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INTERACTION OF PERCEPTUALLY MONITORED AND UNMONITORED EFFERENT COMMANDS FOR SMOOTH PURSUIT EYE MOVEMENTS[1]

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Abstract—When observers tracked a horizontally moving spot, the path of a second spot moving at an angle to the horizontal was radically misperceived. At a signal observers abruptly switched to tracking the second spot, which was then stabilized foveally. Data concerning resulting eye movements and perceptions support a distinction between the "central" motor command, which is found to be formulated solely from the erroneous perception, and the motor command that finally reaches the eye, which, under some specifiable circumstances, has been "peripherally" transformed so that the actual motion of the eye is appropriate to the actual motion of the target.

INTRODUCTION

Several studies have shown that the paths of motion of spots of light moving in the dark are often strikingly misperceived (Dodge, 1904; Ford, 1910; Duncker, 1929; Fujii, 1943; Johansson, 1950; Sumi, 1964a, b; Dichgans, Körner and Voight, 1969; Sumi, 1971; Mack and Herman, 1972; Mack, Fendrich and Sirigatti, 1973; Gogel, 1974; Festinger and Easton, 1974; Coren, Bradley, Hoenig and Girgus, 1975). One explanation of such misperceptions, first suggested by Dodge (1904), is that they arise from a failure of the perceptual system to take adequate account of the smooth pursuit movements of the eyes. In our own work (Festinger, Sedgwick and Holtzman, 1976; Sedgwick and Festinger, 1976) the accurate measurement of eye position during smooth pursuit allowed us to compare the actual, the retinal, and the perceived paths of spots of light moving back and forth in harmonic motion. We found that, when the eye pursues such a spot in the dark, the perceived extent of its motion is much less than the actual extent. Also, the orientation of an untracked spot's path in the dark is radically misperceived when the eye is tracking another spot along a differently oriented path. In this latter case the path along which the untracked spot is perceived to move is quite close to the path it sweeps out on the retina. These data, gathered using a variety of different speeds and extents of tracking motion, suggest that although the perceptual system may have accurate information about the direction in which the eye is moving during smooth pursuit, it attributes a relatively low speed to the eye, almost irrespective of its actual speed.

Perception, in such situations, depends upon information received from the oculomotor system about how the eye is moving. Such extraretinal information can be combined with retinally obtained information in arriving at the perception of a target's motion. Two kinds of extraretinal eye movement information might be available to the perceptual system. One is proprioceptive feedback from the muscles that move the eye; the other is monitoring of the motor commands to those muscles. While current evidence, which is reviewed elsewhere (Skavenski, Haddad and Steinman, 1972; Matin, 1972, 1975), is not totally unequivocal, it appears to us to favor the monitoring of the motor command as the main source of extraretinal information about eye movements that is available to perception.

Errors in perception arising from inadequate extraretinal information concerning smooth pursuit eye movements could conceivably occur from faulty monitoring of the motor command. A more intriguing possibility, however, is that the monitoring is accurate but the motor command itself, at the "central" stage at which it is monitored, does not contain accurate velocity information. A difficulty with this hypothesis is that the actual tracking movements of the eye are usually quite accurate, even in situations in which the perception of the target's path of motion is very inaccurate. This leads us to distinguish between the motor command at the stage at which it is monitored by the perceptual system, which we will refer to as "central," and any subsequent unmonitored transformation of the command, which we will refer to as "peripheral". What must be implied then, if accurate velocity information is not contained in the "central" monitored command, is that the final innervation of the extraocular muscles has been, somehow, transformed "peripherally". This implication needs further investigation.

These conjectures also raise questions concerning the use of perceptual information in formulating "central" motor commands. If these commands are based on perception, then when the perception is in error, as it sometimes is during smooth pursuit, new "central" motor commands also would be in error. A "central" command to pursue a target whose direction of motion was misperceived, for instance, would

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order the eye to pursue in the perceived, rather than the actual, direction of target motion. Thus, there is the possibility that such interdependence of visual perception and the "central" motor command could lead to reciprocal errors: a lack of velocity information in the "central" motor command while the eye pursues one spot could contribute to a misperception of the direction of movement of another target. This in turn could lead to an error in a new "central" motor command to track that target.

The present study was designed to investigate two questions. First, does the "central" motor command rely entirely upon perception? Second, what is the nature of any "peripheral" transformation of that "central" command? We assume that the extraretinal information available to perception accurately reflects the contents of the "central" motor command. The experimental paradigms which we employed were guided by this assumption.

These questions would be difficult to answer unambiguously in a normal tracking situation. Because tracking is never perfect there normally is movement of the target on the retina. This retinal information about target movement would contaminate our assessment of the extraretinal information available to perception. Also, such retinal movement provides feedback on the basis of which any tracking errors can be quickly corrected. Thus it would be difficult to measure any difference that might exist between the "central" motor command and the actual movement of the eye.

These considerations led us to a somewhat complicated experimental paradigm. For the beginning portion of a given trial the eye tracked a spot moving back and forth horizontally in simple harmonic motion. During this time another ("target") spot moved in phase with the tracked spot, but at some angle to the horizontal. At an auditory signal, the observer made a saccadic eye movement to, and began to track, the target spot. As the eye saccaded to the target spot the horizontally moving spot disappeared and, on completion of the saccade, the target spot was stabilized foveally. Since the stabilized target spot then stayed at the center of the fovea no matter what the eye did, a condition of "perfect tracking" was artificially created in which there was no retinal error and hence no need to modify the direction specified by the initial "central" motor command.

This paradigm depended for its success upon the eye continuing to move for some appreciable period with only a stabilized spot on the retina. This was a reasonable outcome to expect since there was no error signal to indicate that any change in what the eye was doing was necessary. Pilot work showed that the eye did reliably saccade to the vicinity of the target spot and immediately go into smooth pursuit which continued for some time. Our pilot work also indicated that the target spot was perceived to continue moving during the period of stabilization.

