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Rapid Communication

Perceived Head-centric Speed is Affected by Both Extra-retinal and Retinal Errors

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When we make a smooth eye movement to track a moving object, the visual system must take the eye's movement into account in order to estimate the object's velocity relative to the head. This can be done by using extra-retinal signals to estimate eye velocity and then subtracting expected from observed retinal motion. Two familiar illusions of perceived velocity—the Filehne illusion and Aubert–Fleischl phenomenon—are thought to be the consequence of the extra-retinal signal underestimating eye velocity. These explanations assume that retinal motion is encoded accurately, which is questionable because perceived retinal speed is strongly affected by several stimulus properties. We develop and test a model of head-centric velocity perception that incorporates errors in estimating eye velocity and in retinal-motion sensing. The model predicts that the magnitude and direction of the Filehne illusion and Aubert–Fleischl phenomenon depend on spatial frequency and this prediction is confirmed experimentally. © 1998 Elsevier Science Ltd. All rights reserved.

Head-centric speed   Spatial frequency   Extra-retinal

INTRODUCTION

If the body and head are stationary, the head-centric velocity of an object (**H**) is the sum of retino-centric (**R**) and eye pursuit velocity (**P**). The visual system could therefore recover head-centric velocity from retinal motion by estimating eye velocity using an extra-retinal signal (von Holst, 1954; Howard, 1982). Given that retinal motion must also be estimated, errors in estimating **R** or **P** will lead to errors in perceived head-centric velocity. $\hat{\mathbf{P}}$ is the estimated pursuit velocity and we assume that it is linearly related to eye speed. Thus, $\hat{\mathbf{P}} = e\mathbf{P}$, where e is the extra-retinal gain factor relating actual to estimated eye speed. $\hat{\mathbf{R}}$ is the estimated retinal image velocity, so making the linear assumption, $\hat{\mathbf{R}} = r(\Omega)\mathbf{R}$, where r is the retinal gain and is affected by several stimulus properties (Ω) including spatial frequency (Campbell & Maffei, 1981; Diener, Wist, Dichgans & Brandt, 1976; Ferrera & Wilson, 1991), dot density (Watamaniuk, Grzywacz & Yuille, 1993), contrast (Thompson, 1982; Hawken, Gegenfurtner & Tang, 1994) and chromatic content (Cavanagh, Tyler & Favreau, 1984). We assume a single value for r for each value of Ω. Our model of perceived head-centric velocity is, therefore:

$$\hat{\mathbf{H}} = r(\Omega)\mathbf{H} + \mathbf{P}[e - r(\Omega)] \tag{1}$$

EXPERIMENT 1: MEASURING RETINAL AND EXTRA-RETINAL GAIN

We tested the model using drifting gratings of different spatial frequency. To measure r, we asked observers to adjust the speed of a test grating (T) until it had the same perceived head-centric speed as a 4·6 deg/sec, 1-c/deg standard grating (S). The test and standard were presented in a two-interval temporal sequence. The eye was stationary ($P = 0$) in both intervals and the spatial frequency (f_T) of the test grating was varied systematically. The upper panel of Fig. 1 displays the speed of the test grating, H_T, when its perceived speed matched the standard's. The standard's speed and spatial frequency are indicated by the arrows. The matching speed increased with decreasing spatial frequency over the range studied, confirming previous reports (e.g. Ferrera & Wilson, 1991).

When the test and standard have the same perceived speed, $[\hat{H}_T = \hat{H}_S]$. Using this equality and equation (1) with $P = 0$, the ratio of retinal gains for the test and standard is:

$$\frac{r(f_T)}{r(f_S)} = \frac{H_S}{H_T} \tag{2}$$

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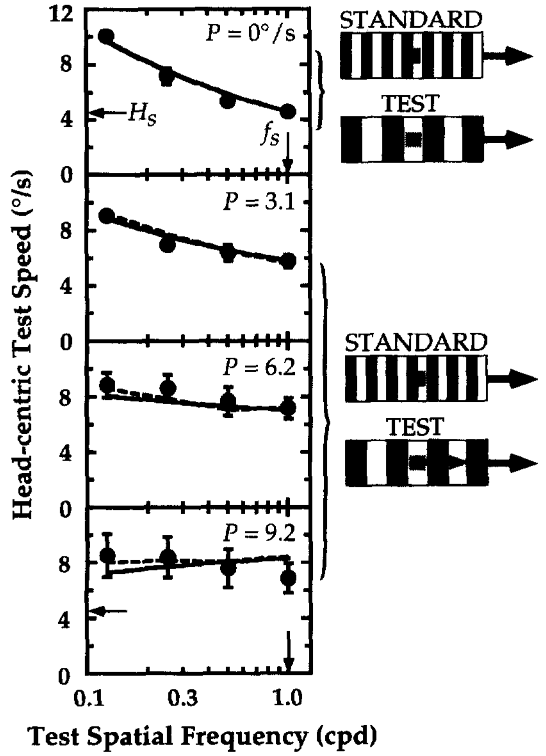

