Vision Res. Vol. 16, pp. 1377 to 1386. Pergamon Press 1976. Printed in Great Britain.

VISUAL PERCEPTION DURING SMOOTH PURSUIT EYE MOVEMENTS[1]

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(Received 19 January 1976; in revised form 23 April 1976)

Abstract—With accurate measurement of eye position during smooth tracking, comparison of the retinal and perceived paths of spots of light moving in harmonic motion indicates little compensation for smooth pursuit eye movements by the perceptual system. The data suggest that during smooth pursuit, the perceptual system has access to information about direction of tracking, and assumes a relatively low speed, almost irrespective of the actual speed of the eye. It appears, then, that the specification of innervation to the extraocular muscles for smooth tracking is predominantly peripheral, i.e. it occurs beyond the stage in the efferent command process monitored by perception.

There are many reports in the literature that indicate inaccurate perception of the paths, extents and velocities of movement of targets that move with reasonably slow velocities on a homogeneous background. The earliest study that bears directly on the issues addressed in this paper is reported by Dodge (1904). Observers were instructed to track a spot of light moving with simple harmonic motion in a darkened room. The eyes engaged in predominantly smooth pursuit eye movements. Dodge reports that the perceived extent of movement of this tracked target was about one third of the perceived extent of motion of another untracked spot that moved simultaneously through an identical physical extent but 180 degrees out of phase with the tracked spot. From examination of the photographic records of the eye movements of his observers, Dodge concluded that the perceptual system had no information at all about smooth pursuit eye movements and that the perceived extent of motion was entirely determined by retinal slip.

This interpretation was disputed by Carr (1907) and the controversy never seems to have been clearly resolved (Dodge, 1910; Carr, 1935). The issue of the extent to which the visual perceptual system compensates for smooth pursuit eye movements was not clearly and directly addressed again until Stoper (1967) investigated the problem. He briefly flashed, in succession, two lines while the observer's eye was engaged in more or less accurate smooth pursuit of a target on a homogeneous ground. The observer's judgments of the relative spatial location of these successive flashes indicate the extent to which this perception takes into account the actual movement of the eye. In his Experiment II, he used interflash intervals of up to 306 msec. His data show that the perception is almost completely determined by retinal location of the flashes, i.e. there is almost no compensation for smooth pursuit eye movements. He states: "Expressed in terms of 'percentage of compensation,' there is never more than 16% compensation for the time intervals used here" (p. 112).

In a further experiment, Stoper explored longer interflash intervals and reports that the compensation for the smooth pursuit eye movements increases as the interval increases. However, even at his longest interval of 1734 msec, the average % of compensation for eye movement is only 64%. Moreover, at these longer time intervals the author reports that the perceptions were very ambiguous.

From the Stoper report one would come to the conclusion that the perceptual system takes relatively little account of the actual eye movement when it is engaged in smooth pursuit. A similar conclusion was reached by Festinger and Easton (1974) in a more indirect manner. Following up an observation by Fujii (1943), they found that, when a target is moved on a homogeneous ground with uniform speed in a square path at a frequency of, say, 0.5 Hz with target speeds of 10°–15°/sec, an observer who follows the target motion with his eyes (head restrained) perceives the path of the target as resembling a pincushion rather than a square. By recording the actual eye movements of observers while following such a target, they were able to compute the exact movement of the target on the retina and showed that the perception closely resembled the form of actual retinal path. This again implies that the perceptual system takes rather little account of actual smooth pursuit eye movements.

There are other related reports in the literature that have been interpreted differently, usually in terms of principles of perceptual organization. Duncker (1929) mounted a light near the rim of a wheel and reports that moving the wheel in a dark room produces the expected perception of cycloid motion of the light. However, if a second light is also mounted at the hub of the wheel, the outer light is then seen to move in a circular path around the center light as the wheel moves. This kind of finding has been interpreted in terms of the dissociation of a common group motion from the total motion, resulting in the perception of the relative motions of the individual lights. Johansson (1950) reports an excellent series of studies guided by this principle of the organization of perception.

[1] The research on which this article is based was supported by Grant Number MH-16327 from the National Institute of Mental Health to Leon Festinger.

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These authors have, understandably, been less concerned about the observer's eye movements and have not measured them. It is likely, as Stoper (1973) points out, that many of these "organizational" phenomena are attributable to the lack of information the perceptual system has concerning smooth pursuit eye movements.

Johansson (1950), for example, reports that if an observer follows a target moving horizontally in simple harmonic motion, a vertically moving spot, which is 90° out of phase with the tracked spot, is perceived to move in a nearly circular path. This vertically moving spot would, of course, sweep out a circular path on the retina if the eye tracked the horizontally moving spot perfectly. The close resemblance of the perception to the likely retinal path might simply indicate the lack of compensation for smooth pursuit eye movements. This is not to say that organizational principles do not at all affect perception. Indeed, the demonstration by Johansson (1971) of the vivid perception of, say, a man walking when the observer only sees the movement of lights attached to limbs and body, argues strongly for the operation of such organizational principles in some circumstances.

In a somewhat different vein, Sumi (1964a, b, 1971) and Gogel (1974) report studies concerning distortion in the perception of the paths of motion of spots moving toward and away from each other at right angles. Again in these studies eye movements are not measured. Gogel did instruct his subjects not to move their eyes but it is not at all certain that such an instruction could be followed in the absence of any fixation point. It is our guess that the reported perceptions in these studies are probably attributable to the lack of compensation for smooth pursuit eye movements by the perceptual system.

