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IS PERCEIVED MOTION A STIMULUS FOR SMOOTH PURSUIT*

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Abstract—Previous investigations have challenged the generality of the claim that perceived motion is an effective stimulus for smooth pursuit eye movements. The experiments extend the scope of these investigations. Three experiments test the hypothesis that perceived motion can serve as the stimulus for pursuit when the eye movement does not generate constraining retinal error information. Observers viewed retinally stabilized displays that elicited the perception that a stationary target was moving or that a moving target was moving faster than it was actually moving. The results failed to confirm the hypothesis. Relevant literature is reviewed. We conclude that perceived movement can act as a stimulus for pursuit only when the "perceptual target" has no retinal counterpart.

INTRODUCTION

We normally direct our gaze to objects in our visual fields which interest us and, if the object we choose to look at happens to be moving, looking at it typically will involve smooth pursuit eye movements. There is no reason to doubt that our perceptions play some role in determining which, among the many objects present, we will look at, if only because looking at something presupposes an awareness that it is there to be looked at. It is not so obvious, however, what role, if any, our perceptions of an object's location or motion play in determining exactly how our eyes will move. This is the question which our research has attempted to answer. The work to be reported concerns only smooth pursuit eye movements and addresses the question of whether our perception of an object's motion as distinct from its retinal image motion, influences or determines how our eyes will track it.

The traditionally accepted view of smooth pursuit has been that it is the oculomotor response to a moving object of interest and serves to maintain its image on or near the fovea. Retinal image motion is taken to be the primary stimulus for smooth pursuit. Recently, however, this view has been called into question by accumulating evidence which appears to suggest that perceived rather than retinal motion is *a* or *the* critical determinant of pursuit eye movements. This evidence includes the following findings. The eye appears to engage in smooth pursuit when stimulated by a stabilized image (Robinson, 1965; Kommerell and Täumer, 1972; Yasui and Young, 1975). Under open-loop testing conditions, when a visual display induces the perception that the amplitude of target motion is greater than actual target motion, the amplitude or gain of smooth pursuit is enhanced (Wyatt and Pola, 1979). Moving cyclopean contours elicit opokinetic nystagmus (OKN) which has a slow drift component (Fox *et al.*, 1978). The slow drift component of OKN is phase locked to the perceived direction of motion in the presence of a reversible motion stimulus (Leguire and Fox, 1978; Ter Braak, 1962). Pursuit is elicited by a discretely displacing, intermittently illuminated target which also elicits apparent movement (Young, 1977; Morgan and Turnbull, 1978). Tracking can be sustained in the absence of any actual target motion when the visual display is such that the tracking itself generates the perception of motion (Lamontagne, 1973; Heywood, 1973; Ward and Morgan, 1978). Finally a moving form which has no retinal counterpart can be tracked (Steinbach, 1976).

This set of evidence has been used to support some version of the view that perceived and not retinal motion is a principle stimulus for pursuit (see for example: Heywood, 1973; Yasui and Young, 1975; Steinbach, 1976, for explicit statements of this view). This is a sharp departure from the earlier view of pursuit. However, this more recent view is itself placed in question by data we recently reported elsewhere (Mack *et al.*, 1979). We found that the eye accurately tracks a stimulus whose motion is *not* perceived because it moves too slowly for its motion to be detected. Furthermore, we found that the eye fails to track a stationary stimulus which appears to move, and tracks the actual retinal motion of a stimulus which appears to move in the opposite direction. Contrary to the view which now ascribes great weight to perceived motion in driving pursuit, these data would appear to suggest not only that perceived motion is not necessary for pursuit, but also that retinal and not perceived motion determines pursuit when the two are in conflict. The apparent discrepancy between these results and those which point to

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the primacy of perceived motion as a stimulus for pursuit presents a problem which the research to be reported attempts to resolve.

Normally the perception of an object's motion is accompanied by an appropriate motion of its image on the retina. There is, therefore, no way of knowing what part each factor plays in the control of pursuit. It is necessary to create conditions in which these two possible sources of oculomotor stimulation are discrepant, if we are to assess their relative contributions to the control of smooth pursuit. For this reason, the stimulus testing conditions to be described all involved a conflict between retinal image motion and perceived motion.

The first experiments were designed to test the hypothesis that our previous failure to find any influence of perceived motion on smooth pursuit was due to the constraining effect of retinal error information. It seemed possible that the capacity of perceived motion to serve as a stimulus for pursuit might be limited to situations in which pursuit eye movements do not cause the image of the apparently moving target to slip away from the fovea of the eye in an inappropriate direction. In each of our previous testing conditions when retinal image and perceived motion were in conflict, any pursuit of the apparent target motion would have done just that. This was not the case in the stimulus conditions examined by other investigators.

To briefly review some of our prior findings: in one instance we induced the appearance of motion in a stationary target by slowly moving a surrounding visual frame which caused an enclosed target to appear to move in the opposite direction. The eye remained fixed on the target and there was no evidence of pursuit. In another condition both target and frame were moved in the same direction but the frame moved faster than the target, causing the target to appear to move opposite the frame, i.e. opposite its actual direction of motion. The eye accurately tracked the retinal motion of the target. These are, of course, both instances of induced motion (Duncker, 1929). In both conditions pursuit of the perceived motion would have displaced the fovea away from the target and, if pursuit serves to stabilize the image of a moving object on the fovea, then pursuit under these conditions would have been counterproductive, at best. This, then, might explain why the perceived motion failed to elicit tracking. However, even if this reasoning is correct, and the results which we are about to report suggest it is not, it should be noted that these data establish restraints on the view that perceived motion is the primary stimulus for pursuit.

