Exp Brain Res (2005) 164: 376–386
DOI 10.1007/s00221-005-2261-6

RESEARCH ARTICLE

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Perceived motion direction during smooth pursuit eye movements

Received: 1 October 2004 / Accepted: 13 December 2004 / Published online: 27 April 2005

Abstract Although many studies have been devoted to motion perception during smooth pursuit eye movements, relatively little attention has been paid to the question of whether the compensation for the effects of these eye movements is the same across different stimulus directions. The few studies that have addressed 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 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.

Keywords Motion perception · Motion direction · Smooth pursuit · Eye movements · Extraretinal signal

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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 and 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 (Von Fleischl 1882; Aubert 1886, 1887) 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 focused 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 (at an angle other than 0 or 180°) with respect to the pursuit target. In the latter case, the problem presented to the visual system is essentially the same as with 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. With both 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 et al. (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 et al. 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 a fairly constant (and high) degree of compensation for all directions.

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 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 and 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 eye movements were not measured in any of them. Because of this, neither the exact eye velocities nor the retinal image velocities are 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 formalised in a simple quantitative model, which essentially is an extension to two dimensions of the classical "cancellation theory" (Von Holst and Mittelstaedt 1950; Von Holst 1954). 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 Fig. 1). Based on the results of Tynan and Sekuler (1982) and McKee and Nakayama (1984), 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 formalise 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:

$$\mathbf{h}' = \mathbf{r} + \mathbf{e} \tag{1}$$

where $\mathbf{h}'$ 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–

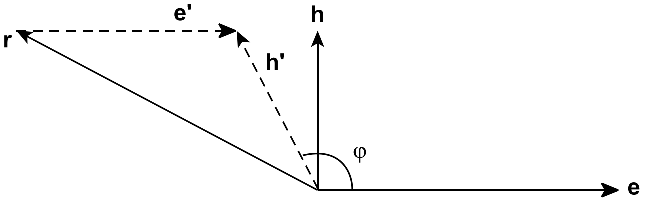

Fig. 1 Geometric representation of the linear model. Vector **e** represents eye velocity, **h** represents the head-centric stimulus velocity and **r** the resultant retinal image velocity. *Primed symbols* indicate estimates by the visual system. In the case depicted, retinal signal gain $\rho = 1$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

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[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.

Fleischl phenomenon, a gain term was introduced, linking the estimate of the eye velocity by the visual system to the actual eye velocity (see for example Wertheim 1987):

$$\mathbf{h}' = \mathbf{r} + \varepsilon\mathbf{e} \tag{2}$$

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 $\epsilon < 1$ (see Wertheim 1994 for a review and for alternative explanations). Wertheim (1994) noted that it is not only the eye movement signal that may err; the retinal image velocity too can be over- or under-estimated. This was stated more explicitly by Freeman and Banks (1998) who introduced a second gain term:

$$\mathbf{h}' = \rho\mathbf{r} + \varepsilon\mathbf{e} \tag{3}$$

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 (Eq. 3) has held up quite well and is able to explain most data on motion perception during smooth pursuit eye movements (see Freeman and Banks 1998; Freeman 1999; Freeman et al. 2000). 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 $\epsilon\mathbf{e}$, respectively) and found that for some observers the data conformed to the linear model, while for others it did not. Recently, the linear combination of retinal velocity and eye velocity in Eq. 3 also has been challenged by some authors (Turano and Massof 2001; Goltz et al. 2003), who introduced an interaction term into the equation, but typically the deviations from linearity they found were small. Wertheim (1994) added extra terms to Eq. 3, which estimate the eye velocity from retinal image characteristics (optic flow) and vestibular inputs, thereby providing an estimate of geocentric instead of head-centric eye velocity. We minimised 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 (Eq. 3) as our starting point.

