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

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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 the 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 eye movement signal that is used by the visual system to increase more than the retinal signal.

Keywords: Motion perception; Motion direction; Pursuit; Eye movements; Extraretinal signal

1. Introduction

In daily life, we encounter many moving objects. The motion of these objects causes their images on our retinae 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

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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, Mateeff, & Hohnsbein, 1986; Mack & Herman, 1978; but see Freeman, Naji, & Margrain, 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 Fig. 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 2, we explored an alternative explanation for the presentation duration effect.

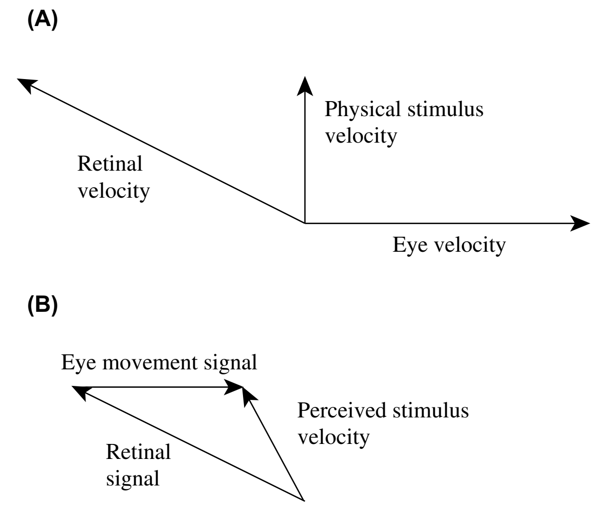

Fig. 1. Perceived stimulus velocity as the sum of a retinal signal and an eye movement signal. (A) Physical (angular) velocities. The retinal image velocity equals the stimulus velocity minus the eye movement velocity. (B) Estimated velocities. The perceived velocity equals the estimated retinal velocity 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. Experiment 1

2.1. Methods

2.1.1. 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.

2.1.2. 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 $\approx 0.15° \times 0.15°$). 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 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 Section 2.2). 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 (≈5.7°). The experiment was performed in total darkness, so the participant could only see the pursuit target and the stimulus dot or the arrow.

2.2. 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°/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°/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°/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.

2.3. Data 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 $\alpha = 0.05$.

2.4. 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 been seen from Fig. 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. 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 and there was only a single small significant interaction effect of these factors with the presentation duration and pursuit target velocity (presentation duration × pursuit target velocity × 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 Fig. 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 ($F(2,10) = 7.753$; $p = 0.032$).

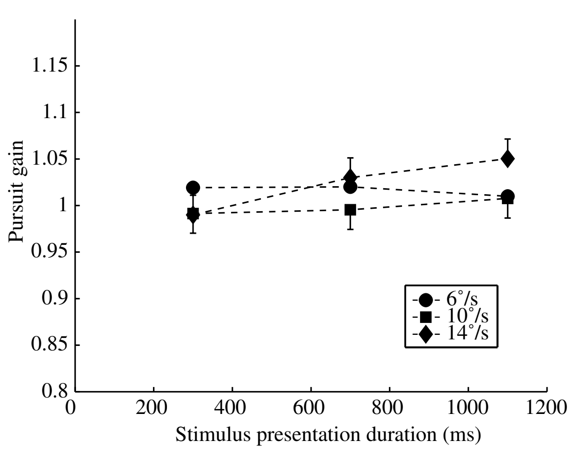

Fig. 2. Pursuit gain as a function of stimulus presentation duration and pursuit target velocity (6, 10, or 14°/s), averaged across six participants. The error bars represent the 95% confidence intervals of the means, based on the MS of the interaction terms of participants and the other factors (presentation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