To assess the hypothesis that the capacity of perceived motion to influence pursuit is restricted to situations in which pursuit does not produce inappropriate retinal error information, we examined tracking using retinally stabilized visual displays which created the impression that a stationary target was moving. Stabilizing the displays served to eliminate all retinal error information that would have been generated by pursuit under normal, closed-loop conditions, and thus, if the hypothesis is correct, should free the eye to follow the perceived target motion. We examined pursuit in two different situations both of which involved the requisite discrepancy between perceived and retinal motion. In one instance, the discrepancy was created by inducing motion in a stationary stimulus, while in the other it was created by a motion aftereffect (MAE) which resulted in the perception that a set of stationary contours was moving.

In both experiments the stimulus patterns were presented on a fast phosphor CRT (p-15) by means of a multiplexer and were controlled by function generators and TTL logic. A neutral density filter placed in front of the display screen eliminated any residual screen glow. The experimenters monitored the display on a matched CRT screen outside of the testing chamber. Eye movements were monitored by an SRI Double Purkinje Image Eye tracker (Cornsweet and Crane, 1973) which has a resolution of less than 2′ and a bandwidth of approx. 200 Hz. Eye movements were recorded on a strip chart recorder (bandwidth 100 Hz). The subjects viewed the display in complete darkness while seated 61 cm from the oscilloscope screen. Head position was maintained by a dental impression bite plate. Horizontal image stabilization was accomplished by feeding the output of the eye tracker into the multiplexer channel displaying the stabilized visual elements. A calibration procedure preceded each testing session and involved the following procedure: the calibration of horizontal stabilization was accomplished by having the subject saccade between 3 points; one center, one 2° to the left and one 2° to the right of center. A point corresponding to the target to be stabilized was visible to the experimenters but not to the subject. The eye-tracker gain and offset controls were adjusted so that successive fixations resulted in a superimposition of the stabilized point on the points being fixated. (Subsequent to this, the stabilized point was made visible to the subject on an otherwise dark CRT screen. If the S's eye tended to slew rapidly either left or right, it was taken as evidence of a small remaining eccentricity of the stabilized target on the fovea, and this tendency was nulled by a small adjustment of the tracker offset control.) Stabilization was checked periodically during the testing of each observer. Although we had no independent measure of the quality of stabilization, a recent report (Kelly, 1979), attests to the capability of the Purkinje Image tracker to produce stabilization of high quality.

EXPERIMENT 1 (INDUCED MOTION DISPLAY)

The target stimulus was a small light point centered within a frame of four additional points which formed a surrounding rectangle 0.5° high and 3° wide. At the

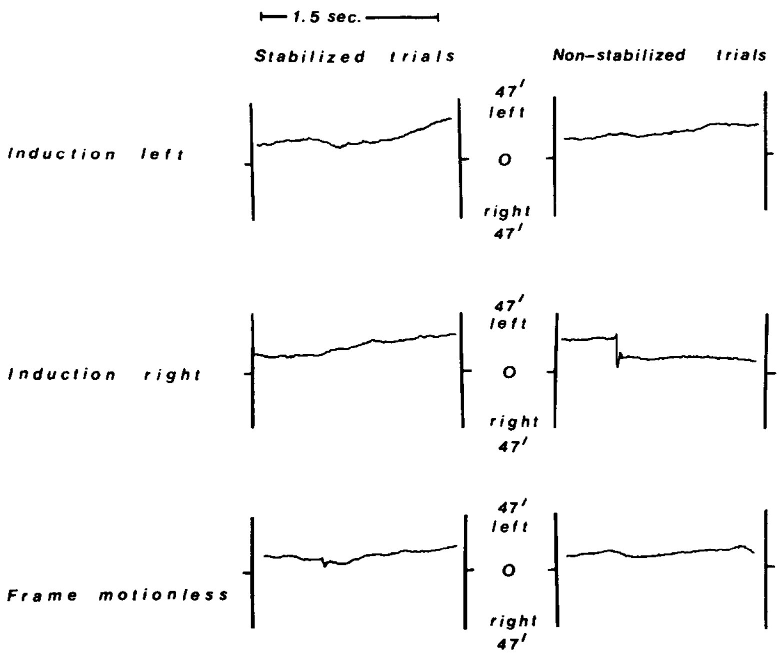

Fig. 1. Eye movement records from Experiment 1. Frame moves 30′/sec in the induction conditions. Target is motionless in all conditions.

onset of every trial the target was at the center of the frame and during a motion trial the frame points moved either leftward or rightward at 30′/sec for 1.5 sec. This quite consistently induced the appearance of counterphase motion in the target. There were two principle testing conditions, one in which the entire visual display was horizontally stabilized and one in which it was not. There were 20 motion trials in each condition; 10 trials of rightward and 10 of leftward frame motion, as well as five no-motion trials in which the display remained stationary. All 50 of these trials were presented in a predetermined, randomized order.

A trial began with instruction to the observer to fixate the target stimulus which was all that was visible. When the eye tracker indicated fixation, the CRT screen became dark and 100 msec later the induction display appeared either stabilized or non-stabilized. Observers were asked to track the fixation target if it appeared to move and to report the direction of its motion at the end of each 1.5 sec trial. These reports were recorded and were analyzed in conjunction with the eye records. Only data from trials in which induced motion was reported were analyzed.

Five observers participated in this experiment, all of whom had normal uncorrected vision.

Results

Induced motion was reported on 100% of all motion trials.