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

$$\mathbf{h}' = (\varepsilon - \rho)\mathbf{e} + \rho\mathbf{h} \tag{4}$$

In our experiment, described below, we presented observers with both collinear and non-collinear motion. Therefore, the variables $\mathbf{h}$, $\mathbf{h}'$ and $\mathbf{e}$ in Eq. 4 represent 2-D 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 $\mathbf{h}'$ to predict the perceived motion direction ϕ:

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

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

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

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

Seventeen 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 1,152×864 pixels and a refresh rate of 100 Hz. Stimulus

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[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.

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 minimise 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 and 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 ≈ 0.15×0.15°). The luminance of both dots was kept low (~0.04 cd/m^2) to minimise afterglowing effects. Both dots were presented against a completely black background (lum. < 0.01 cd/m^2). The pursuit target always moved horizontally at eye height, covering an angle of 20° with a speed of 10°/s (after initial acceleration, see "Procedure" section). 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 (≈ 5.7°). The experiment was performed in total darkness; hence the pursuit target and the stimulus dot or the measurement arrows were the only things that 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 1,000 ms. It then accelerated linearly in 500 ms to 10°/s, moving rightwards or leftwards, respectively. After it reached a speed of 10°/s, it continued moving at this speed until it had covered 20° of visual angle and then disappeared. Pursuit direction was varied to minimise adaptation to the pursuit eye movement (see 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 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. Twenty-four stimulus motion directions were used, sampling the entire range of 0–360° (0–20°, 160–200° and 340–355° in steps of 5°, and 55–135° and 235–315° 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 (±0.5°) 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 min. Between blocks, the lights in the experimental room were turned on for approximately 1 min, to minimise 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 Matin et al 1969, 1970; Mateeff 1978; 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 or fixation respectively) 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 at least half of the trials per combination of stimulus speed and direction did not remain 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 fit 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 12 subjects, less than 1% of the trials in the control condition and about 7% of the 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 Fig. 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 (0–20°, 160–200° and 340–355°) was a systematic deviation of the perceived direction from the physical one of about 10° away from the horizontal 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 12 observers are plotted in Fig. 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

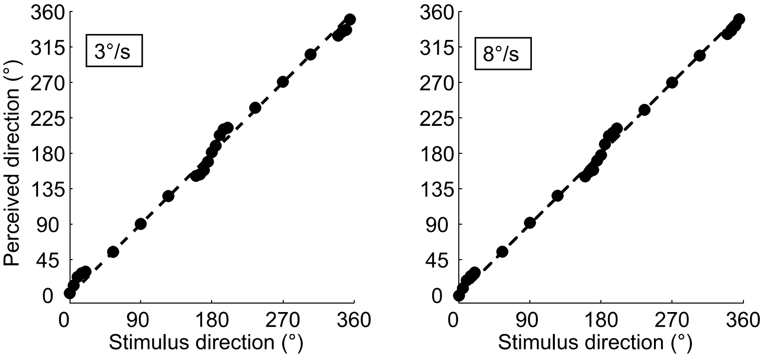

Fig. 2 Perceived stimulus motion direction during fixation as a function of the physical motion direction. The stimulus dot moved at 3°/s (*left panel*) or at 8°/s (*right panel*). Data points represent the average indicated directions for 12 observers (*error bars* representing the 95% confidence intervals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

