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Modification of the Filehne Illusion by Conditioning Visual Stimuli

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During smooth pursuit eye movements made across a stationary background an illusory motion of the background is perceived (Filehne illusion). The present study was undertaken in order to test if the Filehne illusion can be influenced by information unrelated to the retinal image slip prevailing and to the eye movement being executed. The Filehne illusion was measured in eight subjects by determining the amount of external background motion required to compensate for the illusory background motion induced by 12 deg/sec rightward smooth pursuit. Using a two-alternative forced-choice method, test trials, which yielded the estimate of the Filehne illusion, were randomly interleaved with conditioning trials, in which high retinal image slip was created by background stimuli moving at a constant horizontal velocity. There was a highly reproducible monotic relationship between the size and direction of the Filehne illusion and the velocity of the background stimulus in the conditioning trials with the following extremes: large Filehne illusions with illusory motion to the right occurred for conditioning stimuli moving to the left, i.e. opposite to the direction of eye movement in the test trials, while conversely, conditioning stimuli moving to the right yielded Filehne illusions close to zero. Additional controls suggest that passive motion aftereffects are unlikely to account for the modulation of the Filehne illusion by the conditioning stimulus. We hypothesize that this modification might reflect the dynamic character of the networks elaborating spatial constancy.

Motion perception Eye movements Smooth pursuit Perceptual stability

INTRODUCTION

Our visual system conveys a view of the world that remains reassuringly stable in spite of continuous displacements of the retinal image due to eye movements or other kinds of ego-motion. This perceptual stability of the visual world is widely assumed to be based on a comparison between two signals, one corresponding to retinal image slip and another one encoding the movement of the eyes. While the first signal is purely retinal, the second one is usually considered to be of extraretinal origin and in this case referred to as the *corollary discharge* or *efference copy* signal (von Holst & Mittelstaedt, 1950; Sperry, 1950). However, others have preferred the term *reference signal* in order not to exclude the possibility that retinal information might supplement extraretinal information for the encoding of eye motion (see Wertheim, 1994 for review). Irrespective of the question of the nature of the reference signal, perceptual stability is thought to be a necessary consequence of the fact that retinal image slip of a stationary background, resulting from eye movements such as smooth pursuit of a target moving in front, is perceptually cancelled by an eye movement related signal of similar magnitude. Along the same line, the target whose continuous displacement is compensated by smooth pursuit eye movements is perceived as being moving despite the absence of any significant image slip, due to the fact that the reference signal cannot be cancelled by a retinal signal.

A closer look at motion perception during eye movements, however, suggests that this mechanism must be far from being perfect, most probably due to the fact that a reference signal of appropriate magnitude is not or at least not always available. It was Wilhelm Filehne (1922) who first noted that smooth pursuit eye movements may be accompanied by a small albeit significant illusionary movement of stationary objects. According to Filehne, objects seem to move opposite to the direction of eye movement. This, however, is not always the case, since later investigators were able to demonstrate also inverted *Filehne illusions*, i.e. illusionary movements of the visual background in the direction of eye movement, provided the stationary visual background chosen was comparatively large (Wertheim, 1987). More generally, this and other studies pointed towards a profound dependence of the size and the direction of the Filehne illusion on the specific details of the visual configuration prevailing with

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size of the background pattern being only one among other factors (Wertheim 1981; de Graaf & Wertheim, 1988; Wertheim, 1994). While these studies emphasize the importance of the parameters defining the properties of the visual background for the magnitude and direction of the perception of its movement, there is also evidence for factors other than the background properties being involved. One such factor may be age, since Wertheim and Bekkering (1992) reported that older people tend to have an inverted Filehne illusion under visual conditions evoking a normal illusion in younger subjects. In addition, extremely enlarged Filehne illusions have been seen when background patterns were presented to the retinal periphery or when exposure time was very short (Ehrenstein, Mateef & Hohnsbein, 1986; Ehrenstein, Mateef & Hohnsbein, 1987; de Graaf & Wertheim, 1988). These observations could not be explained by a change of the retinal component of the reference signal brought about by the peripheral presentation of the background, since the non-retinal component of the reference signal is assumed to encode about 80% of eye velocity relative to the head and, thus, should have dominated perception (Wertheim, 1994). Rather, the dramatic changes introduced by age and retinal eccentricity suggest a far more dynamic interpretation of given constellations of retinal image slip and eye movement.

The Filehne illusion has first been quantified by Mack and Herman (1973, 1978) who measured the size and direction of the illusion by determining the amount of motion of the background in space that is required to regain the impression of stationarity of the background. At this point of subjective stationarity (PSS) the velocity of the compensatory background movement added is equal in magnitude and opposite in direction to the Filehne illusion. In the case of the classical Filehne illusion the movement of the visual background at PSS is in the same direction as that of eye movement. This indicates that the signal encoding slip of the retinal image of the visual background is larger than the extraretinal signal encoding eye velocity. Obviously, pattern velocity at the PSS can be used as a direct measure of the difference between the retinal and the extraretinal signal (Wertheim, 1987). In the present study a two-alternative forced-choice (2AFC) method was combined with an adaptive staircase procedure in order to measure the Filehne illusion (see below). Surprisingly, first results that we obtained with this method differed from the results reported in the literature in two ways. Firstly, the estimates of the Filehne illusion were generally quite low in our experiments, i.e. a background stimulus was regarded stationary by the subjects when it was actually moving only slightly. Secondly, different start levels of the stair case sequence yielded different Filehne illusions. Specifically, the background speed that induced the percept of stationarity was shifted towards the velocity of visual stimuli presented in the beginning. The present study was undertaken in order to validate these preliminary observations and to explore whether these findings reflect mere biasing effects on thresholds well known in psychophysical research outside the field of motion perception related to ocular pursuit (see e.g. Cornsweet, 1962). We will present experimental evidence suggesting a modification of the Filehne illusion by preceding visual stimuli which might reveal an important genuine property of the underlying mechanisms elaborating spatial constancy during smooth pursuit eye movements.