Figure 1 represents sample eye records from one observer from each of the several testing conditions. These are representative of the eye movement records obtained from all subjects. Inspection of these records clearly reveal no marked differences in the eye movement responses across conditions. Regardless of whether the display was stabilized or not, or whether the target appeared to move right or left, the eye responded in a similar manner. There is thus no evidence that image stabilization freed the eye to follow the perceived motion of the target.

Table 1 presents the mean magnitude of smooth eye displacement for all observers. This was computed by subtracting the saccadic component from the total displacement of the eye on each trial. Individual subject data consistently reflected the patterns evident in the across subject findings. (A similar procedure was used in calculating the mean magnitude of smooth eye displacement in all subsequent experiments.) While these figures show a tendency for the eye to

Table 1. Data summary for experiment 1: mean smooth eye displacement for stabilized and non-stabilized trials in the induction and no-induction conditions

	Stabilized	Non stabilized
Frame moves right		
Induction left	−11.88	−3.83
Frame moves left		
Induction right	−13.63	−0.71
Frame motionless		
No induction	−19.62	−5.14

A (+) indicates eye motion to the right; a (−) indicates eye motion to the left. All entries are in min of arc.

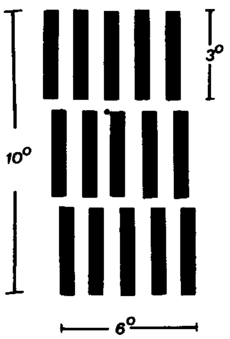

Fig. 2. Stimulus display for Experiment 2. The center set of bars serve as the adapting and test stimulus. Spatial frequency of the grating is 0.7 c/deg. The adapting grating moved left or right at 2 Hz. The black dot indicates the stationary fixation target.

drift leftward on all stabilized trials, there is certainly no evidence that the eye pursued the perceived target motion. Results from the non-stabilized trials reproduce our earlier findings (Mack *et al.*, 1979), that under closed-loop conditions perceived target motion uncoupled from retinal image motion fails to elicit smooth pursuit. The results of this experiment thus failed to provide any support for our preliminary hypothesis and demonstrate that at least under the present testing conditions, perceived motion is completely ineffective in triggering pursuit even when potential retinal error information is eliminated.

EXPERIMENT 2A (MOTION AFTEREFFECT DISPLAY)

In this experiment we used a MAE to produce the perception of pattern motion in a stationary display. This design has the possible advantage of removing any competing image motion from the test display, such as the motion of the surrounding frame in Experiment 1. The display pattern consisted of three bands of vertical, square wave gratings with a spatial frequency of 0.7 c/deg, and an average contrast approaching 1.0. The average luminance of the bright bars was 0.85 cd/m^2. Each band of bars was 3° high and 6° wide and spacing between the bands was 0.5°. The entire display covered an area that was 6° wide and 10° high (see Fig. 2).

The adapting stimulus, the middle band of bars, flanked by two stationary grating bands, moved to the left or right at 2 Hz, generating a consequent rightward or leftward MAE. The upper and lower stationary gratings functioned to provide relative motion which has been shown to be important for producing the aftereffect (Day and Strelow, 1971). The test stimulus was identical to the adapting stimulus except that it remained completely stationary. On half the test trials the test pattern was horizontally stabilized and on half it was not.

Each adaptation period lasted 1 min. During this phase the observer was instructed to fixate a stationary point located just above the center of the middle grating so that his or her eyes would not be pulled by the grating motion. After 1 min of adaptation the screen became dark for 500 msec, after which the test pattern was displayed and remained visible for 1.5 sec. It was either stabilized or not, depending on the nature of the trial. During the test phase no fixation stimulus was present and observers were simply instructed to fixate the upper left corner of the middle grating's center bar, the location corresponding to the position of the fixation point during adaptation. They were instructed to follow the motion of the pattern, if it appeared to move. Observers reported the appearance of pattern motion following each test interval.

Calibration of stabilization preceded all testing. The testing sequence began with four no-motion trials in which the grating was stationary during both adaptation and test. These provided baseline eye movement data. These trials were followed by a series of trials (adaptation and test) which were terminated when the observer reported a MAE on two successive trials. Once a MAE was clearly established, actual testing began. This consisted of four stabilized and four non-stabilized trials, randomly presented, in which the adapting grating moved in one direction only, i.e. left or right. The two concluding trials in the testing sequence were no-motion trials. This entire procedure using the opposite direction of adapting motion was repeated after a minimum rest interval of half an hour which was sufficient time for the MAE to decay. Four observers participated, all of whom had normal, uncorrected vision. Psychophysical estimates of the magnitude of the MAE were obtained in a separate experiment.

EXPERIMENT 2B (ESTIMATION OF MAE MAGNITUDE)

A nulling procedure was used to determine the point of subjective stability (PSS) for the test pattern. The four observers who had participated in Experiment 2A participated in this experiment. Eye movements were again recorded but testing occurred under non-stabilized conditions only. The visual display was identical to the one used in the main experiment except that a real motion, opposing the direction of the apparent motion, was introduced during the test intervals to cancel the aftereffect. There were again two completely separate testing sequences involving adaptation to leftward and rightward pattern motion. A testing sequence consisted of the preliminary no-motion, baseline trials and an initial series of test trials which were again terminated following two successive reports of the MAE. A double random staircase series of trials was then begun. The ascending trials in this series began with zero motion of the test grating while the descending series began with the test grating drifting 30′/sec. The test pattern motion was always opposite the MAE and was therefore in the same direction as the pattern motion present during adaptation intervals. Depending upon whether a trial belonged to the ascending or descending series, the motion of the test pattern was incremented or decremented in 6′/sec steps. The ascending series terminated following two successive reports of the true motion of the grating while the descending series terminated with two successive reports of the MAE. The velocity of the grating which produced the first of each of these reports served as the initial index of the PSS. The mean velocity of the ascending and descending PSS were then averaged and, because there were no significant differences between the mean magnitudes of the leftward and the rightward PSS, these figures were also averaged and the resulting figure then served as the overall estimate of a subject's MAE.

