

TARGET POSITION AND VELOCITY: THE STIMULI FOR SMOOTH PURSUIT EYE MOVEMENTS

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Abstract—Smooth pursuit eye movements are usually thought to be guided only by target velocity. We studied the effectiveness of target velocity and target position (offset from the fovea) as stimuli for pursuit movements. Under open-loop conditions, we used induced (apparent) sinusoidal motion as a "velocity-only" stimulus, and square-wave motion as a "position-only" stimulus. Over a range of frequencies, position stimuli tended to give larger responses, and response velocity increased linearly with target offset. When open-loop sinusoidal target motion was synthesized using appropriate position-only and velocity-only "components", the response was about the same as for real sinusoidal motion, suggesting a dominant role for target position in both cases. Using non-periodic step-ramp stimuli as devised by Rashbass, but in the open-loop, we have commonly observed position-directed pursuit movements.

INTRODUCTION

In order to observe a moving object, a person makes a smooth pursuit eye movement; this is an eye movement with approximately the same velocity as the object, and it tends to stabilize the retinal image of the object at the fovea, thereby allowing the object to be examined with the central retina. In general, a moving object seems to be required to make a pursuit movement and this has led to the widely accepted view that the prepotent stimulus for pursuit eye movements is the velocity of an object. In its original form, this view held that the actual stimulus was the velocity of the retinal image of the object, a signal referred to as retinal slip velocity (Young and Stark, 1963; Puckett and Steinman, 1969; Steinman *et al.*, 1969; Robinson, 1971; Zee *et al.*, 1974). More recently, several studies have suggested that the perception of target velocity may be the most important aspect of stimulus motion for generating pursuit movements (Yasui and Young, 1975; Steinbach, 1976; Young, 1977). This perception is determined in part by retinal slip velocity and in part by such other factors as motion of the eye itself.

The most elegant experimental support for this general perspective comes from a number of experiments by Rashbass (1961), who asked his subjects to visually follow a small target that made a step-ramp motion. That is, the target, which the subject was fixating, jumped away from the fovea in one direction (the step), and made a constant velocity movement (the ramp) in the opposite direction, toward the starting position. If the relation between step size and ramp velocity was selected appropriately, the subject made a pursuit eye movement followed by a saccade: the initial pursuit began before the target crossed its starting position and was made in the direction of target velocity, so that the eye initially led the target motion and was moving away from the target position. The

subsequent saccade was made according to target position. Thus, the pursuit eye movement system seemed to respond mainly to target velocity and not to target position. It appeared that position errors between target and fovea were compensated for exclusively by the saccadic system.

In contrast to this idea of the importance of object velocity for pursuit movements, it has sometimes been suggested (eg. von Kries in von Helmholtz, 1910) that the position of the object relative to the fovea may also in some way contribute to generating pursuit eye movements; however, experimental evidence on this point is very limited. In a study by Robinson (1965), pursuit eye movements not only seemed to match target velocity, but if the eye was lagging slightly behind the target, eye velocity increased allowing the eye to catch up to the target. During such a catching-up movement, eye velocity was opposite to retinal-slip velocity, but was in the direction of target position; thus, this type of behavior would not be expected from a simple velocity sensitive mechanism, but is what would be expected of a mechanism sensitive to target position. In other experiments, Kommerell and Täumer (1972) placed a small afterimage at various eccentricities with respect to the fovea: when their subjects attempted to look at the afterimage, smooth eye movements resulted, and the eye velocity increased with eccentricity of the afterimage. These results are again suggestive of a mechanism sensitive to target position. Unfortunately, from these experiments it is hard to evaluate the importance of a position mechanism in the control of normal pursuit eye movements. In Robinson's study, the mechanism might operate only for very small errors between target and fovea. In the experiments by Kommerell and Täumer, the smooth eye movements may be idiosyncratic, depending on the use of an afterimage. Furthermore, from these experiments, it is not possible to

assess the relative importance of target position and velocity when both are present.

The smooth pursuit eye movement system can be regarded as a closed-loop negative feedback system in which the input is target motion and the output is eye movement. The eye movement serves as negative feedback since it reduces target motion relative to the retina. Previous experiments (Fender, 1962; Dallos and Jones, 1963; Young and Stark, 1963) have shown that opening the negative feedback loop of the pursuit system (i.e. breaking the input/output relationship so that retinal target motion is independent of eye movement) increases the system gain (i.e. the ratio of eye velocity to target velocity). In other words, small target motion gives rise to relatively large eye movements. This high open-loop gain is thought to be the mechanism that brings about accurate tracking under the normal closed-loop conditions encountered in the real world (Zee *et al.*, 1974; Robinson, 1976). Besides this functional importance, a high open-loop gain means that in an open-loop experiment, any change in effectiveness of stimulus gives rise to a clear and easily measured change in magnitude of eye movements. For this reason, we used the open-loop system to investigate the relative contributions of target position and velocity in eliciting pursuit movements. First, we conducted experiments in which we investigated the response of the pursuit system to a "position-only" stimulus and "velocity-only" stimulus, both of which were periodic. Second, we studied the pursuit response to a combination of position and velocity stimuli, again periodic. Third, we looked at the pursuit response to a nonperiodic stimulus, namely a step-ramp stimulus. The results of these studies suggest that both position and velocity are stimuli for the pursuit system, but that position can often be a more powerful influence than velocity. A preliminary report of these findings has been presented (Wyatt and Pola, 1978).

GENERAL METHODS

The present study consisted of several different open-loop conditions in which the subject's task was to visually follow the horizontal motion of a small round target (1.5° in diameter). In most of the conditions, the target motion was periodic, but in one condition its motion was step-ramp. For two conditions, the target appeared in the center of a large frame that consisted of two thin strips forming the upper and lower borders of a rectangle 27° wide and 22° high. The frame oscillated horizontally or, in some instances, was stationary. The purpose of the frame was to influence the subject's perception of motion (see below). We chose a frame of only two horizontal strips with the intent of minimizing activation of the optokinetic system by minimizing vertical edge content. To open the feedback loop in all of the conditions, target motion was stabilized at the retina; that is, regardless of the subject's direction of

gaze, target motion at the retina (oscillatory or step-ramp) was unchanged.