There are some studies in the literature that seem to dispute our conclusions about compensation for smooth pursuit eye movement. Dichgans, Kömer and Voigt (1969) report that the perceived speed of a smoothly tracked target is 63% of the speed perceived when the eye is stationary. Mack and Herman (1972) report only a 10% reduction in perceived extent of motion of a tracked target, which would imply 90% compensation for smooth pursuit eye motion. In both studies, however, the target starts to move instantaneously at a uniform speed. The eye is thus stationary for probably about 150 msec or so while the target is moving at its full speed. The retinal information obtained during this period is undoubtedly excellent and the perceptual system may be capable of integrating such information over time. The situation is, of course, very different if the target moves in simple harmonic motion since little relevant retinal information is obtained during the initial stationary eye period.

Coren, Bradley, Holnig and Girgus (1975) present data on the perceived diameter of a target moving in a circular path in darkness while the observer is instructed to follow the target with his eyes. The reported results would lead to a conclusion of very high compensation for eye movements. Again, however, the target starts moving instantaneously at its full uniform speed. Thus considerable retinal information may be obtained which can be used by the perceptual system. In addition, except for the lowest frequency, this study uses target speeds that the human eye is not capable of following adequately with smooth pursuit motion (Young, 1971).

The issue of whether or not the perceptual system takes smooth pursuit eye movements into account has considerable theoretical importance. It seems likely (Brindley and Merton, 1960; Skavenski, Haddad and Steinman, 1972) that the perceptual system does not have access to inflow information about eye position from the extraocular muscles but only has access to outflow information. In other words, the perceptual system gets information about eye position by monitoring the outflow commands to the oculomotor system. This information would only be complete to the extent that the information contained in that central outflow command is complete. The existing literature indicates that the perceptual system can be grossly inaccurate in its compensation for changes in eye position brought about by smooth pursuit motion and this raises the possibility that the central commands for such movements may be quite general in nature, lacking specific information. By exploring this, we may be able to open a window on the functioning of the oculomotor control system for smooth pursuit eye motion.

The experiments to be reported below are an attempt to collect data that would enable accurate, quantitative assessments about what the perceptual system "knows" about actual smooth pursuit eye movements.

PROCEDURE

In order to assess the amount of information available to the perceptual system concerning smooth pursuit eye movements, the following general procedure was used.

(1) Observers were asked to track a luminous target moving in simple harmonic motion. This kind of motion was chosen since, at appropriate frequencies and velocities, good smooth pursuit motion of the eyes can be sustained.

(2) Measures were obtained concerning (a) the perceived extent of motion of the target, and (b) the perceived direction of motion of another luminous spot moving in phase with the target.

(3) Accurate measures of eye position were recorded throughout so that we could compute the retinal information available to the observer.

(4) Comparing the retinal information available with the measured perception of the observer could provide answers to our basic question, i.e. how much information about the change in eye position over time is available to perception.

The visual display

The visual display contained spots of light moving in the dark. The spots always moved back and forth along linear paths in simple harmonic motion and in phase with each other. The two basic spatial configurations of spot motion which we used are diagrammed in Figs. 1a and b, where the open circles labeled A, B and C represent the spots at the midpoints of their paths, and the lines represent typical extents, positions, and orientations of these paths. Spots A and B always moved along horizontal paths and through equal extents, but the orientation of the linear path of motion of Spot C in Fig. 1b was variable. Spot A was always the tracked spot. Part of the observer's task on each trial was to visually track Spot A as accurately as he could at all times.

Spot B was the adjustment spot, whose offset from the tracked spot was under the control of the observer. The

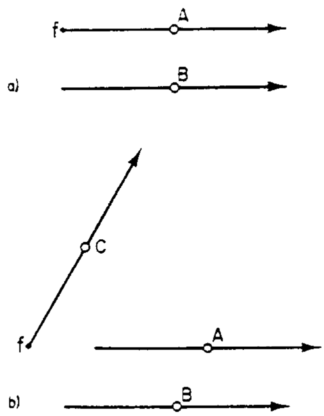

Fig. 1. Scheme of visual displays. (a) Visual display for trials in which the perceived extent of Spot A was measured. Spots A and B represent spots at the midpoints of their paths, always moving horizontally through equal extents. Spot B is the adjustment spot, its vertical offset adjustable to indicate the perceived horizontal extent of Spot A. For control trials, Spot "f" was also present to be fixated while the adjustment was made. Spots A and B remained aligned vertically throughout a trial. (b) Visual display for trials in which the perceived orientation of Spot C was measured. The linear orientation of Spot C varied from trial to trial. Subjects tracked Spot A and adjusted the horizontal offset of Spot B so that the orientation of an imaginary line connecting Spots A and B would be parallel to the perceived orientation of Spot C. For control trials, Spot "f" was also present to be fixated while the adjustment was made.

two-spot display, exemplified in Fig. 1a, was used when measurements were to be made of the perceived extent of motion of the tracked spot. The adjustment Spot B was always directly beneath that tracked spot but its vertical position was variable. The observer's task was to adjust this vertical distance until it appeared equal to the horizontal distance through which the two spots appeared to move on each half cycle.

