Vision Research. Vol. 19, pp. 619 to 632
Pergamon Press Ltd 1979. Printed in Great Britain

THE EFFECT OF EXPECTATIONS ON SLOW OCULOMOTOR CONTROL—I. PERIODIC TARGET STEPS

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(*Received* 6 *February* 1978; *in revised form* 30 *October* 1978)

Abstract—Eye movements were recorded while subjects used saccades to track repetitive target steps at three frequencies (0.25, 0.375 and 0.50 Hz). The eye moved smoothly in the direction of expected target steps at velocities as high as 30′/sec beginning as early as 350 msec before the expected target step. Such anticipatory smooth eye movements were caused by expectations. They were not drifts toward the primary position. The expectation that a target would step and not the expectation that a saccade would be made caused the anticipatory smooth eye movements.

Anticipatory smooth eye movements were found on both horizontal and vertical meridians, before small (10′) as well as large (426′) target steps, with a sequence of target steps in the same direction as well as with square-wave target motion, and in the presence of textured visual backgrounds. They could not be abolished voluntarily and were found in all subjects—the two experienced subjects who knew the purpose of the experiments and also in the three naive inexperienced subjects.

These results suggest that expectations of future target motions have important influences on the activities of the slow oculomotor subsystem.

INTRODUCTION

Slow control, the oculomotor subsystem that is used to maintain the line of sight on stationary targets, is believed to be under visual control. That is, motor commands for slow eye movements are derived from information the oculomotor system receives about motion of the target image on the retina.

The evidence for this belief is as follows: First, the line of sight remains stable when visible targets are stationary. Standard deviations during slow control are only about 2′–3′ (Steinman *et al.*, 1973). A visible target is essential. When the target is removed and the subject is left in darkness, the line of sight steadily drifts away from its former position (Skavenski and Steinman, 1970; Steinman *et al.*, 1973).

Second, not only is a visible target required, but when the target is stationary, the direction of the line of sight cannot be changed voluntarily by means of a smooth eye movement (Dodge, 1903; Yarbus, 1967, p. 160). Directed smooth eye movement (smooth pursuit) requires a smoothly moving target. Furthermore, when the target moves smoothly, the line of sight cannot be kept in place. The eye will move smoothly in the direction of target motion. However, if a stationary target is superimposed on a moving background, the line of sight can, once again, be maintained by slow control as well as it can be maintained when the stationary point is seen in a completely static environment (Murphy *et al.*, 1975). Thus, whether the eye is relatively stationary or moves smoothly does not depend on what a subject wants to do but rather on whether the attended stimulus is stationary or is moving.

The picture just presented describes the general case. There are some exceptions—special situations in which directed smooth eye movements can occur without a moving target. For example, some investigators report finding a rare individual who can make voluntary smooth eye movements without a moving target (Westheimer and Conover, 1954; Heywood, 1972). Also, there are special stimulations which have produced smooth eye movements in a larger population, namely, a vivid after-image (Heywood and Churcher, 1971; Steinbach and Pearce, 1972; Yasui and Young, 1975), active movement of an arm in darkness (Steinbach, 1969; Jordan, 1970), or an illusion of motion (Heywood, 1973; Steinbach, 1976). However, apart from these exceptions it is widely believed that when a stationary target is present, directed smooth eye movements cannot be made in the absence of a smoothly moving target (Alpern, 1972; Cumming, 1976).

This paper challenges that belief. It will be shown that a powerful input to smooth eye movement is provided by expectations of future target motion. Expectations cause the eye to move smoothly away from a stationary point in the direction of the future target motion well before the target begins to move. This effect of expectations on smooth eye movement is not voluntary in the sense that the smooth eye movement in response to expectations cannot be produced voluntarily and cannot be suppressed voluntarily. Such anticipatory smooth eye movements do not require special stimulation of the kind described above. They occur without after-images, moving limbs, or illusions of motion. Anticipatory smooth eye movements are produced exclusively by expectations of future target motion.