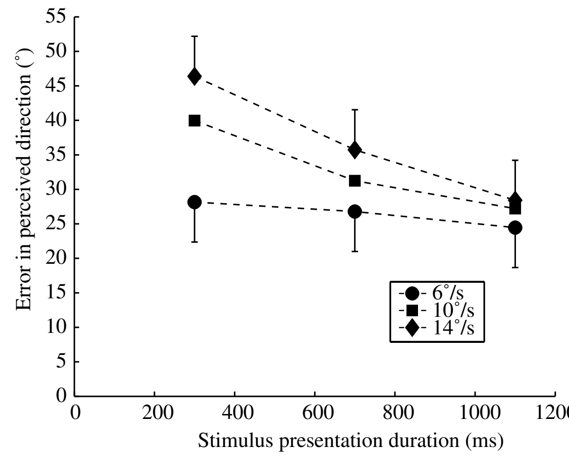

Fig. 3. Errors in perceived motion direction as a function of stimulus presentation duration and pursuit target velocity (6, 10, or 14°/s), averaged across six participants. Positive errors indicate perceived motion directions rotated away from the physical direction towards the retinal motion direction.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

2.5. 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 Fig. 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 smaller 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.

3. Experiment 2

3.1. 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.

3.2. 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 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.

3.3. 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 Fig. 4. Again, pursuit gain was approximately 1 in all conditions. Presentation duration and stimulus location did not have significant effects on the pursuit gain and there was a small significant interaction effect ($F(8,48) = 2.521$; $p = 0.022$).

The average errors in perceived motion direction are represented in Fig. 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. Hence, the location of the stimulus path in the pursuit

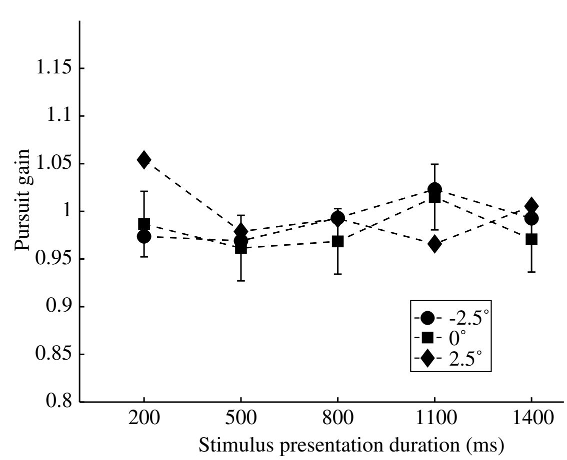

Fig. 4. Pursuit gain as a function of stimulus presentation duration and horizontal stimulus path location (−2.5, 0, or 2.5° relative to the centre of the screen), averaged across seven participants. Error bars as in Fig. 2.

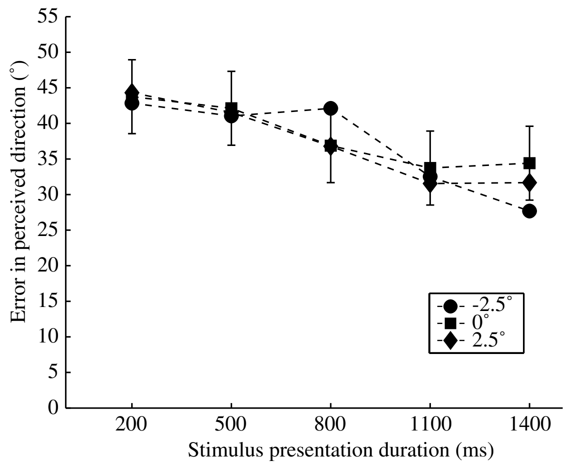

Fig. 5. Errors in perceived motion direction as a function of stimulus presentation duration and horizontal stimulus path location (−2.5°, 0°, or 2.5° relative to the centre of the screen), averaged across seven participants. Positive errors indicate perceived motion directions rotated away from the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

sweep, or, equivalently, the moment during pursuit at which the stimulus was presented, did not have a significant effect on the perceived motion direction.

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.

