THE LOSS OF POSITION CONSTANCY DURING PURSUIT EYE MOVEMENTS

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There is no question that there is some loss of position constancy associated with smooth eye movements. Stationary objects whose images are caused to move across the retina by these eye movements frequently occasion the perception of object motion. This phenomenon, first commented on by Filehne, has been referred to as the Filehne illusion (1922). While there is no generally accepted explanation of it, it has been taken as evidence that, unlike saccadic eye movements, smooth eye movements do not generate information which can serve as compensatory perceptual function (Dodge, 1904; Stoper, 1967, 1973). This view only makes sense, however, if the constancy loss during smooth eye movements is complete, for a less than complete loss suggests that, at least to some extent, image displacements are compensated for by smooth eye movement information.

There are only a few studies which provide quantitative data concerning the magnitude of the constancy loss during smooth eye movements, and the results from these experiments are at odds with each other. One of these was a study of the Filehne illusion (Mack and Herman, 1973). The data from that study indicated that there was only a small loss of position constancy for the background during intervals in which observers pursued a moving stimulus. A version of the nulling technique was used to determine the point of subjective stability for a large background which entirely filled the visual field. The mean point of subjective stability occurred when the background moved with the target at approximately 19% of its velocity, which is more appropriately described as an instance of underconstancy than as a complete failure of constancy.

The hypothesis tendered to account for this partial constancy loss was that it was the result of an underregistration of smooth eye movement velocity, i.e. the perceptual system has information that the eyes are travelling more slowly than their actual rate of movement. The result is that compensation for image displacements of background objects is only partial since it is limited by the under-registration of eye movement velocity.

This hypothesis gains support from the fact that a moving object appears to move more slowly when tracked than when its image paints over the retina (Aubert, 1887, 1861; Fleischl, 1882; Dichgans, Korner and Voigt, 1969; Mack and Herman, 1972, 1973). This phenomenal slowing seems clear evidence of an under-registration of smooth eye movement velocity information. A similar hypothesis has recently been offered by Yasui and Young (1975).

The only other quantitative data concerning the

extent of the constancy loss during smooth eye movements reveals a far greater loss (Stoper. 1967, 1973). These data come from two studies. The first concerned the stimulus conditions for the perception of stroboscopic motion during pursuit, while the other concerned the basis for perceived position. In the first study. Stoper (1967, 1973) adapted a technique devised by Rock and Ebenholtz (1962) to examine whether the perception of stroboscopic motion requires the stimulation of two distinct retinal or spatial points. The Rock and Ebenholtz study involved saccadic eye movements and those investigators found that stroboscopic motion required stimulation from two distinct spatial rather than of two retinal points. Stoper obtained the opposite results using smooth eye movements. In his study, two points were flashed successively while the observer pursued a moving point. Stroboscopic motion was reported only when different retinal loci were stimulated. These results suggests a gross, if not complete, loss of position constancy and are consistent with the view that there is no compensation for image displacements during pursuit.

In Stoper's (1967) other study concerned with perceived position, the subject reported whether the second of two successively flashed points appeared to the right or left of the first while tracking a moving point. Both the temporal interval and the distance between flashes were varied. The results were that, with short interstimulus intervals, the point of subjective alignment for the flashes was much closer to retinal than spatial alignment, but, as the time interval between flashes increased, the point of apparent alignment moved sharply away from retinal in the direction of spatial alignment. With an interstimulus interval of 306 msec there was a 76% mean loss of position constancy, while with a 1734-msec interstimulus interval the mean constancy loss was reduced to 36.2%.

Unlike Stoper's stroboscopic motion results. these results are not consistent with the view that there is no compensation during tracking. However, they do reveal a sharp constancy loss when the interstimulus intervals are brief, and this result does not seem easily explicable in terms of an under-registration of tracking velocity. It is apparently Stoper's view that, taken together, his data support the conclusion that there is no compensation during pursuit and therefore, no position constancy but this conclusion seems unwarranted.

If the position constancy losses curing tracking cannot be fully accounted for by the under-registration hypothesis or by the view that there simply never is any compensation for image displacements, the question arises as to what other factor or factors are responsible?