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There have been prior indications that expectations might influence smooth eye movements. The possibility first appeared in studies of pursuit of sinusoidal motions (Dodge *et al.*, 1930; Westheimer, 1954). These studies revealed that smooth pursuit improved over time and that the eye often tended to change direction before the target changed direction, a phenomenon Dodge *et al.* (1930) called "anticipatory reversal". The influence of expectations on smooth pursuit was investigated, once again, in the early 1960's when linear systems analysis began to be used to model the oculomotor system (e.g. Dallos and Melvill-Jones, 1963; Young and Stark, 1963). These investigators compared smooth pursuit of periodic and aperiodic stimuli. The periodic stimuli were sinusoidal motions. The aperiodic stimuli were either sums of sinusoids (Stark *et al.*, 1962) or bandwidth limited Gaussian noise (Dallos and Jones, 1963; Michael and Jones, 1966). Dallos and Jones modeled the predictor mechanism by assuming that any difference between the response to the periodic and aperiodic patterns was due to operation of the predictor. They proposed that there is a "short-term periodicity detector" that inhibits the predictor when target motion is aperiodic. They also proposed that the operation of the predictor was due to learning in the sense that the oculomotor system must respond repeatedly to the same kind of target motion before it learns the stereotyped response and can predict what the target will do.

This notion of an oculomotor predictor did not sit well with some. St Cyr and Fender (1969) did not believe that a predictor mechanism was responsible for short phase lags during tracking of periodic target motion. They concluded:

> "We find it extremely difficult to visualize a cortical predictor which manages to anticipate target motion by 214 msec regardless of the frequency; and equally, to place much credence in a cortical mechanism which switches the predictor in and out" (St. Cyr and Fender, 1969, p. 1495).

They proposed instead that the short phase lags observed with periodic targets were due, not to prediction, but to time delays that were shorter for periodic than for aperiodic target motions. They proposed that the delay time was a "function of how much information processing takes place within the system" (St Cyr and Fender, 1969, p. 1469). Such delays would be longer for the more complex stimuli because there is more information to be processed. St Cyr and Fender's suggestions were interesting because they pointed out an obvious problem with prior work. Namely, that differences in response to periodic and aperiodic stimuli had been attributed to the operation of a predictor mechanism when, in fact, the differences could have been due to different informational characteristics of the periodic and aperiodic stimuli.

St Cyr and Fender's dismissal of prediction, however, rested on their belief that periodic motions only reduce phase lags. One of them pointed out explicitly that their argument would not hold if periodic motions produce phase *leads* (Fender, 1971). In fact they do. Phase leads had been reported a number of times (Dodge *et al.*, 1930; Westheimer, 1954; Drischel, 1958; Sunderhauf, 1960; Stark *et al.*, 1962, Bornemann *et al.*, 1964) and have been recently confirmed (Winterson and Steinman, 1978).

Despite such evidence for prediction, St. Cyr and Fender's analysis has been influential and the possible role of prediction in controlling slow eye movements has not received attention in recent years. Most recent investigators try to avoid the problem by using unpredictable inputs to study the oculomotor response.

The anticipatory smooth movements which will be described in this paper indicate that the problem cannot be avoided. Prediction plays an important role in oculomotor performance.

METHODS

Eye movement recording

Eye movements were recorded primarily by a contact lens optical lever. Details of this instrument are described in Haddad and Steinman (1973). Its RMS noise level was 9″ in the 4.5° recording field used in the present experiments. Movements of the right eye on either the horizontal or vertical meridan were recorded. The left eye was closed and covered and the head was stabilized by an acrylic dental biteboard.

The voltage output of the optical lever was fed on-line through a 50 Hz filter to a 12-bit analog-to-digital converter (ADC). The ADC, under the control of a minicomputer (Nova 2/10), sampled eye position every 10 msec. Each of these 10 msec samples was the average of 4 analog-to-digital conversions made within the same millisecond. The digitized voltages were stored on LINC tape for later analysis.

Stimuli

Stimuli were generated on a display monitor (Tektronix 604, P-4 phosphor) located 1.31 m directly in front of the subject's right eye. The display was viewed in complete darkness. All stray light was blocked by curtains and baffles.