METHODS

The pursuit target, a red spot (dia 10 min arc), was presented for 0.5 sec in the middle of a 19 in. computer monitor (Mitsubishi, frame rate 72 Hz, 1280 × 1024 pixel). Next the target jumped 15 deg to the left and then moved to the right at a constant velocity of 12 deg/sec spanning a visual angle of 30 deg. Temporally located in the middle of the target sweep a background pattern became visible for 300 msec. This background pattern had an extension of 27 × 27 deg and consisted of 350 white dots (dia 15 min arc) on an otherwise dark screen. The dots moved *en bloc* left-or rightwards, each dot which had reached the border of the pattern was replaced by a freshly plotted new dot on the opposite side.

Eight paid and naive subjects, male and female students aged between 22 and 33 yr, were seated in front of the monitor at a viewing distance of 57 cm in a dark room. They were instructed to maintain their head in a fixed position supported by a head-and-chin rest and to track the target as accurately as possible. In this fashion subjects first performed a saccade to the left and then smooth pursuit eye movements to the right. Subjects were asked to report what direction of background motion they experienced during pursuit by pressing one of two alternative keys related to leftward and rightward background motion respectively. With a latency of 0.5 sec the next trial was started.

The 2AFC method assumes that the observer will decide randomly what answer he gives whenever he has the impression that the background stimulus is not moving. Therefore, a stimulus velocity that results in 50% right and 50% left answers after repeated presentation defines the PSS in our experiments. In order to determine this velocity, different background velocities were presented to the observer following an adaptive staircase procedure termed PEST [Parameter Estimation by Sequential Testing (Taylor & Creelman, 1967; Lieberman & Pentland, 1982)]. This PEST procedure begins by offering background movement at some arbitrary start level and choses a new background velocity after a finite number of trials. The choice of new velocities depends on the results obtained in preceding trials and, consequently, on the history of the whole run. In the present study, first a background moving at a velocity of either +4 or −4 deg/sec (rightward and leftward, respectively) was presented to the observer. Starting from one of these two levels further background velocities were displayed that gradually approached the PSS, i.e. the velocity, which gave right and left responses with equal probability. The strategy

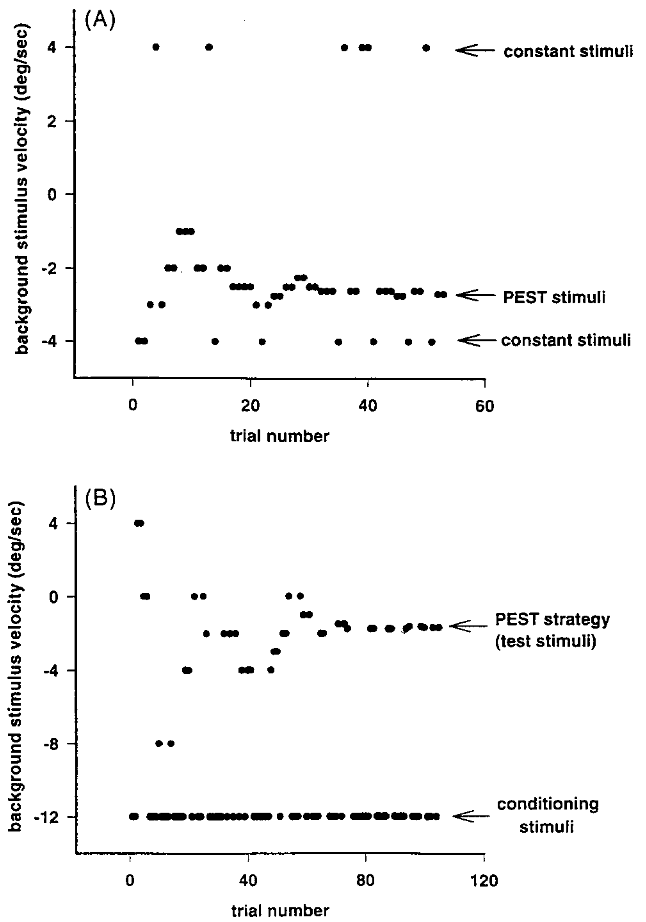

FIGURE 1. Temporal sequence of background stimulus velocities that are presented to the observer during a typical measurement of Expt I (A) and Expt II (B). Each dot marks one trial, intertrial intervall: 0.5 sec. Negative stimulus velocities indicate direction opposite to eye movements.

was finished when the background velocity of the next trial differed less than 0.01 deg/sec from the preceding one. In this case the background velocity presented in the final trial served as an estimate of the background velocity yielding subjective stationarity. When the procedure had not converged within 40 trials it was stopped as well and a probit analysis (McKee, Klein & Teller, 1985) with subsequent χ^2 goodness-of-fit test was applied on the responses in order to estimate the background velocity yielding equally probable right and left decisions. The temporal sequence of a typical run is shown in Fig. 1(A). As can be derived from this figure, the PEST procedure converged towards a background velocity of -2.34 deg/sec by running through oscillations that became smaller over time. We will refer to such a sequence of trials yielding an estimate of the PSS as a "measurement" of this threshold. In addition to and independent of trials with background movement determined by PEST ("PEST stimuli"), background stimuli moving at a fixed velocity (here ± 4 deg/sec, alternatively) were presented. These "constant stimuli" were originally designed to prevent fatigue of the subjects that was expected to emerge after repeated presentation of background movement close to the PSS.