FIGURE 1. Matched head-centric speeds as a function of spatial frequency and eye pursuit speed. Each panel plots the head-centric speed of the test at the match point as a function of the spatial frequency of the test grating. Upper panel: Test and standard gratings viewed with the eye stationary. Data points are the means from three observers (the first author, TCAF, and two naive observers); error bars are ±0.5 SD. Arrows indicate the spatial frequency and speed of the standard. Lower panels: Test grating viewed with eye moving at 3.1, 6.2 or 9.2 deg/sec; standard viewed with the eye stationary. Data points are the means from the same three observers; error bars are ±0.5 SD. Solid curves show model predictions with

$\tilde{r}(f_T)$

determined from the data in the upper panel and with $\tilde{e} = 0 \cdot 6$. Dashed curves represent model predictions using measured eye movements to estimate P in Equation (3). The stimuli were vertical sinusoidal gratings (mean luminance = 24.6 cd/m^2, contrast = 0·80) displayed at 67.5 Hz and viewed monocularly from 57.3 cm. They were displayed in a 15 deg by 5 deg rectangular window with a black surround. A 0.9 × 0.9 deg black square centered in the rectangular window contained a small fixation point. Stimulus duration was 700 msec, preceded by a 400-msec display at mean luminance that contained the rectangular window and the fixation point. In test intervals involving an eye pursuit, the fixation point and window started to move 400 msec before the grating appeared. The test interval always appeared first unless otherwise stated. The direction of eye pursuit was left or right with equal probability; direction was cued by the initial location of the fixation point and window. Environmental features were made invisible by performing the experiments in a dark room, by viewing the stimuli through an aperture that occluded all non-essential parts of the room and CRT, and by keeping the observer light adapted. Test speed was adjusted using a 1-up/1-down staircase procedure. The estimated match point was the mean of the last eight reversals. Each observer completed at least four staircases per condition. Eye movements were recorded using a limbus eye tracker mounted on a bite bar. The eye tracker was calibrated prior to each experimental session using standard procedures. Eye position was sampled at 300 Hz. Eye speed was determined by low-pass filtering the position record, computing the derivative of the filtered record with respect to time, removing saccades using an amplitude criterion of 10 deg/sec, and then computing the mean velocity over the remaining record in which the grating was visible. The mean pursuit gain was 0.85 and did not vary with target speed or spatial frequency.

Changes in the ratio (H_S/H_T) manifest changes in retinal gain as a function of spatial frequency because $r(f_S)$ is fixed. It follows that the data points in the upper panel of Fig. 1 show how retinal gain varies with spatial frequency up to an unmeasurable scale factor, $r(f_S)$. The results indicate a factor of two increase in $r(f_T)$ from 0.125–1 c/deg.

If the observer makes a smooth eye movement during the test interval then:

$$H_T = \frac{H_S}{\tilde{r}(f_T)} + P\left[1 - \frac{\tilde{e}}{\tilde{r}(f_T)}\right] \qquad (3)$$

where $\tilde{r}(f_T) = [r(f_T)/r(f_S)]$ and $\tilde{e} = [e/r(f_S)]$. We estimated the value of $\tilde{e}$ by having observers adjust the speed of a test grating, viewed during a pursuit eye movement, to match the apparent head-centric speed of a standard grating, viewed with the eye stationary. The lower three panels of Fig. 1 display the average speed settings for three observers when the standard was drifting at 4.6 deg/sec in the same direction as the eye pursuit during the test interval. The panels show the data for pursuit target speeds of 3.1, 6.2, and 9.2 deg/sec. If observers made settings by equating the retino-centric speeds of the test and standard gratings, the data in the lower three panels would be the same as the data in the upper panel except for shifts upward by the pursuit speed. For example, the mean test speed settings for $P = 9.2$ deg/sec would be 19.3, 16.4, 14.6, and 13.8 deg/sec. Clearly, the data are inconsistent with the use of a retino-centric strategy.

