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THE PERCEPTION OF OBJECT MOTION DURING SMOOTH PURSUIT EYE MOVEMENTS: ADJACENCY IS NOT A FACTOR CONTRIBUTING TO THE FILEHNE ILLUSION

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Abstract—During smooth pursuit eye movement performance often an illusory motion of background objects is perceived. This so called Filehne illusion has been quantified and explored by Mack and Herman [*Q. J.exp. Psychol.* **25,** 71–84 (1973); *Vision Res.* **18,** 55–62 (1978)]. According to them two independent factors contribute to the Filehne illusion: (1) a subject relative factor, viz. the underregistration of pursuit eye movements by the perceptual system, and (2) an object relative factor, viz. adjacency of the pursued fixation point and the background stimulus. The evidence of the present experiment supports the former but rejects the latter as a contributing factor. Instead of the concept of adjacency, an alternative theoretical extension of the subject relative factor is offered.

Smooth pursuit eye movements   Object motion   Filehne illusion   adjacency

INTRODUCTION

Visual perception of object movement can be understood as the outcome of a comparison between two signals, a retinal signal, encoding retinal image movement, and a reference signal, encoding the movements of the retinae in space. Only when the magnitudes of the two signals differ significantly (at least one JND: see Wertheim, 1981), object motion is perceived; otherwise retinal image motion is interpreted as due to eye movements and the object is perceived as stationary. However, since Filehne (1922) it is known that during smooth pursuit eye movements (made to a moving fixation point), stationary objects, whose images consequently move across the retinae, often appear to move in the direction opposite to the eye.

This phenomenon, known as the Filehne illusion, has been nicely quantified by Mack and Herman (1973). They measured the compensatory velocity that a large background stimulus had to be given to restore its subjective stationarity. This compensatory motion indeed always turned out to be in the direction of the eye movement. At the point of subjective stationarity (PSS), the magnitudes of retinal and reference signals are equal by definition. Thus, since subjective stationarity is reached by decreasing the retinal image velocity of the background stimulus, actual eye velocity must have been underrated in the reference signal. Therefore Mack and Herman concluded that the Filehne illusion is a consequence of this underregistration of pursuit ocular velocity in the reference signal.

In a later paper Mack and Herman (1978) mentioned an additional factor that contributes to the Filehne illusion; a factor which is unrelated to the comparison mechanism mentioned above. They claimed that close adjacency of a small background stimulus dot and a moving fixation point will cause a substantial increase of the Filehne illusion. This claim was based on their observation that the Filehne illusion is less pronounced when the background stimulus dot was visible for 1.2 sec than when it was visible for only 0.2 sec. Their argument was that with very brief exposure of the background stimulus, the images of the untracked background stimulus dot and the tracked fixation point are close together and therefore subject to the biasing effect of object relative motion cues.

When the background stimulus dot is seen for longer, the two images become separated and consequently the salience of object relative displacement cues decreases. The perceived motion of the background stimulus will then be determined mainly by subject-relative information i.e. by the outcome of the comparison of retinal and reference signals. This results in a much smaller Filehne illusion because it is now caused by only one factor; the underregistration of ocular velocity.

Mack and Herman tested their adjacency hypothesis with an additional experiment in which the moving fixation point disappeared while the background stimulus dot was briefly exposed, thus eliminating object relative displacement cues. This indeed resulted in a small Filehne illusion, similar to that in their original long background stimulus exposure condition. This suggested that background stimulus exposure time per se does not affect the Filehne illusion. However, their data are somewhat difficult to interpret because the eye velocity of their (highly trained) subjects shows a sudden drop after disappearance of the fixation point, i.e. during the background stimulus exposure. Since the reference signal may have been affected by this change in eye velocity, the reduced Filehne illusion could also have been caused by this factor.

To test the adjacency hypothesis of Mack and Herman more thoroughly we performed an experiment in which background stimulus exposure time was varied while adjacency remained constant, but with continuous visibility of the moving fixation point. For this purpose we needed a background stimulus pattern which was always projected onto the same part of the retinae during the pursuit eye movement. Therefore we used a window through which only part of a large background stimulus pattern was visible and had this window move with the same velocity as the fixation point.