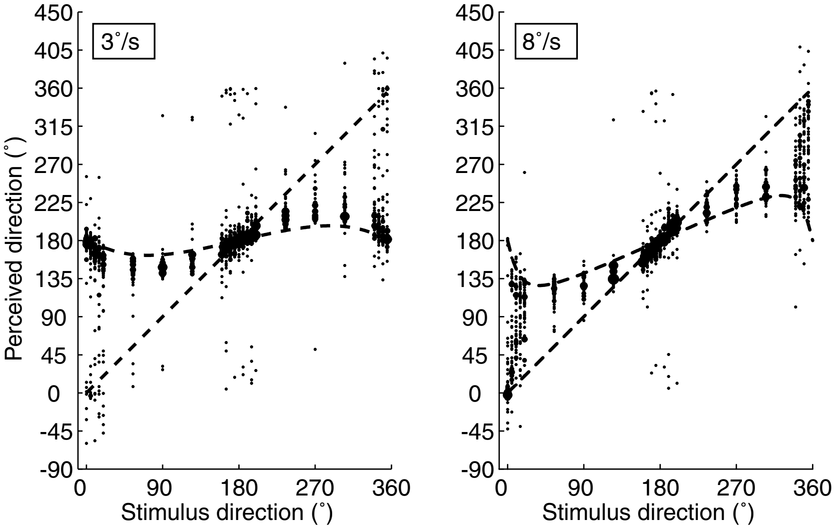

Fig. 3 Perceived stimulus motion direction during horizontal pursuit as a function of the physical motion direction. The *left panel* shows the data from the 3°/s condition, the *right panel* those from the 8°/s condition. The figures represent the aggregate data of 12 observers, classified in 1° bins, 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

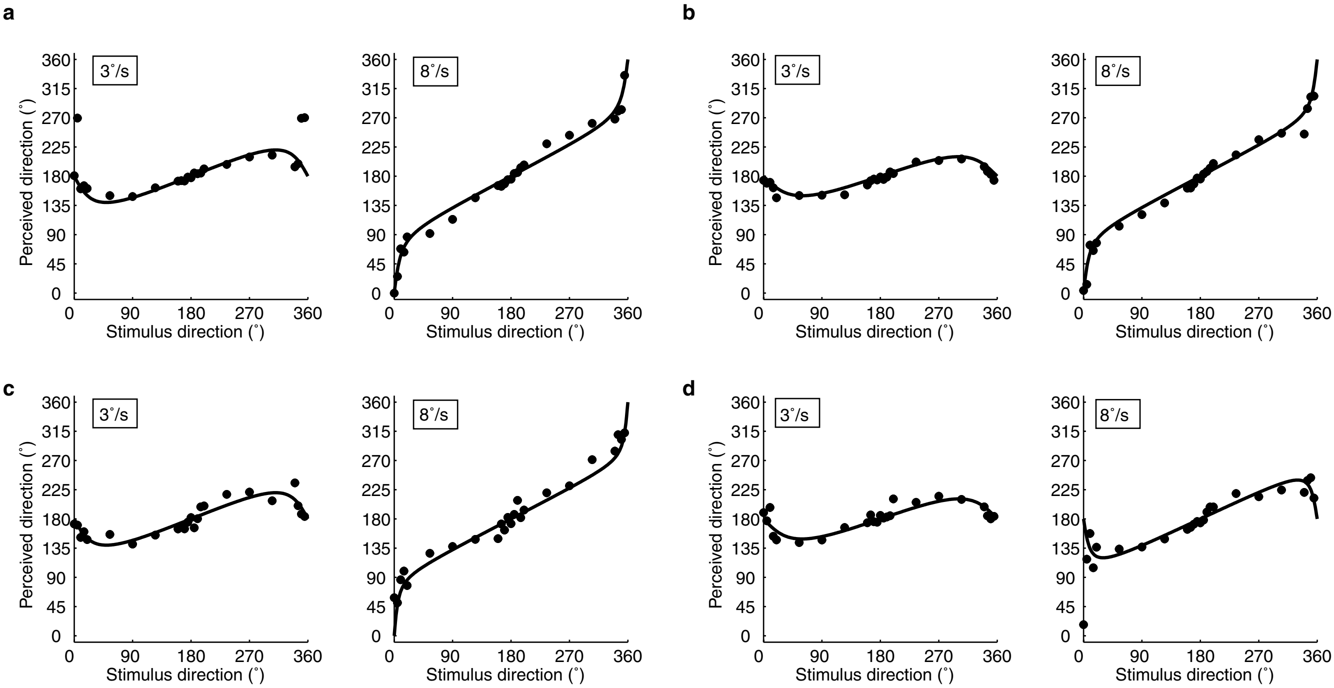

Fig. 4 Perceived stimulus motion direction data from four participants (panels *a*, *b*, *c*, *d*, corresponding to participants 1, 2, 8 and 11 in Table 1). The *data points* represent the average indicated motion direction per stimulus direction. The *lines* show the best fitting model curves

makes 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 and the 8°/s conditions were generally quite different. In the 3°/s condition, 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° 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 for instance Fig. 4d). Errors increased with deviation of the stimulus direction from the horizontal and decreased again around the opposite direction (180°).