Our aim then was to infer the direction specified by the "central" motor command from the perceived direction of target motion during "perfect tracking" and also to examine the nature of "peripheral" transformation by comparing this "central" command with what the eye actually did.

PROCEDURE—I

Apparatus

The position of the right eye, with the left eye occluded, was monitored by a double Purkinje image eye tracker developed and described by Cornsweet and Crane (1973). This system provides continuous analog voltage outputs for the vertical and horizontal components of eye position over a range of $16° \times 16°$ of visual angle with less than 4′ of arc noise.

The eye tracker output is somewhat non-linear with respect to direction of gaze, however, and these non-linearities, as well as the overall scale of the output, vary somewhat among observers. Accordingly, the first experimental session for each observer was set aside to collect eye position data appropriate for the calculation of a linearity correction matrix and scale factors. The calibration procedure is described in detail by Festinger *et al.* (1976).

Computer-controlled visual displays were presented in total darkness on a Hewlett-Packard 1310 oscilloscope equipped with a p15 phospher, which leaves virtually no persistence (decays to 10% in 3 μsec). Each observer viewed displays from a distance of 1 m with head held in place by a biteboard and forehead rest. The experimenter could visually monitor the observer's eye movements on an oscilloscope located outside the eye tracker room.

During the experiment, a baseline correction was calculated at the beginning of each trial to correct for variations in how the observer was positioned in the tracker apparatus. During each trial, eye position was sampled and digitalized every 2 msec by computer, and linearity, scale, and baseline corrections were applied. When a spot in the display was to be foveally stabilized, that spot was presented every 2 msec at the position corresponding to the observer's calculated direction of gaze. There are several possible sources of inaccuracy in this stabilization procedure. These include the 3′–4′ of arc noise level of the eye tracker, a lag of 2–3 msec between the time that the eye moves and the time this movement is reflected in the output of the tracker, and possible errors of measurement in the determination of the linearity, scale, and baseline corrections. Eccentric stabilization resulting from some combination of these errors was probably the cause of repeated saccades that occurred during the stabilization period on occasional trials. Such trials were discarded. We also included control conditions that would allow us to assess the extent to which smaller stabilization errors might have influenced the direction of smooth pursuit during stabilization.

Tracking conditions

An example of the configuration of spots used for the prestabilization period of each experimental trial is shown in Fig. 1A. Three vertically aligned spots, spaced at $\frac{1}{2}°$ intervals, moved back and forth together along horizontal paths in simple harmonic motion at 0.4 Hz over a 6° extent. A "target" spot moved in simple harmonic motion back and forth nearby along a straight path at some angle to the horizontal. The horizontal component of motion of the target spot was always in phase with the horizontally moving spots. Spot configurations were designed so that, at the mid-point of each half cycle of motion, the target spot was 4° directly above the middle one of the three horizontally moving spots.

The observer was instructed to track the middle horizontally moving spot[3] until a tone was sounded, which was

[3] Three spots moving together were used in this display because we wanted the observer's tracking during this initial portion of each trial to be as good as possible. It has been demonstrated that the efficacy of pursuit is enhanced by the presence, in close proximity, of additional spots surrounding the spot to be tracked (Hundley, 1976).

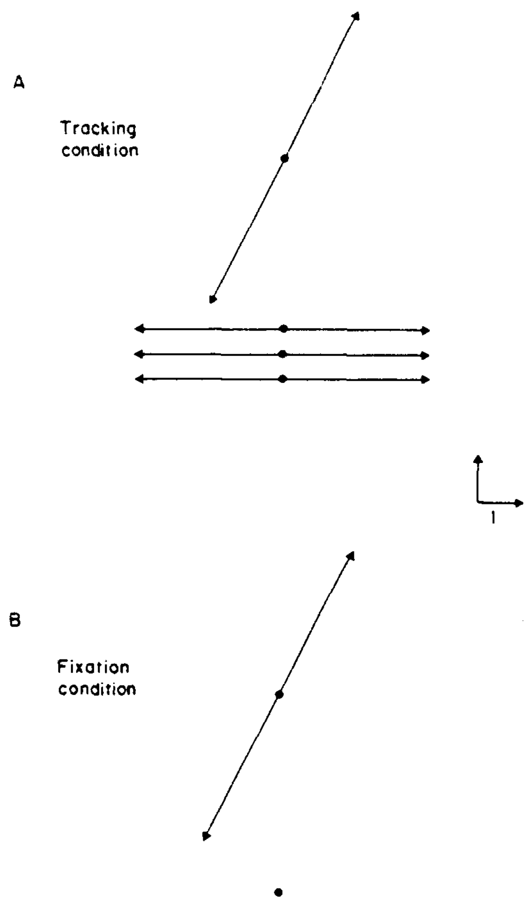

Fig. 1. (A) Visual display for tracking conditions with spots represented at the midpoint of their paths. During the pre-stabilization period, observers pursued the middle horizontally moving spot. The spot moving at an angle to the horizontal is the "target" spot. (B) Visual display for fixation condition with "target" spot represented at the midpoint of its path. During the pre-stabilization period, observers fixated the stationary spot.

a signal to look at and follow the target spot. At the beginning of the first saccade following the tone, the horizontally moving spots disappeared. When the saccade was completed, the target spot was replaced with a foveally stabilized spot. The stabilization period lasted 1.25 sec after which a central fixation spot appeared for 5 sec, a new baseline correction was calculated, and a new trial was initiated.

In order to obtain saccades with little or no horizontal component, a cumulative average of saccadic latencies following the tone was maintained for all trials, and the time at which the tone sounded was adjusted to maximize the likelihood that the saccade to the target spot would occur at the midpoint of a half-cycle, when the target spot was directly above the tracked spot. The tone sounded on either the fifth or sixth rightward half-cycle.

A stabilized spot was not presented if the saccadic latency following the tone exceeded 600 msec or if the eye did not saccade into a 1° square window centered around the target spot. Under such circumstances a central fixation spot appeared instead, a new baseline was calculated, and the trial was repeated. If the observer blinked during the half-cycle in which the tone was to sound, or during the previous cycle, the tone was delayed one cycle. If a blink occurred during stabilization, the trial was immediately terminated, and was then repeated.