4. General discussion

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 (to be reported elsewhere) 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, Ehrenstein, and Hohnsbein (1987). 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 an 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 discarded 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) and Wertheim and 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 setup can affect the outcome. For instance, contrary to the studies mentioned in Section 1, 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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References

Algom, D., & Cohen-Raz, L. (1984). Visual velocity input-output functions: the integration of distance and duration onto subjective velocity. *Journal of Experimental Psychology: Human Perception and Performance, 10*(4), 486–501.

Becklen, R., Wallach, H., & Nitzberg, D. (1984). A limitation of position constancy. *Journal of Experimental Psychology: Human Perception and Performance, 10*(5), 713–723.

Berthoz, A., Pavard, B., & Young, R. L. (1975). Perception of linear horizontal self-motion induced by peripheral vision (linear vection): basic characteristics and visual-vestibular interactions. *Experimental Brain Research, 23*, 471–489.

Brown, R. H., & Conklin, J. E. (1954). The lower threshold of visible movement as a function of exposure-time. *American Journal of Psychology, 67*, 104–110.

Cohen, R. L., & Bonnet, C. (1972). Movement detection thresholds and stimulus duration. *Perception and Psychophysics, 12*(3), 269–272.

De Graaf, B., & Wertheim, A. H. (1988). The perception of object-motion during smooth-pursuit eye movements: adjacency is not a factor contributing to the Filehne illusion. *Vision Research, 28*, 497–502.

Dichgans, J., & Brandt, T. H. (1978). Visual–vestibular interaction: effects on self-motion perception and postural control. In R. Held, H. W. Leibowitz, & H.-L. Teuber (Eds.). *Handbook of sensory physiology* (vol. 8, pp. 755–804). Springer: Berlin.

Ehrenstein, W. H., Mateeff, S., & Hohnsbein, J. (1986). Temporal aspects of position constancy during ocular pursuit. *Pflügers Archiv—European Journal of Physiology, 406*, R15, 47.

Festinger, L., Sedgwick, H. A., & Holtzman, J. D. (1976). Visual perception during smooth pursuit eye movements. *Vision Research, 16*(12), 1377–1386.

Filehne, W. (1922). Über das optische Wahrnehmen von Bewegungen. *Zeitschrift für Sinnesphysiologie, 53*, 134–144.

Freeman, T. C. A. (1999). Path perception and Filehne illusion compared: Model and data. *Vision Research, 39*(16), 2659–2667.

Freeman, T. C. A. (2001). Transducer models of head-centred motion perception. *Vision Research, 41*, 2741–2755.

Freeman, T. C. A., & Banks, M. S. (1998). Perceived head-centric speed is affected by both extra-retinal and retinal errors. *Vision Research, 38*(7), 941–945.

Freeman, T. C. A., Naji, J. J., & Margrain, T. H. (2002). Head-centred motion perception in the ageing visual system. *Spatial Vision, 15*(2), 117–127.

Giaschi, D., & Anstis, S. (1989). The less you see it, the faster it moves: Shortening the "on-time" speeds up apparent motion. *Vision Research, 29*(3), 335–347.

Goltz, H. C., DeSouza, J. F. X., Menon, R. S., Tweed, D. B., & Vilis, T. (2003). Interaction of retinal image and eye velocity in motion perception. *Neuron, 39*, 569–576.

Hansen, R. M. (1979). Spatial localization during pursuit eye movements. *Vision Research, 19*(11), 1213–1221.

Johnson, C. A., & Leibowitz, H. W. (1976). Velocity–time reciprocity in the perception of motion: foveal and peripheral determinations. *Vision Research, 16*, 177–180.

Johnson, C. A., & Scobey, R. P. (1980). Foveal and peripheral displacement thresholds as a function of stimulus luminance, line length and duration of movement. *Vision Research, 20*, 709–715.

Leibowitz, H. W. (1955). The relation between the rate threshold for the perception of movement and luminance for various durations of exposure. *Journal of Experimental Psychology, 49*(3), 209–214.

Loftus, G. R., & Masson, M. E. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin and Review, 1*(4), 476–490.