The first experiment focuses on factors which might account for the conflicting results. There are several clear differences between the methods used by Mack and Herman to study the Filehne illusion and those used by Stoper to study perceived position during pursuit which might be responsible for the discrepant outcomes. The difference which would appear most critical would seem to concern the temporal parameters controlling background exposure. Our Filehne study involved a continuously visible background and yielded only a very partial constancy loss. Stoper found that as the interval between presentation of background stimuli increased, the magnitude of the constancy loss decreased. This suggests the possibility that there is some common factor controlling or influencing the magnitude of the constancy loss which may have been affected in similar ways at the longest interstimulus interval in Stoper's study and by presenting a continuously visible background in our study. That is, it seems possible that increasing the interval between presentation of background stimuli may affect factors responsible for the constancy loss in much the same way as increasing the interval during which the background stimulus is continuously visible. If true, then exposing the background briefly but continuously should produce a large constancy loss, similar to that obtained by Stoper with a brief interstimulus interval, while exposing it for a longer period should result in a much smaller constancy loss, similar to that obtained in our study of the Filehne illusion and at Stoper's longest interstimulus intervals.1

For this reason, in the first experiment, it is the duration of background exposure which is manipulated and its apparent motion or stability assessed. In order to obtain an estimate of position constancy unconfounded by the possible tendency of a large surround to appear stationary (Duncker, 1929), a phenomenon we believe might have reduced the amount of constancy loss in our earlier study, the background stimulus in these studies was a single point marginally smaller than the tracking target and thus comparable to the background stimuli used by Stoper.

To insure the accuracy of tracking, all eye movements were monitored and recorded with a Cornsweet Double Purkinje Image tracker (Cornsweet and Crane, 1973), and only those trials in which there were no major breaks in tracking were used.

The duration of background exposure differentiates the two testing conditions. In one condition (Short Interval), the background was visible for 0.2 sec. In the other condition (Long Interval), the background was visible for 1.2 sec.

METHOD

Apparatus

The observers sat in light-tight chamber which also housed the optical section of the eye tracker and the display oscilloscope, both of which rested on a rigid table. Mounted on the table was an X, Y, Z axised milling attachment which held a head rest-bite plate combination that kept the observer's head immobilized. The oscilloscope display screen (Tektronix Model 5103 N with a fast phospor. P31) was located 35 cm in front of the observer's right eye which was the eye monitored by the eye tracker. A 0.25-in. smoked Plexiglas filter was placed in front of the screen to reduce any residual glow.

The output of the eye tracker and the function generator which controlled the motion of the display were recorded on separate channels of an oscillograph. Temporal intervals were recorded by the event markers. A second oscilloscope outside the light-tight chamber permitted the experimenter to monitor the display.

Visual display

The display consisted of the pursued target, which was a 0.5° vertical line, and the background point. The background point bisected the target when they were aligned. The target moved from left to right at a constant velocity (5° sec) over a 15° path. When the target reached the midpoint of its path (7.5°), the background stimulus appeared, aligned with the target and moved at a velocity which was varied on each trial from stationary to 5° sec in either the same or opposite direction as the target.

In the Long Interval condition, the background point remained visible for 1.2 sec. during which time the target travelled 6°. In the Short Interval condition, the background appeared at the same point but remained visible for only 0.2 sec, during which time the target travelled 1°. The order of testing conditions was counterbalanced across observers. Observers were instructed to track the target from left to right and were informed that a point would appear during the middle of the presentation. At the end of each trial, they were to report whether the point was "moving to the right, to the left, or was stationary".

The background velocity was set to 0 for the first six trials. This provided an initial measure of the illusion and gave observers an opportunity to practice tracking in the actual experimental condition. One potential subject was rejected in this period because he was unable to continue smooth tracking when the background point appeared. Following these initial trials, the direction and velocity of background motion was varied in a random double staircase design (Cornsweet, 1962) in 0.25% sec steps until the velocities that were consistently judged as motion "with" and motion "against" the target were obtained for each observer in three consecutive presentations.

In the Long Interval condition, any trial in which there was a saccade at the onset of the background, or in which there were more than two saccades during the interval when the background was visible, was rejected and immediately repeated. In the Short Interval condition, any trial in which a saccade occurred while the background was resent was rejected and immediately repeated. Trials were rarely repeated more than twice. In the Long Interval condition, 8.6° , of the trials were repeated once: 0.5° , were

¹ It should be noted that there is another major difference between the Stoper and Mack and Herman study: Stoper's study involving varying interstimulus intervals concerned the perceived position of background stimuli. while the Mack and Herman study concerned the perceived motion of the background. While this is an important difference, it does not seem the one most likely to account for the discrepant results. Primarily this seems true because of Stoper's stroboscopic motion study, where the dependent variable was apparent motion and the data, like that from the brief interstimulus interval condition in the experiment on perceived position, suggest no compensation. In the current work, we continued to examine perceived motion and stability rather than perceived position. since it is the apparent motion or stability of objects whose images are caused to move over the retina by movements of the observer which defines position constancy.

repeated twice and none were repeated more than twice. In the Short Interval condition, 8.9% of the trials were repeated once; 3.4% were repeated twice and 1.9% were repeated more than twice.