In one condition the window (through which the background stimulus pattern was visible) was centered around the fixation point, so both the background stimulus and the fixation point were presented foveally. Therefore adjacency was high and constant, irrespective of the duration of the background stimulus. In another condition the window again moved with the same velocity as the fixation point, but now it was presented in the retinal periphery. The background stimulus pattern was thus always projected onto the same peripheral area of the retinae whilst the pursued moving fixation point was always presented foveally. So here adjacency was low but still constant, irrespective of the duration of the background stimulus exposure. Within both these "high" and "low" adjacency conditions we then varied the period during which the stimulus pattern was visible.

Suppose differences in adjacency were indeed the underlying reason for the difference in the strength of the Filehne illusion between the short and long stimulus duration conditions in the Mack and Herman study. Then the duration of the background stimulus exposure should have no effect within the present conditions where adjacency is kept constant. There should, however, be a significant difference in the strength of the Filehne illusion between the "high" and "low" adjacency conditions. According to Mack and Herman, the condition with low adjacency should cause a small Filehne illusion and the condition with high adjacency should cause a substantial one.

Two control conditions were included. In one of them the window remained stationary in the visual field rather than on the retina. Thus adjacency then varied between the short and long background stimulus exposure in the same way as in the Mack and Herman study. In the second control condition the full background stimulus pattern was visible. Here, during the performance of a pursuit eye movement, adjacency remained high and constant in the foveal areas but varied in the peripheral areas of the retinae between short and long background stimulus exposure.

APPARATUS

A moving fixation point (a small plus sign), the pursuit stimulus, was swept with a constant velocity of 12 deg/sec across a CRT screen (a Hewlett-Packard high-speed graphics display model 1321A with a rapidly decaying phosphor [P4]). Then, temporally located in the middle of this sweep a background stimulus pattern was made visible for a fixed exposure time of either 0.3 or 1.5 sec. This background stimulus pattern was a 30 × 30 deg array of randomly positioned white dots (dot diameter 10.8 min of arc, interdot distance at least 1.2 deg) that could be moved en masse in either horizontal direction. In three conditions only part of the background stimulus pattern was visible through a 6 × 6 deg window. This window was created by localised Z-modulation, and possessed fuzzy borders to prevent sudden (dis)appearance of the dots at its edges. In two of the three conditions the window moved with the same velocity and in the same direction as the fixation point. In the first, the foveal window condition (FovW) the window was placed symmetrically around the fixation point, which ensured foveal perception of the stimulus pattern during the pursuit eye movement. In the second, the peripheral window condition (PerW), the midpoint of the window was positioned 20 deg vertically above the fixation point. Thus the stimulus pattern always projected onto the same area of the peripheral rètinae during smooth pursuit. In the third condition, the stationary window condition (StatW), the window did not move but remained stationary in the middle of the screen.

In a last condition, the large pattern condition (NoW), no window was used and the complete 30 × 30 deg background stimulus pattern was visible on the screen.

Eye movements were measured with an IR reflection device mounted on a frame of spectacles (Haines model 52). Eye movements were monitored on line with a BBC computer, which also controlled the stimuli on the CRT screen. In parallel, the eye movements were digitized (sample rate 100 Hz), stored and analysed with an IBM AT computer. The experimental environment was completely dark. Average luminance of the dot pattern on the screen was 2×10^{-4} cd/m^2.

Subjects were seated in a dentist chair, the head completely fixed in a rigid (vacuum) cushion which was attached to the headrest of the chair. The viewing distance was 52 cm.

METHOD

After calibration of the IR eye movement recording system, subjects were instructed to track the moving fixation point with their eyes. Then, near the middle of the fixation point sweep, the background stimulus pattern was made visible, in such way that exposure time was symmetrical around the exact midpoint of the sweep. To determine the point of subjective stationarity (PSS) of the background stimulus two thresholds were measured. One was the threshold for perceiving background stimulus motion in the direction opposite to the eyes, i.e. opposite to the direction in which the fixation point moved (against-threshold). The other was the threshold for the perception of background stimulus movement in the same direction as the eyes (with-threshold). The PSS was defined as the midpoint between these two thresholds.

Thresholds were measured using the single staircase method. At the end of each sweep of the fixation point the subject reported verbally whether the background stimulus had been perceived as stationary or as moving in the same or opposite direction to that of the fixation point. Then the experimenter increased or reduced the background stimulus velocity by 0.35 deg/sec, depending on the subjects response. (Actually initial steps of 2.6 and 1.3 deg/sec were used to converge quickly onto the threshold area.) Mean background stimulus velocity across the first six consecutive turning points of a staircase served as the threshold stimulus velocity. For each sweep on which a turning point had occurred, the eye movement trace was stored and the eye velocity was computed exclusively during the background stimulus exposure period. The mean of these six eye velocity values served as the ocular velocity score associated with that particular threshold. Trials with bad tracking on which saccades occurred during the stimulus presentation were discarded.