The solid curves in Fig. 1 are the predictions of equation (3) with $\tilde{r}(f_T)$ determined from the data in the upper panel and with $\tilde{e}$ as a free parameter. The best fit was obtained with $\tilde{e} = 0.6$. Eye movements were measured while the observers collected these data. They were quite accurate and did not vary with systematically with spatial frequency. Thus, the ability to pursue targets in the presence of gratings of different spatial frequencies cannot explain the data. This was confirmed by computing the mean of the measured pursuits across observers for each spatial frequency and pursuit target speed. The dashed curves are the predictions of equation (3), using these means to estimate P. The best fits were obtained with $\tilde{e} = 0.56$.

Equation (3) assumes that $\tilde{e}$ is not a function of P. We examined this assumption by allowing $\tilde{e}$ to vary across pursuit target speed. The best fits were obtained with $\tilde{e} = 0.63$, 0.54 and 0.57, respectively. The similarity of these values suggests that $\tilde{e}$ does not vary with P for the conditions studied.

EXPERIMENT 2: REVERSING THE FILEHNE ILLUSION

When an observer makes a pursuit eye movement while being presented a target stationary with respect to the head, the target usually appears to move opposite to the eye movement (Filehne, 1922). The conventional explanation for the Filehne illusion is that the gain of the extra-retinal, eye-velocity signal (e) is less than 1, so it under-estimates actual eye speed during pursuit move-

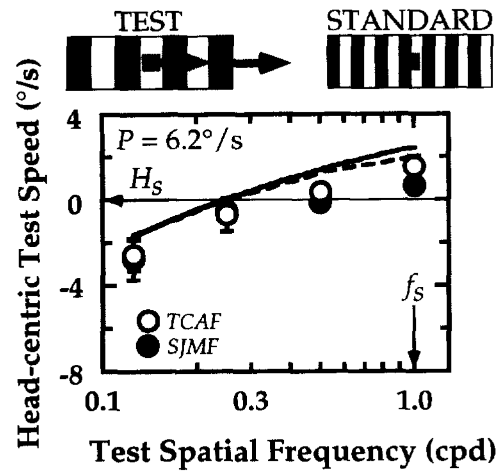

FIGURE 2. The Filehne illusion as a function of spatial frequency. The test grating was viewed with the eye moving at 6.2 deg/sec; the 1-c/deg standard grating was stationary and viewed with the eye stationary. The physical speed of the test grating at the match point is plotted against the test's spatial frequency. Data points are the means from two observers (the first author, TCAF, and a naive observer, SJMF); error bars are ±0.5 SD. Solid curves show model predictions with $\tilde{r}(f_T)$ determined from the data in Figure 1 and with $\tilde{e} = 0.6$. Dashed curves represent model predictions using measured eye movements to estimate P in Equation (3). The mean pursuit gain was 0.88 and did not vary with target speed or spatial frequency. All other details are the same as Figure 1.

ments (Mack & Herman, 1973, 1978; Wertheim, 1987; Yasui & Young, 1975). The implicit assumption is that the retinal gain (r) is 1. We examined this classic illusion in the context of our model.

Setting $H_S = 0$, equation (3) becomes:

$$H_T = P\left[1 - \frac{\tilde{e}}{\tilde{r}(f_T)}\right] \qquad (4)$$

For a given pursuit speed, P is constant and we assume that $\tilde{e}$ is constant as well. When $\tilde{r}(f_T) > \tilde{e}$, the equation predicts that H_T must have the same sign as P for the target to appear stationary, a prediction consistent with previous work (e.g. Mack & Herman, 1973, 1978). However, when $\tilde{r}(f_T) < \tilde{e}$, which could occur at low spatial frequencies where retinal gain is low, the equation predicts that H_T must be *opposite* in sign from P for the target to appear stationary (see also Wertheim, 1987).

Observers adjusted the speed of a test grating, viewed during a pursuit eye movement, until it appeared to have the same head-centric speed as a stationary 1-c/deg grating, viewed with the eye stationary. The results are presented in Fig. 2. At test frequencies greater than 0·5 c/deg, the test speed at perceived stationarity was in the direction of the eye pursuit. However, at frequencies of 0·25 c/deg and lower, the test had to move in a direction opposite to the pursuit to be perceived as stationary. The solid curve represents the model predictions with $\tilde{r}(f_T)$ and $\tilde{e}$ values determined from the data in Fig. 1. The model also exhibits a reversed Filehne illusion for low-frequency targets. The dashed curve represents model predictions using measured eye movements to estimate P.