Three tracking conditions were used, which differed only in the path of the target spot. On the basis of our previous work with very similar configurations (Festinger *et al.*, 1976), we knew that the perceived orientation of target spot motion for each tracking condition would be close to the retinal path swept out by the target spot. Since tracking of the horizontally moving spots would be very good, the perceived path of the target could be closely approximated by the orientation of its path of motion relative to the horizontally moving spots. Therefore, we used the orientation of this relative path of motion as our estimate of what the perceived path of target motion would be. We will refer to this as the "estimated perceived" path. By physical path, we refer simply to the orientation of the target spot's path in physical space. Orientations for target spot paths located above the horizontally moving spots are measured counter-clockwise from the horizontal and are given positive signs; those for targets located below the horizontally moving spots are measured clockwise from the horizontal and are given negative signs. Each of the three tracking conditions is identified by both the physical path and the "estimated perceived" path of the target, the physical path given first.

The vertical component of target spot motion was 6° for all tracking conditions, while its horizontal component varied among conditions in order to produce paths of target spot motion at three different angles to the horizontal. Tracking Condition 63°/117° was designed so that its physical path and its "estimated perceived" path were symmetrical around 90°. Tracking Condition −63°/−117° was identical to Tracking Condition 63°/117°, except the target spot was located below the horizontally moving spots; these two conditions were mirror images of each other relative to the horizontal axis. Tracking Condition 34°/63° was designed so that the "estimated perceived" path was identical to the physical path of the target spot for Tracking Condition 63°/117°.

Fixation conditions

Conditions in which the eye was stationary prior to the period of stabilization were run as controls for the tracking conditions. An example of the configuration of spots used for the pre-stabilization period of each fixation condition is shown in Fig. 1B. These conditions differed from tracking conditions in that the three horizontally moving spots were replaced by a single stationary spot which the observer was instructed to fixate until the tone was sounded. At the midpoint of each half-cycle the fixation spot and target spot were aligned vertically and separated by 4°. The sequence of events for fixation conditions was identical to that for tracking conditions.

Each fixation condition is designated by a single number which refers to the physical path of the target spot, but which should also be a good approximation to its perceived path. Two fixation conditions were run for each tracking condition; one corresponding to the physical path and the other to the "estimated perceived" path. Only five different fixation conditions were needed because Fixation Condition 63° served as both the physical path control for Tracking Condition 63°/117° and the "estimated perceived" path control for Tracking Condition 34°/63°.

Nonstabilized conditions

Pilot work showed that there were occasional trials on which, during stabilization, the eye did not maintain smooth pursuit motion. The occurrence of such a trial usually disrupted subsequent trials. Therefore, tracking conditions and fixation conditions were always embedded in a larger number of nonstabilized fixation trials. These nonstabilized trials were intended to help maintain the expectation that the target spot would continue along its prior path when the eye began to follow it. Nonstabilized trials were identical to fixation conditions with the following exceptions. First, instead of a stabilized spot appearing after the saccade to the target spot, the nonstabilized target spot continued to be displayed. Second, tracking time for the target spot varied from 1.25 to 5 sec. And third, the tone sounded at any one of five approximately evenly spaced intervals in the rightward or leftward half of the fifth or sixth cycle. The varied tracking times and tone latencies for the nonstabilized trials were intended to minimize the predictability of the tone latency and target tracking duration.

Perceptual measures

Pilot work indicated that often, if the observer was required to make perceptual reports of the stabilized spot's path, the eye would move to the target spot, but fail to execute any tracking whatsoever, perhaps waiting to see what the spot did. Once this occurred, subsequent trials were affected as well. Accordingly, we did not attempt to measure the observer's perceptions until we had collected a complete set of eye movement data. At that time the observer's perceptual experiences during the experiment were discussed in detail. We probed to find out whether or not, at any time, the target appeared to change its orientation at the time of stabilization or during the period of stabilization. We then ran additional tracking trials and, after each trial, asked the observer to describe and to draw what was seen. In most cases such trials continued as long as the observer maintained smooth pursuit during stabilization. We were thus able to obtain some detailed perceptual information about the period of stabilization without interfering with the collection of eye movement data.

Observers and sequence of events

Three paid volunteers participated in the experiment. All had normal visual acuity as measured by the Keystone Visual Efficiency Battery, exhibited adequate tracking without any observable systematic drift during a practice session, and knew nothing about the purposes of the experiment. After calibration, observers participated in the

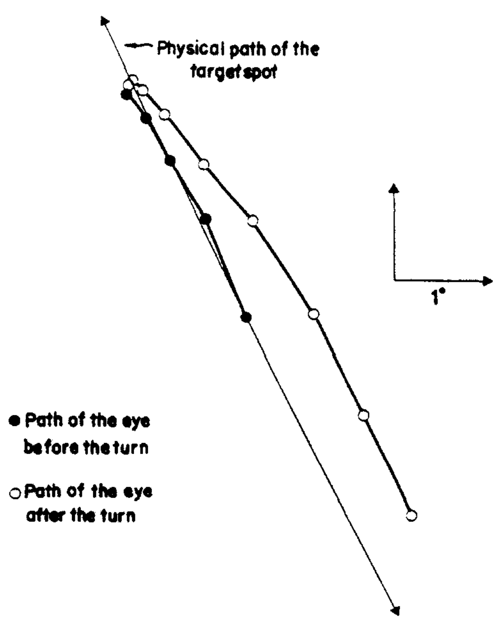

Fig. 2. Path of the eye during stabilization for one trial from Fixation Condition 117°. Straight lines were fitted to the eye position data for each of thirteen successive 100 msec intervals. The direction and extent of the physical path along which the target spot moved prior to stabilization is indicated by the thin line. This line is positioned so that its midpoint coincides with the beginning of the eye's path.

experiment for two further days, during which data were collected on four trials of each of the three tracking conditions and on two trials of each of the five fixation conditions. For each experimental trial, three nonstabilized trials were run, but were not considered in the analysis. Trials were run in blocks of five with approximately 2 min rests between blocks. If, during stabilization, the observer made a saccadic eye movement or failed to track, and this was detected on the oscilloscope located outside the eye tracker room, the trial was repeated at the end of that day. Each session lasted approximately 2 hr.