Experiment I

The first series of measurements was designed to test if different start levels of PEST influenced the estimates of the Filehne illusion. Two different start levels (+4 and -4 deg/sec) were compared in six out of the eight subjects mentioned above. The constant stimulus speed was ± 4 deg/sec, the probability of a constant stimulus coming next instead of a PEST stimulus was 0.2 [again see Fig. 1(A) for an example].

Experiment II

The hypothesis that a given stimulus may affect the perception of the following one was tested in Expt II by making use of the constant stimuli which were presented now at just *one* given velocity. Figure 1(B) shows a typical run from Expt II with the constant stimulus moving at -12 deg/sec. Since Expt II was designed to test if constant stimuli would influence the perception of PEST stimuli, we will refer to the two also as "conditioning stimuli" (CS) and "test stimuli" (TS), respectively. The CS velocity used in Expt II ranged from -28 to +28 deg/sec in steps of 8 deg/sec. Thus, each of the eight subjects participated in eight measurements differing in the velocity of the CS. The sequence of velocities was randomized for each subject. As fatigue was regarded a crucial factor affecting the subjects' responses there was a selfdetermined rest usually lasting up to 10 min after each measurement. No rest was allowed during the course of the measurement itself. The only interruption of the psychophysical procedure resulted from repeated insufficient smooth pursuit evoking recalibration of the eye position signal (see below). Each measurement usually lasted between 10 and 15 min. Subjects were tested for a duration of 1, 1.5 or 2 hr a day. Thus, 3–6 measurements could be made during one session. Subjects consistently reported that the measurements were quite demanding, but did not feel stressed or tired. Experiment II was performed in two modifications: in the "eyes tracking during presentation of conditioning stimuli" (ETCS) version subjects tracked the moving target when CS were shown. In the "eyes stationary during presentation of conditioning stimuli" (ESCS) version of Expt II the observer was required to fixate a stationary target in the middle of the screen while the conditioning background moved. So, trials with a moving (TS) and with a stationary target (CS) were intermixed under this latter condition. In the ESCS version CS speed was varied over a range from -32 to +16 deg/sec in order to yield retinal image slip velocities similar to those prevailing under the ETCS condition. The PEST start level was kept invariantly at +4 deg/sec, the probability for the presentation of a CS being 0.5.

Eye movements were measured using an infrared reflection system (CCD eyetracker, AmTech, Weinheim, Germany) at a sampling rate of 200 Hz. Eye records were stored and analyzed on-line with a computer which also controlled the motion of the target and the presentation of the stimuli. Deviations of eye position from target position exceeding 2 deg were fed back to the subjects

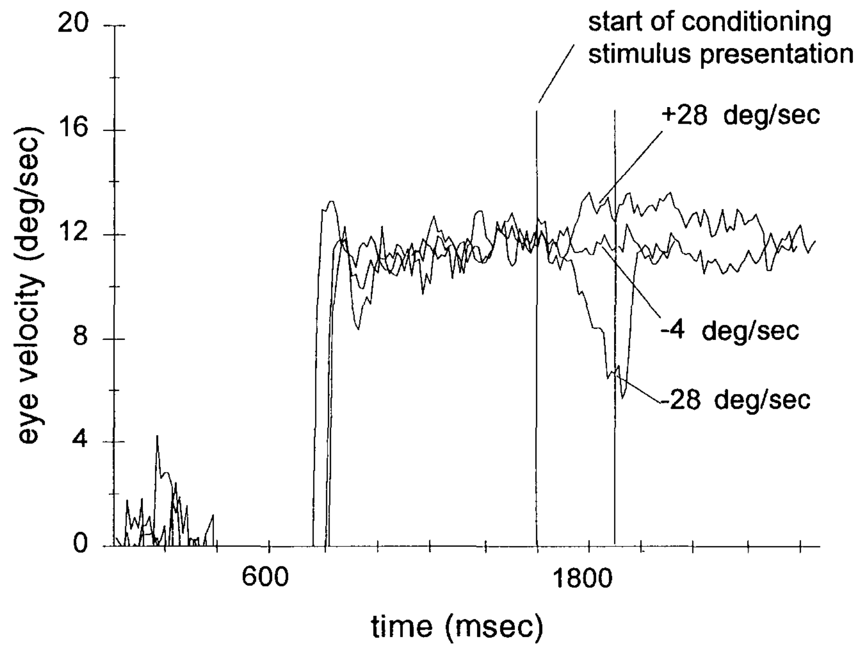

FIGURE 2. Intraindividual means of ocular velocity in one selected subject who displayed a pronounced modulation of his pursuit gain when moving background stimuli (CS) were presented. Vertical bars mark start and stop of the presentation of CS. The magnitude of CS speed is indicated above or below the corresponding ocular velocity record in each case.

acoustically as errors. Three errors in sequence led to recalibration. Trials with insufficient pursuit as defined before were ignored by PEST and excluded from the later analysis. For each conditioning velocity level two different means over all valid trials were calculated in order to characterize pursuit performance: (i) mean velocity of smooth pursuit eye movements during presentation of CS; (ii) mean ocular velocity during presentation of TS.

