofdstuk 2 wordt een oplossing voor deze schijnbare tegenspraak gegeven. De waargenomen bewegingsrichting voor het hele bereik van stimulusrichtingen (0° tot 360° ten opzichte van de richting van het volgdoel) werd gemeten. Deze waargenomen bewegingsrichtingen bleken goed te kunnen worden beschreven door het klassieke lineaire model van bewegingswaarneming tijdens oogvolgbewegingen. Volgens dit model is de waargenomen snelheid gelijk aan de som van de geschatte retinale snelheid van de stimulus en de geschatte oogsnelheid, waarbij deze proportioneel zijn met respectievelijk de werkelijke retinale bewegingssnelheid en de oogbewegingssnelheid. De beide proportionele constanten ('gains' genoemd) bepalen dus de waargenomen beweging. Het lineaire model beschreef de data van het experiment in Hoofdstuk 2 goed met een constante verhouding van beide gains, wat impliceert dat de mate van compensatie voor de effecten van oogvolgbewegingen constant is voor verschillende bewegingsrichtingen van de stimulus. De data in Hoofdstuk 2 laten ook zien dat het verschil dat eerder was gevonden tussen collineaire en niet-collineaire beweging kan worden verklaard door een verschil in de gebruikte stimulusnelheden. Wij vonden een lagere mate van compensatie bij een hogere stimulusnelheid.

Als er eenzelfde compensatiemechanisme werkzaam is bij collineaire en niet-collineaire bewegingswaarneming, dan zou men ook verwachten dat factoren die

de waargenomen snelheid van collineaire beweging beïnvloeden een soortgelijk effect hebben op de waargenomen niet-collineaire beweging. In Hoofdstuk 3 werd één van die factoren bestudeerd: het effect van de aanbiedingsduur van de bewegingsstimulus. Bij collineaire beweging zorgt een langere aanbiedingsduur ervoor dat de fouten in de waarneming die het gevolg zijn van oogvolgbewegingen kleiner worden. De Filehne illusie bijvoorbeeld (de illusoire beweging van een stilstaand object tijdens een oogvolgbeweging: Filehne, 1922; Mack & Herman, 1973), wordt minder sterk bij een langere aanbiedingsduur (De Graaf & Wertheim, 1988; Ehrenstein, Mateeff, & Hohnsbein, 1986; Mack & Herman, 1978). Wij verwachtten daarom dat de illusoire helling van de waargenomen baan van een verticaal bewegende stimulus die aangeboden wordt tijdens een horizontale oogvolgbeweging eveneens zou afnemen met toenemende aanbiedingsduur. Dit is precies wat we vonden. De resultaten van een tweede experiment lieten zien dat dit effect van aanbiedingsduur niet kon worden toegeschreven aan een verandering in de mate van compensatie in de loop van de tijd, onafhankelijk van de aanbiedingsduur. Op grond van de resultaten van de twee experimenten in Hoofdstuk 3 concludeerden we dat de oogsnelheid zoals die geschat wordt door het visuele systeem en gebruikt wordt om te compenseren voor de effecten van oogbewegingen op de retinale beeldbeweging beïnvloed wordt door de aanbiedingsduur van de stimulus.

Eén van de problemen bij het vergelijken van studies naar de waarneming van collineaire en niet-collineaire beweging tijdens oogvolgbewegingen is dat er verschillende perceptuele maten zijn gebruikt. In collineaire bewegingsstudies wordt het effect van de oogbewegingen over het algemeen afgeleid van de waargenomen snelheid, terwijl in niet-collineaire bewegingsstudies de waargenomen richting daarvoor wordt gebruikt. Dit maakt beide groepen studies uiteraard moeilijk te vergelijken. Hoofdstuk 6 geeft de resultaten van twee experimenten waarin waarnemers zowel de snelheid als de richting van de stimulus beoordeelden. Hiervoor werd een nieuw onderzoeksparadigma ontwikkeld. De resultaten lieten zien dat, net als in de Hoofdstukken 2 en 3, het effect van de oogvolgbewegingen gelijk was voor collineaire en niet-collineaire beweging. Bovendien bleek ons nieuwe paradigma uitermate geschikt te zijn om bewegingswaarneming tijdens oogvolgbewegingen te bestuderen.