The subject sat in a dark room facing a rear-projection screen at a distance of 114 cm. All stimuli were projected on this screen and viewed monocularly with the left eye. The position of the target was controlled by a first surface mirror mounted on a galvanometer pen-motor. For periodic target motion, the pen-motor was driven by a function generator, and for step-ramp motion, the motor was driven by a configuration of operational amplifiers. To obtain the open-loop condition, a signal of horizontal eye position was added to the signal creating target motion. Frame position was controlled by a mirror mounted on a second galvanometer pen-motor. This pen-motor was driven either by the function generator or by a signal of horizontal eye position. The eye position signal was obtained from an infrared scleral reflection system (Narco Bio-Systems, Inc.), which has an output linear to several parts in a hundred over a range of $\pm 20^\circ$ and a resolution of about 0.25° . The eye position signal was differentiated to yield an eye velocity signal, and both of these, together with stimulus events, were recorded on a Grass polygraph. In cases where details of saccadic eye movements were not of interest, the pen-motor amplifier could be used with a 60 Hz notch filter.

An experimental session on a single day consisted of a series of trials during which the subject tracked either periodic or step-ramp target motion. To calibrate the eye position record, the subject fixated, in turn, three fixation lights located straight ahead and 15° to either side of straight ahead. To set and check stabilization, the open-loop target was turned on during this fixation sequence: the criterion for good stabilization was that the target be seen by the experimenter to be located at each fixation light in turn. In particular, for periodic target motion, the criterion was that the target oscillate symmetrically about each fixation light. Stabilization could be determined to an accuracy of 0.25–0.5° at each point. The stabilization

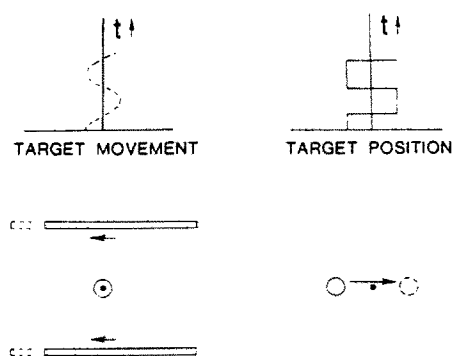


Fig. 1. Right: the "position-only" condition. The target (circle) executes square-wave motion on the retina, jumping back and forth across the fovea (solid dot). Left: the "velocity-only" condition. The frame moves back and forth, inducing apparent motion of the target which is stabilized at the fovea.

was checked before and after each trial, and if a substantial change occurred during the trial, the trial was discarded. The velocity record was calibrated by a ramp signal equivalent to an eye movement of 30 deg/sec. This was done once per session. Since the differentiation circuitry was not altered during a session, the velocity calibration for a given trial was proportional to the position calibration for that trial.

The subjects in these experiments were males between the ages of 20 and 40 with refractive states varying from emmetropic to 5 D myopic. A total of 8 subjects participated in these experiments. We present here the data of two, both familiar with the experiments. However, their data was essentially the same as that obtained from other subjects, most of whom were naive.

EXPERIMENTS WITH SEPARATE POSITION AND VELOCITY STIMULI

The stimulus most often used for studying the gain of the open-loop pursuit system has been a target moving sinusoidally (Fender, 1962; Young and Stark, 1963). We could not use this stimulus to study the separate contributions of target position and velocity because any real target motion of this type has both non-zero target position and velocity. Thus, we devised two open-loop conditions, one consisting of a "position-only" stimulus, and the other consisting of a "velocity-only" stimulus.

Methods

For the first of the above conditions the stimulus was horizontal square-wave target motion (0.5, 0.75 and 1.0 Hz) stabilized around the fovea. That is, the target stepped back and forth symmetrically from one side of the fovea to the other, regardless of the subject's direction of gaze (Fig. 1). Peak-to-peak square-wave amplitude was varied from 0.5 to 6°, and thus, target offset to each side of the fovea was 0.25 to 3°. Since target velocity on the retina was zero except for the instant of transition, this could be considered a "position-only" condition. (The low frequencies at which some of these experiments were carried out argue against any significant contribution by apparent motion.) For the second condition, the target was stabilized at the fovea and had no real motion of its own; however, it was located in the center of a large frame (Fig. 1) that oscillated sinusoidally from side to side (0.5, 0.75 and 1.0 Hz). Peak-to-peak amplitude of frame motion was varied from 5 to 120°. Unlike the target, the motion of the frame was not stabilized at the retina. The effect of such a frame is that it induces apparent motion of the target in a direction opposite to the frame motion (Duncker, 1929; Wallach, 1959; Wyatt and Pola, 1979). Thus, the target appeared to move sinusoidally at the same frequency as the frame, but in counterphase (180° out-of-phase) to the frame. Since the target was always located on the fovea this could be considered a "velocity-only" condition.

The position-only and velocity-only conditions were run in separate experimental sessions, generally on different days. In a session for the position-only condition, a trial lasted 20–40 sec during which the subject tracked the target at one square-wave frequency and amplitude. The order of amplitude presentation was varied from one trial to another in a quasi-random manner, but frequency was generally held constant. At least 3–4 trials were run at a given frequency and amplitude, usually over several sessions. The pooled data from these several trials were used in subsequent analysis. In a session for the velocity-only condition, the arrangement of trials was made on a similar basis to the above.

Results

Figure 2 shows some results from the two experimental conditions at a stimulus frequency of 0.75 Hz. In the position-only condition, the square-wave motion (in this case 2° peak-to-peak) elicited sinusoid-like eye movements of about 10° amplitude peak-to-peak. (The spike-like events in the velocity record of these eye movements reflect the occurrence of saccades.) In the velocity-only condition, sinusoidal slow eye movements also occurred, but their amplitude was small, only about 2° peak-to-peak. These eye movements were in phase with induced motion, and out of phase with frame motion: this can be seen clearly in the inset, where eye position (dashed line) is traced on the same time axis as the frame position (solid line). These eye movements were oppositely directed to those expected if the frame acted as an optokinetic stimulus. Since the target was always on the fovea, few or no saccades were made. It should be noted that this is the first time that slow eye movements have been shown to occur in response to induced target velocity in the absence of any other stimulus. [One earlier study showed an augmentation of a vestibular eye movement, that was probably the consequence of apparent motion of a target (Yasui and Young, 1975), while another described augmentation of a pursuit response as a consequence of enhancing the perceived motion of a target (Wyatt and Pola, 1979).]

Figures 3 and 4 show the results for the position-only and velocity-only conditions at the three frequencies used. For the position-only condition, the mean value of the peak smooth eye movement velocity is plotted as a function of square-wave amplitude. For the velocity-only condition, peak smooth eye movement velocity is plotted as a function of amplitude of frame motion. Error bars show ± 1 SD.