Results

Table 2 presents the psychophysical data as well as data indicating the ratio between eye motion and nulling target motion for all trials and for the subset of trials which served as the index of the PSS from Experiment 2B. The latter ratios specify what proportion of the actual grating motion was pursued during the testing intervals in which, on the average, the grating actually appeared stationary to the observer. The calculated overall mean velocity which nulled the MAE was 13.9′/sec which resulted in a mean nulling displacement of 20.85′ suggesting that our viewing conditions in Experiment 2A were adequate for producing the desired MAE. It seems reasonable to assume that a similar MAE was experienced in Experiment 2A since testing conditions were similar.

Figure 3 presents representative samples of eye records from one subject from each of the six testing conditions of Experiment 2A. It should be noted that all subjects in this experiment consistently reported a MAE during testing intervals. The sample eye movement records pictured in Fig. 3 again provide no evidence of tracking the perceived motion regardless of whether the records were obtained under open- or closed-loop conditions.

Table 3 summarizes the eye movement data from Experiment 2A. It presents the mean magnitude of smooth eye displacement in each of the six testing conditions. It is evident that whatever drift there was, was completely random across conditions and was comparable to that typically observed when a stationary target is monocularly fixated (Nachmias, 1961). Once again then, there were no differences between stabilized and non-stabilized conditions and no differences between rightward and leftward MAEs. We thus again failed to confirm our preliminary hypothesis, and found, as in the previous experiments, that perceived motion alone fails to elicit pursuit even when the possibility of constraining retinal error is eliminated.

Discussion

Not only did these results fail to confirm our hypothesis, they also failed to resolve the problem of why the perception of motion seems to play a role in pursuit under some conditions but not under others. The present experiments must be included among those which fail to show any influence of perceived motion on pursuit. This outcome seemed particularly surprising in light of a recent report (Wyatt and Pola, 1979) that perceived induced motion enhances pursuit gain under open-loop conditions.

Wyatt and Pola (1979) examined smooth pursuit under open-loop conditions when the perceived motion of a target was enhanced by the counterphase motion of a large flanking surround. They compared the eye movements in this condition with those in the presence of the stabilized target alone. In both conditions the stabilized target oscillated 2° horizontally and symmetrically across the fovea. They report that the amplitude of the pursuit movements was greater when the inducing frame was present. Since the counterphase motion of the frame enhanced the perceived motion of the target without altering its retinal motion, the authors quite reasonably argue that the increase in amplitude is caused by the increase in perceived motion.

Since the pursuit targets in Experiments 1 and 2 were both retinally fixed whereas the target in the Wyatt and Pola study oscillated over the fovea, we thought it might be this difference which accounted for the very different outcomes. Perhaps retinal target motion is a precondition for a perceptual influence on pursuit. To test this speculation we attempted to replicate and extend the Wyatt and Pola study. We examined pursuit again under open-loop conditions using the motion of a frame to enhance or reduce the apparent motion of an oscillating target.

EXPERIMENT 3

The visual display was presented on a large, 40 × 30 cm, fast phosphor (p-15) oscilloscope screen.

Table 2. Mean magnitude of MAE and ratio between eye motion and nulling target motion for all trials and the subset of trials which served as the index of PSS from Experiment 2A

Mean magnitude MAE	Eye motion/target nulling motion (All trials)	Eye motion/target nulling motion at PSS
13.9′/sec (20.85′)	0.60	0.60

Figure in parentheses is mean nulling displacement at PSS.

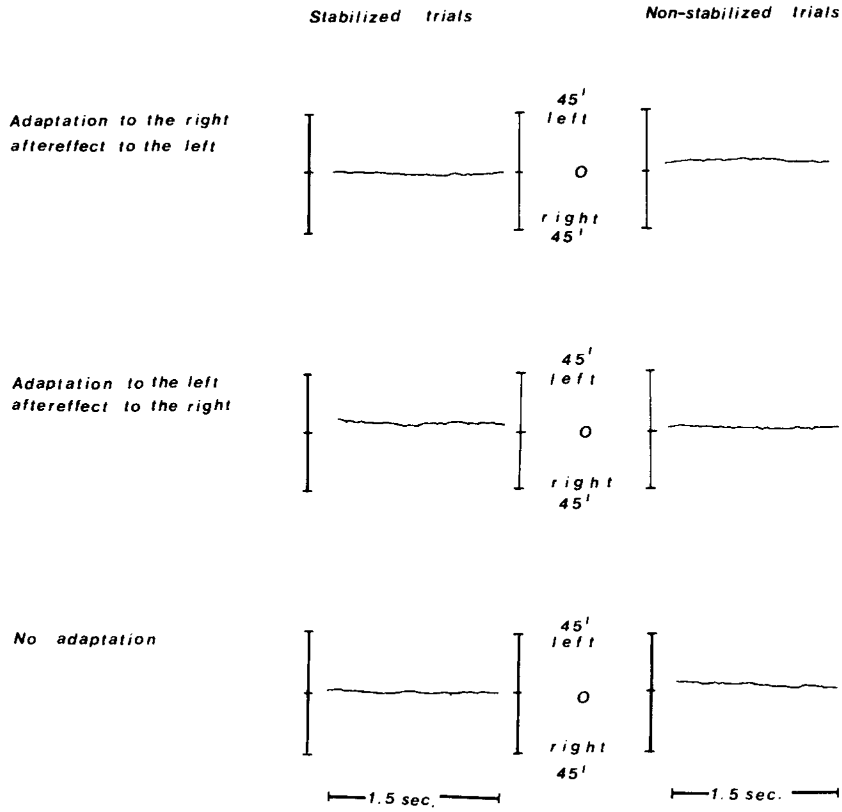

Fig. 3. Eye movement records for one subject from Experiment 2. Representative eye movement records for the 1.5 sec test period following adaptation are shown for each observational condition.