To insure that differences in the apparent motion of the background were due to the character of the display and were not the effect of different rates of eye movement, it was necessary to calculate eye movement velocity. The mean rate of eye movement was computed from the last 10 trials for each observer. The rate of tracking with no background present was computed for the last 0.2-sec interval that was free of saccades prior to the onset of the background. The rate of tracking with the background present was computed from the 0.2-sec interval in which the background was present in the short interval condition and was the mean of three saccade-free 0.2-sec intervals; the first 0.2-sec interval, the last 0.2-sec interval, and a 0.2-sec interval in the center of the total interval in which the background was present in the Long Interval condition.

Six paid observers with 20/20 vision were recruited from the New School student population.

RESULTS

The mean rate of eye movement in the Long Interval condition during background exposure was 4.26° /sec or 87% of that with no background present (4.88° /sec). In the Short Interval condition, the mean rate of eye movement during background exposure was 4.85° /sec or 98% of that with no background present (4.95° /sec). The similarity in eye movement velocities rules out the possibility of accounting for differences in the strength of the illusion in terms of gross differences in eye movement rate.

In the initial presentation with the background stationary, the Filehne illusion occurred 61% of the time in the Long Interval and 58% of the time in the Short Interval condition.

The mean background velocity judged stationary in the Long Interval condition was 0.96° /sec $(t_5 = 2.381, P < 0.05)$ in the same direction as the target, while in the Short Interval condition it was 3.35° /sec $(t_5 = 4.022, P < 0.01)$ in the same direction as the target. These figures represent a 19 and a 67°_{0} loss of constancy, respectively. The mean difference between conditions is 2.40° /sec $(t_5 = 4.792, P < 0.005)$. (See Table 1 for a summary of this data.)

The probability of a veridical response in saccadefree trials was 0.43 while the probability of a correct response in trials in which a saccade occurred was 0.40. Thus the differences between conditions cannot be attributed to the difference in the quality of tracking.

DISCUSSION

The finding of a larger loss of constancy in the Short as compared to the Long Interval condition suggests that duration of background visibility is, in fact, a critical factor influencing the magnitude of the

Table 1. Mean loss of constancy in Experiments 1. II and III expressed in \sqrt{sec} and \sqrt{a}_{o}

Experiment	/sec	0 V
1	<u></u>	
Long Interval	0.96	19
Short Interval	3.35	67
II (invisible target)	0.79	16*-26+
III (3 sec)	2.23	74

Table 2. Median loss of constancy in Experiments I. II and III expressed in /sec and °,

Experiment	/sec	0 0
[<u> </u>
Long Interval	1.00	20
Short Interval	3.95	79
[] (invisible target)	0.44	9*-15+
111 (3 /sec)	2.35	78

* Based on 5 sec.

+ Based on 3 sec.

constancy loss. The most obvious next question is: why should this be? A possible answer is that, during tracking, when the image of an untracked "background" object falls close to the image of the tracked object (Short Interval condition), the perception of the untracked object may be determined by its position or displacement relative to the tracked one, i.e. perception of it may be determined by object-relative information. This is consistent with the perceptual principle of adjacency which states that. "the effectiveness of cues bettween objects is an inverse function of object separation" (Gogel, 1974, p. 425).² Thus when background object and target are adjacent. object-relative displacement of position may be perceptually salient and may determine the perception of background movement or position. When this happens, the result is a major loss of position constancy, virtually indistinguishable from that which would be caused by a complete absence of compensatory eye movement information. As the separation between background object and tracking target increases (Long Interval condition), the salience of object-relative displacement also decreases, with the result that the perception of the background becomes more a function of the relationship between the position or movement of its retinal image and eye position or eye movement information. The percept is now determined by subject- rather than object-relative information. When this occurs, the position constancy loss is much less since the registered eye movement is only partially unable to account for the eve movement produced image displacements.³

This explanation is at least congruent with the results of Experiment I, since, in the Short Interval condition, the background and tracking target were never separated by more than 2° , whereas in the Long Interval condition, the maximum separation between background and target was 12° . However, because the initial 0.2 sec of background exposure in the two conditions are identical, it is necessary to assume that judgements in the Long Interval condition are at least partially based on the final moments of the tracking trial.