In the position-only condition, peak eye velocity increased monotonically with square-wave amplitude at each frequency. For large amplitudes of target offset, smooth eye movement velocities in excess of 40 deg/sec often occurred. The straight lines, fitted by eye, suggest that within the range of amplitudes investigated the increase was approximately linear. There is, however, a suggestion in the data of both subjects

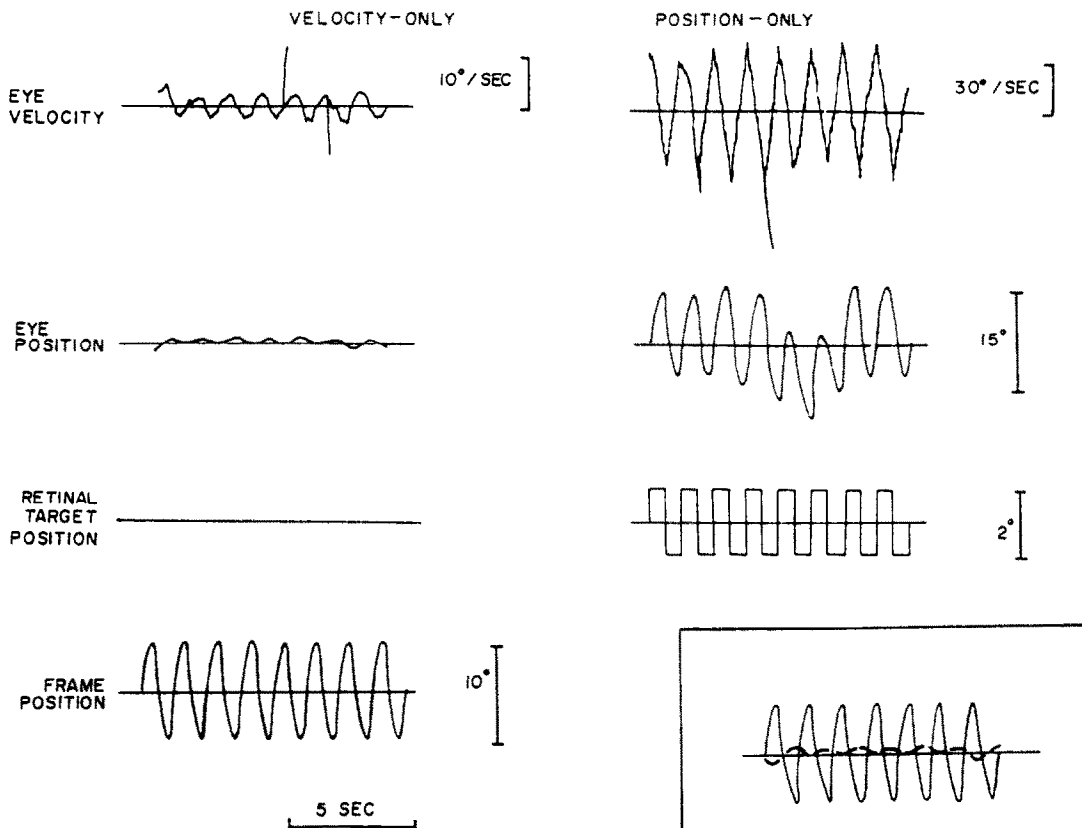


Fig. 2. Typical responses to the "position-only" condition (right) and the "velocity-only" condition (left) at 0.75 Hz. For each condition, target position is shown relative to the fovea. In the "position-only" condition, there is square-wave target motion on the retina, with the target first on one side, then on the other side of the fovea. In the "velocity-only" condition, there is no retinal target motion. Frame position is shown relative to the head. In the "velocity-only" response, eye movement is approximately 180° out-of-phase with frame motion, i.e. eye movement is in phase with induced target motion. This is evident in the inset: frame position (continuous line) and eye position (broken line) are plotted on the same time axis.

that at 1 Hz the response saturated with increasing amplitude of offset. Another feature of both sets of data is that the straight line fit to the data appears to intercept the ordinate at velocities that are greater than zero (about 10 deg/sec for JP and 20 deg/sec for HW). This indicates that for very small target offsets from the fovea, the pursuit response had a relatively high velocity.

In the velocity-only condition, eye velocity was much smaller in general than was the case in the position-only condition. A consistent feature of the velocity-only data is that as the frame motion increased beyond about 40° (at each frequency), eye velocity either reached a more or less constant value or decreased. (However, these data show a large variance relative to the mean, so this statement is made with caution.) It is clear, furthermore, that as frequency increased, the response for a given amplitude of frame motion decreased. It seems likely that both of these trends in the data are consequences of changes in induced apparent motion resulting from changes in amplitude and frequency of frame motion.

EXPERIMENTS WITH COMBINATIONS OF "POSITION-ONLY" AND "VELOCITY-ONLY" STIMULI

The findings so far described indicate that both target position and apparent velocity are stimuli for smooth pursuit eye movements. But the data do not show the relative influence of these two stimuli when they occur simultaneously, as is usually the case. The object of the following experiments was to present a stimulus consisting of a combination of a position-only stimulus plus a velocity-only stimulus. Each component of the combination stimulus was determined to be equivalent to the position component or the velocity component of a real sinusoidal stimulus. We could then compare the eye movements in response to the combination stimulus with the eye movements in response to the real sinusoidal stimulus. If the response to the combination stimulus was similar to the response to the real sinusoidal stimulus, this would provide an estimate of the relative contribution of the position and velocity components of a real stimulus. It also would support a tentative

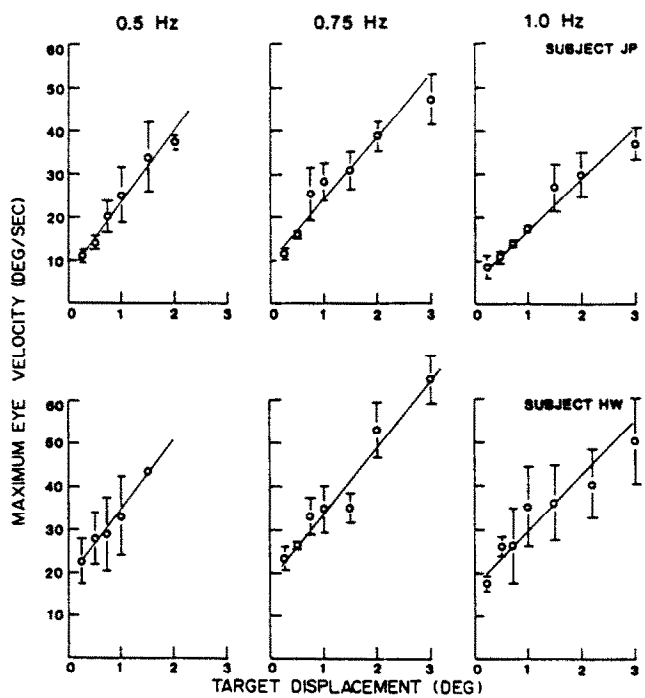


Fig. 3. Maximum pursuit eye movement velocity plotted against displacement of target off the fovea in the "position-only" condition. During square-wave motion, the target is first right of the fovea, then left of the fovea by the same amount. The upper three graphs give the data for one subject (JP) at three frequencies, and the lower graphs give the data for another subject (HW). Straight lines were fitted by eye to each set of data points. Error bars represent ± 1 SD.