The linear model (Eq. 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 Fig. 4 refer to participants 1, 2, 8 and 11, respectively). Generally, the

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

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

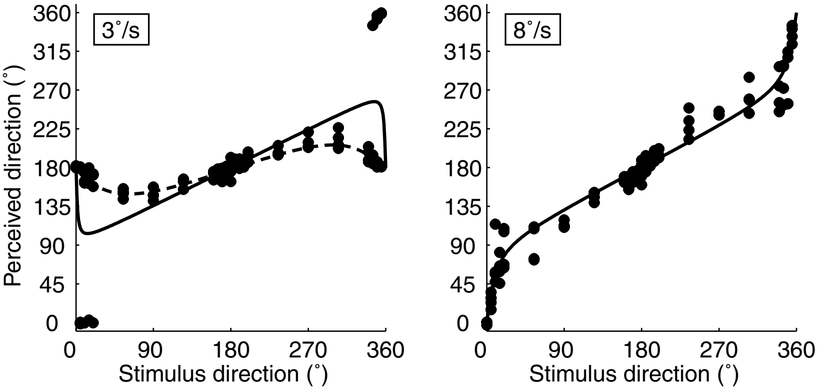

Fig. 5 Individual data points of perceived direction from one participant (*left panel*: 3/s condition; *right panel*: 8/s condition). The *continuous line* indicates the best fitting model curve with the outliers included; the *dashed line* that after removal of the outliers (only for the 3/s condition)

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 0.80 in the 3°/s condition and 0.90 in the 8°/s condition). Participants 7 and 10 were the two participants with high variances mentioned before and, consequently, with lower $R^{2\prime}$s. Some of the other participants showed low $R^{2\prime}$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 been seen from the fitted model curve in Fig. 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 Fig. 5). The resulting gain ratios and R^2 values 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 Fig. 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,

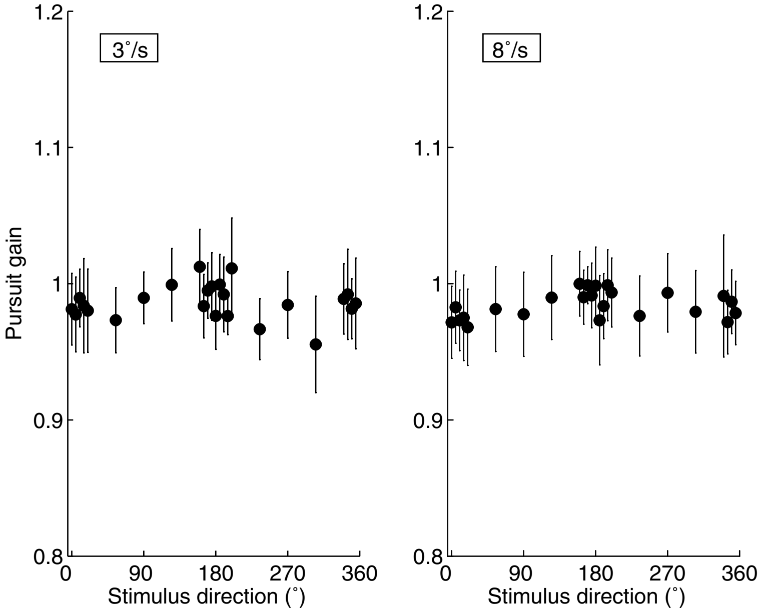

Fig. 6 Ocular pursuit gain as a function of stimulus direction for the 3°/s condition (*left panel*) and the 8°/s condition (*right panel*). *Symbols* represent the mean pursuit gain across 12 participants, with the *error bars* representing the 95% confidence intervals across observers