RESULTS—1

Before proceeding with a quantitative analysis of the eye position data, we examined $X-Y$ plots of eye movements during the period of stabilization for each trial. Figure 2 shows an $X-Y$ plot of eye position for thirteen successive 100 msec intervals for one typical trial from Fixation Condition 117°. For this trial, and for fixation conditions in general, eye movements during stabilization were characterized by a period of decelerating smooth pursuit along a relatively straight path; a turn at approximately the time the target spot would have turned; and acceleration of pursuit back along a similar path. For each fixation condition the path of the eye both before and after it turned was close to the physical path of the target spot prior to stabilization.

Figures 3 and 4 are examples of $X-Y$ plots of data collected for two of the tracking conditions. As with fixation conditions, there was a period of decelerating smooth pursuit, a turn, and a period of accelerating smooth pursuit.

Tracking Condition 34°/63°, illustrated in Fig. 3, was also similar to the fixation conditions in that the path of the eye, both before and after it turned, was close to the physical path of the target spot. This was not true, however, of Tracking Condition 63°/117° as illustrated in Fig. 4. For this condition the path of the eye before it turned was intermediate between the physical and "estimated perceived" paths of the target spot, while the path of the eye after the turn was strikingly close to the latter. Qualitative observations such as these led us to perform the following quantitative analysis.

Since the eye did move along straight paths during stabilization, as illustrated in Figs 2, 3, and 4, the orientations of best fitting straight lines were calculated, one for the eye position data preceding, and another for the data following, the turn. For this analysis we needed to specify an objective criterion for when the eye turned. Eye speeds, in degrees of visual angle per second, were computed for thirteen successive 100 msec intervals (the duration of stabilization plus 50 msec) of eye position data. A speed criterion was established whereby the "turn" was indicated by the interval or intervals in which eye speed fell below 2° of visual angle per sec. Only those trials were analyzed for which there was adequate data for calculating the path of the eye both before and after the turn.

We also calculated the average orientation of the retinal path swept out by the target spot during the three full cycles immediately prior to stabilization (for details of this computation see Festinger et al., 1976). These computations allowed us to check whether or

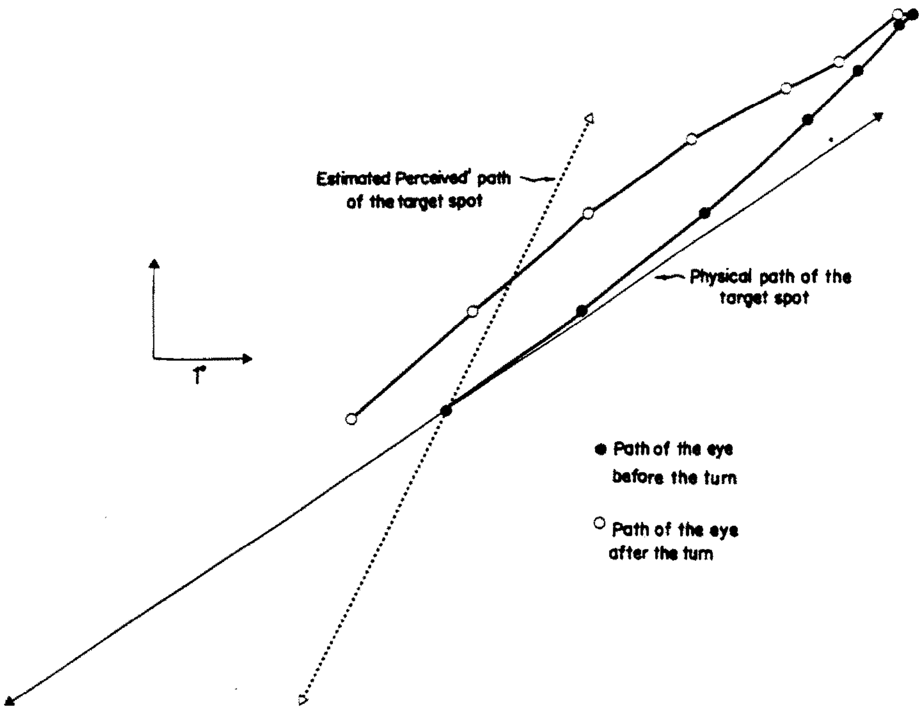

Fig. 3. Path of the eye during stabilization for one trial from Tracking Condition 34°/63°. Straight lines were fitted to the eye position data for each of thirteen successive 100 msec intervals. The directions and extents of the physical and "estimated perceived" paths of the target spot prior to stabilization are indicated by the thin solid line and the dashed line, respectively. These two lines are positioned so that their midpoints coincide with the beginning of the eye's path.

not, prior to stabilization, the eye fixated accurately in fixation conditions, and tracked accurately in tracking conditions.