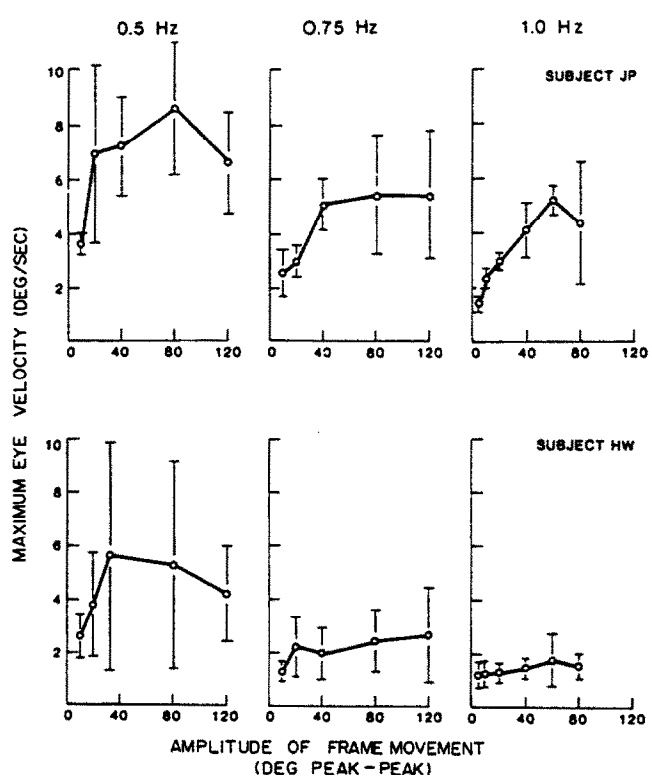


Fig. 4. Maximum pursuit eye movement velocity plotted against amplitude of frame motion in the "velocity-only" condition. Data for two subjects are shown at three frequencies.

assumption that apparent (induced) velocity elicits a response similar to real velocity.

Methods

To see the relative contributions of position and apparent velocity we used a group of three open-loop conditions. (1) We looked at pursuit eye movements when the stimulus was simply the target moving sinusoidally with an amplitude of 3° peak-to-peak (Fig. 5, bottom). (2) We looked at pursuit when the stimulus was the "position component" of the sinusoidal motion of the first condition (Fig. 5, top). The stimulus for this was square-wave target motion with the same time-average offset from the fovea as the sinusoidal motion. (A squarewave of amplitude 1.95° peak-to-peak has the same area under each half cycle of the curve as does a sine wave of amplitude 3° peak-to-peak.) (3) We looked at pursuit when the stimulus was the sum of the "position component" and "velocity component" of the sinusoidal motion (Fig. 5, middle). The stimulus for this was the square-wave position stimulus of the second condition, together with the inducing frame. The frame was adjusted to add apparent sinusoidal motion to the stimulus, equal in amplitude to the real sinusoidal motion of the first condition (i.e. 3° peak-to-peak).

Within a daily session, the three conditions were compared at one of three frequencies (0.5, 0.75 and 1.0 Hz). The conditions were presented in quasi-random order over trials, each trial lasting 20–40 sec. Each condition was repeated at least twice within a session, with a total of at least six repetitions across all sessions.

Selection of the inducing frame motion for the combination "position plus velocity" stimulus. The selection of appropriate frame motion for the third stimulus above, requires some further explanation. It must be remembered that, for example, with a position-only stimulus the eye executes smooth movements. During these movements, the subject perceives substantial target motion, even in a totally dark room. This perception presumably comes from an internal signal of the eye movement itself, since there is neither retinal target motion nor target motion relative to a background (Wyatt and Pola, 1979). It is necessary therefore to distinguish between total perceived motion and "input" perceived motion. For example, in the case of real sinusoidal open-loop target motion, retinal target motion is the input motion, and during a high-gain open-loop response, perceived motion often greatly exceeds input motion (Wyatt and Pola, 1979). (An exaggerated case is pursuit of a position-only stimulus, when input motion is zero, but perceived motion is substantial.) When induced (apparent) motion is being used as part or all of the input stimulus, the distinction between input and total perceived motion becomes more complicated.

We adopted the following direct approach to the combined stimulus: (a) We measured the amplitude of eye movements in the response to the open-loop pos-

ition component of the sinusoidal motion (condition 2; Fig. 5, top). (b) We performed psychophysical experiments under closed-loop conditions. The subject tracked a target moving with the same frequency as the experimental target of condition 2 with an amplitude equal to the amplitude of eye movements found in the open-loop responses of condition 2. After tracking in the dark, the subject estimated the perceived extent of closed-loop target motion by a successive matching technique (Wyatt and Pola, 1979): after pursuit for a number of cycles, target amplitude was set to zero, dim lights were turned on, and the subject adjusted target motion (while tracking the target) to match the previously tracked target in its perceived extent of motion.

(c) The lights were extinguished again, and target amplitude was set at the same value as in (b). The inducing frame was also turned on, either stationary or executing small oscillatory movements (2.5 or 5° peak-to-peak) either in phase with, or in counterphase to, the target. The subject tracked the target for a number of cycles and again estimated the perceived extent of motion using a successive match. The change in perceived motion produced by the frame (match in c—match in b) was noted.

Since these psychophysical experiments were closed-loop, the eye movement was very nearly the same with and without the frame present. Therefore, the augmentation of perceived motion produced by the frame under these conditions is a good estimate of the "input" effect of the frame that occurs when the frame is added to the square-wave stimulus under open-loop condition 2. (Keeping the eye movement constant should hold the perception resulting from eye movement constant, so that the observed change in perception is due to the frame alone.) From these experiments, we were able to select the frame motion that, when added to ongoing eye movement of appropriate amplitude, would produce an increase in perceived motion equal to the perceived motion of the real sinusoidal target (i.e. 3° peak-to-peak). Strictly speaking, this would be valid for the open-loop only if a change in the amplitude of eye movement due to the frame did not alter the "input" effect of the frame. Since the open-loop eye movements did not increase by more than 30–60% as a consequence of adding the frame (see below), and since the effect of adding a frame to an ongoing closed-loop pursuit is a very slow function of pursuit amplitude (unpublished observations), this appears to be a reasonable approximation. As discussed previously (Wyatt and Pola, 1979), the perceived extent of motion of a target tracked in the light is about the same as the perceived motion of the same target in the dark, when the subject fixates a mark and lets the target sweep across the retina. Thus, our matching condition was a reasonable measure of the frame effect in terms of perceived motion of a target actually moving across the retina.