Hoewel Hoofdstuk 5 niet direct betrekking had op collineaire vs. niet-collineaire bewegingswaarneming, vormde het experiment dat in dit hoofdstuk beschreven wordt in feite de motivatie om de relatie tussen bewegingswaarneming met beide klassen van stimuli te bestuderen. We gebruikten in dit hoofdstuk dezelfde niet-collineaire bewegingsstimulus als in Hoofdstuk 3 (een verticaal bewegend puntje) om de relatie tussen de compensatie voor oogbewegingen in localisatie en bewegingswaarneming tijdens oogvolgbewegingen te bestuderen. Op grond van de aangegeven begin- en eindpunten van de stimulusbeweging werd de richting van de waargenomen stimulusbaan voorspeld en vergeleken met de feitelijk aangegeven richting. Hoewel zowel de aangegeven als voorspelde bewegingsrichtingen afweken van de fysieke, verticale richting, was deze fout groter voor de richting voorspeld op grond van de localisatie. Op grond van de literatuur werd dit verschil verklaard in termen van extra factoren die localisatie tijdens oogvolgbewegingen beïnvloeden ten opzichte van bewegingswaarneming, zoals verschillende signaallatenties en asymmetrieën in de retinale bewegingsrichting.

Het lineaire model en alternatieven

De tweede onderzoekslijn in dit proefschrift betrof de vraag hoe goed het klassieke lineaire model bewegingswaarneming tijdens oogvolgbewegingen beschrijft. Dit model, uitgebreid beschreven in de Hoofdstukken 2, 4, 6 en 7, is gebaseerd op het eenvoudige idee dat het visuele systeem een schatting van de oogsnelheid optelt bij de geschatte retinale beeldsnelheid om tot een bewegingspercept te komen (Freeman & Banks, 1998; zie ook Von Holst, 1954; Von Holst & Mittelstaedt, 1950; Wertheim, 1990, 1994). Fouten en illusies in bewegingswaarneming tijdens oogvolgbewegingen worden verklaard in termen van de gains van de twee signalen. Ondanks zijn eenvoud is dit lineaire model in staat om verschillende fenomenen die optreden tijdens oogvolgbewegingen goed te beschrijven, zoals de reeds genoemde Filehne illusie en het Aubert-Fleischl fenomeen (een bewegend object lijkt langzamer te bewegen wanneer het gevolgd wordt met de ogen dan wanneer het gezien wordt tijdens fixatie: Aubert, 1886, 1887; Dichgans, Wist, Diener & Brandt, 1975; Von Fleischl, 1882; zie Wertheim & Van

Gelder, 1990, voor een alternatieve verklaring in termen van verhoogde drempels voor bewegingszien tijdens oogvolgbewegingen). Zoals beschreven in Hoofdstuk 2 bleek het lineaire model ook de waargenomen bewegingsrichting van stimuli die gezien worden tijdens oogvolgbewegingen goed te beschrijven. Hoofdstuk 4 laat zien dat het lineaire model de resultaten van een moeilijke snelheidsmatchingtaak tijdens sinusoidale oogvolgbewegingen eveneens goed beschreef. Deze studie was opgezet om potentiële latentieverschillen tussen het retinale signaal, dat de retinale beeldsnelheid encodeert, en het oogbewegingssignaal, dat de rotatiesnelheid van de ogen encodeert, te onderzoeken. Hoewel het lineaire model de data van de meeste waarnemers goed beschreef, waren de latentieverschillen die hieruit afgeleid worden erg variabel, wat het trekken van kwantitatieve conclusies met betrekking tot deze latentieverschillen bemoeilijkte. Op grond van de resultaten concludeerden we dat de gevonden latentieverschillen mogelijk de invloed van een visuele component in het oogbewegingssignaal laten zien. Dit zou betekenen dat het lineaire model mogelijk onjuist of incompleet is. Om deze mogelijkheid verder te onderzoeken werden in de Hoofdstukken 6 en 7 expliciete toetsingen van het lineaire model, vergeleken met twee non-lineaire modellen, uitgevoerd. In Hoofdstuk 6 werden deze modellen toegepast op de snelheidsmatches van de twee experimenten waarin waarnemers zowel snelheid als bewegingsrichting van de bewegingsstimulus moesten beoordelen (zoals hierboven beschreven). Het model van Turano en Massof (2001) bleek de data iets beter te fitten dan het lineaire model en het non-lineaire model van Freeman (2001). Hoofdstuk 7 geeft een review van deze modellen. In dit hoofdstuk worden de modellen toegepast op andere, reeds bestaande, datasets en kom ik tot hetzelfde resultaat. In het model van Turano en Massof zijn de retinale beeldsnelheid en de oogsnelheid zoals die geschat worden door het visuele systeem non-lineair gerelateerd aan de fysieke snelheden. Verder bevat dit model een interactie van de retinale beeldsnelheid en de oogsnelheid in de schatting van de oogsnelheid. De betere fits van het Turano en Massof model lijken daarom te impliceren dat het oogbewegingssignaal niet alleen is gebaseerd op extraretinale informatie (een efferentiekopie van het oculomotorsignaal), maar ook op eigenschappen van het retinale beeld. Dit komt overeen met eerdere theoretische ideeën (Wertheim, 1990, 1994), met psychofysische resultaten (Goltz, DeSouza, Menon,