² Most relevant is Gogel's finding that this principle operates in induced motion (1974).

³ Bridgeman (1972) presents evidence that neurons in the visual cortex of awake monkeys are differentially sensitive to object and subject-relative motion. This would provide a neuronal basis for this distinction between subject- and object-relative motion cogently stressed by Wallach (1968).

This analysis also provides a possible explanation for the increase in position constancy reported by Stoper as the interval between the stimuli whose position was to be judged increases, as well as an alternative explanation for the results of his stroboscopic motion experiment. The increase in position constancy in the experiment on perceived position could reflect the decreasing salience of object-relative position as a determinant of perceived position, since, as the interstimulus interval increased, so did the separation between the stimulus whose position was to be judged and the tracking target. This should have had the effect of reducing the tendency to perceive its position relative to the tracking target, thereby increasing the amount of position constancy. The sharp losses of constancy obtained with the short interstimulus intervals could be attributed to the fact that, in these conditions, flashed and tracked stimuli were always adjacent, their separation did not exceed 3. so that the position of the judged stimulus was likely to have been determined by its position relative to the tracking stimulus.

In Stoper's stroboscopic motion experiment when the inducing stimului were flashed in the same retinal (different physical) positions, their images both fell about 0.2° to the right of the image of the tracking stimulus. If, because of this substantial adjacency amounting almost to superposition, the position or motion of the flashed stimuli is determined by position or displacement relative to the tracking stimulus. one would predict no change in perceived position and no reports of motion since position relative to the tracking stimulus was identical. There were no motion reports in this condition. When inducing stimuli were flashed in the same physical location (different retinal locations), the two stimuli had different positions relative to the tracking stimulus which, given stimulus adjacency, is the condition in which motion or a change in position should be perceived. and it was. Even more to the point is Stoper's finding that, in this condition, stroboscopic motion was reported only when the two inducing flashes were separated by a visual angle not greater than about 2, which meant that the first flash fell 0.2 to the right of the tracking stimulus and the second fell 1.8° to its left. When the retinal separation was greater. and therefore the distance of the image of the second flash from the tracking image was greater. no stroboscopic motion was reported, which is consistent with

⁵ Stoper (1973) has argued that this is the basis for the reported difference in results.

the principle of adjacency that governs the effectiveness of image relations in determining perception.⁴

Alternatively, the difference between the results of the two conditions of Experiment I could be attributed to the difference between the foveal and parafoveal motion thresholds. The threshold for motion detection is lower for the fovea than for the periphery (Leibowitz, Johnson and Isabelle, 1972).

The results of the Long Interval condition are consistent with the under-registration hypothesis, since the constancy loss was small and could have been a function of under-registered eye movement velocity when object-relative displacement was no longer perceptually dominant. Data from Experiment IV supports this inference.

Since the results of this condition are comparable to those found earlier by Mack and Herman (1973), they confirm the fact that the difference between those results and Stoper's (1967) showing a much larger loss of constancy cannot be attributed to the size of the backgrounds employed in these studies.⁵ since, in both the Long and Short Interval conditions, the background stimulus was small and comparable in size to the background stimulus used by Stoper, and yet there was a significant difference in the magnitude of the position constancy loss between these conditions.

The fact that reports of the Filehne illusion, the perception of background motion during pursuit when the background is actually stationary, were twice as frequent in both conditions of this experiment compared to the Mack and Herman's (1973) results (60°_{0} vs 30°_{0}) supports the hypothesis that a large background viewed during pursuit will tend to be perceived as stationary, and so will reduce the Filehne illusion.

Experiments II and III examine the possibility that peripheral/foveal motion detection differences might be responsible for the results of Experiment I, and explore the influence of object-relative displacement on the perception of the background during tracking. This is accomplished with two conditions which are identical with respect to the retinal locations and duration of exposure of the background stimulus and differ only with respect to whether or not there is relative displacement between target and background. If we are correct in attributing the large loss of position constancy in the Short Interval condition of the first experiment to the displacement of the background relative to the tracking stimulus because the two were always contiguous, then duplicating that condition while eliminating relative displacement should vield a much smaller loss of constancy comparable to that obtained in the Long Interval condition. Obtaining such results would not only support the credibility of the relative displacement explanation of the large constancy losses during tracking. but would also rule out the possibility that the differences between the two conditions were the result of foveal peripheral threshold differences. These results would also lend support to the under-registration hypothesis, since, if there is a constancy loss and it is small when relative displacement is eliminated, it seems likely that it is the result of the partial inadequacy of smooth eye movement information. This hypothesis is tested in Experiment IV.