The three-spot display, exemplified in Fig. 1b, was used when measurements were to be made of the perceived direction of motion of the vertically moving Spot C. The path of the adjustment spot was always 1° below the path of the tracked spot, and the horizontal offset of the adjustment spot from the tracked spot was variable. The observer's task with these displays was to adjust this horizontal offset until the orientation of the imaginary line connecting the tracked Spot A and the adjustment Spot B appeared to parallel the orientation of the path of motion of Spot C.

To obtain control measures of perception of extent or direction of motion while the eye was stationary, the identical displays were used with the addition that in each case a stationary fixation spot was added at the point labeled "f" in Fig. 1.

The visual displays were generated digitally by a Nova 2 computer linked, through an oscilloscope control containing two 13 bit digital to analogue converters, to a Hewlitt Packard 1310 oscilloscope, equipped with a p15 phosphor. The decay time of this phosphor is less than 3 μsec so that the moving spots left essentially no physical trace behind them. A contrast screen served to effectively remove any general glow from the oscilloscope face. The observers viewed the display in total darkness from a distance of 1 m with head held in place by a bite board and forehead rest.

Measurement of eye position

The position of the observer's right eye (left eye always occluded) was monitored by a double Purkinje image eye tracker, which has been described in detail elsewhere (Cornsweet and Crane, 1973). Briefly, the eye tracker operates by measuring the relative position of the two images created by reflecting a beam of i.r. light off of the front surface of the cornea and the rear surface of the lens. When appropriately calibrated, the eye tracker output provides two continuous analog voltage signals proportional to horizontal and vertical eye position over an approx 16 by 16° field with a noise level less than 4′ of arc.

Because the measurement involves a comparison of two reflections from the eye which do not change relative to each other for translational movements of the eye, one major source of inaccuracy is eliminated. The raw output of the eye tracker, however, is not linear with respect to direction of gaze and these non-linearities vary somewhat from observer to observer. In addition, different observers required different scale factor adjustments, probably due to differences in the radius of curvature of the cornea, of the rear of the lens, and the size of the eyeball. The accuracy of the eye position data is hence primarily determined by the accuracy of calibration and the correction for non-linearities. Accordingly, the first 2-hr session with each observer was devoted to gathering calibration data. The observer fixated a spot of light that jumped in a quasi-random path through 81 positions forming a 9 × 9 square matrix. At each spot position the median eye position was computed and recorded. The data from eight such trials were used to empirically construct a two dimensional matrix of correction vectors and to compute a scale factor for the observer.

The voltage outputs from the eye tracker corresponding to the horizontal and vertical components of eye position were sampled every 2 msec, converted to digital form with 12 bit resolution, corrected for linearity and scale factor and stored in the computer. Every 2 sec the accumulated data were written out on magnetic tape for permanent storage.

Measures of perception

The observers' adjustments of Spot B in Fig. 1 were also under the control of the computer. The observer had access to a two way switch which was monitored every 2 msec by the computer through a general purpose digital interface. Depending on the position of the switch, the computer gradually moved Spot B to the left or the right (or up or down). When the observer was satisfied with the adjustment, pushing a second switch, also monitored by the computer, caused the trial to end. The computer then printed out the exact position of Spot B in relation to Spot A.

Experimental design

Data were collected from observers in three different conditions designed to answer somewhat different questions.

Condition 1. The purpose here was to assess whether the information concerning smooth pursuit eye movements that was available to perception varied as the speed of the actual eye movements varied. Three observers with no previous relevant experience, who knew nothing about the purposes of the experiment, were used. They were all paid volunteers.

In this condition, the extent of motion of the tracked spot was always 4°. Four different frequencies of simple harmonic motion were used, namely 0.125, 0.25, 0.50 and 1.00 Hz. The corresponding maximum speeds of the tracked spot at the center of its excursion were about 1.6, 3.1, 6.3 and 12.6 deg/sec. At each frequency there were six experimental trials using the two-spot display (Fig. 1a) to obtain measures of the perceived extent of motion of the tracked spot. On three of these trials the initial separation between the tracked spot and the adjustment spot was 0.25° and on the other three it was 4.18°. Six fixation control trials for extent settings were also run at each frequency at each of three extents, namely 1°, 2° and 3°, chosen from pilot work to bracket the settings made on the experimental trials.

In the experimental trials using the 3 spot display (Fig. 1b) in which the perceived orientation of the path of the untracked spot was measured, that spot always had a vertical component of motion of 4° of visual angle, but the horizontal component of its motion was varied from trial to trial in order to obtain different orientations of its path of motion. For each frequency eight different orientations were chosen so that the retinal paths, if the eye were to track the target (Spot A) perfectly, would cluster in 5° steps between 60° and 75° and between 105° and 120°, measured counter-clockwise from the horizontal. The avoidance of the 90° area and the variation in orientation was intended to prevent the development of habitual responses. Two trials were run at each orientation, the adjustment spot having an initial horizontal offset of 3° to the left or to the right of the tracked spot. Fourteen fixation control trials were run at each frequency, two at each of seven physical orientations, ranging in 15° steps from 30° to 120°. These values were also chosen from pilot work to bracket the perceptions on the experimental trials.

The experiment was run in four, approx 2-hr sessions with all of the 42 trials for a given frequency contained within a single session. Each session was run on a separate day. Within each session all four kinds of trials (experimental and control, extent and orientation) were mixed together in a random, counter-balanced order.