The following trials were omitted from the analysis: one tracking trial and one fixation trial because the eye turned very early; two tracking trials because eye speed failed to exceed 2° per sec following the turn; and fourteen tracking and seven fixation trials because one or more saccades occurred during the stabilization period. Of all these trials, seven tracking

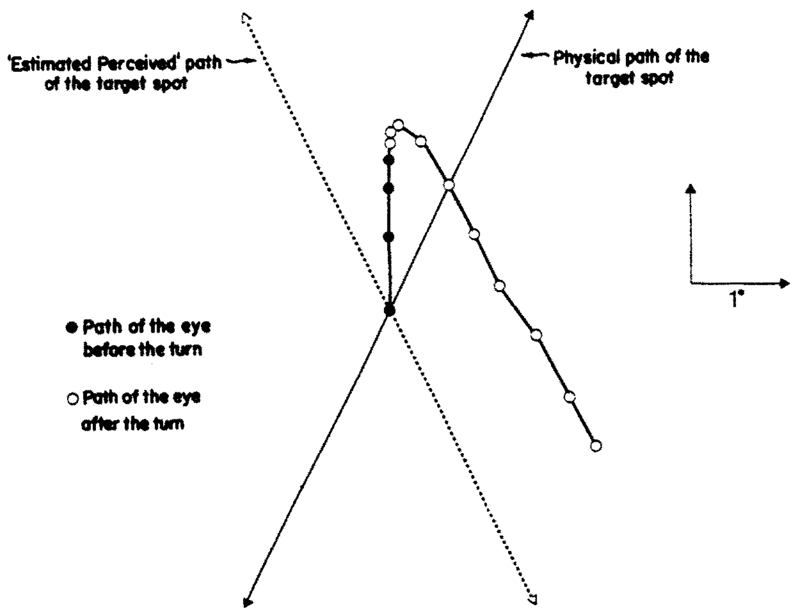

Fig. 4. Path of the eye during stabilization for one trial from Tracking Condition 63°/117°. Straight lines were fitted to the eye position data for each of thirteen successive 100 msec intervals. The directions and extents of the physical and "estimated perceived" paths of the target spot prior to stabilization are indicated by the thin solid line and the dashed line, respectively. These two lines are positioned so that their midpoints coincide with the beginning of the eye's path.

Table 1. Average retinal paths of the target spot prior to stabilization and paths of the eye during stabilization for fixation and tracking conditions

	Path of the target spot	N	Retinal path of the target spot	Path of the eye before the turn	Path of the eye after the turn
Fixation conditions	34°	7	34° (0.12)	37° (3.98)	41° (2.44)
	63°	9	64° (0.26)	52° (4.48)	54° (2.31)
	117°	12	117° (1.14)	127° (0.50)	122° (3.36)
Tracking conditions	34°/63°	15	62° (0.75)	34° (7.66)	38° (3.50)
	63°/117°	24	115° (0.78)	84° (1.64)	119° (5.44)

Figures in parentheses give the inter-subject standard deviation.

trials and four fixation trials were detected as aberrant during the experimental session and were repeated at the end of the day's run. Also, fifteen additional trials (thirteen tracking and two fixation) that were run at the end of the experiment, when observers made perceptual judgments, were included for analysis. A total of thirty-nine tracking trials and twenty-eight fixation trials comprised the data for the analysis.

When rectified by taking their absolute value, the results for Tracking Condition −63°/−117° are similar to the results for Tracking Condition 63°/117°. This is also true of the corresponding pairs of fixation conditions. Therefore, the rectified data for conditions with paths below the horizontal are combined with the corresponding conditions having paths above the horizontal. The data for our three observers are similar and so are averaged together and presented in Table 1. Each value represents the average for the three observers with each observer given equal weight. The inter-subject standard deviations are presented for each condition.

Retinal path of the target spot before stabilization

As can be seen from Table 1, the retinal and physical paths of the target are very close for all fixation conditions. This is expected if, prior to stabilization, observers accurately maintained fixation of the stationary spot. For each tracking condition, the retinal path of the target spot is quite close to its "estimated perceived" path. Because the "estimated perceived" path is calculated on the assumption of perfect tracking of the horizontally moving spot, this result is consistent with good tracking during the prestabilization period.

Path of the eye during stabilization

Table 1. shows that during stabilization in fixation conditions, the path of the eye, both before and after the turn, is close (within 12°) to the physical path of the target spot prior to stabilization. The differences that do exist tend to be reliable across observers because the inter-observer variability is low. We may conclude that whatever small errors in stabilization may have existed did not have a large effect on the direction of smooth pursuit.

For Tracking Condition 34°/63°, the path of the eye during stabilization is close to the physical path control condition. The average paths of the eye before and after the turn are 34° and 38° for this tracking condition as compared to 37° and 41° for Fixation Condition 34°.

Tracking Condition 63°/117° differs from Tracking Condition 34°/63° in three important ways. First, the path of the eye is never close to the physical path control condition. Second, there is a large difference between the average paths of the eye before and after it turns. And finally, the path of the eye after it turns is close to the "estimated perceived" path control condition. The average path of the eye before it turns is 84° for this tracking condition, as compared to 52° for Fixation Condition 63°, and 127° for Fixation Condition 117°. Thus, the average path before the turn for this tracking condition is approximately midway between that found for the two relevant control conditions. After the eye turns, however, the average path for this tracking condition is 119°, as compared to 122° for its "estimated perceived" path control (Fixation Condition 117°). The average paths of the eye before and after it turns thus differ by 35° for Tracking Condition 63°/117°.

Perceptual reports

Our observers were questioned thoroughly about what they had seen during the experiment. They were also given additional tracking trials in which they were specifically asked to pay attention to the path of the target spot. No observer ever realized that how the target spot was moving was influenced by how the observer's eye was moving. Each of them reported that when they went to follow the target spot it continued moving along the path it had been following, turned, and came back along the same path. Even under repeated questioning no observer reported that the target spot appeared to change its course after it turned. When observers were asked to draw what they saw during the additional trials that were run, they always drew the same orientation of target spot path before and after the turn.

The uniformity with which observers reported that the path of the target spot during the 1.25 sec of stabilization resembled its path before stabilization might suggest that they were responding on the basis of their expectations rather than their perceptions. There is evidence that this was not the case. As mentioned previously there were occasional trials on which saccades occured during stabilization. In these instances the observers' drawings accurately showed jumps in the target path. This supports our assumption that observers were reporting their actual perceptual experience.