⁴ This analysis does not, however, appear to account for the small constancy loss found by Mack and Herman (1973), since in that experiment some part of the background was always adjacent to the tracking target and according to this explanation, at least that part of the background should always have appeared to move and did not. The reason for this we argue, is not that the object-relative displacement explanation is wrong, but rather that when the background is large relative to the tracking target, it becomes the perceptual frame of reference and as a result tends to be perceived as stationary (Duncker, 1929). This tendency for a large surround to appear stationary counteracts the localized displacement between part of the background and tracking target which then results in a very reduced loss of position constancy.



Fig. 1. Sample records of good tracking: Experiment II.

EXPERIMENT II

Experiment II is a modified replication of the Short Interval condition of the first experiment. The tracking target was replaced by an "invisible" target during the 0.2-sec interval in which the background point was visible. Since the background was visible only when the tracking target was not. relative displacement between the two was completely eliminated. An "invisibile target" was created by training observers to track a visible target which disappeared for an interval. They were trained to continue to track during this blank interval. The learning was facilitated by the tendency to continue to smooth track for a brief period (approx 0.2 sec) after a tracked moving target disappears. With practice, observers were able to lengthen this interval to over 0.5 sec. In order to participate, an observer had to be able to smooth track with no saccades during the target blanking interval. (One potential observer was not able to reach this criterion and was rejected.)

METHOD

Apparatus and visual display

The apparatus and visual display were essentially the same as that used in the Short Interval condition of Ex-

periment I, except that the target was not visible during the interval in which the background was present. The target disappeared 0.2 sec before the onset of the background and reappeared 0.1 sec after its offset. Thus the display consisted of the target moving 5 /sec from left to right for 1.3 sec over a 6.5 path, followed by a blank field for 0.2 sec. Then the background point appeared 1 to the right of the spot where the target had disappeared and remained visible for 0.2 sec. The background then disappeared leaving a blank screen for an additional 0.1 sec. followed by the reappearance of the target which then travelled 6² before disappearing.

Observers

Six naïve paid observers with 20/20 vision were recruited from the New School student population.

EXPERIMENT III

Examination of eye movement records in Experiment II revealed that the mean rate of tracking fell to 3.02° /sec when the target was not visible, or to 59% of the tracking rate when the tracking target was visible $(5.12^{\circ}/\text{sec})$. (See Figs. 1 and 2 for sample eye movement records.) Therefore, any difference in the strength of the illusions found in the Short Interval condition of Experiment I and in Experiment II



could have resulted from the different rates of eye movement as well as from the presence or absence of a visible tracking target while the b-ckground was present. In order to secure a condition which differed from Experiment II only in terms of the presence of the target during the exposure of the background, Experiment III was run as a replication of the Short Interval of Experiment I using a 3% sec target.

The same observers were used as in Experiment II

Procedure

The procedure was identical to the Short Interval condition of Experiment 1 with the following exceptions. The target was moving at 3° sec instead of 5° sec. In order to obtain a background exposure during 1° of target travel, the temporal interval during which the background was visible was lengthened to 0.33 from 0.2 sec. to compensate for the reduced target velocity.

RESULTS

In Experiment III (visible target), the mean rate of eye movement during the interval in which the background was present was 3.10° /sec, or only 3°_{00} greater than in Experiment II (3.02° /sec, invisible target); therefore, any differences in the magnitude of the illusions cannot be attributed to gross differences in the eye movement rates.

In the initial presentation with the background stationary, the Filehne illusion occurred 67% of the time in Experiments II and 81% of the time in Experiment III. In Experiment II, the background was judged to be stationary when it was moving at a mean rate of 0.79° /sec with the target ($t_5 = 2.039$, P < 0.05). This is a 26% loss of constancy with regard to 3% sec eye movement. Although the mean eye movement rate when the background was present in Experiment II was 3.02° /sec, it is possible that the drop in eye movement velocity was the result of the presence of the background in an otherwise blank field, and that the registered velocity was based on the eye movement velocity during the totally blank interval. If this were the case, the constancy loss would be more approprionately computed with regard to 5°/sec eye movement (16%). The background was judged to be stationary in Experiment III when it was moving at a mean rate of 2.23°/sec with the target, a 74% loss of constancy ($t_5 = 7.228$, P < 0.001). The difference between the constancy loss in Experiments II and III, 1.44° /sec, is significant ($t_5 = 3.952$, P < 0.01).