In many cases, a stationary frame was sufficient to appropriately increase the perceived motion of the

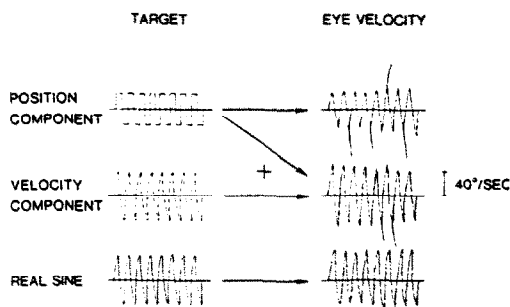


Fig. 5. Responses to combined "position-only" plus "velocity-only" stimulus. Pursuit eye movement velocity is shown for three stimulus conditions: (bottom) Real sinusoidal target motion, 3° peak-to-peak; (top) Square-wave motion—the "position component" of the sinusoidal motion shown at the bottom—with the same time-average offset from the fovea as the sinusoidal motion (here, 0.95°); (center) Square-wave target motion as at top, plus frame inducing an additional apparent target motion of 3° peak-to-peak. See text.

open-loop target. However, when frame motion was required, either in phase or in counterphase, the frame motion was driven by a signal of eye movement appropriately scaled. The signal was used either direct or inverted, depending on whether the frame motion had to be in or out of phase. By using the eye movement signal to drive the frame, we insured that the phase of the frame did not shift with respect to the phase of the eye.

Results

The response of the pursuit system to the three stimulus conditions at 0.75 Hz is shown in Fig. 5. A striking feature of these data is that the pursuit movements in response to "synthesized" sinusoidal motion (i.e. condition 3; Fig. 5, center line: position plus velocity components of the real sinusoid) were very similar to the pursuit movements in response to the real

sinusoidal motion (Fig. 5, bottom). Furthermore, the pursuit response to the position component apparently accounts for about 75% of the response to the "synthesized" stimulus. In other words, the difference between the response to target position (condition 2) and the response to real sinusoidal motion (condition 1) was relatively small, and the contribution of the apparent motion (which is small) makes up the difference.

The results from the experiments described above, together with similar data at 0.5 and 1.0 Hz, are plotted in Fig. 6. The mean value of the smooth peak eye velocity is shown for each condition. At each frequency, the pursuit movement velocity in the "synthesized" sine condition (open circles) may be compared to the real sine condition (solid circles). With the exception of the 1.0 Hz data for HW, the responses in the two conditions were quite similar. Furthermore, the response to the position component of the combined stimulus appears to have constituted most of the response to the stimulus (compare squares to open circles).

EXPERIMENTS WITH TRANSIENT STIMULI: OPEN-LOOP STEP-RAMP (RASHBASS) EXPERIMENTS

The vigorous pursuit movements that occurred in the preceding experiments in response to the position stimulus appear to be at variance with the findings of Rashbass (discussed in the Introduction) that indicated that the pursuit system responded to velocity and not to position. With appropriate selection of stimulus parameters, we were able to replicate the observation that Rashbass made under closed-loop conditions. However, when we used step-ramp stimuli under open-loop conditions, our results were quite different for many values of input parameters.

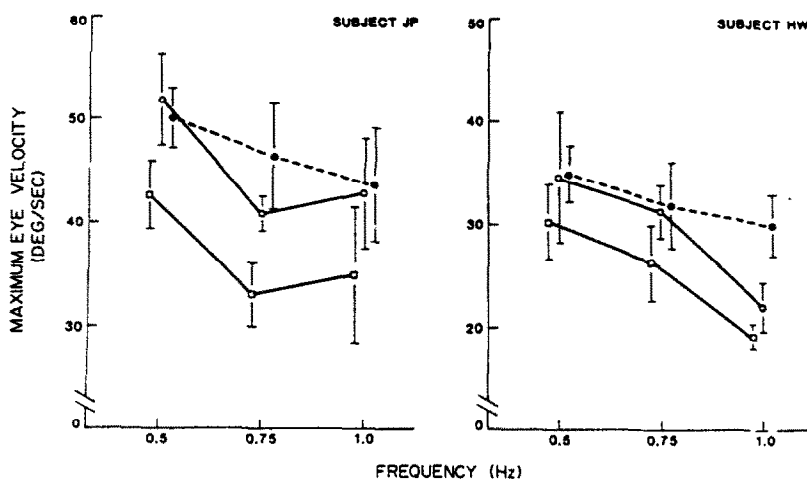


Fig. 6. The combined "position-only" plus "velocity-only" experiment—summary of results. Maximum pursuit eye velocity is shown for the three conditions: sinusoidal target motion (\bullet), "position component" of sinusoidal motion (\square), and sum of "position component" plus "velocity component" (\circ).

Methods

The size of the step was constant (2°), but the velocity of the ramp was varied (16, 8, 4, 2 and 1 deg/sec). The target, at first foveally located, made a horizontal step-ramp motion which the subject was instructed to follow as quickly as possible. A trial consisted of a series of at least five individual responses to step-ramp presentations with ramp velocity held constant. Ramp velocity was varied from trial to trial in a quasi-random manner, and each velocity was used on at least two or three separate occasions. In these experiments, the direction of the step-ramp was the same within and across trials. To see whether the eye movement response was dependent on this repetition of direction, we also performed these experiments with "two-way" randomization (step polarity randomly varied, with ramp direc-

tion opposite to the step) and with "four-way" randomization (step and ramp directions varied randomly and independently; results from trials with step and ramp in the same direction are discarded). Again, a trial consisted of a series of individual responses to step-ramp presentations with a given ramp velocity. The stimuli during the series were in random directions according to the "two-way" or "four-way" procedures.