Condition 2. Results obtained in Condition 1 could be affected by the fact that, on any one day, an observer experienced only one frequency of spot motion. The question may be asked whether more, or different, information would be available to the perceptual system if frequencies were mixed within each day. Two additional naive observers were run to answer this question.

This condition was identical to Condition 1 except that all four frequencies were mixed on each day. In order to maximize the mixing of frequencies within each session, the number of trials per session was increased and we did not mix measurements of extent with measurements of orientation on the same day. All of the orientation measurements were presented on two successive days and all of the extent measurements were made on a third day. Each session contained an equal number of trials at each of the four frequencies of spot motion, the trials being arranged in a random counterbalanced order with the restriction that the same frequency never occurred on two successive trials.

Condition 3. To separate the variables of frequency and velocity two more naive observers were run in a series of trials similar to the previous ones. Now, however, the frequency of harmonic motion of the spots was held constant at 0.5 Hz while the velocity of motion was varied by varying the extents through which they moved. Three extents of motion of the tracked spot were chosen, namely 2°, 4° and 8°. The horizontal components of motion of the untracked spot in the orientation trials were adjusted to give the same retinal angles, with perfect tracking, as were used in Conditions 1 and 2. The same range of orientation controls was also used.

For each of the three physical extents, six experimental trials were run on which perceived extent was measured. On three of these the initial vertical separation of the tracked and adjustment spots was 0.25°, and on the other three was 6.25°. Six extent measurement control trials were also run at 0.5°, 1° and 1.5° for the 2° extent controls; 1°, 2° and 3° for the 4° extent controls; and 2°, 4° and 6° for the 8° extent controls.

The experiment was run in three sessions, and analogously to Condition 1, all the trials for a given extent of motion of the tracked spot were run within the same session.

Analysis of data

The linearized data from the eye tracker specify rather precisely the angular orientation of the observer's right eye at 2 msec intervals. By subtracting this eye position information from the known positions, in terms of visual angle, of each of the spots in the display at each time interval, we can calculate the motion of each of these spots relative to the moving eye. These calculations tell us what retinal information exists and our subsequent analysis is based on the assumption that this retinal information is available, in some fairly accurate form, to the perceptual system.

If the eye movements of the observers contained no saccades the analysis of our data would be straightforward. Our data show, however, that at all speeds of the tracked spot, even the slowest, saccadic eye movements do occur. To ignore the many half-cycles in which saccades occurred would seriously bias the data. Since our purpose is to assess the amount of information the perceptual system has about smooth pursuit eye movements, certain decisions had to be made about how to treat these saccadic eye movements.

It seems plausible to assume that the perceptual system has sufficient information to be able to discount retinal motions produced by saccades. This does not involve the assumption that the perceptual system has accurate extraretinal information about the saccadic eye movement itself. To the extent that the saccadic eye movement is executed in order to bring the target from some relatively peripheral point on the retina onto the fovea, the perceptual system has retinal information, before the saccade, concerning the distance of the target from the fovea, and also has information, after the saccade, about the extent to which that distance was reduced.

Since we want to calculate a combination of everything the perceptual system knows except for possible information about smooth pursuit movements, we must also make some assumption about how the saccadic and smooth pursuit systems interact. There are two somewhat different assumptions that could be made. It is possible that the saccadic eye movement, when it occurs, replaces the smooth pursuit motion of the eye. That is, the smooth pursuit system might be turned off for the duration of the saccade and then turned on again at its conclusion. On the other hand, it is possible that the saccade, when it occurs, is superimposed on the ongoing smooth pursuit motion which continues unabated as a component of the total eye movement.

Close examination of our eye movement data persuades us that the second possibility is more likely to be correct. There are two main reasons for this. First of all, there are never any pauses of the eye following a saccade. At the completion of the saccade the eye immediately moves in smooth pursuit. Secondly, there are never any marked modifications of the velocity of smooth pursuit motion from before to after a saccade. Following a saccade the eye movement appears to be a smooth continuation of the pursuit movement preceding the saccade. We have, consequently, assumed in our calculations, that the saccades are superimposed onto continuing smooth pursuit motion.

To be precise, the velocities of the eye over 20 msec periods before and after the saccade are averaged and this average velocity is assumed to have been maintained by the smooth pursuit system for the duration of the saccade. The magnitude of the saccade is calculated as being the total change in eye position from before to after the saccade minus the distance the eye is calculated to have moved in smooth pursuit during that period. The eye movement records are then corrected to remove this calculated magnitude of saccade. When these corrected eye positions are subtracted from the known spot positions in our visual displays, the result is a combination of information available from the retina and from saccades. We will call this "retinal information."

To summarize the relevant "retinal information" for trials on which we measured the perceived orientation of the non-tracked, vertically moving spot, we calculated a best fitting straight line to the "retinal path" swept out by that vertically moving spot for each half cycle of spot motion. For trials on which we measured the perceived extent of movement of the tracked spot we calculated, for each half cycle, the extent of "retinal motion" swept out by the tracked spot. In both kinds of trials, we obtained a single estimate by averaging the last ten half cycles up to the final one prior to the completion of the observer's setting. At low frequencies of spot motion the observer frequently completed the setting in less than 10 half cycles. In such cases all but the first and the final half cycles were averaged. All of the eye movement data were visually examined on a computer controlled display. Half cycles during which the observer blinked or during which the tracker lost the eye (both relatively infrequent occurrences) were excluded from the analysis.