An examination of individual data from Experiment II reveals a skewed distribution caused by an extreme score from one observer. The mean value of these scores was 0.79° /sec, whereas the median value was 0.44° /sec. Since the value of the mean was increased by this one extreme score, it is possible that the significance of the loss of constancey may be artifactual. A binomial test, which is less affected by a single extreme score, confirmed that the loss of constancy when relative displacement is eliminated is significant.

Because the distribution of scores was skewed, the median becomes a better descriptive statistic tan the mean. (In all other conditions there was little difference between means and medians.) Consequently, all further comparison with the results of Experiment II are made with nonparametric statistics. Table 1 presents a summary of the results from all experiments stated both in terms of means and medians.

DISCUSSION

These results support a relative displacement explanation of the large constancy losses found in the Short Interval condition of Experiment I and in Experiment III. In both cases, the tracking target was present and contiguous to the background and the constancy losses were large. However, when relative displacement is eliminated, as it is in Experiment II. there is a sharp reduction in the loss of constancy, despite the fact that these conditions are comparable in all other respects. Because the constancy losses in Experiment II and in the Long Interval condition of Experiment I are of comparable magnitude, it suggests that they probably have a similar cause and that is the under-registration of smooth eve movement velocity. On the strength of these findings, it also seems possible to argue that Stoper's results can be explained in these terms.

There is an alternative explanation for the results of Experiments II and III, which should be considered. It is, at least at first glance, conceivable that the difference in the magnitude of the constancy loss merely reflects the well-documented difference between the subject- and object-relative motion detection thresholds (e.g. Shaffer and Wallach, 1966). Since the subject-relative threshold, which is based solely on absolute retinal image displacement, is known to be considerably higher than the object-relative threshold, which is based on relative-retinal displacement, the smaller loss of constancy in Experiment II (all object-relative displacement eliminated) might simply be another instance of the higher detection threshold for subject-relative motion. Were this the case, the results would provide no evidence of compensation. Careful consideration of this possible explanation, however, leads to its rejection.

If this explanation is to account for the data the following must be true. Motion of the background stimulus in the direction opposite to the pursuit eye movement should generally be reported, since motion of the stimulus in that direction increases its retinal velocity. It is. A physically stationary stimulus which displaces on the retina at the rate of the eye movement (approx 3[°]/sec) should appear to move in the direction opposite to the eye motion for at least some of the time, since a retinal image displacement in that direction of about 3³ sec should be at or above the subject-relative detection threshold. The stationary target is in fact perceived to move against the eye on 67% of the trials, a fact consistent with this explanation. The probability of veridically reporting stimulus motion in the direction of the eye motion should decrease as the rate of motion in that direction increases, since increasing velocity in that direction decreases retinal velocity or retinal displacement. In fact, the point of subjective stability should be located at the velocity of background motion in the direction of the eye motion which is just below the subject-relative threshold, and all stimulus motion in that direction which is faster cannot be detected. This was distinctly not found. The point of subjective stability

occurred when the background moved with the eye at a mean velocity of 0.79° /sec. All motion in that direction faster than 0.79° /sec was consistently reported correctly. Thus as the retinal velocity decreased from about 2.2° /sec (eye movement minus stimulus movement), the subjects correctly reported the stimulus motion. (Since the direction of retinal motion was always opposite the eye movement, this explanation also demands that motion in the direction of the eye motion should never be reported accurately and it was.) On these grounds, then, this explanation of the results of Experiments II and III must be rejected.

Given the cogency of this argument, the explanation we have offered becomes more attractive. Ultimately, however, the validity of the under-registration hypotheses as an explanation for the loss of position constancy on the Long Interval condition of Experiment I and in Experiment II rests on showing that the degree to which a stimulus moving at 5[°]/sec is phenomenally slowed by pursuit is approximately equal to the degree to which position constancy is lost in these two experiments.⁶ It will be remembered that we assumed that the phenomenal slowing of a tracked target represents the under-registration of smooth eye movement velocity information. Experiment IV examines this question.

EXPERIMENT IV

Method

Visual display. The visual display consisted of a target, a 0.5° vertical line which travelled over a 15° horizontal path, and a fixation point at the center of the path of the target. Although only one target was visible at a time, two targets were actually used, a standard target which moved at a constant rate of 5° /sec, and a second target (target 2) which could be set to move at a velocity varying from 2 to 8° /sec.