Results

Figure 7 shows typical open-loop responses to step-ramp stimuli, with a step size of 2° , and various ramp velocities. These experiments were performed using two-way randomization (see above). When the ramp velocity was 16 deg/sec, so that the target recrossed its initial (pre-step) position in 0.125 sec, the

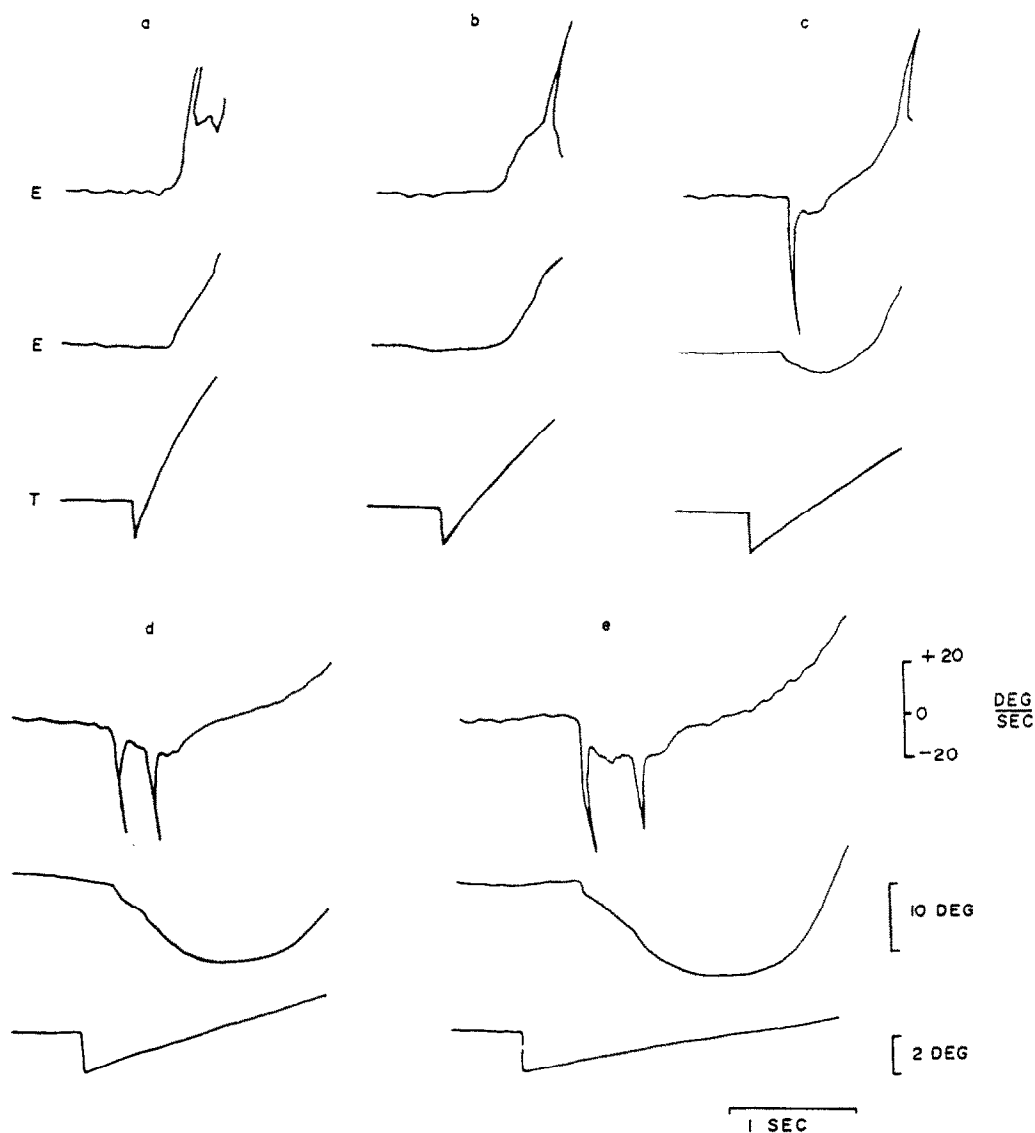


Fig. 7. Responses to open-loop step-ramp stimuli. Eye position (E) and eye velocity (\dot{E}), for stimuli (T) with constant 2° step size and decreasing ramp velocity from (a) to (e). (a) 16 deg/sec, (b) 8 deg/sec, (c) 4 deg/sec, (d) 2 deg/sec, (e) 1 deg/sec. Position-directed smooth movements are apparent in (c), (d) and (e).

response was a pursuit movement in the direction of the ramp, which is in line with traditional results. However, when the ramp speed was reduced to 4 deg/sec, a pursuit movement (often preceded by a saccade) was sometimes observed to occur in the direction of the step, i.e. in the direction of target position. As the ramp speed was successively slowed to 2 deg/sec, and finally 1 deg/sec, the response to the step in target position continued to increase. At 1 deg/sec, the eye made a 15° excursion in the direction of the step. Pursuit movements with various forms of randomization were similar; however, pursuit velocity tended to be slightly less than in the non-randomized case. Responses to the step-ramp stimuli showed considerable variation between subjects; some subjects showed many saccades and only small and sluggish position-direction pursuit movements, while others made only a single saccadic attempt at fixation prior to a vigorous position-directed smooth movement. A feature of our results that was found for all subjects for step-ramp stimuli, is that the reaction-time between the onset of the step and the pursuit eye movement was generally greater than 200 msec. This was true whether the velocity of the ramp was low or high, as seen in Fig. 7. This is notably longer than the reaction time usually reported for pursuit eye movements (which is about 125 msec).

DISCUSSION

It has often been assumed that the predominant stimulus for smooth pursuit eye movements is the velocity of a moving target. A role for target position has sometimes been suggested (e.g. von Kries, in von Helmholtz, 1910) and included in models for completeness (e.g. Young, 1977), but there has been only limited experimental evidence to support this view directly (e.g. Kommerell and Täumer, 1972). Experimental work has used techniques that restrict the ability to control stimulus parameters, and it has not previously been possible to use stimuli with known amounts of both position (offset from the fovea) and velocity. Our results support the view that target position is a stimulus for pursuit eye movements, and furthermore that target position can often be a more powerful stimulus than target velocity. The fact that, in most of the experiments reported here, we compared the effects of foveal-offset-of-a-real-target to apparent-motion-of-a-target leaves open the possibility that some of our findings are peculiar to the use of apparent motion, which may be a weaker stimulus for pursuit movements than real motion. However, in the "synthesis" experiments, we were able to obtain eye movements similar to responses to real sinusoidal target motion by using a combination of apparent motion and real target offset "equivalent" to the sine motion. This suggests that the apparent motion we used bears a close relation to real motion in driving the pursuit system, and, given our results, that target offset provides most of the drive to the pursuit system.

Furthermore, in the step-ramp experiments we pitted real target offset against real target velocity, and at low to moderate velocities the pursuit response tended to favor the offset over the velocity.