The determination of a PSS took about 10–15 min, after which rest was allowed in normal light conditions. Then the IR eye movement recording system was calibrated again. In each of the four conditions (FovW, PerW, StatW and NoW) two background stimulus exposure durations were used, lasting either 0.3 or 1.5 sec. Thus eight PSS measurements were obtained for each subject, presented in random order. The order of the "with-threshold" and the "against-threshold" in a PSS measurement was balanced between conditions. All 10 (male and female) subjects were paid, and naive with respect to the hypothesis. They were between 20 and 33 years old.

RESULTS

The results of two subjects were excluded from analysis because they could not perform proper smooth eye movements in the experimental situation. The remaining eight subjects had no such problems. The sudden appearance of the background stimulus did not disrupt the smooth eye movement nor did it change ocular velocity (see Fig. 1). Mean ocular velocity was 11.44 deg/sec across all conditions. An ANOVA performed on the ocular velocity scores revealed no significant differences in eye movement velocity between short (0.3 sec) and long (1.5 sec) background stimulus exposure situations nor between any of the eight PSS measurement groups.

However, an ANOVA performed on the PSS background stimulus velocity scores revealed a significant difference ($F = 3.14$; d.f. = 21,21;

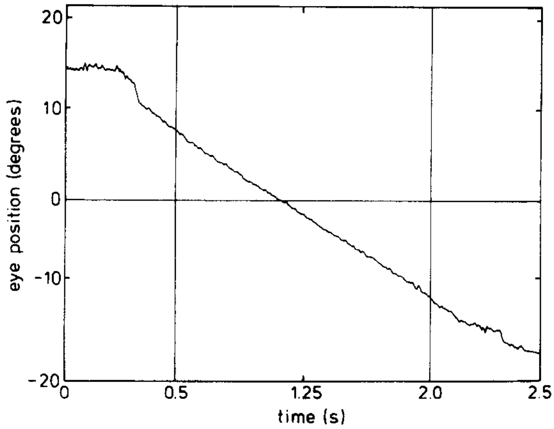

Fig. 1. Example of smooth pursuit eye movement performance during the long stimulus exposure situation (1.5 sec between vertical bars).

$P < 0.01$, 12% variance explained) in the strength of the Filehne illusion between short and long background stimulus exposure durations. The illusion was always stronger in the brief background stimulus exposure situation (see Fig. 2).

The strength of the Filehne illusion was also significantly different between the four background stimulus conditions ($F = 12.7$; d.f. = 3,21; $P = < 0.001$. 28% variance explained). Post-hoc Newman–Keuls analysis revealed that the illusion was significantly stronger in the PerW condition than in all other conditions ($P = < 0.01$), which did not differ significantly from each other (see Fig. 2).

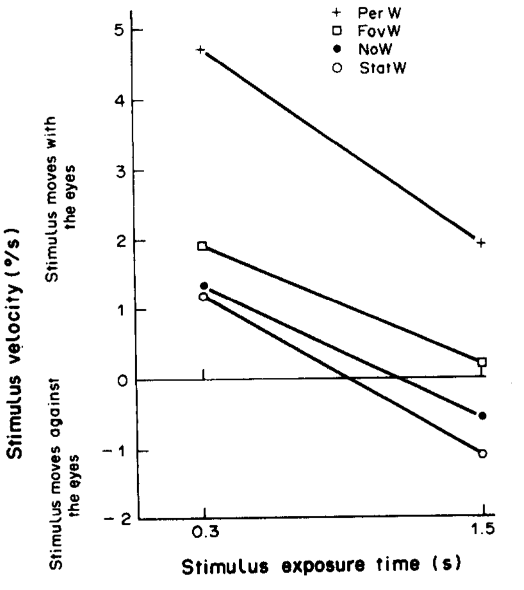

Fig. 2. Compensatory stimulus velocity at the point of subjective stationarity (group means of eight subjects). The extent of stimulus velocity—with the eyes—quantifies the strength of the Filehne illusion. Note the difference in strength of the Filehne illusion within all conditions between short and long stimulus exposure durations. In addition, the Filehne illusion is stronger in the peripheral window (PerW) than in all other conditions.