Each trial began with target 1 at the left of the field and the fixation point visible. The fixation point then disappeared and target 1 began to move. When target 1 reached the end of its path, it jumped back to the start position, was eliminated and replaced by target 2, the fixation point was again visible, and target 2 traveled across the field at a present velocity.

Procedure. In the experimental condition which provides a measure of the apparent velocity of a tracked target moving in a blank field, observers were instructed to fixate

⁶ We did not examine the phenomenal slowing of a pursued target travelling at 3^{2} /sec since in an earlier experiment, using a different testing procedure, we examined this phenomenon with a target speed of 3.5^{2} sec. Data from that earlier experiment suggested that we would not be likely to find differences between a 5 and a 3²/sec target speed (Mack and Herman, 1973).

It is doubtful that the amount of drift had a great effect on the results, since a Kendel r test for rank order of the mean amount of drift and the mean amount of underestimation of target velocity for each observer proved not to be significant. (r = 0.18, s = 5, P = 0.138). This supposition is supported further by the fact that the two subjects showing the least amount of drift, 0.1 and 0.08 had mean underestimations of velocity of 0.75 and 0.28⁺/sec, respectively, and the mean of these two subjects (0.51⁺/sec) is no different from the mean underestimation of all eight subjects. Finally, the subject with the greatest mean drifts. 0.97⁺/sec showed a mean underestimation of only 0.46 /sec. the fixation point, and then to shift fixation to the target (1), ignore the fixation point, and to follow target 1 when it started to move. When the target returned to the start position, observers fixated the central fixation point when it reappeared and maintained fixation while target 2 transversed the field. After target 2 returned to the start position, the observer reported whether it appeared faster or slower than target 1.

The procedure for the control condition, which provides a measure of the apparent velocity of the same target in the same field when the eye is fixating an imaginary point rather than tracking the target, was exactly the same, except that the observers were instructed to fixate the central fixation point and to maintain fixation where the fixation point had been after it disappeared and not to track target 1 while it traversed the field.

The velocity of target 2 was varied in 0.25 /sec steps on successive trials in either an ascending or descending order until the observer reported that target 2 appeared to be faster than target 1 on three consecutive ascending trials. or slower on three consecutive descending trials. Then the order was reversed. Each observer received four ascending and four descending series in both conditions and the conditions were counter-balanced. Eight observers were tested.

RESULTS

The overall mean velocity estimate during fixation is 4.53³/sec, or 9% less than the target was actually travelling, while the overall mean velocity estimate during tracking is 4.08⁵/sec, or 18% less than the target was actually travelling. The median difference in velocity between fixating and tracking is 0.46⁵/sec. The mean difference is 0.45⁵/sec ($t_7 = 4.044$, P < 0.005), which represents a 10% underestimation relative to the apparent velocity of the untracked target.

Eye movement records reveal that the mean rate of eye movement in the tracking condition was 4.92°/sec, while the mean rate of drift when the observer was fixating an imaginary point was 0.42°/sec in the direction that the target was travelling.⁷ Drift occurred in 82 of the 128 trials sampled and was absent in the remaining 46 trials. The direction of drift, when it occurred, was almost exclusively in the direction which the target was travelling. On only one trial was there drift in the opposite direction.

DISCUSSION

The finding of an underestimation of the velocity of a tracked target in an otherwise blank field compared to the perceived velocity of the target when the observer was fixating an imaginary stationary point provides further supporting evidence of the under-registration hypothesis. The median underestimation found was 0.46° /sec or 10% less than the perceived velocity during fixation, which is virtually equal to the median loss of constancy found in Experiment II.

The close correspondence between the amount of constancy loss of the background when the observer is tracking in the absence of a visual target (Experiment II) (no relative displacement), and the amount of the underestimation of the velocity of a tracked target (Experiment IV) supports the hypothesis that smooth eye movement information is used to compute motion and stability but is under-registered, producing the small loss of constancy.

CONCLUSION

The results of these experiments appear to suggest that there may be two factors responsible for the position constancy losses during pursuit. The first is the under-registration of velocity. It accounts for the loss of constancy when the perception of background objects is determined by the relationship between eye movement and image movement information. (This is a rather standard account of perceptual underconstancy. For example, the underconstancy of size is generally attributed to inadequate distance information.) The second factor is the displacement of the background relative to the tracked target, when the background and target are adjacent, which may account for the very substantial losses of constancy which can occur during smooth pursuit. The failure to make the distinction between object-relational (exocentric) cues to motion and eye movement-retinal image displacement information (egocentric) may therefore lead to the erroneous conclusion that smooth eye movement information is not involved in the perception of the motion and stability of the background.