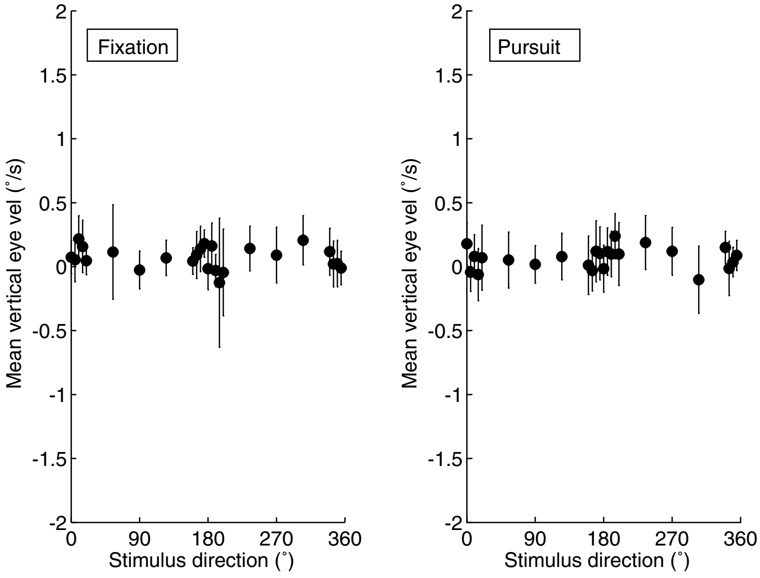

Fig. 7 Average vertical eye movement velocity as a function of stimulus direction for the 3°/s condition (*left panel*) and the 8°/s condition (*right panel*). *Symbols* represent the mean vertical eye velocity across 12 participants, with the *error bars* representing the 95% confidence intervals across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

indicating that the horizontal pursuit was hardly affected by the appearance of the stimulus dot (Fig. 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 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 (Rauber and Treue 1998, 1999; Grunewald 2004).

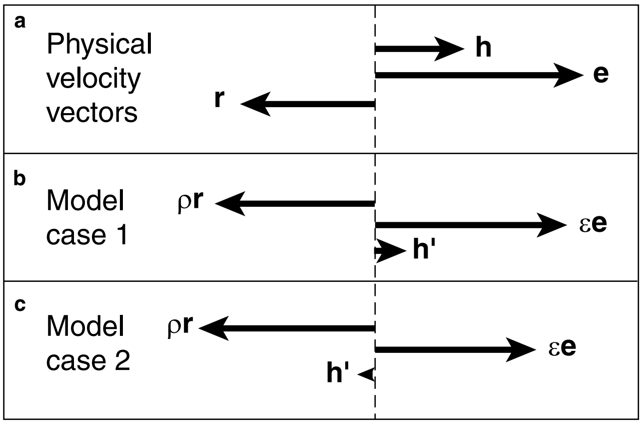

Fig. 8a–c A demonstration of the possible effects of small changes in signal gains on the perceived motion direction. **a** Physical velocity vectors for head-centric stimulus velocity (h), eye velocity (e) and retinal image velocity (r). **b** Model prediction of the perceived head-centric velocity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

The linear model, described by Eq. 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, as we hypothesised, 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 and 8°/s). The gain ratio was much higher in the lower speed condition. This explains the inconsistencies between results from earlier studies. Swanston 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