The display, as far as possible, was identical to that described by Wyatt and Pola. However, it was reduced in size by 25% in order to fit on the display scope. To keep testing conditions as comparable as possible to Wyatt and Pola, all other stimulus parameters were reduced by 25% as well.

The display consisted of two horizontal lines, 20.25°, vertically separated by 16.5°, which served as the inducing frame and flanked the central target which was a small light point. The frame oscillated through 15° at a frequency of 0.5 Hz, while the target oscillated through 1.5°. The observer viewed the display from a distance of 45.7 cm while his/her head was held in place by a dental impression bite plate. Stabilization was accomplished in the manner described earlier.

Table 3. Data summary for Experiment 2: mean smooth eye displacement for stabilized and non-stabilized trials in adaptation and no-adaptation conditions

	Stabilized	Non-stabilized
Aftereffect to the right	−3.37	+5.00
Aftereffect to the left	−0.25	+0.50
No aftereffect	+5.48	+2.25

A (+) indicates eye motion to the right; a (−) indicates eye motion to the left. All entries are in min of arc.

There were three different conditions: target alone (T); target and frame, with the frame moving counterphase to the target (FA); and target and frame moving in phase (FW). This last condition (FW) was designed to produce the perception that the target was either moving much less than it is or that it was actually moving in the opposite direction. The perceived motion of the target should be enhanced in the FA condition, which is a repeat of the Wyatt and Pola induction condition. In every instance the subject was asked to fixate and follow the target and report the average distance through which it had appeared to move within a trial. To do this the observer used a potentiometer to adjust the distance between two light points which appeared on the scope at the end of every trial so that the distance between them reflected this perception.

On half the trials these points were initially close together, while in the remaining trials they were maximally separated. Each trial lasted 30 sec. On the first trial the spot-target appeared alone and was not stabilized. This was followed by six trials in which the target was stabilized. They occurred in the following order: T; FW; FA; FW; FA; T.

Three subjects were formally tested, two of whom were sophisticated and one of whom was naive as to the purpose of the experiment. An additional three observers were tested but their data is not reported

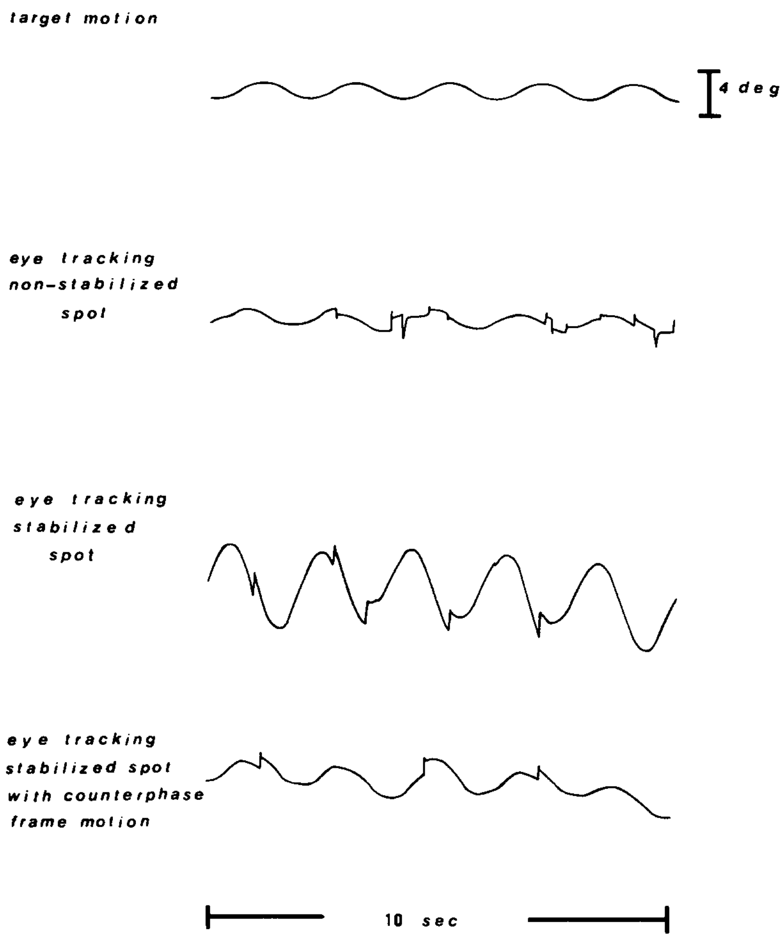

Fig. 4. Eye movement records for three observational conditions in Experiment 3. In all conditions target motion was sinusoidal with an amplitude of 1.5°. The uppermost trace illustrates the amplitude of target motion. All records are recorded on same time base.

since it is not complete. Their data are consistent with the results which are reported.