The stimulus used in the initial experiments was a single diffraction limited point that stepped back and forth through 99′ along the horizontal meridian at one of three frequencies (0.25, 0.375 or 0.50 Hz). In other words, the point stepped once every 2, 1.5 or 1 sec. These frequencies are within the range of frequencies used in prior studies (Stark *et al.*, 1962; Dallos and Jones, 1963). Its motion was controlled by a function generator (Tektronix 501). On any given trial the point stepped between either primary position and a position 99′ to the right of primary, or between primary position and a position 99′ to left of primary. The point, whose intensity was 1 log unit above foveal threshold, jumped against a dark background. The output of the signal generator was not only sent to the display monitor but was also fed to a channel of the ADC. During each trial the eye and stimulus channels were sampled at the same time so that a digital sample of target position was obtained for each digital sample of eye position.

Subjects

Five subjects participated in the experiments. The main subjects were Steinman and Kowler. Both were experienced in eye movement experiments and knew the purpose of the present research. The three other subjects (WL, AK, and MW) who participated had never served in an eye movement experiment and were, and remained, naive as to the purpose of these experiments. The eye movements of the naive subjects were recorded by an SRI Double Purkinje Image Tracker that will be described later.

Only one of the experienced subjects (Steinman) had previously tracked target motions similar to those employed in the present experiments.[2] Kowler had no prior practice of tracking target steps in the laboratory, so her data, as well as the data from the naive subjects, represents her first performance in such tracking tasks.

Procedure

Trials, which lasted 25 sec, were started 100 msec after the subject pressed a button which began data acquisition. The target was in motion before the first trial and continued to step during intertrial intervals. The subjects were instructed to use saccades to track each target step. They were asked to wait until they saw the target step before making a saccade to the new position and to use a single saccade whenever possible.

Twenty-five second trials were also recorded while the subjects used slow control to maintain the line of sight on a stationary point in each of the three positions (primary, left 99′, or right 99′) the target occupied during the tracking trials. During these trials, which were run in the same recording sessions as the tracking trials, the subjects knew that the target would stay in place.

All subjects were tested for their ability to make a directed voluntary smooth eye movement at the beginning and at the end of the series of experiments. This was done by asking them to move smoothly, back and forth, between two stationary targets. None of the five subjects demonstrated any ability to make voluntary directed smooth eye movements. They used saccades exclusively to shift the line of sight.

Data analysis

Digitized eye position samples were analyzed by computer programs whose principal task was to calculate eye velocity during intersaccadic intervals. Average eye velocity was computed for successive 50 msec periods beginning 500 msec before each target step and ending 150 msec after each target step. Occasionally, subjects made small saccades (on the order of 5′–10′) while waiting for the target step. Fifty msec intervals that contained such saccades were discarded. The onset and offset of these miniature saccades were detected by acceleration criteria that were chosen empirically for each subject by inspection of analog records of eye position in which saccades detected by the computer program were marked by flags. Typical acceleration criteria were 75′/sec^2–100′/sec^2. The criteria were chosen to make it very unlikely that miniature saccades would be included in drift velocity estimates. This led occasionally to a high velocity drift being called a miniature saccade and its removal from the estimate of intersaccadic drift velocity. Only a smaller number of 50 msec samples (5%) were discarded for this reason.

The latency of the first saccade made in response to each target step was also measured. The onsets of these large saccades were detected most accurately by using both velocity and acceleration criteria, namely, the first change in eye position of a least 15′ between two 10 msec samples and an increase in eye velocity of at least 200′/sec between two successive pairs of 10 msec samples. This proved to be an accurate way of detecting the large saccades made in response to the target steps. The computer program's detection of saccades was confirmed by inspection of analog records of the eye and stimulus position in which flags marked the onset of the saccades detected by the program. Only very rarely were large saccades missed or inappropriate large saccades detected (1%). These cases were eliminated from subsequent analyses.

Saccadic latency was measured to be sure that the instruction to wait for each target step was followed. Steps where saccadic latency was less than 100 msec (2%) were eliminated from subsequent analyses in all experiments except one, whose object was to examine intersaccadic drifts before such short latency saccades.

RESULTS

Characteristics of anticipatory smooth eye movement with periodic target steps

The eye begins to drift in the direction of the target step before the step occurs. The representative eye movement records reproduced in Fig. 1 show that the eye drifts in the direction of the target step well before the step occurs. Both subjects made anticipatory smooth eye movements at the three step frequencies used. Such anticipatory smooth eye movements were seen on the first trial for each subject. They appeared automatically, requiring no practice, training, or special effort on the part of the subject.