Since all of our studies were conducted in the open-loop condition, there is a question about the applicability of our findings to normal everyday closed-loop circumstances. While the relation between open- and closed-loop is quantitatively defined for technological control systems, it is by no means clear that a similar relation holds for a biological system such as the pursuit eye movement system, with all of its nonlinearities and apparently volitional characteristics. Nevertheless, in recent experiments, where careful measurements have been made, there is suggestive evidence that the closed-loop system requires and employs target position as an input stimulus. Williams and Fender (1979) have described experiments with a moving row of dots, which they called a "pure velocity" stimulus, because information about target position was absent or ambiguous. From experiments in which subjects attempted to match eye velocity to target velocity, they concluded that the smooth pursuit system is "a sloppy velocity control system." While it is difficult to relate our "velocity-only" stimulus, using apparent motion of a foveal target, to their "pure velocity" stimulus, using real motion of a row of dots, our results suggest that target position can be more important than velocity for accurate pursuit and their findings seem to be consistent with this view. Experiments with both monkeys and humans (Eckmiller and Mackeben, 1978a, b; Lisberger *et al.*, 1977) have shown that, during tracking of sinusoidal target motion, the eye often accelerates in the smooth pursuit mode, reducing errors of target position relative to the fovea. In the monkey studies, pursuit movements eliminated errors as large as 4°.

Step-ramp stimuli

Perhaps one of the most interesting aspects of our experiments is the large magnitude of the position effect found with step-ramp stimuli. This finding shows that a pursuit response to target position does not require periodic stimuli. However, a previous study did not show a clear pursuit response to target position for step-ramp stimuli (Fender, 1962); instead, slow eye movements occurred primarily in the direction of target velocity. In other words, when the target stepped off to one side of the fovea, the subject made sawtooth-like eye movements, with smooth pursuit movements away from target position (in the direction of target velocity), interspersed with saccades made toward the target. We have observed this type of response, but with only 1 out of 8 subjects, and we thus conclude that the majority of people show a position-dominated pursuit movement under appropriate stimulus conditions.

Our results with step-ramp stimuli seem to contradict Rashbass' findings, with closed-loop step-ramp stimuli, which appeared to show that the pursuit sys-

tem responded only to ramp velocity and not to the position offset produced by the step. However, this contradiction may only be apparent, since for higher velocity ramps such as those used by Rashbass, we also found that pursuit eye movements were in the direction of the ramp. Only when ramp velocity was low did we find position-directed pursuit movements. A simple explanation for this difference in response to high and low velocity ramps can be provided if we assume that the pursuit system has two properties: the first is that the pursuit response to target position takes a relatively long time to develop to full strength. There is some evidence for this: when a subject first tracks open-loop square-wave target motion, the resulting periodic smooth eye movement increases in amplitude with time (our unpublished observations). The second property is that the response to target velocity can compete with the response to target position when the two are oppositely directed. Given these two properties, when a step-ramp stimulus with high ramp velocity is presented, the target ramp crosses back over the fovea before a position-directed pursuit movement can develop, so the eye follows the ramp. In addition, the high velocity ramp is a relatively strong velocity stimulus in itself, which may help target velocity to "win out," as stimulus, over initially-weak target position. When ramp velocity is low, however, target offset in the direction of the step occurs for a long enough time for the position response to develop. Also, since the low velocity ramp is a weak velocity stimulus, it may not compete effectively with target offset, with the result that the eye turns in the direction of the step. In our series of pursuit responses to step-ramp stimuli with decreasing ramp velocity (Fig. 7), the shift from velocity-directed to position-directed pursuit response is clear. In Rashbass' closed-loop step-ramp experiments, velocity-directed pursuit movements were shown in response to higher velocity ramps, which corresponds to our open-loop results. However, it is not possible to perform meaningful closed-loop step-ramp experiments with low velocity ramps, since the initial response is a saccade which eliminates the error between target and fovea, removing the need for a position-directed pursuit movement.

A striking feature of pursuit eye movements to the open-loop step-ramp stimuli is that the reaction time to the onset of the movements was generally more than 200 msec. This is significantly longer than the usual closed-loop reaction time of pursuit movements (at least for a simple ramp stimulus), which is about 125 msec (Robinson, 1965). The longer reaction time can be explained plausibly using the two properties proposed above: when a step-ramp stimulus is provided, the pursuit response to target position is ini-

tially weak and approximately cancels out the response to velocity, so the eye remains stationary momentarily. In the case of a low velocity ramp, as the response to target position grows in strength, it overcomes the velocity response and the eye turns in the direction of the target. For higher velocity ramps, the velocity "wins out," but the position offset delays the response by competing with velocity until the ramp significantly reduces the offset.

Increased reaction time to step-ramp stimuli occurs in closed-loop as well as open-loop conditions: an examination of the original data of Rashbass (1961) shows that the reaction time of about 125 msec for a ramp stimulus increases to 150–200 msec for a step-ramp stimulus. Robinson (1965) noted a similar increase in reaction time, stating that "the initial target step has not gone unnoticed by the smooth pursuit system." The competitive mechanism that we have proposed to account for the open-loop result could reasonably be expected to operate in the closed-loop condition as well.

Stimulus predictability

So far, we have made only passing reference to the "predictability" of the stimuli used in the various experiments. It is well known that the pursuit eye movement system responds differently to predictable than to non-predictable stimuli; in particular, the gain is generally larger for the former. It has been suggested that the pursuit system operates at a more fundamental level in responding to nonpredictable stimuli (Stark *et al.*, 1962).

It may be that predictable stimuli are particularly conducive to the function of the position-directed pursuit mechanism, and are therefore responsible in part for the vigorous eye movements we have observed in response to position stimuli. If this is so, then, since most naturally occurring targets for visual pursuits are relatively predictable (see below), the position mechanism is likely to function quite frequently.

Stimulus predictability was originally dealt with as a dichotomy, i.e. a stimulus was either predictable or not (Stark *et al.*, 1962). However, Michael and Melvill-Jones (1966) showed that predictability could be treated as a continuous variable, inversely related to bandwidth of target motion: using bandlimited noise to control target position, they noted a regular decline in the accuracy of pursuit as bandwidth increased. In this sense, sinusoidal target motion (or the fundamental component of square-wave target motion) is zero-bandwidth and therefore highly predictable. What does not seem to be usually recognized is that stimuli such as step-ramp stimuli are also very predictable *after they start*. This can be seen on an intuitive level (after onset, the motion is a constant velocity ramp), and can also be related to the findings of Michael and Melvill-Jones (the onset of a ramp is effectively a broad-band stimulus, while the late part is effectively narrow-band).*

* For this to hold formally, we need to make the plausible assumption that the eye movement system deals with the bandwidth of target motion over some finite interval prior to the instant in question.

From this more general perspective on predictability, it may be seen that many stimuli we normally pursue are predictable after the onset of the stimulus—for example, a person walking, a moving car, or a bird in flight. Our results using predictable stimuli would therefore seem to reflect the system behavior under circumstances that occur rather commonly in visual pursuit.