The fact that when there is a conflict between the object and subject relative percepts of the background, the object-relative percept, because of stimulus adjacency is salient, is not at all surprising. It is consistent with many other perceptual events. It is generally the case that under circumstances in which an object-relative percept is likely, and is in conflict with a subject-relative one, the object-relative percept will suppress the subject-relative one. To cite only two familiar examples: one is the induced motion of a small stationary object produced by a larger surrounding object which is moving. The enclosed object is predictably perceived to move by virtue of its displacement relative to its surround despite the fact that it does not displace relative to the subject and the subject-relative percept is the veridical one. The other familiar example is the rod and frame phenomenon. A spatially vertical rod may appear tilted when it is enclosed in a tilted rectangular frame. If it does, it is by virtue of its orientation relative to its visual frame and not by virtue of its orientation with respect to the self, information about which is certainly available to the perceptual system and if used would result in a veridical percept.

A clear advantage then of the explanation of the position constancy loss during smooth eye movements offered here, is that it makes perception during pursuit no exception to what we know about perception in general. Were it the case that the perception of the background objects during pursuit were strictly determined by the activity of their retinal images, it would be a clear anomaly. Only under very reduced stimulus conditions is perception generally determined solely by proximal information. Acknowledgements—This research was supported by grant GB 38670 from NSF and Ey 01135 from NIH. It was E. Herman's doctoral thesis research. We are grateful to Dr. Melvin Komoda for his advice and assistance.

REFERENCES

- Aubert H. (1887) Die Bewegungsempfindungen. Pflügers Arch. ges. Physiol. 40, 459-480.
- Aubert H. (1861) Eine scheinbare bedeutende Drehung von Objekten bei Neigung des Kopfes nach rechts oder links. Virchow's Arch. path. Anat. Physiol. 26, 381-393.
- Bridgman B. (1972) Visual receptive fields sensitive to absolute and relative motion during tracking. Science 118, 1106-1108.
- Cornsweet T. (1962) The staircase method in psychophysics. Am. J. Psychol 75, 485-491.
- Cornsweet T. and Crane H. (1973) Accurate two-dimensional eye tracker using first and fourth Purkinje images. J. opt. Soc. Am. 63, 921-928.
- Dichgans J., Korner F. and Voigt K. (1969) Comparative scaling of afferent and efferent motion detection in man: linear function with different slopes. *Psychol. Forsch.* 32, 377-395.
- Dodge R. (1904) The participation of eye movements in the visual perception of motion. *Psychol. Rev.* 11, 1-14.
- Duncker K. (1929) Über induzierte Bewegung. Psychol. Forsch. 12, 180-259.
- Filehne W. (1922) Ueber das optische Wahrnehmen von Bewegungen. Z. Sinnesphysiol. 53, 134-145.
- Fleischl E. V. (1882) Physiologisch-optische Notizen. Sitzungsber. k. Akad. Wiss. Wien 86, 17-25.
- Gogel W. C. (1974) Relative motion and the adjacency principle. Q. Jl exp. Psychol. 26, 425-437.
- Leibowitz H. W., Johnson C. A. and Isabelle E. (1972) Peripheral motion and detection and refractive error. Science 177, 1207-1208.
- Mack A. and Herman E. (1973) Position constancy during pursuit eye movements: an investigation of the Filehne illusion. Q. Jl exp. Psychol. 25, 71-84.
- Mack A. and Herman E. (1972) A new illusion: the underestimation of distance during pursuit eye movements. *Percept. Psychophys.* 12, 471-473.
- Rock I. and Ebenholtz S. C. (1962) Stroboscopic movement based on change of phenomenal location rather than retinal location. Am. J. Psychol. 75, 193-207.
- Shaffer O. and Wallach H. (1966) Extent-of-motion thresholds under subject-relative and objective-relative conditions. Percept. Psychophys. 1, 446-451.
- Stoper A. (1967) Vision during pursuit eye movements: the role of oculomotor information. Unpublished doctoral dissertation, Brandeis University.
- Stoper A. (1973) Apparent motion of stimuli presented stroboscopically during pursuit eye movements. Percept. Psychophys. 7, 201-211.
- Wallach H. (1968) Informational discrepancy as a basis of perceptual adaptation. In *The Neuropsychology of Spatially Orientated Behavior* (Edited by Treedman S.). Dorsey Press, Illinois.
- Yasui S. and Young L. (1975) Perceived visual motion as effective stimulus to pursuit eye movement system. *Science* 190, 906–908.