Anticipatory smooth eye movements are responses to an expectation and are not caused by a tendency of the eye to drift to the primary position in the orbit. This is shown by the histograms in Fig. 2. Each graph contains four distributions of 50 msec eye velocities. Two of the distributions in each graph are for rightward steps, one for steps toward and the other for steps away from primary. The other two distributions are for leftward steps, again toward and away from primary.

As these graphs illustrate, the eye drifts to the right while expecting rightward steps and to the left while expecting leftward steps. Note that drift velocities were almost the same when steps were towards or away from the primary position. Thus, anticipatory smooth eye movements are not drifts toward the primary position of the eye in the orbit. A convenient consequence of this result is that all further analyses will show the response for a given step direction pooled over the primary and eccentric positions.

As the eye drifts in the direction of the expected target step, its velocity steadily increases over time. This is illustrated by Fig. 3 which shows the time course of the development of the anticipatory smooth eye movements. Each function plots mean 50 msec velocity samples for corresponding periods of time relative to the step averaged over all steps for a particular frequency and direction. Two things are apparent. First, the anticipatory smooth eye movements begin about 350 msec before the step after which drift velocity increases with time at a fairly constant rate. Second, drifts are faster for the higher frequencies.

The eye drifts at velocities higher than those found during typical slow control. Figure 4 shows how drift velocities before expected rightward and expected leftward steps differ from drift velocities when the subjects used slow control to maintain the line of sight on a stationary point, knowing full well that the target would *not* step (the center function in each graph).

It is clear that a substantial portion of drifts while expecting target steps were faster than drifts when target steps were not expected. Summary statistics of the distributions plotted in Fig. 4 show that mean 50 msec velocities before expected steps were much

[2] Steinman had done this twice before (Timberlake *et al.*, 1972; Winterson and Steinman, 1978). In both cases phenomena of the kind studied extensively in this paper were observed but not reported because they were not directly related to the purpose of these other studies.