DISCUSSION—I

In this experiment we were interested in whether or not the "central" motor command to follow a new target is based solely on the prior perceived motion of that target and in whether or not unmonitored "peripheral" processes can transform the "central" command. Our tracking conditions created situations in which, prior to the formulation of a new "central" command to track a target spot, the perceived path of that spot was different from its physical path. As soon as the "central" motor command was executed, the target spot was stabilized on the fovea so that there was no retinal error for which to correct. The path of the eye specified by that "central" command can be inferred from the perceived path of the stabilized target spot on the assumption that the information contained in the "central" motor command is accurately monitored by the perceptual system. "Peripheral" transformation of this "central" motor command can be deduced from systematic discrepancies between the perceived path of the stabilized target spot and the actual path of the eye.

Observers' reports indicate that the target was always perceived to move along the same path when it was stabilized as it did during the pre-stabilization period. On the assumption that the new "central" command was accurately monitored by the perceptual system, this implies that the "central" motor command to track the target spot was based solely on perceptual information about its path. Thus, we can conclude that the "central" motor command, like the perceptual system, does not take accurate account of ongoing tracking prior to stabilization.

Given this conclusion, the eye movement data demonstrate that the "central" motor command can be transformed by "peripheral" processes. First, for Tracking Condition 63°/117°, the path of the eye during the portion of the stabilization period before the turn was intermediate between the pre-stabilization physical and "estimated perceived" paths of the target spot. In this case "peripheral" transformation seems to have partially compensated for ongoing tracking. This "peripheral" transformation could be accounted for by assuming that during tracking of the horizontally moving spot there was a build-up of some ongoing "peripheral" activity that was then partially added to the new "central" command to track the target spot. Second, for Tracking Condition 34°/63°, the path of the eye during the stabilization period, both before and after the turn, was close to the physical path of the target spot during the pre-stabilization period. Thus, it seems that for this tracking condition, "peripheral" transformation of the new "central" motor command fully compensated for ongoing tracking. It is of particular interest that this compensation occured both before and after the eye turned. This implies that ongoing "peripheral" activity, established through pursuit of a horizontally moving spot, is capable of continuing through the sequence of deceleration, turn, and acceleration in the opposite direction.

On the other hand, for Tracking Condition 63°/117°, the ongoing peripheral activity did not continue through the turn. For this condition the path of the eye after it turned was close to the "estimated perceived" path of the target spot prior to stabilization. It seems likely that the actual movement of the eye in this case accurately reflected the path specified by the "central" motor command.

These results raise some difficult questions concerning the functioning of the oculomotor system. Particularly, the difference between the two tracking conditions in the path of the eye after it turned raises the question of why the ongoing "peripheral" activity was added to the "central" motor command in one condition and not in the other.

We can approach this question by asking what the critical difference was between these two tracking conditions. These different interactions might have arisen from differences in the perceived paths of the target spot prior to stabilization. For Tracking Condition 34°/63°, in which ongoing "peripheral" activity was added to the "central" motor command, horizontal tracking prior to stabilization was in the same direction as the horizontal component of the "estimated perceived" target motion. For Tracking Condition 63°/117°, in which the effect of ongoing "peripheral" activity ended at the turn, horizontal tracking was in the opposite direction.

One hypothesis that suggests itself, then, is that whether ongoing peripheral activity does or does not sum with a new "central" command depends upon whether the direction of ongoing horizontal tracking and the horizontal component of the perceived target motion are the same or opposite before that new command is executed. If this hypothesis is correct, then whenever the prior perceived path of the target spot is less than 90°, summation throughout stabilization should be obtained. Summation should not exist past the turn whenever the prior perceived path of the target spot is greater than 90°. Therefore, for any condition in which the "estimated perceived" path of the target spot prior to stabilization is less than 90°, tracking during stabilization should be close to the physical path of the target spot. For any condition in which the "estimated perceived" path of the target spot prior to stabilization is greater than 90°, tracking during the portion of the stabilization period following the eye's turn should be close to the "estimated perceived" path. This hypothesis implies an abrupt discontinuity around 90°.

Alternatively, it may be that the transition is not abrupt but continuous. It may be that the interaction of the ongoing "peripheral" activity with the "central" motor command varies continuously from complete summation to no summation depending upon how much the path specified by the new "central" motor command differs from the path of ongoing tracking.

Our next experiment was intended to provide data that would allow us to choose between these two hypotheses.

PROCEDURE—2

The procedure for this experiment differed from that of the previous experiment only in the number of conditions used and in the paths of the target spots used for the different conditions. A total of six tracking conditions were used in this experiment. These were: 35°/66°, 40°/75°, 45°/84°, 50°/93°, 55°/102°, and 60°/111°. Note that the "estimated perceived" paths of target spot motion for three of these conditions were less than 90°, and for the other three were greater than 90°.

Twelve fixation conditions with physical target motion corresponding to the "estimated perceived" and physical paths of the target spot for the six tracking conditions were employed as controls.

Two paid volunteers, satisfying the same criteria as in the previous experiment, were run. Five 2 hr sessions were necessary to collect a complete set of data, eight replications of each tracking condition, and two replications of each fixation condition, for a total of seventy-two trials. For each stabilized trial three non-stabilized trials were run but were not considered in the analysis.

Because of illness, one of our observers was unable to complete the experiment. Thus, for this observer, we obtained only about half of the intended number of replications for most conditions and did not obtain any data for Fixation Conditions 35°, 45°, and 93°.

RESULTS—2

Eye position data were analyzed using the method employed in the previous experiment. Nine trials were rejected because eye speed failed to exceed 2° per sec following the eye's turn, and one trial was rejected because a saccade occurred during the stabilization period. In addition, we rejected three trials on which one observer began tracking the target spot before the tone sounded. Of these thirteen rejected trials, six were detected as aberrant during an experimental session and were repeated at the end of the day's run. Five trials during which perceptual judgments were made were also analyzed. A total of seventy-six tracking trials and forty fixation trials comprised the data for the analysis.