Fixation and pursuit

As mentioned earlier, position-directed pursuit may function more generally during normal closed-loop pursuit than has been suggested by most experiments using closed-loop targets. (This is because saccades usually frustrate attempts to use low-velocity closed-loop targets.) This view is supported by preliminary findings (Pola and Wyatt, 1979) that subjects can make slow eye movements to slow—and even stationary—closed-loop targets if their saccadic mechanism is prevented from achieving fixation. If pursuit of targets, especially slowly-moving targets, uses position-directed pursuit, it is natural to suggest that the same mechanism acts to hold the eye on a stationary target. This would remove the distinction between tracking two targets moving at velocities of, say, 0.1 deg/sec and 0 deg/sec. (Usually, the first case would be described as “pursuit” and the second as “fixation.”) In other words, the position mechanism for smooth pursuit eye movements may be the same as the mechanism for visual fixation. It has, in fact, been shown that slow eye movements are sufficient to fixate a stationary target (Steinman *et al.*, 1973).

The proposed importance of a position signal for controlling gaze provides an explanation for the observation by Mack *et al.* (1979) that apparent motion does not elicit pursuit responses in closed-loop conditions. They performed experiments similar to our “velocity-only” experiment (Fig. 1), except that they used a closed-loop fixation target. Under those conditions, a strong position signal would act to hold the eye stationary in spite of the apparent motion induced by the frame. With our stabilized fixation target, slow eye movements do not give rise to a conflicting position signal.

In conclusion, our results indicate that both position and velocity act as stimuli for pursuit eye movement, possibly under a wide variety of everyday circumstances. We suggest that models attempting to account for pursuit system behavior should include both position and velocity channels at the input stage of the system.

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REFERENCES

- Dallos P. J. and Jones R. W. (1963) Learning behavior of the eye fixation control system. *IEEE Trans. Automatic Control* AC-A, 218–227.
- Duncker K. (1929) Über induzierte bewegung (Ein Beitrag zur Theorie optisch wahrgenommener Bewegung). *Psychol. Forsch.* 12, 180–259. Translated and extracted in *A Source Book of Gestalt Psychology* (prepared by Ellis W. D.). Routledge & Kegan Paul, London (1938).
- Eckmiller R. and Mackeben M. (1978a) How does a monkey keep a slowly moving light spot on both foveas? *Invest. Ophthalm. visual Sci.* 17, Suppl., 271.
- Eckmiller R. and Mackeben M. (1978b) Pursuit eye movements and their neural control in the monkey. *Pflügers Arch. ges. Physiol.* 377, 15–23.
- Fender D. H. (1962) The eye movement control system: evaluation of a model. In *Neural Theory and Modelling* (Edited by Reiss R. F.). University Press, Stanford.
- Helmholtz H. von (1866) *Handbook of Physiological Optics*, 3rd edn (1909). Translated by Southall J. P. C. (1924) reprinted by Dover, New York (1962). Notes on §29 by Kries J. von, p. 271.
- Kommerell G. and Täumer R. (1972) Investigations of the eye tracking system through stabilized retinal images. In *Cerebral Control of Eye Movements and Motion Perception* (Edited by Dichgans J. and Bizzi E.). Karger, Basel.
- Lisberger S. G., Evinger L. C. and Johnson G. W. (1977) Smooth pursuit tracking of periodic and non-periodic targets in man. *Abstr. 7th Ann. Meet. Soc. Neurosci.*, p. 156.
- Loomis J. M. and Nakayama K. (1973) A velocity analogue of brightness contrast. *Perception* 2, 425–428.
- Mack A., Fendrich R. and Pleune J. (1979) Smooth pursuit eye movements: is perceived motion necessary? *Science* 203, 1361–1363.
- Michael J. A. and Melvill-Jones G. (1966) Dependence of visual tracking capability upon stimulus predictability. *Vision Res.* 6, 707–716.
- Pola J. and Wyatt H. J. (1979) Smooth pursuit eye movements to stationary targets. *Invest. Ophthalm. visual Sci.* 18, Suppl., 103.
- Puckett J. de W. and Steinman R. M. (1969) Tracking eye movements with and without saccadic correction. *Vision Res.* 9, 695–703.
- Rashbass C. (1961) The relationship between saccadic and smooth tracking eye movements. *J. Physiol.* 159, 338–362.
- Robinson D. A. (1965) The mechanics of human smooth pursuit eye movement. *J. Physiol.* 180, 569–591.
- Robinson D. A. (1971) Models of oculomotor neural organization. In *The Control of Eye Movement* (Edited by Bach-y-rita P. *et al.*). Academic Press, New York.
- Robinson D. A. (1976) The physiology of pursuit eye movements. In *Eye Movements and Psychological Processes* (Edited by Monty R. A. and Senders J. S.). Erlbaum, Hillsdale, N.J.
- Stark L., Vossius G. and Young L. R. (1962) Predictive control of eye tracking movements. *IEEE Trans. Human Factors in Electronics* HFE-3, 52–57.
- Steinbach M. J. (1976) Pursuing the perceptual rather than the retinal stimulus. *Vision Res.* 16, 1371–1376.
- Steinman R. M., Skavenski A. A. and Sansbury R. V. (1969) Voluntary control of smooth pursuit velocity. *Vision Res.* 9, 1167–1171.
- Steinman R. M., Haddad G. M., Skavenski A. A. and Wyman D. (1973) Miniature eye movement. *Science* 181, 810–819.
- Wallach H. (1959) The perception of motion. *Scient. Am.* 201, 56–60.
- Williams R. A. and Fender D. H. (1979) Velocity precision in smooth pursuit eye movements. *Vision Res.* 19, 343–348.

- Wyatt H. J. and Pola J. (1978) Position and velocity: the stimuli for smooth pursuit eye movements. *Invest. Ophthal. visual Sci.* **17**, Suppl., 139.
- Wyatt H. J. and Pola J. (1979) The role of perceived motion in smooth pursuit eye movements. *Vision Res.* **19**, 613–618.
- Yasui S. and Young L. R. (1975) Perceived visual motion as effective stimulus to pursuit eye movement system. *Science* **190**, 906–908.
- Young L. R. (1977) Pursuit eye movement—what is being pursued? In *Control of Gaze by Brain Stem Neurons* (Edited by Baker R. and Berthoz A.). Elsevier/North Holland Biomedical Press, Amsterdam.
- Young L. R. and Stark L. (1963) Variable feedback experiments testing a sampled data model for eye tracking movements. *IEEE Trans. Human Factors in Electronics* HFE-4, 38–51.
- Zee D. S., Friendlich A. R. and Robinson D. A. (1974) The mechanism of downbeat nystagmus. *Archs Neurol.* **30**, 227–237.