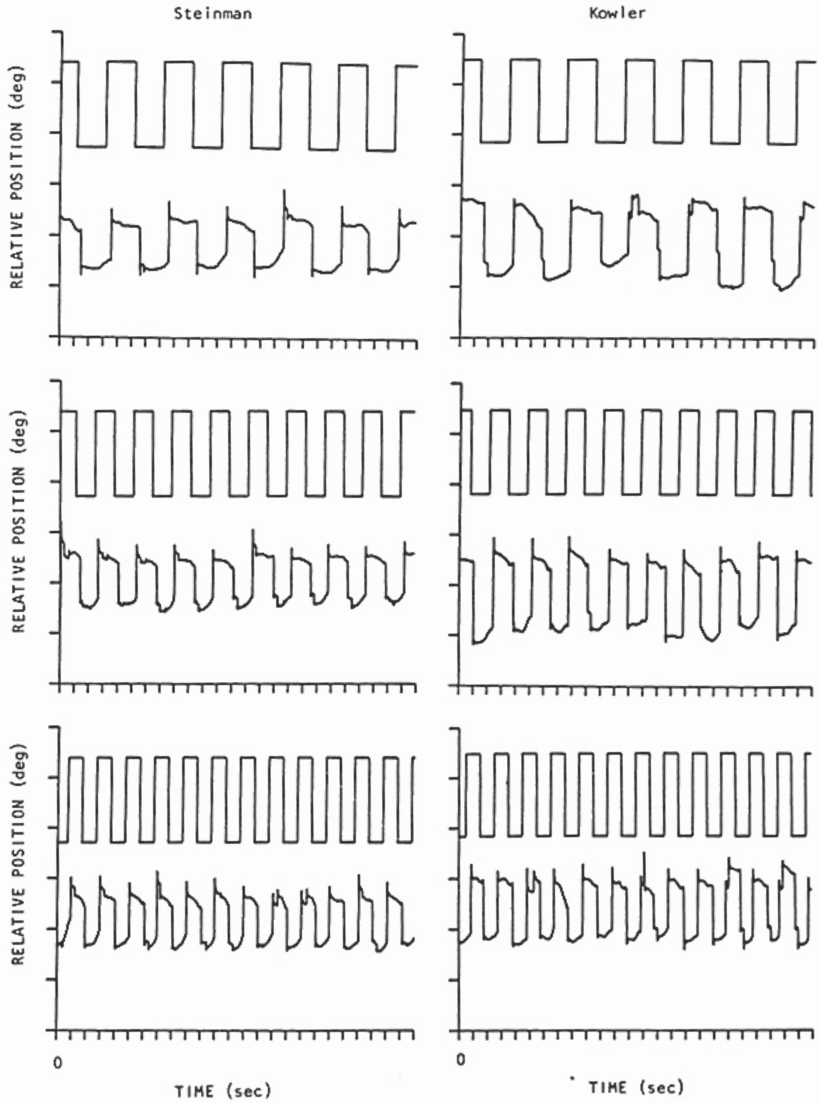

Fig. 1. Horizontal anticipatory smooth eye movements (bottom traces in each graph) with periodic target steps (top traces in each graph) at 0.25 Hz (top graphs), 0.375 Hz (middle graphs), and 0.50 Hz (bottom graphs). The time scale shows 1 sec intervals. The position scale shows 1° distances. The records begin at $T = 0$. Upward displacements of the traces signify movements to the right.

higher than velocities when steps were not expected, that is, mean 50 msec velocity for Steinman before rightward steps averaged over all three frequencies was 15.8′/sec (S.E. = 0.24, $N = 3503$), before leftward steps was −9.9′/sec (S.E. = 0.21, $N = 3604$). When steps were not expected, mean 50 msec velocity was 0.2′/sec (S.E. = 0.14, $N = 4001$). Summary statistics of Kowler's distributions show the same thing, namely, mean 50 msec velocity before rightward steps was 8.9′/sec (S.E. = 0.19, $N = 5109$), before leftward steps was −13.0′/sec (S.E. = 0.20, $N = 4890$), and when steps were not expected mean 50 msec velocity was −2.2′/sec (S.E. = 0.17, N = 3939).[3]

Anticipatory smooth eye movements are not restricted to the horizontal meridian. Anticipatory smooth eye movements were prominent on the vertical meridian when vertical target steps were expected. This is shown in Table 1 where mean 50 msec vertical eye velocities before expected upward and downward steps are compared to mean 50 msec vertical velocities when steps were not expected. The velocity distributions were somewhat more variable than those for the horizontal meridian, but it is clear that drifts before vertical target steps were pronounced.

Anticipatory smooth eye movements do not change with practice. Most treatments of the role of prediction in smooth pursuit have stressed the notion that the predictive components of the response develop over time as the oculomotor system learns to respond in a stereotyped way to repetitive stimulation (Stark *et al.*, 1962; Dallos and Jones, 1963). However, anticipatory smooth eye movements do not show characteristics suggestive of a learning process. They were present on the first trial and did not change with

[3] Negative signs indicate leftward direction.