Retinal path of the target spot before stabilization

The average retinal paths of the target spot during the pre-stabilization period show that there was good fixation or tracking in all conditions. For each fixation condition, the average retinal path is within 1° of the physical path of the target spot. In each tracking condition the deviation of the retinal path from the "estimated perceived" path is less than 2°, always in the clockwise direction. The standard deviation of the retinal paths, within any condition, is less than 2°.

Path of the eye during stabilization

The path of the eye during stabilization for fixation conditions tended to be close to the prior physical path of the target spot as shown in Fig. 5. The data in Fig. 5 are plotted so as to facilitate comparison between these control conditions and their corresponding tracking conditions. Thus, there is a double abscissa. The control for any tracking condition's "estimated perceived" path is plotted at the same position on the abscissa as is the control for the physical path of that same tracking condition. Since the data for the two observers are similar, they are presented graphically in combined form. The paths of the eye before and after the turn are indicated by the filled and open circles, respectively. For conditions in which data were collected for both observers, each circle represents the average of the two observers, each given equal weight.

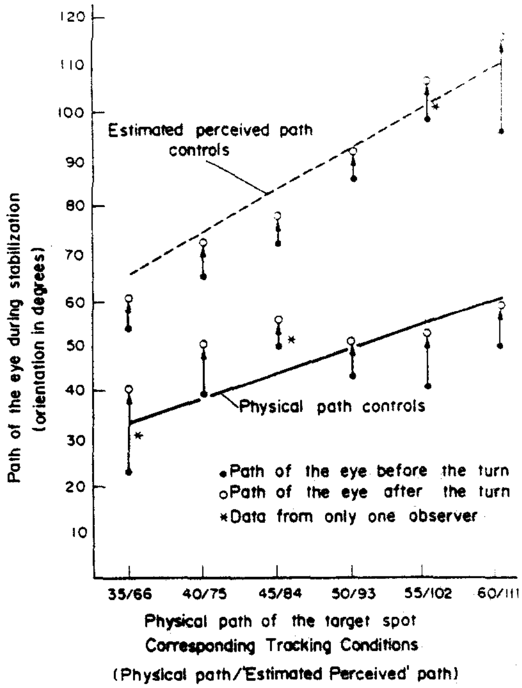

Fig. 5. Path of the eye during stabilization for fixation conditions. To facilitate comparison with Fig. 6, the "estimated perceived" path control for each tracking condition is plotted at the same position on the absicissa as its physical path control. Except where noted by a star, each circle represents the average of two observers, each given equal weight.

As can be seen in Fig. 5, the data tend to fall near the diagonal lines that represent perfect correspondence between path of the eye and the physical path of the target spot. The path of the eye after the turn is at a consistently larger angle than before the turn, the difference ranging from 2° to 20°.

Figure 6 shows the comparable data for the tracking conditions. The solid and dotted lines in the figure represent perfect correspondence between the path of the eye during stabilization and the prior physical path and prior "estimated perceived" path, respectively, of the target. Paths of the eye before and after the eye turned are again indicated by the filled and open circles.

The data for our two observers are similar (the average difference in eye path between observers was less than 4°), and so we averaged the data giving each observer equal weight. The intra-subject standard deviations for each condition ranged from 2° to 16°, with an average of approximately 7°.

The results show a discontinuity in the eye movement data between tracking conditions with "estimated perceived" paths of the target spot less than 90° and "estimated perceived" paths greater than 90°. For the three tracking conditions with "estimated perceived" paths less than 90°, the path of the eye after

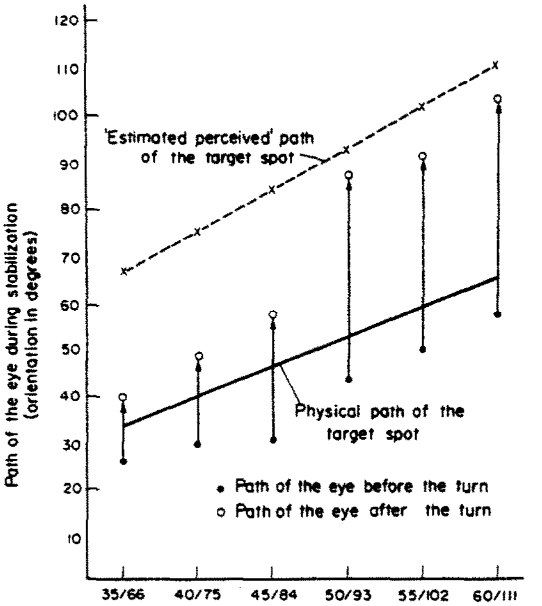

Fig. 6. Path of the eye during stabilization for tracking conditions. Each circle represents the average of two observers, each given equal weight.

it turns is close (within 10°) to the comparable physical path control conditions shown in Fig. 5. For the three tracking conditions with "estimated perceived" paths greater than 90°, the path of the eye after it turns is close (within 15°) to the comparable "estimated perceived" path control conditions. This results in a difference of 29° between Tracking Condition 45°/84° and Tracking Condition 50°/93° in the path of the eye after the turn. The largest difference between any other two adjacent tracking conditions is only 12°.

On the other hand, when the path of the eye before the turn is examined, all tracking conditions are close to their comparable physical path control conditions. For each tracking condition, except 45°/84° (for which the difference is 19°), the difference between the path of the eye before it turns and that for its comparable physical path control condition is less than 10°.

Perceptual reports

As in the previous experiment, observers reported that they never saw the target spot change its course when they went to follow it, nor did they ever observe any difference in the orientation of its path before and after it turned. For one observer, additional trials were run, and she was questioned after each trial and asked to draw what she saw. There was no ambiguity in her reports. She had perceived the target during stabilization to move along the same path before and after it turned, and at the same perceived orientation as that of the target spot prior to stabilization. We were unable to run additional trials for the observer who did not complete the experiment.