Mack, A., & Herman, E. (1973). Position constancy during pursuit eye movement: an investigation of the Filehne illusion. *Quarterly Journal of Experimental Psychology, 25*, 71–84.

Mack, A., & Herman, E. (1978). The loss of position constancy during pursuit eye movements. *Vision Research, 18*, 55–62.

Masson, M. E. J., & Loftus, G. R. (2003). Using confidence intervals for graphically based data interpretation. *Canadian Journal of Experimental Psychology, 57*(3), 203–220.

Mateeff, S. (1978). Saccadic eye movements and localization of visual stimuli. *Perception and Psychophysics, 24*(3), 215–224.

Mateeff, S., Ehrenstein, W. H., & Hohnsbein, J. (1987). Constancy of visual direction requires time to develop. *Perception, 16*(2), 253 (A229).

Matin, L., Matin, E., & Pearce, D. G. (1969). Visual perception of direction when voluntary saccades occur. I. Relation of visual direction of a fixation target extinguished before a saccade to a flash presented during the saccade. *Perception and Psychophysics, 5*(2), 65–80.

Matin, L., Matin, E., & Pola, J. (1970). Visual perception of direction when voluntary saccades occur: II. Relation of visual direction of a fixation target extinguished before a saccade to a subsequent test flash presented before the saccade. *Perception and Psychophysics, 8*(1), 9–14.

Meyer, C. H., Lasker, A. G., & Robinson, D. A. (1985). The upper limit of human smooth pursuit velocity. *Vision Research, 25*(4), 561–563.

Schalen, L. (1980). Quantification of tracking eye movements in normal subjects. *Acta Oto-Laryngologica, 90*(5–6), 404–413.

Swanston, M. T., & Wade, N. J. (1988). The perception of visual motion during movements of the eyes and of the head. *Perception and Psychophysics, 43*(6), 559–566.

Treue, S., Snowden, R. J., & Andersen, R. A. (1993). The effect of transiency on perceived velocity of visual patterns: A case of "temporal capture". *Vision Research, 33*(5-6), 791–798.

Turano, K. A., & Massof, R. W. (2001). Nonlinear contribution of eye velocity to motion perception. *Vision Research, 41*(3), 385–395.

Tynan, P. D., & Sekuler, R. (1982). Motion processing in peripheral vision: Reaction time and perceived velocity. *Vision Research, 22*(1), 61–68.

Van der Geest, J. N., & Frens, M. A. (2002). Recording eye movements with video-oculography and scleral search coils: a

direct comparison of two methods. *Journal of Neuroscience Methods, 114*, 185–195.
Von Holst, E. (1954). Relations between the central nervous system and the peripheral organs. *British Journal of Animal Behavior, 2*, 89–94.
Von Holst, E., & Mittelstaedt, H. (1950). Das Reafferenzprinzip (Wechselwirkungen zwischen Zentralnervensystem und Peripherie). *Die Naturwissenschaften, 37*(20), 464–476.
Watson, A. B., Barlow, H. B., & Robson, J. G. (1983). What does the eye see best? *Nature, 302*, 419–422.
Watson, A. B., & Turano, K. (1995). The optimal motion stimulus. *Vision Research, 35*(3), 325–336.
Webb, N. A., & Griffin, M. J. (2003). Eye movement, vection, and motion sickness with foveal and peripheral vision. *Aviation, Space, and Environmental Medicine, 74*(6), 622–625.
Wertheim, A. H. (1987). Retinal and extraretinal information in movement perception: How to invert the Filehne illusion. *Perception, 16*(3), 299–308.
Wertheim, A. H. (1994). Motion perception during self-motion: The direct versus inferential controversy revisited. *Behavioral and Brain Sciences, 17*(2), 293–355.
Wertheim, A. H., & Van Gelder, P. (1990). An acceleration illusion caused by underestimation of stimulus velocity during pursuit eye movements: Aubert–Fleischl revisited. *Perception, 19*(4), 471–482.