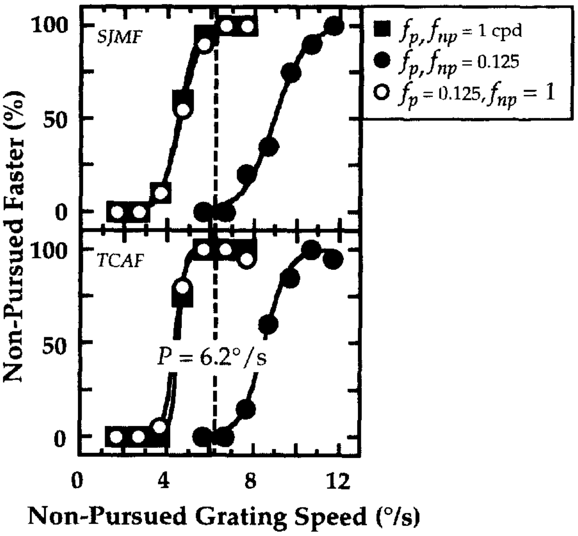

FIGURE 3. The Aubert–Fleischl phenomenon as a function of spatial frequency. Observers reported on each trial whether a pursued or non-pursued grating appeared to move faster relative to the head. The speed of the non-pursued grating was varied according to the method of constant stimuli. The upper and lower panels show the psychometric functions for the two observers. The percentage of responses that the non-pursued grating appeared faster is plotted as a function of the speed of the non-pursued grating. The pursuit speed was always 6.2 deg/sec as indicated by the vertical dashed line. Solid curves are best-fitting logistic functions. Each point is based on 20 trials. The filled squares represent the data when the spatial frequency of the pursued and non-pursued gratings was 1 c/deg. The filled circles represented the data when the frequency of the two gratings was 0.125 c/deg. The open circles represent the data when the frequency of the pursued grating was 0.125 c/deg and the frequency of the non-pursued grating was 1 c/deg.

EXPERIMENT 3: REVERSING THE AUBERT–FLEISCHL PHENOMENON

A moving object typically appears to move slower when it is tracked with a pursuit eye movement than when it is not (Aubert, 1886; Fleischl, 1882). To experience the Aubert–Fleischl phenomenon, an observer must compare perceived head-centric speeds for the same moving target when it is pursued and not pursued. According to equation (3), the perceived head-centric speed of a pursued target will not depend on spatial frequency because, with accurate pursuit, there is no retinal motion and, therefore, variations in $r(f)$ have no effect. However, perceived speed with eyes stationary will vary with spatial frequency (Fig. 1). For this reason, the implications of equation (3) are not only that the magnitude of the Aubert–Fleischl phenomenon should vary as a function of spatial frequency (Dichgans, Wist, Diener & Brandt, 1975), but that its direction should vary, too. Applying equation (1) to pursued and non-pursued intervals separately and setting the results equal:

$$H_{np} = P\left[\frac{\tilde{e}}{\tilde{r}(f_{np})}\right] \qquad (5)$$

where the subscript np denotes the non-pursued grating. The data of Figs 2 and 3 indicate that $\tilde{e} \approx 0.6$ and the data of Fig. 1 indicate that $\tilde{r}(f_{np}) \approx 1$ and 0.5 for 1 and

0.125 c/deg, respectively. Thus, for a frequency of 1 c/deg, equation (5) predicts that non-pursued and pursued targets will appear to move at the same head-centric speed when the former moves at 0.6 P. However, for a frequency of 0.125 c/deg, the two gratings will have the same perceived speed when the non-pursued grating moves at 1.2 P. Thus, the model predicts a reversal of the Aubert–Fleischl phenomenon at low spatial frequencies.

To test this prediction, we asked observers to indicate the speeds at which pursued and non-pursued gratings of the same frequency (1 or 0.125 c/deg) appeared to move at the same head-centric speed. The speed of the pursued grating and accompanying fixation point was always 6.2 deg/sec and the speed of the non-pursued grating was varied. The two gratings were presented sequentially and observers indicated which appeared to move faster with respect to the head. The filled symbols in Fig. 3 represent the results. At 1 c/deg, a classic Aubert–Fleischl phenomenon is observed; the non-pursued grating must move slower with respect to the head than the pursued grating in order to have the same perceived speed. However, at 0.125 c/deg, the opposite is observed. Specifically, the non-pursued grating must move faster than the pursued grating to have the same perceived head-centric speed. Thus, the Aubert–Fleischl phenomenon can indeed be reversed.