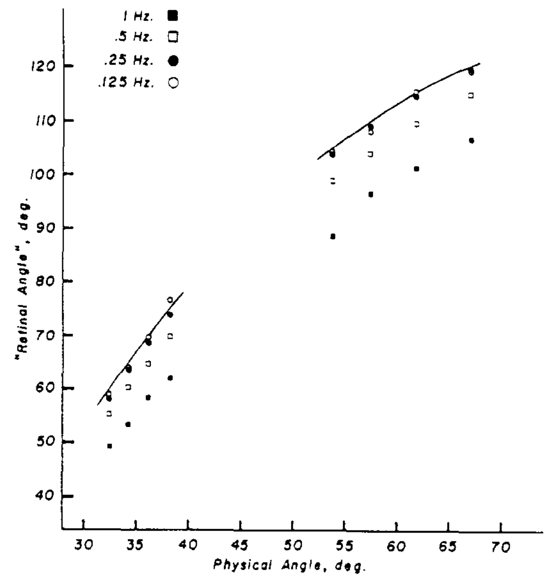

Fig. 2. Relationship between "retinal angle" and physical angle for Spot C at each frequency employed. Each point represents the average setting of five subjects for a given frequency and physical angle. Spot C's "retinal angle" (measured counterclockwise from the horizontal) is computed from the best straight line fitted to the "retinal information". The solid curve indicates the "retinal angle" that would correspond to perfect smooth pursuit of the eye.

RESULTS

Our data concern the perception of paths and extents of motion of moving luminous spots on a totally contourless ground while the eye, itself, is engaged in smooth pursuit motion. In the absence of stationary contours in the visual field, these perceptions can be based on two sources of information only. There is potential information available from the paths swept out on the retina, paths which are a joint function of the spot motion and the eye motion. There is also potential extraretinal information available about saccadic and about smooth pursuit eye movements. The data enable us to examine the extent to which information about smooth pursuit eye movements contributes to the visual perception. We will examine the data on this point separately for the perception of the path of the nontracked spot and the perception of the extent of motion of the tracked spot.

Perception of the path of the nontracked spot

The measures of the perception of the path of Spot C can be expressed as the perceived angle (measuring counter clockwise from the horizontal). The slopes of the best straight lines fitted to the "retinal information" were also converted to "retinal angles" for comparison with the perception.

The smooth pursuit motion of the eye is, of course, never perfect. How adequate it is depends on the frequency (and velocity) of the motion of the tracked spot. In our data, the tracking is least adequate at 1 Hz and improves steadily up to 0.25 Hz. At 0.125 Hz the eye frequently moves faster than the spot and many of the interspersed saccades are counter to the direction of smooth pursuit motion.

Because of the differing adequacy of the smooth pursuit motion, the computed "retinal angle" of Spot C differs for different frequencies of the same physical constellation of spot motions. Figure 2 presents these average "retinal angles" for each frequency and each physical constellation of spots. The data represent the averages of five subjects, three run with only one frequency on each day and two run with the four frequencies mixed together each day (Conditions 1 and 2). These two conditions are combined because there are no discernable differences between them on these measures. The solid curve indicates the "retinal angle" that would correspond to perfect smooth pursuit motion of the eye. With these differences among frequencies in mind, the remainder of the presentation of data will be with respect to these "retinal angles."

The main result is easily stated. The perception of the direction of motion of the nontracked spot is much closer to the "retinal angle" than to the physical angle. Figure 3 shows the relation between perceived angle and retinal angle. Each point on the figure is the average of two measurements at a given physical angle for each of the five subjects mentioned above. Each subject is represented by 32 points, eight physical angles each at four different frequencies. The straight line that runs through the plotted points is the line of exact correspondence between perceptual angle and "retinal angle." The curved lines in the lower part of the figure indicate exact correspondence of perceptual angle and physical angle.

From the data in Fig. 3 we cannot be certain about the exact extent to which the perception is dominated by the "retinal angle" since any pyschophysical measurement may be affected by constant errors. It was for this reason that control measurements were obtained while observers fixated the stationary point labeled "f" in Fig. 1. Examination of these control measurements reveals, however, that this choice of a control situation was very unfortunate. With Spots A, B and C all in the periphery, the distance between the spots had a large effect on the measures, thus

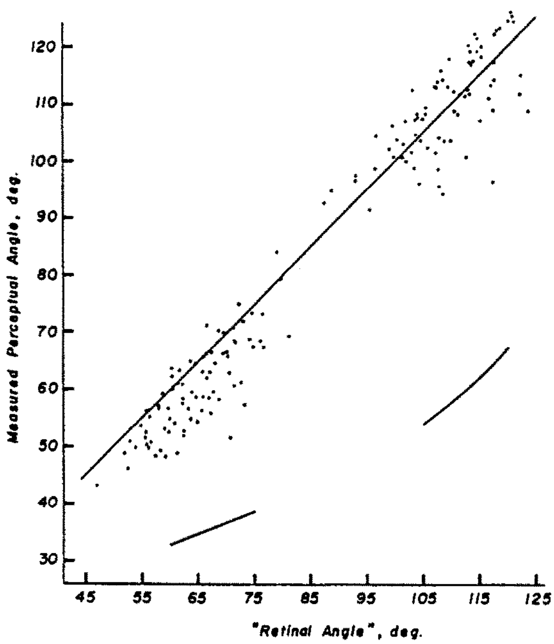

Fig. 3. Relationship between "retinal angle" and perceived angle for Spot C. Each point is the average of two measurements at a given physical angle. Each subject is represented by 32 points—eight physical angles at four frequencies. The straight line represents exact correspondence between perceived angle and "retinal angle". The curved lines represent exact correspondence between perceived angle and physical angle.

particularly distorting the control data for oblique angles. Our control data seem quite useless.