Results

The FW condition failed to produce consistent perceptual results, and therefore the data from this condition will not be reported. We suspect that this condition, which was intended to reduce perceived target motion or alter its perceived direction, failed to do so consistently because, as the eye moved to capture the target which was moving in phase with the frame, the target was carried along with the eye, significantly reducing or changing the relative displacement between target and frame which is the basis of the induced motion. (Were the frame also to have been stabilized, this would not have occurred. We chose not to stabilize the frame in order to conform to the Wyatt and Pola design.) This was not a problem in the FA condition where target and frame were moving out of phase, since, for the most part, pursuit of the relentlessly oscillating target exaggerated the relative displacement which is the basis for the induced enhancement of target motion. Observers generally perceived more target motion in this condition.

Figure 4 provides a representative sample of eye records from the T and FA testing conditions. What is immediately obvious from these eye motion traces is that tracking amplitude was substantially reduced when the counterphase frame was present. This is, of course, the opposite of what Wyatt and Pola report and the opposite of what would be predicted if perceived motion were to exert an influence over the control of pursuit. Figure 5 presents a summary of the results. It is clear from the inspection of the bars showing perceived target excursion that the presence of the counterphase frame successfully and markedly enhanced perceived target motion. In fact, the increase in perceived target motion was approximately threefold compared to the target-only, stabilized condition. Despite this, there was a sharp reduction, four to fivefold, in pursuit amplitude in this condition. Amplitude of pursuit was greatest when the stabilized spot alone (T) was visible. In this condition the eye engages in futile pursuit of the elusive target; its

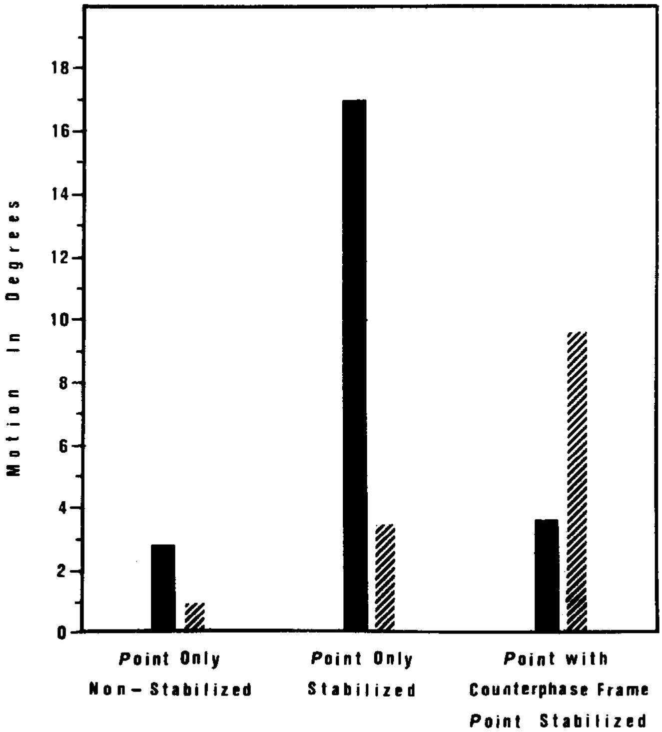

Fig. 5. Eye motion and psychophysical data for three observational conditions in Experiment 3. Data show means for three subjects. The black bars give eye motion amplitude in degrees. The striped bars give psychophysical motion reports in degrees.

motion in one direction restrained only by the phase reversals of the target.*

While we are completely at a loss to explain the difference between our results and those reported by Wyatt and Pola, we think that the reduction in pursuit amplitude found in our induction conditions may reveal the influence of the counterphase frame on the oculomotor control of pursuit which appears to have placed restraints or acted as a brake on the sweeps of the eye. However, whatever accounts for the difference between our results and those of Wyatt and Pola, we clearly again have no evidence that perceived motion influences pursuit eye movements, even when the image of the stabilized target stimulus displaces over the retina.

Our consistent and complete failure to find any evidence that the visual perception of an object's motion affects the smooth motions of the eyes, led us to look again at other situations reported to be effective in demonstrating the influence of the perception of motion on pursuit. The report of most interest is one belonging to a class of demonstrations in which the tracked target has no retinal counterpart. For example, there are a number of demonstrations that smooth eye motions may be elicited by non-visual stimuli such as: a subject's hand moving in the dark (Steinbach and Held, 1968; Jordan, 1970); the imagined motion of a swinging pendulum (Deckert, 1964), or a moving sound source (Gauthier and Hofferer, 1976), and the report of smooth eye motions during REM sleep (Fuchs and Ron, 1968). The report that moving cyclopean contours elicit OKN (Fox *et al.*, 1978) may also belong in this category. A particularly striking example of this class of observations which, like pursuit of cyclopean contours, depends upon a visual stimulus with no obvious retinal counterpart, has been described by Steinbach (1976). He reported that an anorthoscopically presented stimulus can be tracked. He found that an ellipse or circle moved back and forth behind a narrow vertical slit, and revealed only through the slit, can be pursued despite the fact that all that is present on the retina are two small elements moving up and down out of phase and changing slope. Since there is no appropriately displacing stimulus which could serve as the horizontal pursuit target, this appears to be a case where perception must be playing a central role in the control of pursuit. Since this stimulus configuration appears to

* We examined whether the decrease in target size might be responsible for the difference in our results. To that end we repeated the reported experiment with the same observers using a square each side of which was 1.5°. The results were completely consistent with the data reported for the point-target. In the target-only stabilized condition the mean perceived motion was 3.43° and the mean eye motion was 9.7°. In the counterphase-frame condition the mean perceived motion was 10.48° and the mean eye motion was 3.04°.

finally provide clear evidence of the influence of perceived motion on the control of pursuit, we chose to examine eye movements during observation of such a stimulus.