RESULTS

Eye movements

Smooth pursuit eye movements in general are characterized by a high degree of variability which is

TABLE 1. Eye movement velocity during presentation of background stimuli

CS velocity (deg/sec)	Horizontal eye movement velocity (deg/sec) during presentation of		Retinal image slip velocity of CS (deg/sec)
	CS	TS	
ETCS condition			
−28	10.36 ± 1.77	10.34 ± 1.34	−38.36
−20	10.34 ± 0.92	10.35 ± 1.05	−30.34
−12	10.84 ± 0.71	10.71 ± 0.54	−22.84
−4	10.98 ± 0.63	10.81 ± 0.61	−14.98
4	11.01 ± 0.81	10.70 ± 0.71	−7.01
12	11.23 ± 1.17	10.33 ± 0.99	0.77
20	11.66 ± 1.12	10.81 ± 0.88	8.34
28	12.28 ± 1.41	10.39 ± 1.31	15.72
ESCS condition			
−32	−0.64 ± 0.61	10.60 ± 0.99	−31.36
−24	−0.71 ± 0.22	10.40 ± 0.88	−23.29
−16	−0.85 ± 0.27	10.29 ± 1.12	−15.15
−8	−0.71 ± 0.33	10.38 ± 1.09	−7.29
0	0.18 ± 0.49	10.04 ± 1.07	−0.18
8	0.87 ± 0.28	10.45 ± 1.35	7.13
16	0.95 ± 0.35	10.09 ± 1.16	15.5

For each experiment characterized by a different level of CS velocity interindividual means and SDs of smooth pursuit velocity during presentation of CS or TS were calculated. Positive values of stimulus and eye movement speed denote direction from left to right. The difference between CS velocity and smooth pursuit yields the actual retinal image slip velocity of conditioning background stimuli.

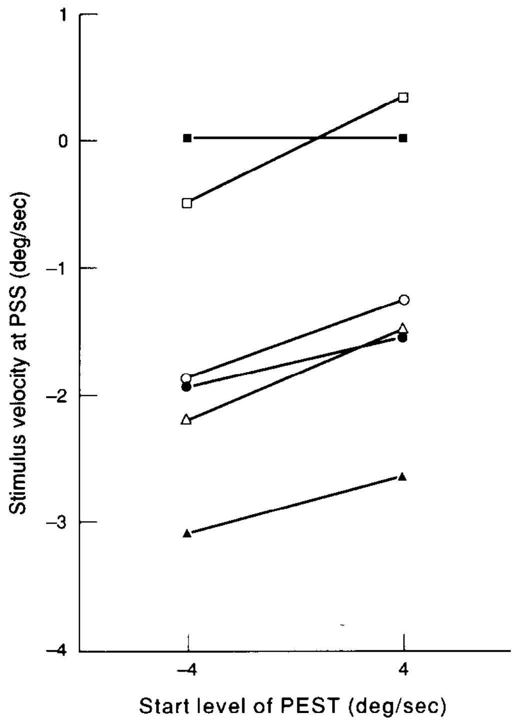

FIGURE 3. Effect of the start level of the PEST strategy on the Filehne illusion: stimulus velocity at the PSS for two different start levels. Six subjects were tested, each subject is represented by an individual symbol. Positive velocities at the PSS mean that the background stimulus actually has to move in the same direction as the eyes to cause the sensation of stationarity (Filehne illusion); negative velocites at PSS denote physical background motion opposite to the eyes (inverted Filehne illusion).

further increased by the properties of the visual background. Structured visual backgrounds like the one used in the present study tend to impair smooth-pursuit eye movements (Yee *et al.*, 1983; Keller & Khan, 1986; Kimmig, Miles & Schwarz, 1992; Mohrmann & Thier, 1995). It would therefore be inappropriate to relate perception of background velocity to the velocity of the target, rather than to the actual eye velocity. Although we had adopted demanding pursuit accuracy criteria in order to exclude trials of grossely impaired pursuit, even the remaining trials revealed an influence of the visual background on eye velocity. This is illustrated in Fig. 2, which shows the eye movements of one of our subjects, whose pursuit turned out to be exceptionally susceptible to the presentation of a visual background. The three curves plotted in Fig. 2 represent the intraindividual means of eye velocity based on trials (Expt II, ETCS condition) with CS moving at one out of three different velocities (−28, −4 or +28 deg/sec). While pursuit was roughly compensatory before the presentation of the structured visual background, 130 msec after the background had been turned on, the eye velocity records started to diverge, depending on the velocity of the background. Whereas background motion in the direction of pursuit induced some slight overtracking, background motion opposite to the direction of pursuit caused considerable undertracking, at least at the higher of the two background speeds tested. Eye velocity in this latter condition averaged 9.89 deg/sec over the presentation time of the visual background. Table 1 summarizes the group means of eye velocity during the presentation of the visual background for all subjects, separately for CS and TS in the two variants of Expt II (ETCS vs ESCS). Although the group means show the same tendency of overtracking for background motion in the direction of pursuit and undertracking for background motion opposite to the direction of pursuit, already suggested by the example shown in Fig. 2, this background influence did not reach statistical significance due to the large intra-and interindividual variability of the responses (one-way ANOVA with the factor conditioning stimulus velocity, $P > 0.1$).