There is also another consideration that limits what we can say about absolute magnitudes of effects in Fig. 3. There is a possible question that might be raised as to whether our method of measurement itself might not have encouraged reliance on retinal information. We can say, however, that perceptions that are close to "retinal angles" are obtained with other methods of measurement also. In preliminary work we asked observers to estimate the angle of the perceived path or to draw it. Our basic results seem quite independent of the method of measurement. It is still possible, nonetheless, that the exact absolute quantities of difference between "retinal angle" and perception might be, to some extent, influenced by our method.

We can, however, compare different frequencies since, whatever the constant errors, they should be roughly the same. With these problems in mind we may examine the data more carefully to see if there are differences in the extent to which the smooth pursuit eye motion is taken into account perceptually in the various frequency conditions. Since the frequencies varied over an eight-fold range, and hence the smooth pursuit eye velocities also varied over a considerable range, we may look to see whether the perceptual system takes account of these differences.

Figure 4 illustrates the computations on which the rest of our analysis of the data is based. Since we know the "retinal angle" and the perceived angle, we can calculate the distance that the perceptual system assumed the eye to have moved in smooth pursuit.

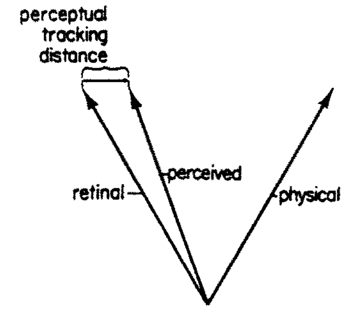

Fig. 4. Computation of "perceptual tracking distance". Arrows (from right to left) indicate typical physical, perceived, and retinal paths of motion of a spot of light while the eye smoothly tracks another spot of light (not shown) which is moving horizontally. The "perceptual tracking distance", which is the distance that the perceptual system assumes the eye to have moved in smooth pursuit, is the horizontal component of the difference between the perceived and retinal paths of motion.

In the figure we have labeled this "perceptual tracking distance." We can also compute the average distance per half cycle that the eye actually did move in smooth pursuit. These data are presented in the upper half of Table 1.

It can be seen that, while the extent of the actual smooth pursuit eye movement varies from 3.2° at 1.0 Hz to a full 4° at 0.125 Hz, the amount of eye movement that the perceptual system seems to know about is small. There is, however, a systematic tendency for the "perceptual tracking distance" to increase somewhat for lower frequencies at which the eye actually moves in smooth pursuit over a larger extent. To interpret this trend it is helpful to examine the comparable data from the two additional subjects for whom the frequency was held constant at 0.5 Hz while the actual extent of movement of the tracked spot was either 2°, 4° or 8° (Condition 3). The range of actual horizontal eye movement for these two subjects is, of course, much greater. These data are presented in the lower half of Table 1.

These two observers both show negative values for "perceptual tracking distance." To take this at face value would mean that the perceptual system acts as if the eye were moving in a direction opposite to its actual motion. Since this is not sensible, we must interpret these negative values as reflecting constant errors of measurement, emphasizing again the caution that must be exercised in interpreting absolute magnitudes in the data.

Table 1. Calculations based on perceived angle: average "perceptual" and actual distance of smooth pursuit eye movement (deg of visual angle)

	Tracked spot extent = 4°			
Hz =	1.0	0.5	0.25	0.125
"Perceptual"	0.04	−0.01	0.21	0.49
Actual	3.22	3.71	3.94	4.01
	Frequency = 0.5 Hz			
Extent =		8°	4°	2°
"Perceptual"		−0.61	−0.56	−0.29
Actual		7.45	3.72	1.88

Table 2. Perceived extent of tracked spot (deg of visual angle)

	Tracked spot extent = 4°			
Hz =	1.0	0.5	0.25	0.125
One frequency per day	1.34	1.29	1.28	1.31
Mixed in same day	2.33	2.35	2.61	2.76
	Frequency = 0.5 Hz			
Extent =		8°	4°	2°
One extent per day		2.05	1.36	1.04

Again, however, if we compare these values across the different extents of motion of the tracked spot, it seems clear that the perceptual system does not take into account much about the distance that the eye actually moves in smooth pursuit. Here we have an appreciable range of distance the eye travels, from about 7.5° down to about 1.9°. Nevertheless the differences in "perceptual tracking distance" remain very small. It seems clear that there is not much correspondence between the "perceptual tracking distance" and the actual distance the eye moves.

Perception of extent of movement of the tracked spot

If the perceptual system knows little about the distance over which the eye moves in smooth pursuit, then we should also expect to obtain evidence of this in the perception of the extent of movement of the tracked spot. These measurements were much more difficult for the subjects to make, and are more variable. Again, unfortunately, we cannot apply any proper correction for possible constant errors of measurement because the control measures that we did obtain are quite inappropriate. Again, they seem inappropriately distorted because of the distance in the visual periphery at which the measurement had to be made.