EXPERIMENT 4

The anorthoscopic stimulus was simulated on a fast phosphor CRT. A circle, 2° in diameter was swept back and forth on the CRT through 2° at 0.5 Hz. Gating logic to the scope's intensity input allowed it to be visible only when it crossed a narrow, 14′ vertical window on the screen. Eye movements were recorded both during observation of the anorthoscopic stimulus and while the subject looked at a completely visible circle moving back and forth in an identical manner. Following each observation interval the observer adjusted two points of light which appeared on the scope face so that they were separated by the distance through which the observed figure had appeared to move. The observer was instructed to look at the display and follow the motion of the perceived form when it was apparent.

Initially what is seen when viewing this anorthoscopic display are short line segments dancing up and down, together and apart, in a vertical column. When anorthoscopic perception occurs, the dancing line segments suddenly become the outline of a perceived circle which appears to be moving back and forth revealing itself through a slit in the CRT. When this happens, the boundaries of the simulated slit are marked by vivid subjective contours. Since figure perception tends to be intermittent under these conditions, the observers were asked to depress a switch which they held in their hands whenever the moving form was perceived. A trial lasted 60 sec. Seven observers were tested.

RESULTS

Figure 6 presents a representative sample of eye records obtained from one subject while he tracked the visible circle, the anorthoscopically presented circle, and while observing the anorthoscopic display but failing to perceive the organized form. Inspection of these eye traces reveal, as Steinbach reported, that it is possible to track an anorthoscopic stimulus. The quality of the tracking, however, is degraded when compared with the tracking of the continuously visible moving stimulus. More striking is the contrast between the eye records obtained when the subject viewed the anorthoscopic display but failed to perceive the circle and the eye records obtained during an interval when the anorthoscopic percept had been achieved. In general, there was no evidence of tracking except when the observers reported seeing the anorthoscopic figure.

Table 4 provides a summary of these results. The difference between tracking a real and an anorthoscopic circle is clear. The stimulus is actually displacing through 120′. When the stimulus is completely visible the amplitude of the pursuit closely matches the amplitude of stimulus displacement. On the other hand, when the stimulus is anorthoscopically presented, the amplitude of the smooth eye motion is enormously reduced. There is also a marked reduction in the *perceived* amplitude of stimulus displacement under anorthoscopic conditions, but this reduction is much less than the reduction in the amplitude of smooth pursuit. It should also be noted that there

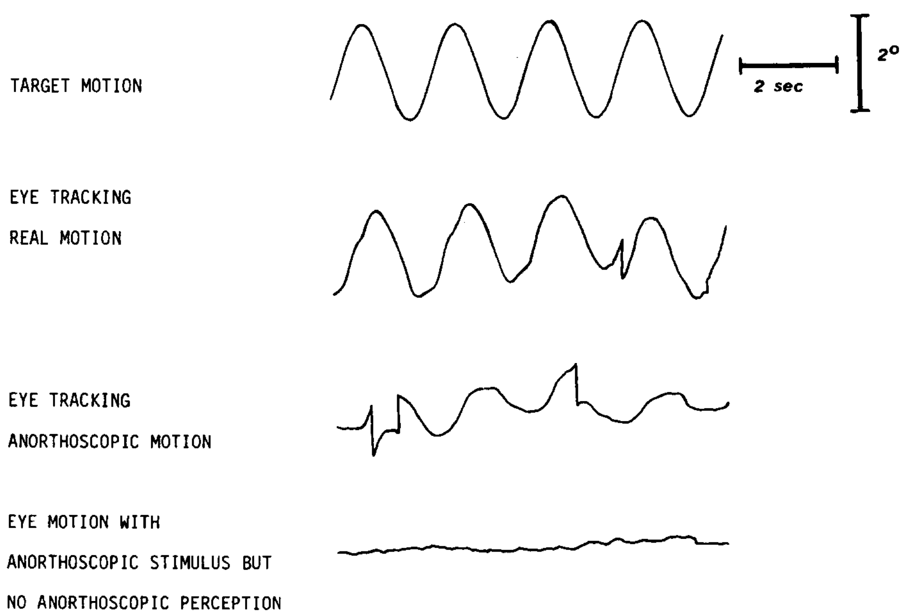

Fig. 6. Eye motions during attempted pursuit of real and anorthoscopic stimuli in Experiment 4. Subjects tracked a 2-deg circle which was swept sinusoidally back and forth at 0.5 Hz. In the anorthoscopic condition, the figure moved behind a simulated 14′ slit.

Table 4. Eye movement and perceived displacement with real and anorthoscopic stimuli in Experiment 4

Subject tracks:	Mean extent eye displacement	Mean judgment target displacement	Eye displacement as % of judged target displacement
Actual motion	116.03	115.44	102.98
Anorthoscopic motion	29.92	90.08	39.72

All entries are in min of arc.

were no intervals of tracking the anorthoscopic stimulus which were not interrupted by frequent saccades which is not the case when an observer is tracking a normally visible, moving stimulus.

Thus, while it is indeed true that it is possible to track an anorthoscopic stimulus, the eye substantially undertracks the simulated object's displacement. More importantly, it grossly undertracks the *perceived* displacement, and tracking quality is poor. Nevertheless, this is a clear case where perceived and not retinal motion serves as a stimulus for pursuit, since only when the perception of an integrated figure in motion is achieved, is any tracking possible.