DISCUSSION—2

The data concerning the path of the eye following its turn support the hypothesis that a new "central" motor command for smooth pursuit eye movement can interact with ongoing "peripheral" activity in two distinct ways. The new command can continue to sum with ongoing "peripheral" activity, in which case the path of the eye is close to the physical path of the target spot. Alternatively, the summation of the new "central" command with ongoing "peripheral" activity can cease when the eye turns. In this case, the path of the eye after its turn is close to the "estimated perceived" path of the target spot. It appears that summation continues after the eye turns if the horizontal component of the new "central" motor command is in the same direction as prior ongoing horizontal tracking.

For all the tracking conditions in this experiment, the summation of the new "central" motor command with ongoing "peripheral" activity before the eye turned appears to have been nearly complete. This result differs from that obtained in Tracking Condition 63°/117° in the previous experiment. In that condition the path of the eye before it turned was intermediate between the physical and the "estimated perceived" paths of the target spot, which suggested only partial summation. Why we found partial summation for this condition in our first experiment and did not find it for closely comparable conditions in our second experiment is not clear. It may be that the clue lies in the fewer and more easily distinguishable conditions in the first experiment. That the number and variety of conditions employed can affect tracking during stabilization is also evident in the larger differences between the path of the eye before and after the turn in the fixation conditions of our second experiment as compared to the first experiment.

Some partial summation is also hinted at in the data from our second experiment. For tracking conditions with "estimated perceived" paths of less than 90° there is some indication that the differences in the path of the eye before and after the turn are greater than for their physical path control conditions. The pattern of differences across these conditions suggests that summation may decrease somewhat as the "estimated perceived" path of the target spot approaches 90°. This gradual change is small, however, in comparison with the change that occurs from less than 90° to greater than 90°.

THEORETICAL CONSIDERATIONS AND CONCLUSIONS

We have distinguished between the actual movement of the eye and the "central" motor command which orders those movements. We have defined the "central" command as the motor command at that stage at which it is monitored perceptually. Our conclusions depend upon the assumption that this monitoring provides the perceptual system with accurate information about the orientation of the path of the eye specified by the "central" motor command.

Several aspects of our data make this assumption seem reasonable. First, the similarity between the perceived paths of target spot motion before and during stabilization is accounted for if the "central" motor command is formulated entirely on the basis of perceptual information before stabilization, and if the perception during stabilization is then based on an accurate monitoring of that "central" command. Second, the assumption of accurate monitoring is supported by the data for conditions with "estimated perceived" paths of target spot motion greater than 90°. For these conditions, during stabilization, the path of the eye after the turn and the perceived path of the target spot were similar. A simple explanation of this result is that the "central" command is accurately monitored perceptually and is unaltered, in this situation, by "peripheral" transformation.

If this assumption is correct, we may then conclude that the "central" motor command is formulated entirely on the basis of what is visually perceived. When perception is in error, the "central" motor command is also in error. We can also conclude that the "central" motor command can be transformed at a "peripheral" processing stage; that is, a stage at which it is unmonitored. This transformation has the effect, under most of the circumstances which we observed, of "correcting" the "central" motor command so that the eye moves in accordance with the movement in the physical world. This effect seems to be accomplished by summing the "central" motor command with unmonitored "peripheral" activity associated with the prior movement of the eye. Such a summation of the "central" motor command with ongoing "peripheral" activity suggests a system whose operation may be functionally appropriate overall, despite the absence of information "centrally".

The "central" motor command, however, does not always summate with ongoing "peripheral" activity. Under some circumstances the effect of "peripheral" activity appears to cease so that the eye moves along the path indicated by the "central" command, a path quite different from the one along which the target spot was moving prior to stabilization. This result, which can be regarded as a tracking error, is produced by circumstances which are, of course, highly unusual. Whether the limitations in the smooth pursuit system revealed here would produce observable tracking errors in ordinary situations is another question. If errors did occur, it is expected that they would be corrected quickly through the use of error information from the retina.

The concepts of "central motor command," "ongoing peripheral activity," and "peripheral transformation of the central motor command" refer to processes about which we are able to say very little. To conceptualize the functioning of the smooth pursuit system in this way helps to make sense out of its complicated interactions with the visual perceptual system, but many questions remain. Why summation sometimes continues and sometimes ceases when the eye turns, and why in our first experiment we observed evidence of partial summation before the eye turned but found no such evidence in the second experiment, are questions that require further investigation.

Several secondary results emerged from our data. It is clear that a specific pattern of smooth pursuit eye movements, closely resembling prior target spot motion, can be elicited during stabilization. Other studies have already shown, through the use of afterimages and other techniques (Westheimer and Conover, 1954; Deckert, 1964; Steinbach, 1969; Mack and Bachant, 1969; Jordan, 1970; Heywood and Churcher, 1971; Steinbach and Pearce, 1972; Heywood, 1973; Yasui and Young, 1976; Steinbach, 1976), that smooth pursuit activity can be carried out without the target having any significant velocity on the retina. The data from our fixation conditions extend this result by showing the accuracy with which the direction of tracking during stabilization is able to match the direction of previous target spot motion. Furthermore, our data show that even in the absence of retinal error information, the direction of eye motion is reversed at approximately the time the target spot would have reversed direction. This appears to be direct evidence for an internal clock that can be set in rhythm with periodic target motion, as has been suggested elsewhere (Robinson, 1968).

Finally, those instances in our experiments in which the perceived path of the stabilized target spot differed strikingly from the actual path of the eye bear directly on the question of whether information from the extraocular muscles can be used effectively in the perception of the direction of motion. These perceptions of the direction of motion of a single foveally stabilized spot of light, in otherwise total darkness, must have been derived from extraretinal information. Our explanation of these effects is that the perceptual system obtains eye movement information by monitoring the "central" motor command, while actual eye movement can be affected by an unmonitored "peripheral" transformation of this command. Any information that the perceptual system receives from the extraocular muscles would, presumably, accurately reflect the direction of actual eye movement. One is forced to conclude from these discrepancies between actual direction of eye movement and the perceived direction of motion of the stabilized target spot that, if the perceptual system does make use of any extraretinal inflow information about the direction of smooth pursuit eye movement, that information can at best be very crude.

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