Tweed, & Vilis, 2003) en met modellen die gebaseerd zijn op fysiologische gegevens (Pack, Grossberg, & Mingolla, 2001). Alles bij elkaar laten de resultaten van de Hoofdstukken 2, 4, 6 en 7 zien dat het lineaire model nog steeds een nuttig instrument is om experimentele data te beschrijven, aangezien de fouten die dit model maakt in de beschrijving van de snelheidsmatches in deze hoofdstukken tamelijk klein zijn. Het grote voordeel van het lineaire model als een instrument om de data te beschrijven is dat het eenvoudig is, analytisch gefit kan worden en één enkele, gemakkelijk te interpreteren parameter heeft. Als een algoritmisch model van hoe ons brein compenseert voor de gevolgen van oogvolgbewegingen in bewegingswaarneming lijkt het niet volledig. Waarschijnlijk zijn de schattingen van de retinale beeldsnelheid en van de oogsnelheid die het visuele systeem gebruikt non-lineair gerelateerd aan de fysieke snelheden en interacteren ze.

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Curriculum Vitae

Jan Souman was born on July 28th, 1969, in Oldebroek. After completing his secondary education (VWO) at the Reformed High School in Amersfoort, he studied Theology at the Theological University of the Reformed Churches in the Netherlands, in Kampen. Already before graduating in Theology in 1996 with the specialization New Testament, he started to study Psychology part-time at Utrecht University, in an attempt to extend his knowledge and skills in a more empirical science. Besides his Psychology study, he worked for one year in a bookshop and for three years as a project manager of three car parks. Also, he taught statistics to undergraduate students as a student-assistant at the Methodology and Statistics Department of the Faculty of Social Sciences of Utrecht University. After he finished his Masters in Theoretical and Experimental Psychology with honours, doing a practical at the Free University of Amsterdam under supervision of prof. dr. Jan Theeuwes, dr. Peter Starreveld and prof. dr. Jan Kroeze and a graduation project at TNO Human Factors in Soesterberg, under supervision of prof. dr. Lex Wertheim, prof. dr. Jan Kroeze and dr. Frank Kooi, he started working in 2000 as a postgraduate student in the Helmholtz Research School (Department of Psychonomics, Utrecht University), under supervision of prof. dr. Lex Wertheim and, initially, prof. dr. Jan Kroeze and later dr. Ignace Hooge. From 2000 to 2002 he was also active as a junior lecturer in the Methodology and Statistics Department of Utrecht University. During his Ph.D. project, Jan spent several months working with dr. Tom Freeman in Cardiff, Wales. From June 2005, he will be working as a researcher with dr. Marc Ernst, in the Max Planck Institute for Biological Cybernetics in Tübingen, Germany.

Jan Souman werd op 28 juli 1969 geboren in Oldebroek. Nadat hij het VWO doorlopen had aan de Gereformeerde Scholengemeenschap in Amersfoort, studeerde hij Theologie aan de Theologische Universiteit van de Gereformeerde Kerken in Nederland, in Kampen. Al voordat hij in 1996 afstudeerde in de specialisatie Nieuwe Testament, begon hij Psychologie in deeltijd te studeren aan de Universiteit van Utrecht, in een poging zijn kennis en vaardigheden in een meer empirische wetenschap uit te breiden. Naast zijn psychologiestudie werkte hij gedurende één jaar in een boekhandel en was hij drie jaar lang projectmanager van drie parkeer garages. Ook gaf hij als student-assistent statistiek aan eerste- en tweedejaars studenten bij de vakgroep Methodologie en Statistiek van de Faculteit Sociale Wetenschappen van de Universiteit van Utrecht. Nadat hij cum laude zijn doctoraalbul in de Theoretische en Experimentele Psychologie had gehaald, op basis van een stage aan de Vrije Universiteit van Amsterdam onder begeleiding van prof. dr. Jan Theeuwes, dr. Peter Starreveld en prof. dr. Jan Kroeze en een afstudeeronderzoek bij TNO Technische Menskunde in Soesterberg, onder begeleiding van prof. dr. Lex Wertheim, prof. dr. Jan Kroeze en dr. Frank Kooi, begon hij in 2000 als assistent-in-opleiding in de Helmholtz Onderzoeksschool (vakgroep Psychonomie, Universiteit Utrecht), onder begeleiding van prof. dr. Lex Wertheim en, van aanvankelijk prof. dr. Jan Kroeze en later dr. Ignace Hooge. Van 2000 tot 2002 was hij tevens actief als junior-docent bij de vakgroep Methodenleer en Statistiek van de Universiteit Utrecht. Gedurende zijn promotieproject werkte Jan gedurende enkele maanden samen met dr. Tom Freeman in Cardiff, Wales. Vanaf juni 2005 zal hij als onderzoeker werkzaam zijn bij het Max Planck Instituut voor Biologische Cybernetica in Tübingen, Duitsland, waar hij zal samenwerken met dr. Marc Ernst.