DISCUSSION

What is it about the anorthoscopic stimulus which permits the perception of a figure in motion to be a stimulus for pursuit? We believe the answer is that the feature of the anorthoscopic display which enables perception to serve as a stimulus for pursuit is the very aspect of these displays which make them compelling evidence for the influence of perception on pursuit; namely the fact that the perceptual stimulus for pursuit has no retinal counterpart. We suggest that it is because the anorthoscopic figure has no retinal image counterpart, because it is an achievement of organizational processes which are integrating temporal inputs, that the eye is free to follow its perceived path of motion. We know from the work described above, when a target stimulus has a retinal counterpart, it is the retinal stimulus which controls how the eye will track it. However, where perception "creates" the target and therefore there is no retinal feedback which can constrain or inhibit pursuit, then the perceived motion may serve as the pursuit stimulus, although because tracking quality is degraded in these conditions, it would seem that perceived motion unsupported by retinal motion is far from an ideal stimulus.

This construction is supported by a finding recently reported by Levine and Lackner (1979), which also suggests that this absence of a retinal counterpart is at the heart of all the phenomenon in which there is pursuit of non-visual targets. They found that observers could track, at least part of the sensed motion of their restrained arm while in complete darkness when the motion was induced by vibration of their biceps muscle. However, they report that if a small light is placed on the observer's vibrated hand which now appears to move along with his hand, there is no longer any evidence of tracking eye movements. Thus when the perceived motion has no retinal counterpart, it elicits tracking, whereas when there is a retinal image counterpart, produced by the visible target light, it alone controls the oculomotor response. Since the image of the light does not displace, there is no tracking.

None of the remaining alleged demonstrations of the influence of perceived motion on pursuit provide compelling evidence against this reasoning. The finding that pursuit is highly correlated with the perceived direction of motion when an observer views a reversible motion pattern (Ter Braak, 1962; Leguire and Fox, 1978), may be discounted as evidence that perception governs pursuit since these demonstrations involve displays with contours moving in opposite directions. A retinal motion is present to initiate and sustain tracking in either direction. All that can be argued reasonably from these results is that perceptual processes participate in the selection of which of the retinal motions is to be followed. The remaining demonstrations are all ones in which the image of a tracked target is held, or appears to be held stable on the fovea. Since in each of these cases pursuit occurs with an apparently stationary retinal target which seems to move, they have been taken as evidence of perceived motion pursuit. The prototypical case is pursuit of a foveal afterimage (Heywood and Churcher, 1971; Yasui and Young, 1979).* Reports that observers can sustain pursuit while viewing a stroboscopically lit array of identical stimuli (Lamontagne, 1973; Heywood, 1973) or while viewing dynamic, random noise (Ward and Morgan, 1978), pro-

* Pursuit with a foveal afterimage has been otherwise accounted for by Hedlun and White (1959) and Doeschotte (1954) who suggested that the smooth eye movements in this situation may not be normal pursuit, but rather represent the response of a more primitive mechanism. "By maintaining the retinal image at a fixed position regardless of eye movements, the optical feedback necessary for normal pursuit is eliminated, thus making the eye the slave of a more primitive mechanism with its own individually characteristic rhythm" (Hedlun and White, p. 730). One advantage of this view is that it avoids a difficulty faced by the perceived motion account of afterimage tracking, namely that of accounting for the reversals in tracking direction at the end of each oscillatory swing. It can hardly be perceived motion which accounts for these reversals.

vided that an actually moving stimulus is present to initiate tracking, fall into this category as do the reports of tracking of stroboscopic motion (Westheimer, 1954; Young, 1977; Morgan and Turnbull, 1978).*

In none of these instances do we believe it necessary nor in fact correct to invoke perceived motion as the stimulus for pursuit since the information that accounts for the perception of motion maybe, and probably is, given directly to the oculomotor system. In each case in which a foveal stimulus remains or appears to remain foveal while the eye is moving (the conditions which characterize accurate tracking of an actually moving stimulus), the perception of motion is generally attributed to the output of a motion comparator which matches a corollary discharge or extraretinal eye motion signal against the concomitant retinal reafference and signals motion when these two inputs do not sum to zero (Von Holst, 1950). There is considerable reason to believe that the oculomotor system has direct access to this motion signal and no reason to assume that the oculomotor system must get this information by way of higher order perceptual processes.†

CONCLUSION

In conclusion then, we believe that assertions attributing a dominant role to perceived motion in the control of pursuit are incorrect. Perception is usually able to exert only an indirect influence on the control of pursuit eye movements through the selection of a visual target. Its direct influence would seem to be limited to those instances in which the selected target has no retinal image counterpart. When the perceived stimulus does have a retinal counterpart, it is this which controls pursuit with no contribution from perception. The pursuit system acts to stabilize this image on the fovea of the eye. This conclusion is consonant with the earlier, widely accepted, view of pursuit which maintained that retinal and not perceived motion is the primary stimulus. Unlike this earlier view, however, our construction allows for the influence of perception under highly restricted conditions and thus provides a possible way of accounting for the reports of pursuit in the absence of any visual stimulus at all.

* While we cannot account for the initiation of pursuit when the observer perceives stroboscopic motion, we reject the view that perceived motion is the eliciting stimulus since Morgan and Turnbull (1978) found that pursuit persists with interflash intervals too long to generate the appearance of continuous motion. Once tracking is initiated, pursuit of stroboscopic motion is simply another instance of pursuit of a stimulus which seems to remain retinally stable.

† There is considrable evidence that the corollary discharge and comparator signals are more central to the oculomotor control system than to the perceptual system. In most situations in which the comparator signal conflicts with other sources of motion information, such as relative retinal displacement, our perceptions are determined by this latter information and are generally unaffected by the comparator output. The clearest example of this is, of course, induced motion, where the relative retinal displacement between images leads us to misperceive stationary objects as moving or moving objects as moving in the wrong directions, whereas were perception to be based on the comparator output, our perception in these situations would be veridical. We have shown that in such cases pursuit is not impaired.

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