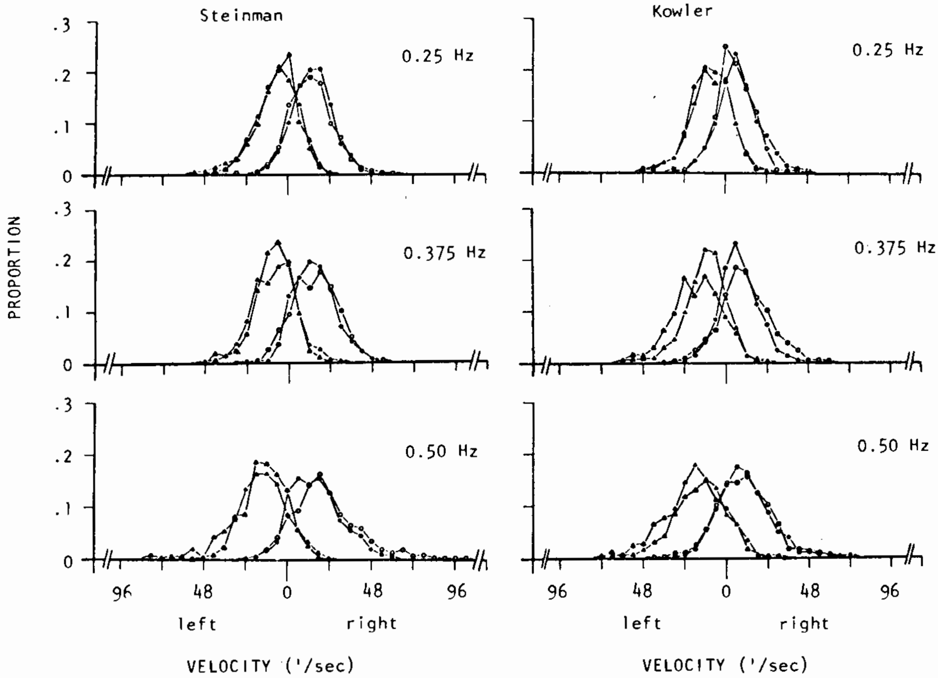

Fig. 2. Velocity histograms of horizontal anticipatory smooth eye movements with periodic target steps. Histograms contain 50 msec velocity samples beginning 350 msec before and continuing to 150 msec after the target stepped. Circles signify rightward steps and triangles leftward steps. Filled symbols signify steps away from primary, open symbols steps toward primary. Each histogram contains about 700 samples.

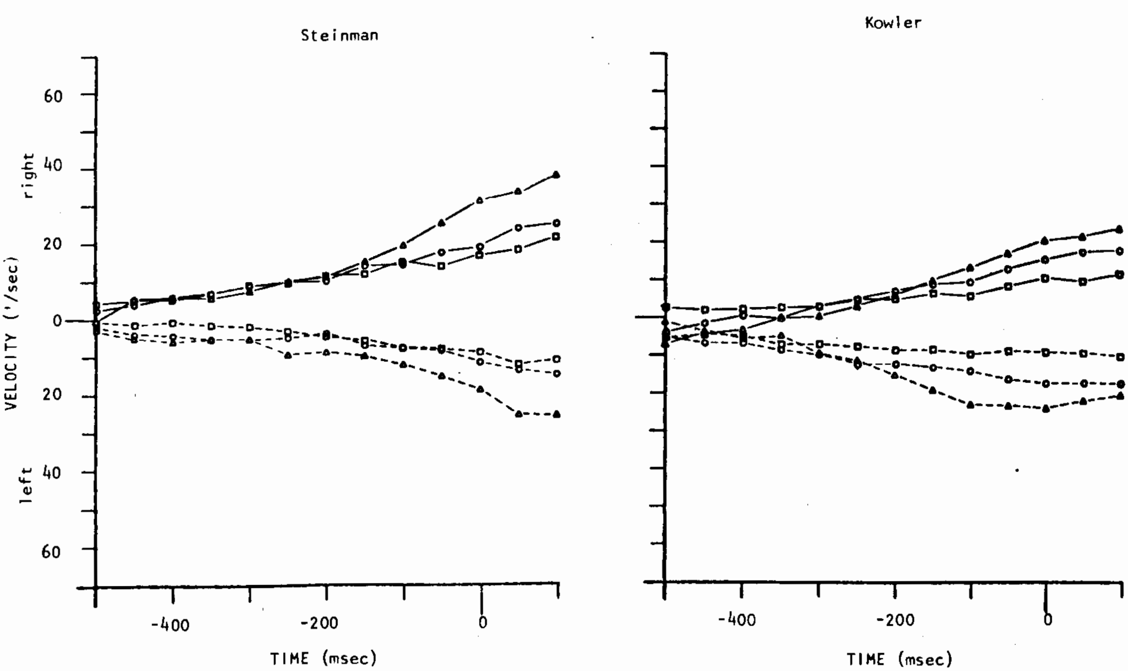

Fig. 3. Time course of horizontal anticipatory smooth eye movement velocity with periodic target steps. The step occurred at $T = 0$. Squares signify 0.25 Hz, circles 0.375 Hz, and triangles 0.50 Hz. Solid lines are for rightward steps, dashed lines for leftward steps. Each datum point is the mean of about 130 50-msec velocity samples.