In the ESCS variant of Expt II, subjects were required to fixate a stationary target while the conditioning stimulus was presented. As can be seen in the lower part of Table 1, the eyes tended to move slightly with the background, rather than to remain completely stationary. Unlike the effect of background motion on pursuit, this effect on stationary fixation was statistically significant (one-way ANOVA with the factor conditioning stimulus velocity, $F = 24.9$, d.f. = 6,47, $P < 0.001$).

Although the background influence on pursuit did not reach significance we felt it would be preferable to relate background motion perception to the actual eye velocity as estimated by averaging eye velocity over background presentation time. All calculations of retinal background image slip are based on these estimates of eye velocity.

Experiment I

Figure 3 plots the background velocity at PSS as a function of the starting level of PEST for the six subjects tested. Although the interindividual variation was considerable, with background velocity varying between −3.07 and 0.03 deg/sec for the −4 deg/sec start level of PEST, and between −2.64 and 0.34 deg/sec for the +4 deg/sec start level, there was a consistent shift of background velocity at PSS towards more positive levels when PEST started from a positive level as opposed to PEST starting from the negative level in five out of the six subjects. This shift averaged 0.48 deg/sec (SEM 0.12) and was statistically significant (paired *t*-test, $P = 0.011$). It was not attributable to differences in the performance of smooth pursuit eye movements under the two conditions. Specifically, group means and SDs of eye velocity during presentation of PEST stimuli were 10.43 ± 0.24 and 10.33 ± 0.43 deg/sec for the +4 and −4 deg/sec start levels, respectively.

Experiment II: influence of CS on the Filehne illusion

In Expt II CS caused a profound modification of the Filehne illusion, which under certain circumstances could get even close to the size of the retinal background image slip (see below). The amount of modification of the Filehne illusion was primarily determined by the size and direction of the retinal slip of the CS, whereas the

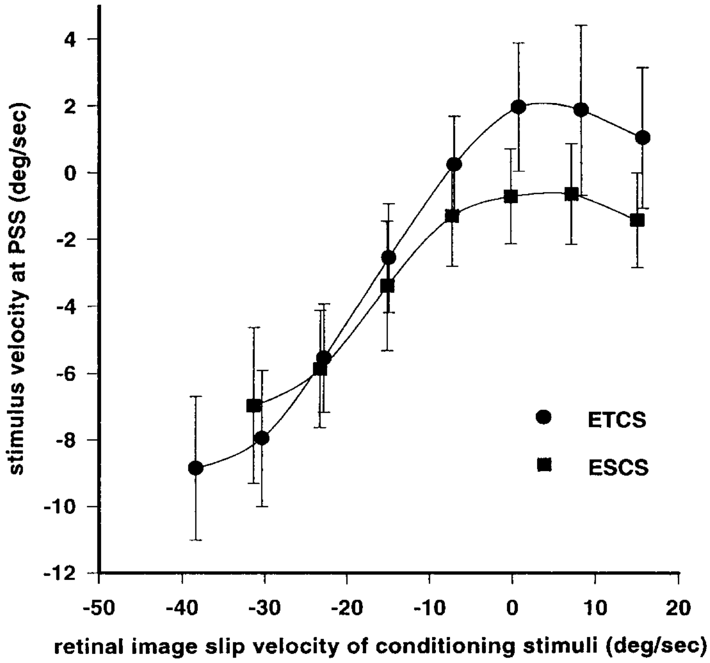

FIGURE 4. The effect of CS on the Filehne illusion: test stimulus velocity at the PSS as a function of the retinal image slip velocity of conditioning stimuli (means of eight subjects, error bars signify 1 SE above and below means). CS were presented to the subjects with their eyes directed to a moving or a stationary target (ETCS or ESCS respectively). Positive velocities at the PSS reflect the classical Filehne illusion, negative speeds at the PSS indicate inverted Filehne illusions.

oculomotor response during presentation of the CS, i.e. whether the eyes maintained stationary fixation as in the ESCS condition or tracked the moving target as in the ETCS condition was secondary. The paramount importance of the retinal slip of the CS image is demonstrated by Fig. 4, which plots the background velocity at PSS as a function of retinal image slip of the CS for both oculomotor response conditions. The two curves are roughly sigmoidal indicating that the Filehne illusion increased with increasing CS image slip for CS movement directed opposite to the direction of target movement in test trials and conversely Filehne illusions close to zero for CS image slip in the direction of target movement. The mean Filehne illusion for a CS slip of -38.36 deg/sec under ETCS condition, for example, was 9.36 deg/sec and could reach 13.5 deg/sec in selected subjects. The dependence of the Filehne illusion on the CS image slip was highly significant for both the ETCS and the ESCS condition (one-way ANOVA with the factor retinal image slip of the conditioning stimulus; ETCS, $F = 40.6$, d.f. = 7,53, $P < 0.001$; ESCS, $F = 17.03$, d.f. = 6,47, $P < 0.001$).

Although CS image slip was the major determinant of the Filehne illusion, the oculomotor response was not without any effect. The curve plotting the estimate of the Filehne illusion as a function of CS image slip for the ETCS condition was somewhat steeper than the one for the ESCS condition, with the former crossing the latter at 20–25 deg/sec CS image slip and the ETCS condition yielding larger Filehne illusions for large negative CS image slip than the ESCS condition. Moreover, only the ETCS condition gave rise to "classical" Filehne illusions up to 2 deg/sec (i.e. illusory motion opposite to the direction of pursuit) for CS image slip in the direction of eye movement in the test trials. Two-way ANOVA with the factors retinal image slip and oculomotor response condition showed that the somewhat larger effectiveness of CS image slip in the ETCS condition was significant ($F = 15.8$, d.f. = 1, $P < 0.001$).