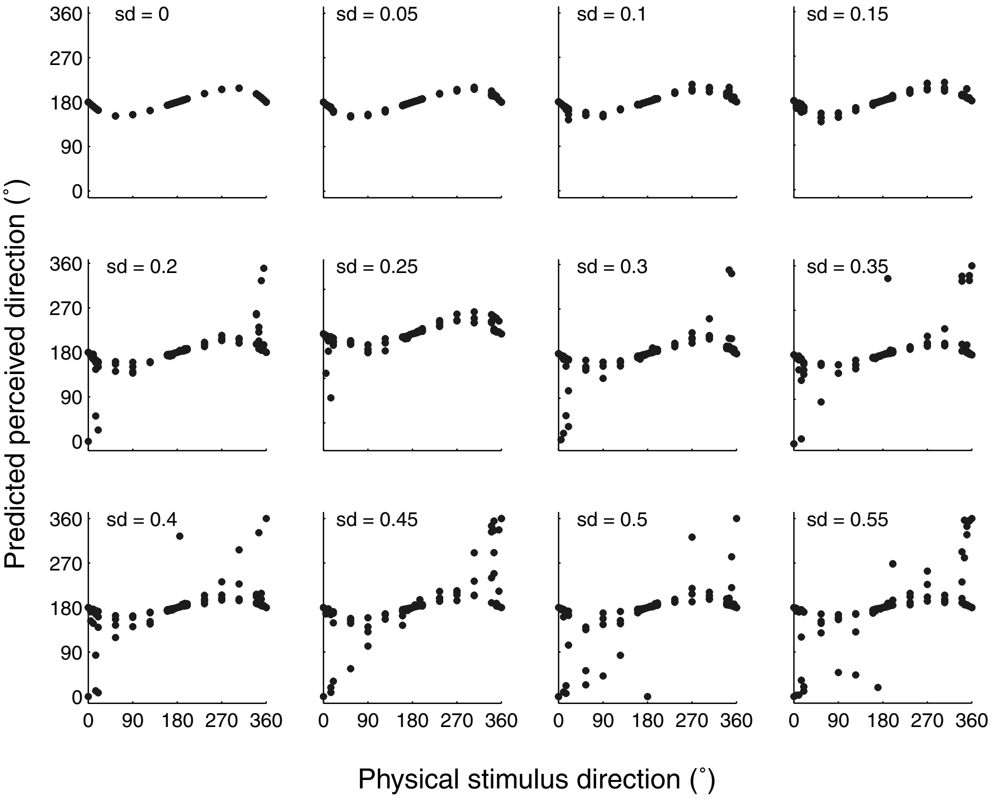

Fig. 9 Simulation of the effect of a noisy gain ratio. The gain ratio is sampled from a normal distribution with a mean of 0.37 and an increasing standard deviation (SD). Four replications per stimulus direction were simulated for a stimulus speed of 3°/s and an eye movement velocity of 10°/s

long) presentation of the stimulus dot in the studies by Wallach et al. (1985) and Swanston 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 (Mack and Herman 1978; Ehrenstein et al. 1986; De Graaf and Wertheim 1988).

The effect of noise in the signals

Some participants in our experiment showed bimodally-distributed data for stimulus directions around 0 and 360° (see Fig. 5 for an example). Figure 8 shows that, for these stimulus directions, the linear model predicts that the amplitude of the perceived velocity vector $\mathbf{h}'$ 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 $\mathbf{h}'$ to flip its direction from 0 to 180° or vice versa. One possible source of these variations might be the variability in pursuit gain (in the actual eye velocity) between trials, which would also cause variability in retinal speed. Although the pursuit gain was quite constant (see Fig. 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.

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 (to the right, since we plotted all of 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 ($\mathbf{h}-\mathbf{e}$) will be in the opposite direction. According to the linear model, the perceived head-centric velocity $\mathbf{h}'$ equals the sum of the estimated retinal velocity $\rho(\mathbf{h}-\mathbf{e})$ and the estimated eye velocity $\epsilon\mathbf{e}$. 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° (veridical). On a next trial, the retinal signal gain ρ might be slightly higher than in Fig. 8b and the eye movement signal gain ϵ lower (Fig. 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 (Fig. 9). The data of participant 1 in the 3°/s condition (plotted in Fig. 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 been seen from Fig. 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 Fig. 5. Hence, a simple extension of the linear model can easily account for the bimodally-distributed data.

Conclusions

The classical linear model (Eq. 3) accurately 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 The authors would like to thank Dr. Herbert Hoijtink for his advice on modelling the data.

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[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.

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