When a target is pursued, there is no retinal motion, so the perceived head-centric speed should be determined by extra-retinal, eye-velocity information alone. This implies in turn that the perceived head-centric speed of a pursued grating should not vary with spatial frequency. We tested this prediction by presenting pursued and non-pursued gratings of 0.125 and 1 c/deg, respectively. The results are the unfilled symbols in Fig. 3 and they are essentially identical to the results obtained when both targets were 1 c/deg. Thus, as predicted by the model, the spatial frequency of the pursued target has no effect on the Aubert–Fleischl phenomenon.

OTHER ACCOUNTS

Post and Leibowitz (1985) hypothesized that the size of extra-retinal signals depends on "pursuit effort", defined as the difference between the outputs of gaze-stabilization and pursuit mechanisms (see also Raymond, Shapiro & Rose, 1984). They also assumed that retinal-motion processing is veridical. According to the hypothesis, when the eye moves across a stationary background, the gaze-stabilization system attempts to keep the eye stationary with that background; consequently, the pursuit effort must increase to keep the eye moving. Although this hypothesis has not been quantified, it could conceivably predict the data of Figs 1–3 if we assume that the gaze-stabilization system is stimulated more at low than at high spatial frequencies. Another hypothesis is that perceived object motion depends not only on retinal speed and eye velocity, but also on a "reference signal" produced by vestibular and optokinetic inputs (Wertheim, 1987, 1994). The magnitude of the reference signal supposedly varies depending on the spatiotemporal frequency and size of the stimulus, but presumably has only one value at any time. This reference-signal hypothesis could incorporate errors in the estimation of retinal motion, but Wertheim has not specified those errors.

We tested the pursuit-effort and reference-signal hypotheses in the following way. Two grating patches were presented to the left and right of a stationary fixation point. In the *simultaneous* condition, the gratings appeared at the same time moving in opposite directions (away or toward the fixation point). The spatial frequency of the test grating was 0.125 c/deg and that of the standard was 1 c/deg; the speed of the test was varied from trial to trial and the speed of the standard was always 4.6 deg/sec. After each presentation, observers indicated which patch appeared faster. In the *sequential* condition, two intervals were displayed in temporal sequence; each had the same spatial arrangement as in the simultaneous condition. The spatial frequencies of both gratings were 0.125 c/deg in the test interval and 1 c/deg in the standard interval. The gratings again moved in opposite directions in each interval. Observers indicated the interval containing gratings that appeared to move faster. According to the pursuit-effort and reference-signal hypotheses, there could be an effect of spatial frequency in the simultaneous condition because the two patches contain different frequencies and, therefore, the pursuit effort or optokinetic potential could differ depending on the motions of the two spatial frequencies. However, there should be no effect of spatial frequency in the sequential condition because, at each instant, the pursuit effort or optokinetic potential from one grating is offset by that from the other. These hypotheses, therefore, predict that different settings will be observed for the two conditions. In contrast, our model predicts no difference. We tested four observers; three were naive to the hypotheses. In contrast to the predictions of the pursuit-effort and reference-signal hypotheses, the mean matching speeds were similar in the two conditions: 6.7 (SD = 1.8) and 7.7deg/sec (SD = 0.6) in the simulaneous and sequential conditions, respectively. Thus, in their current form, the pursuit-effort and reference-signal hypotheses cannot account for these data, but our model can.

CONCLUSIONS

Previous accounts of head-centric velocity perception have assumed that retinal motion processing is veridical, but this assumption is refuted by a wide variety of data. Our model assumes that velocity percepts are subject to errors in extra-retinal, eye-velocity signals *and* in retinal motion signals. We have shown that two oft-cited illusions of head-centric motion perception—the Filehne and Aubert–Fleischl illusions—are the consequence of both sorts of errors. As predicted by our model, reversals occur in the directions of the two illusions. The model and data presented here imply that perceived self-motion during eye movements (Royden, Banks & Crowell, 1992; Warren & Hannon, 1988) may well be affected by the spatial-frequency content of the stimulus. Our observation may, therefore, have important implications for the construction of visual aids such as image intensifiers, virtual reality displays, and low-vision aids.

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