Experiment III: is the modulation of the Filehne illusion due to a motion aftereffect?

One possible explanation of the observed modification of the Filehne illusion by conditioning image slip is an adaptation process related to the motion aftereffect (MAE). It is well known that after prolonged stimulation of the retina by motion over the retina, whether generated by patterns moving continuously in a certain direction with immobile eyes or by tracking eye movements across a stationary visual environment, a subsequently presented stationary pattern seems to move in a direction opposite to that of the adapting stimulus (e.g. Wohlgemuth, 1911; Barlow & Hill, 1963; Anstis & Gregory, 1965). In our experiments repeated exposure to CS moving to the left during stationary fixation (ESCS) or in combination with smooth pursuit to the right (ETCS) should cause a MAE to the right. This MAE might override the Filehne illusion inducing a large illusory motion of the test background to the right, requiring a large compensatory external displacement at the PSS to the left.

While we cannot rule out that the MAE contributed somewhat to the modification of the Filehne illusion, there are two observations which suggest that this contribution is not significant. The first observation

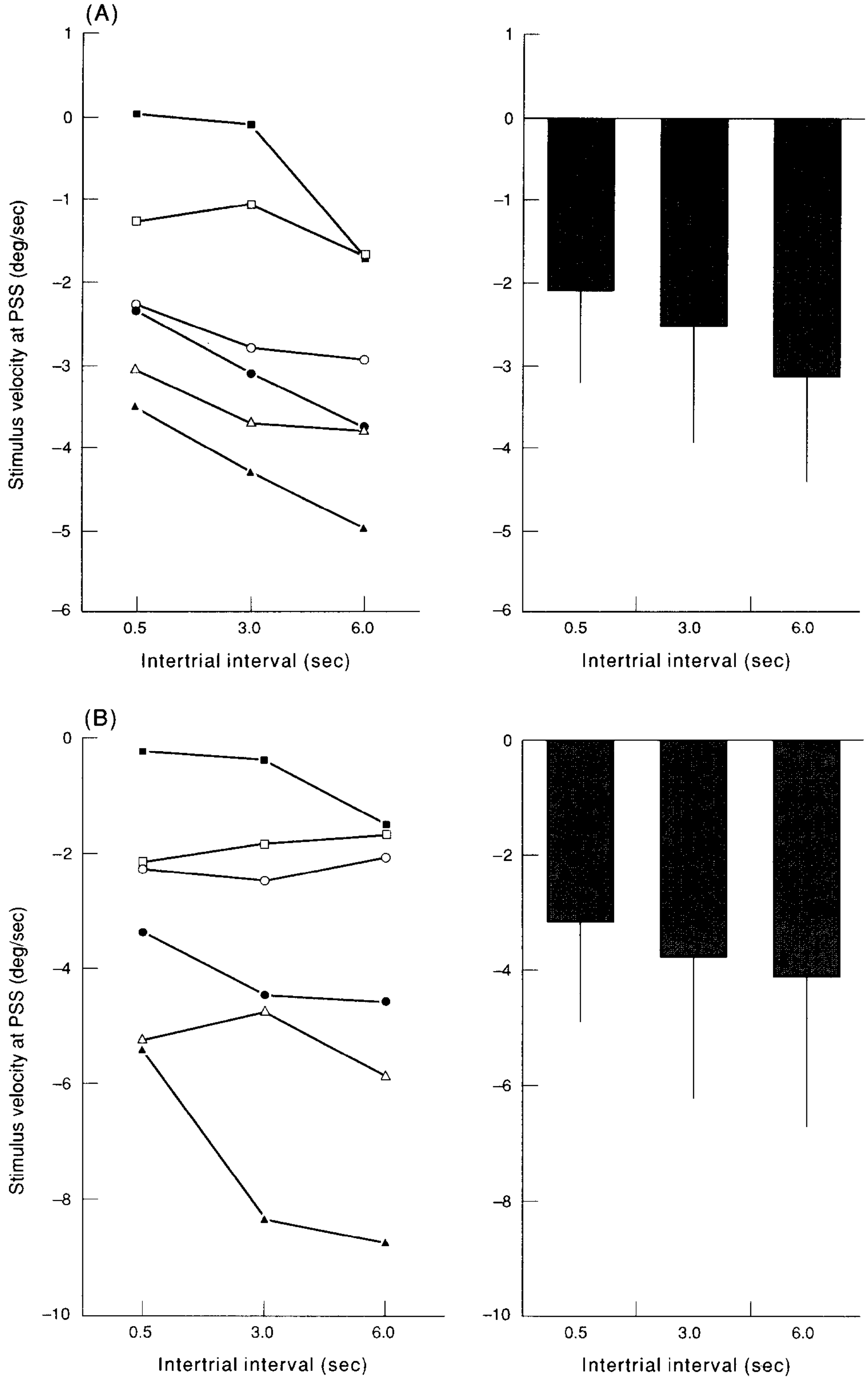

FIGURE 5. Time dependency of the effect of CS on the Filehne illusion: compensatory test stimulus velocity at the PSS as a function of intertrial interval. Six subjects, represented by different symbols. CS motion was −4 deg/sec to the left while subjects tracked a target moving at 12 deg/sec to the right (A) or CS moved at 16 deg/sec to the left with subjects keeping their eyes fixed on a stationary target (B).

relates to the time course of the MAE. The MAE is known to decay exponentially in time (see e.g. Keck & Pentz, 1977) with maximum estimates of the time constant being in the order of about 20 sec. In other words, the MAE is expected to decrease to about 0.74 of its initial value within the first 6 sec, which is the order of the magnitude of the intertrial interval used in Expt III. The dependence of the modification of the Filehne illusion on the intertrial interval was studied in more detail in six out of the eight subjects exposed to a CS velocity of −4 deg/sec (ETCS) and −16 deg/sec (ESCS). Hence, each condition was expected to result in a retinal image slip of approx. −15 deg/sec (see Table 1). Similarly to Expt II, measurements differing in oculomotor responses (ETCS and ESCS condition) or intertrial intervals (0.5, 3 and 6 sec) were varied in each subject in a random manner.