Table 2 presents the data on the perceived extent of movement of the tracked spot. The means are presented separately here for the three subjects who experienced only one frequency per day and the two for whom frequencies were mixed because their results on this measure are different. It can readily be seen that in the one frequency per day situation the perceived extent is just a bit more than 30% of the true extent of spot movement. In the mixed frequency situation it is almost two-thirds of the true extent. We will comment below on the possible reasons for this difference.

When frequency was held constant at 0.5 Hz and the actual extent of movement of the tracked spot was varied there is a relationship, clearly, between the true extent and the perceived extent. When the true extent was 2°, the perceived extent was 1°; when the true extent was 8°, the perceived extent was 2°. Clearly the perceived extent is not, here, a constant percentage of the true extent of movement.

The data in Table 2 do not tell us much, however, since these numbers reflect the combination of "retinal information" about movement of the tracked spot and information about smooth pursuit eye movements. We want to subtract the "retinal information" from the perceived extent in order to estimate the "perceptual tracking distance." Table 3 presents these data together with the means of the actual extent of smooth pursuit eye movements. The rather large values for extent of eye movement at 0.25 and 0.125 Hz in the second row of the table are entirely attributable to one subject. It can readily be seen that when the true extent was constant at 4° and frequency varied, the "perceptual tracking distance" is considerably smaller than the actual distance of smooth pursuit eye movement.

One thing that emerges here, however, is the fact that as the frequency decreases the "perceptual tracking distance" increases. We noted this as a suggestion in the data on the perceived angle of movement of the nontracked spot, but here it is a very clear and pronounced effect. On the other hand, for the subjects for whom frequency was held constant while the actual extent was varied, there is only a very small increase in "perceptual tracking distance" for an almost fourfold increase in the actual distance that the eye moved in smooth pursuit. These data suggest that the "perceptual tracking distance" is primarily dependent, not upon the distance the eye moves, but upon the time it takes the spot to move through a half cycle. When this time is held constant at 0.5 Hz, the calculated "perceptual tracking distance" does not change much in spite of large changes in the extent of actual smooth pursuit eye movements. When this time per half cycle varies over an eight-fold range (from 1.0 to 0.125 Hz) the "perceptual tracking distance" changes considerably even though there are only small changes in the actual extent of smooth pursuit eye movements.

This would suggest that the perceptual system does not have direct information, however imperfect, about

Table 3. Calculations from perceived extent of the tracked spot: average "perceptual" and actual distances of smooth pursuit eye movement (deg of visual angle)

			Tracked spot extent = 4°			
		Hz =	1.0	0.5	0.25	0.125
One frequency per day	"Perceptual"		0.30	0.97	1.46	1.77
	Actual		2.93	3.67	4.19	4.45
Mixed in same day	"Perceptual"		1.58	2.07	2.66	2.86
	Actual		3.25	3.72	4.05	4.10
			Frequency = 0.5 Hz			
		Extent =		8°	4°	2°
One extent per day	"Perceptual"			1.34	1.10	0.88
	Actual			7.28	3.73	1.85

Table 4. Average "perceptual" and actual speed of smooth pursuit eye movement (deg of visual angle/sec)

Computation based on		Hz = 1.0	0.5	0.25	0.125
Perceived angle	"Perceptual"	0.08	−0.01	0.10	0.12
	Actual	6.44	3.71	1.97	1.00
Perceived extent (1 Hz/day)	"Perceptual"	0.60	0.97	0.73	0.44
	Actual	5.86	3.67	2.09	1.11
Perceived extent (mixed Hz)	"Perceptual"	3.16	2.07	1.38	0.72
	Actual	6.50	3.72	2.02	1.10

the distance the eye travels in smooth pursuit. Rather it would seem that there is some information about the speed with which the eye moves and that this information is integrated over time. If this were the case then the relevant thing to ask would be what the perceptual system knows about the speed of the smooth pursuit eye movement. We can look at the data from this point of view by dividing the calculated "perceptual tracking distance" by the time for one half cycle of spot movement yielding a measure of "perceptual tracking speed" averaged over the half cycle. The results of these computations are presented in Table 4 both for the measurements of angle of the spot moving with a vertical component and for the measurements of extent of the tracked spot. The values are not repeated for the variable distance condition since at 0.5 Hz the time per half cycle is 1 sec and, consequently, the numbers in Tables 1 and 3 already represent the "perceptual tracking speed."

We may see, in Table 4, that when this computation is based on the perceived angle of the non-tracked spot, the "perceptual tracking speed" is rather constant, about 0.1°/sec over a wide range of actual average smooth pursuit eye speeds. The same is true for the computations based on perceived extent of motion of the tracked spot in the "one frequency per day" condition. Although the "perceptual tracking speed" seems to increase somewhat from 0.125 to 0.5 Hz it falls again at 1 Hz. The differences in absolute magnitude between the above two computations might well be due to constant errors associated with the specific measurement procedures.