DISCUSSION

The results confirm Mack and Herman's finding that background stimulus exposure time is critical for the strength of the Filehne illusion. However, adjacency between background stimulus and fixation point seems not to be the underlying cause. There was a significant difference in the strength of the Filehne illusion within conditions where background stimulus exposure time was varied even though adjacency was kept constant (FovW, PerW). In addition, according to the Mack and Herman hypothesis, there should be differences in the strength of the Filehne illusion between conditions with different levels of adjacency. In fact there was a difference. The condition responsible, the peripheral window condition which had the lowest adjacency, produced the largest Filehne illusion. This seems to imply an effect of adjacency opposite to what was predicted. But actually adjacency is not a determinant at all, because all other conditions, *despite their different levels of adjacency*, did not differ significantly from each other.

Consequently, adjacency must be rejected as a contributing factor for the Filehne illusion. How then should one explain the importance of background stimulus exposure time for the strength of the illusion? Let us briefly explore a possible answer. We endorse the view (Mack and Herman, 1973) that underregistration of ocular velocity in the reference signal causes the Filehne illusion, but claim that the reference signal does not merely refer to eye velocity alone but is a signal whose purpose is to register the velocity of the retinal surface in space. The reference signal is therefore proposed to be the result of a parallel processing of (1) efferent ocular (eyes in their orbits) and (2) afferent vestibular (headmovement) velocity information and (3) additional afferent retinal optokinetic information. The latter kind of information is available in the smearing of images of background objects across the retina, and is known to have the potential to generate a perception of selfmotion (Helmholtz, 1962; Dichgans and Brandt, 1978; Berthoz and Droulez, 1982; Schmidt *et al.*, 1985). Selfmotion implies movement of the retinae in space. So optokinetic stimulation implies information about movement of the retinae in space. Physiological evidence for such an integration of information from at least these 3 sources stems from electrophysiological measurements of mossy fibers in the cerebellar flocculus (of monkeys). These fibers receive converging inputs from structures related to visual, oculomotor and vestibular functions (Noda, 1985; Ito, 1982; Miles and Lisberger, 1981; Lisberger *et al.*, 1987; Buttner and Waespe, 1984). Examples of mossy fiber visuomotor unit responses to a combination of retinal smear information, eye velocity information and head velocity information (Noda, 1985) give a strong indication that the reference signal originates in the flocculus.

With psychophysical methods Wertheim (1987) demonstrated that retinal afferent stimuli with optokinetic potential (i.e. rather large stimuli with low spatial frequency which move across the retinae for at least one second) do indeed affect, namely increase the magnitude of, the reference signal.*

On the basis of these arguments we think it is reasonable to assume that integration of ocular velocity information, head velocity information and optokinetic information can normally optimize the gain of the reference signal so that the Filehne illusion will not occur. But when the head of a subject is fixed and the background stimulus presented has no optokinetic power (e.g. it is small and/or very briefly presented), then the gain of the reference signal is less than one, due to (underregistered) ocular velocity information only, and this causes the Filehne illusion.

In their (1978) experiments, Mack and Herman used a single small background stimulus dot, which was presented for a very short (0.2 sec) or a little, but crucially, longer (1.2 sec) time. In the brief exposure situation visual (i.e. optokinetic) modulation of the reference signal could not play a role. But, according to our explanation, a small visual component in the reference signal may have been induced in the long background stimulus situation, slightly increasing reference signal size. This explains why Mack and Herman found a somewhat smaller Filehne illusion in the latter condition.

In the present experiment we used more or less the same background stimulus exposure durations as Mack and Herman did, but a much larger background stimulus pattern. In our long exposure situation this must have induced a larger visual component in the reference signal. The Filehne illusion did indeed disappear in three conditions and became much smaller in the fourth, peripheral, condition.

The question remains why the overall strength of the Filehne illusion was significantly larger in the peripheral window condition than in all other conditions (Fig. 2). We think that besides time there is another factor determining the strength of the illusion, namely position on the retina. It seems reasonable to assume that retinal eccentricity affects the build-up of visual modulation of the reference signal. Possibly the peripheral retinae require a larger area of stimulation or a longer background stimulus exposure. Future research will deal with this matter.

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*The hypothesis that optokinetic stimulation affects the magnitude of the reference signal does not necessarily imply that this happens only when self motion is consciously experienced. There may be a perceptual threshold. In other words, the reference signal might already be affected before sensations of self motion reach consciousness [see Dichgans and Brandt (1978) for a similar suggestion that optokinetic stimulation may affect object motion perception before it affects ego motion perception].

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