Figure 5 plots the background velocity at PSS as a function of the intertrial interval for each individual subject and for the group of six for the ETCS [Fig. 5(A)] and the ESCS [Fig. 5(B)] condition. Although a one-way ANOVA with the factor intertrial interval revealed no significant effect under either condition (ETCS or ESCS), the comparison of the group means obtained for the different intervals showed a clear tendency for a slight increase of the inverted Filehne illusion with rising intertrial intervals [mean difference (0.5 sec vs 6 sec): −1.08 deg/sec for ETCS; −0.91 deg/sec for ESCS], i.e. opposite to what would be expected if the MAE played a role.

Secondly, subjects usually did not experience a MAE if a conditioning trial was followed by a stationary background rather than a test trial or a further CS. In this modification of the standard procedure, subjects were asked to simply watch the stationary background and to report verbally if they experienced a drift of the background to either side. Only one out of the six subjects reported a small drift of the stationary background, when the intertrial interval was reduced to 0.5 sec. All other subjects perceived a completely stationary background even for 0.5 sec intertrial intervals.

DISCUSSION

The results of the present study demonstrate that the perception of self-induced background motion during smooth pursuit eye movements can be influenced by preceding visual stimuli. As eye velocity during presentation of the TS was constant throughout all conditions of Expt II (see Table 1), it has to be concluded that identical constellations of retinal image slip and eye movement can lead to different perceptions as indicated by a large modification of the Filehne illusion. The major determinant of this modification was the retinal image slip of the CS preceding test trials. Specifically, the point of perceived stationarity was shifted consistently towards the direction of motion of these CS. However, the slight, albeit, significant differences between the ETCS and ESCS conditions argue against retinal image slip being the sole basis of the modification of the Filehne illusion. Retinal shifts caused a more pronounced modification when they were at least partially due to eye movements.

Biasing effects on psychophysical responses are well known (see e.g. Cornsweet, 1962; Helson, 1964). There is experimental evidence that a subject's response to a given stimulus in a series of stimuli presented during a psychophysical measurement depends not only on the characteristics of the given stimulus, but also, albeit to a lesser degree, on the values of all the stimuli that have already been presented—a finding referred to as anchoring effect, series-effect etc., and variedly attributed to adaptation or "response frequency equalization" (Erlebacher & Sekuler, 1971) to mention but a few of the mechanisms discussed. Independent of the mechanism, the result, in most cases, is that the threshold is shifted towards the middle of the set of stimuli that have been presented. In this context the large modulation of the Filehne illusion might be regarded nothing but a further example of such a biasing effect. There is one major finding that is not compatible with this interpretation: a strong modification of motion perception took place only after the presentation of CS drifting *against* the direction of the eye movement. In this case a huge inverted Filehne illusion resulted, whereas the Filehne illusion was quite small and invariant for CS moving with the eyes. As far as we can tell, a comparable directional asymmetry has never been found for the biasing effects considered earlier. However, an asymmetric modulation of responses similar to that of the Filehne illusion in the present study has been observed in earlier studies of eye movement related motion perception. Thus, Wallach, Becklen and Nitzberg (1985) found that background motion is more accurately perceived when it is in the same direction as the eye movement as compared to background motion and eye movement directed oppositely. As to the perception of the velocity of the tracked target itself, Brenner (1993) noted that background motion opposite to target motion strongly affects perceived target velocity. Conversely, background stimuli moving in the same direction as the target are uneffective. While the exact mechanisms of the asymmetric modulation in these experiments remain unclear, it is close to hand to assume that the interaction between non-visual, eye movement related signal and visual information seems to be essential.

To our knowledge, the literature does not contain any hints suggesting a modification of the Filehne illusion comparable to the one reported here. This is most probably due to the fact that fast moving background stimuli have not been used in earlier studies. Actually, we originally introduced fast moving stimuli in Expt I in order to break up the sequence of close to threshold test stimuli thereby making the presentation less tiring. We decided to vary the speed of these constant stimuli systematically because of the finding that different PEST start levels resulted in different Filehne illusions. This latter dependency obviously poses a serious problem. How can the Filehne illusion be veridically measured after all without biasing the observer? By the same token, one may wonder if the modification of the perception of self-induced image slip by preceding visual stimuli might have unnoticedly affected some of the results reported in the literature on the Filehne illusion. Could it be that alternative procedures to measure the Filehne illusion preferred by most of the earlier studies are less prone to modification? The most common method used has been introduced by Wertheim (see e.g. de Graaf & Wertheim, 1988). He measured the PSS and thereby the Filehne illusion by determining the midpoint between two thresholds: one was the threshold for perceiving background stimulus motion in the same direction as the eyes, the other was the threshold for the perception of motion in the opposite direction. These thresholds were determined separately by increasing or decreasing the background velocity until the subjects were just able to notice the motion of the background. Background velocity was then changed in the opposite way until stationarity was perceived again, and so on. Threshold was defined as the mean of background velocities related to the first six consecutive turning points. Our results show that the modifying capacity of a visual stimulus is the larger the larger the resulting background image slip is provided background motion occurs opposite to the direction of smooth pursuit. Thus, at least background stimuli used by Wertheim in order to determine the threshold for visual motion opposite to the direction of eye motion should have been capable of modifying the observers' perception. Specifically, prolonged presentation of patterns that move consistently opposite to the eyes should have led to a deflection of the threshold in the same direction, i.e. the threshold should have been systematically overestimated in these studies. As a consequence, the PSS defined as the midpoint between the two different thresholds should have been shifted towards negative values, too. In other words, these considerations suggest that there does not seem to be a bias-free measure of the Filehne illusion.