The data are strikingly different, however, for the subjects in the situation in which all frequencies were mixed in each day. For these subjects there is a clear, and almost constant, relationship between "perceptual tracking speed" and actual speed of the eye. The reason for this probably lies in the different procedure used. In this condition, not only were all frequencies mixed together on each day but all the measurements of perceived extent of motion of the tracked spot were done on one and the same day. It is possible that the mixture somehow enabled the perceptual system to obtain better information about eye velocity. If this were the case it is puzzling that the same information was not available, or at least not used, in connection with the perception of the path of the non-tracked spot. After all, the various frequencies were mixed together for those measurements as well. It is also possible, however, that a measurement artifact exists because the repeated trials of the same 4° spot movement may have introduced extraneous cues and enabled the subjects to make certain assumptions. Such a factor would not have affected the perception of the path of movement of the non-tracked spot since the physical angles were being varied.

A word should be said about the control data that we have not used. If the data had been presented with respect to the controls the following effects would exist:

(1) Calculations based on perceived extent of motion of the tracked spot become more variable. Values of "perceptual distance" in Table 3 change by amounts ranging from −0.08 to +0.68. The trends, or absence of trends, in Tables 3 and 4 remain substantially unaffected.

(2) Calculations based on perceived path of motion of the nontracked spot are affected. About 0.5 (range of 0.39–0.59) gets added to each of the "perceptual distances" in Table 1. This is entirely due to the distorted control values for oblique angles. Consequently, if we had used the control data, the "perceptual speed" values in the first row of Table 4 would also increase and would show a slight but steady decrease from left to right.

DISCUSSION

The data presented above were collected under conditions in which any information about smooth pursuit eye movement must be derived from some possible extraretinal signal. It is clear that, under these conditions, the perceptual system takes into account very little about smooth pursuit eye movements. Some information seems to exist, however, and it is important to ask where this information comes from.

In principle, it is possible that such information could be based on afferent (inflow) signals from muscle spindles in the extraocular muscles or from Golgi tendon organs associated with these muscles. In a muscle system in which the load on the muscles never varies, as is true of the ocular system, information from these receptors concerning change of length and tension of the muscles might provide position information. There is, however, a fair body of evidence that they do not provide such information to the perceptual system. This evidence has been reviewed frequently (Merton, 1964; Skavenski *et al.*, 1972; Festinger and Easton, 1974).

The same evidence also indicates that the perceptual system does obtain information about eye position and eye movement by somehow monitoring the central nervous system's efferent commands (outflow) to the oculomotor system. To state it briefly, the perceptual system knows where the eye is insofar as it knows where the eye was told to go. This fact has important implications for the interpretation of the data we have presented. It means that where the perceptual system knows, apart from retinal information, about eye movement is an indication of the informational content of the efferent command at the point at which it is monitored.

Let us then look at the data from this point of view. We know from our data that precise instructions about speed are not monitored centrally. Let us, tentatively, accept the guess that, for the experimental condition in which measurements for all frequencies were collected on the same day, the perception of extent of movement of the tracked spot was influenced by cues extraneous to the issue with which we are concerned. The remainder of our data indicate that, over a wide range of actual speeds of smooth pursuit eye motion, the perceptual system assumes nearly the same speed. Just what this assumed speed is is open to question. Probably the estimate of 0.1°/sec derived from the perception of the angle of the non-tracked spot is too low. From the data on extent of movement of the tracked spot, the estimate would be that this assumed speed is one degree per second or less. In any event, we can guess that the perceptual system knows that the eye is moving, does not know much about the speed of that movement, and assumes some low value for this speed of movement.

It is, hence, consistent with the data to imagine that the central command that is monitored contains merely an instruction for the eye to move. For example, the central command may simply activate the smooth pursuit system. If the more peripheral smooth pursuit system cannot function effectively over a very wide range of speeds without adjustment of some parameters of the system, then the central command might also occasionally contain further instructions to reset some parameters. Thus the perceptual system might sometimes have information that the eye was moving faster, or more slowly, than previously. When the eye is engaged in repetitive tracking of simple harmonic motion the perceptual results of such a system would be consistent with what we have found.

It also seems clear that the perceptual system knows the direction in which the eye moves in smooth pursuit. The tracked spot, for example, always was perceived to move horizontally. Therefore, the central command that is monitored must also contain information about the direction of movement.

This implies that the central command for smooth pursuit eye movements is rather general, containing only information about direction and starting movement. Yet, we must remember that the eye does execute rather accurate smooth pursuit movements. If the necessary information is not all contained in the central command, the actual calculation of the innervation to the extraocular muscles must be accomplished more peripherally, i.e. somewhere in the efferent transmission system past the point at which the central command is monitored.

If we are correct about this system, some difficult questions arise: What information does the peripheral sub-system use to execute the accurate smooth pursuit eye movements? It seems plausible to imagine that the peripheral sub-system does get information from muscle spindles and uses this, together with information about retinal slip of the target.

This, then, raises another question. How does the peripheral sub-system know which of the several possible moving points is the "target" and what retinal slip to use in its computations? We would conjecture that the designation of "target" is accomplished simply by a central command to the saccadic system that brings that "target" to the fovea. If, during smooth pursuit motion, the "target" got too far from the fovea, the central system would have to intervene to bring it back to the foveal area in order for the peripheral sub-system to be able to function adequately.

The peripheral sub-system would have to be more sensitive to retinal slip in the neighborhood of the fovea than in the periphery. The direction of appropriate retinal slip for the target would also have to be specified. It is relevant here that Miles (1975) reports that the flocculus, an area involved in smooth pursuit movement, contains cells that are sensitive to retinal movement in specific directions primarily near the fovea. Much more evidence is needed before these questions can be settled.

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