The most obvious interpretation of the modulation of the perception of self-induced background motion observed in the present study is that it results from an adaptation process known as the MAE. As already mentioned in the Results, the MAE occurs when prolonged motion over the retina takes place, whether generated by patterns moving continuously in a certain direction or by eye movements across a stationary pattern. It is well established that the MAE gets stronger with longer presentation times of the adapting stimulus and shorter intervals between the adapting stimulus and the presentation of the test background. In the case of our experiment, the presentation time of the inducing stimulus, the CS, was comparatively short, probably explaining our finding that only one out of the six subjects experienced a weak MAE, when probed with a stationary background following the CS. However, even in this subject a MAE was only observed when the intertrial interval was 0.5 sec, whereas a MAE was not experienced with longer intervals. Not only this lack of a significant classical MAE under the conditions prevailing in our experiment but also the lack of an effect of varying the intertrial interval on the modification of the Filehne illusion is inconsistent with the view that a MAE can account for our finding of a modification of the Filehne illusion. It is usually assumed that the MAE decays exponentially with a time constant of less than 20 sec. Although the decay of MAE can be decreased by darkness or by a homogeneously illuminated non-textured pattern in the post-adaptation period, the latter prevailing in the present experiment, the MAE is hardly detectable for more than 25 sec and usually the MAE speed will decline to seven-tenths of the maximal speed within the first 6 sec (see e.g. Spigel, 1962; Keck & Pentz, 1977; Verstraten, Fredericksen, Grüsser & van der Grind, 1994). However, the modification of the Filehne illusion did not become smaller but, if anything, larger when the intertrial interval was increased from 0.5 to 6 sec.

We will therefore explore an alternative interpretation of the modification of the Filehne illusion by preceding visual inputs in the context of the inferential theory of motion perception (Wertheim, 1994). The inferential theory assumes that motion is perceived if retinal image slip differs significantly from an internal reference signal based on both, retinal and extraretinal information. What does the major finding, namely the occurance of a dramatically increased inverted Filehne illusion induced by CS moving in the direction opposite to the eyes, mean in terms of this theory? It obviously means that the reference signal must have been increased considerably thereby allowing it to override the retinal image slip signal. Obviously we have to ask if this increase of the reference signal results from an increase of its retinal component, its non-retinal component or both? Two contrary versions of the inferential theory have to be considered in an attempt to come up with an answer. The first version held by Wertheim suggests that the extraretinal component underestimates eye velocity and moreover is constant. It is supplemented by a retinal component mainly representing eye-movement induced optic flow. Within the framework of this theory it seems conceivable that the repetition of brief instances of excessive image flow by the presentation of CS might have the potential to load up the reference signal to highest values. In other words, the increased reference signals would have a retinal origin.

Conversely a non-retinal origin is suggested by the second version of the inferential theory, held by Post and Leibowitz (for review see Raymond & Shapiro, 1984; Post & Leibowitz, 1985). Unlike the Wertheim version of the inferential theory the latter version allows for a modification of the non-retinal component as well. The reason is that Post and Leibowitz suggested that the extraretinal signal is not proportional to actual eye velocity but to the central effort invested in voluntary control of eye motion. In order to account for our finding of an increased inverted Filehne illusion by conditioning visual stimulation, one would have to assume that the presentation of antagonistic CS might increase this central effort. Supporting this assumption, the analysis of eye movement showed that smooth pursuit was indeed impaired during display of CS that moved in a direction opposite to that of the eyes. The need to override a strong optokinetic stimulus may thus have caused an enlarged central command signal and thereby an enlarged reference signal. Both explanations are hypothetical and cannot be distinguished on the basis of the data available. In any case, we have to assume that the modification of the reference signal is stable for at least 6 sec, the upper intertrial interval used.

From a teleological point of view, the profound modification of the reference signal might be considered as detrimental. Would not one prefer a system using a stable reference signal, reliably cancelling any eye movement (and more generally) any self-motion induced retinal image slip in order to guarantee perceptual stability of our visual environment? Actually, a stable, non-modifiable reference signal would be rather useless towards this end. Since both the neuronal signal encoding retinal image slip and the retinal component of the reference signal depend on a number of visual parameters such as spatial frequency or luminance, only the capability to continuously re-update the size of the reference signal will warrant a good match between self-induced retinal image slip and the reference signal. Furthermore a re-updating of the reference signal might also become necessary if for instance due to aging or disease the non-retinal component should change. Therefore, rather than indicating a sloppy system subserving perceptual stability, our finding of a modification of the Filehne illusion by conditioning visual stimuli might reflect a very useful property of this system, namely the capability to continously re-update the reference signal, which under conditions more natural than the ones prevailing in our experiments will warrant perceptual stability.

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