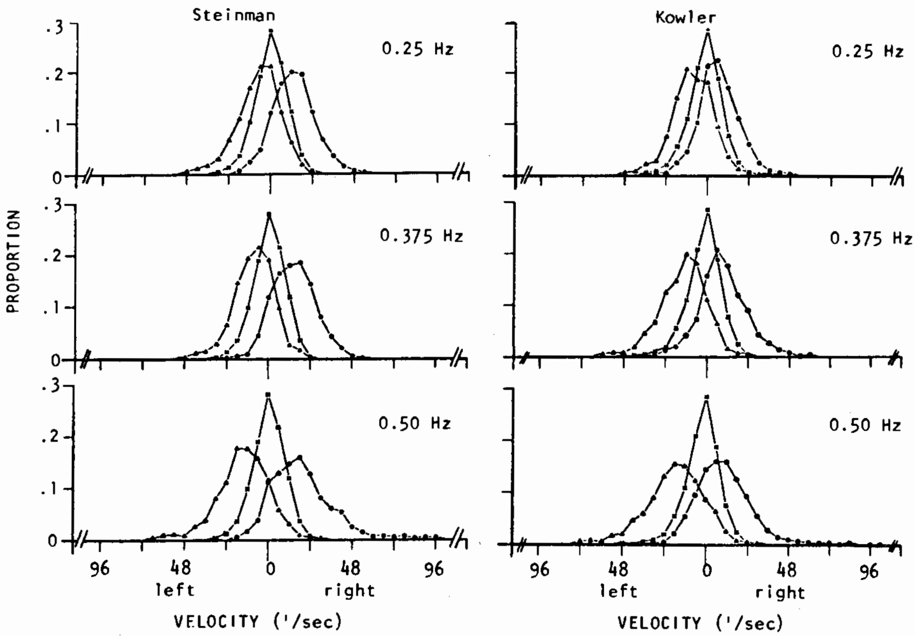

Fig. 4. Velocity histograms when horizontal periodic target steps were expected and when steps were not expected. Circles signify rightward steps, triangles leftward steps, and crosses no steps. Histograms for target steps contain 50 msec velocity samples beginning 350 msec before and continuing to 150 msec after the target stepped. Histograms, when no step was expected, are based on entire 25 sec trials when the target was located at primary, 99′ to the right, or 99′ to the left. Each histogram for target steps contains about 1400 samples. Each histogram, when no step was expected, contains about 4000 samples.

practice. Figure 5 shows two things: Drift velocities were as fast during the first half of the 25 sec trials as they were during the last half of the trials (top graphs). Also, they were as fast during the first half of the experimental sessions as during the last half (bottom graphs). Thus, the effect of expectations on smooth eye movements did not change with practice, suggesting that the effect of expectations does not depend on learning a new oculomotor response. This result does not really conflict with the results of Dallos and Jones (1963) who actually found that the gain and phase of sinusoidal tracking did *not* change with practice (see their Figs 6 and 7). They ignored their result when they went on to incorporate notions of learning in their model of smooth pursuit.

To sum up what we have seen thus far: when re-

Table 1. Mean 50 msec vertical eye velocities (MV) when vertical periodic target steps were expected at three frequencies (F) and when steps were not expected for subjects Steinman and Kowler. Velocities before upward (U) and downward (D) steps are shown separately

	Steinman		Kowler	
F	MV ('/sec)	N	MV ('/sec)	N
0.25 Hz				
U	13.5 (0.62)	627	4.7 (0.56)	519
D	−18.9 (0.61)	619	−15.9 (0.69)	518
0.375 Hz				
U	13.8 (0.87)	494	11.5 (0.81)	488
D	−21.7 (0.88)	486	−25.5 (1.04)	464
0.50 Hz				
U	13.8 (0.97)	446	23.1 (1.01)	386
D	−24.9 (0.94)	415	−31.5 (1.27)	406
Overall				
U	13.7 (0.46)	1567	12.2 (0.45)	1393
D	−21.4 (0.45)	1520	−23.7 (0.57)	1388
No steps	−1.3 (0.21)	4081	0.1 (0.26)	4066

S.E. are given in parentheses and the number (N) of 50 msec samples is also shown. Means for target steps are based on samples beginning 350 msec before and continuing to 150 msec after the target stepped. Means, when no step was expected, are based on entire 25 sec trials when the target was located at primary, 99′ up, or 99′ down. Negative signs indicate downward direction.

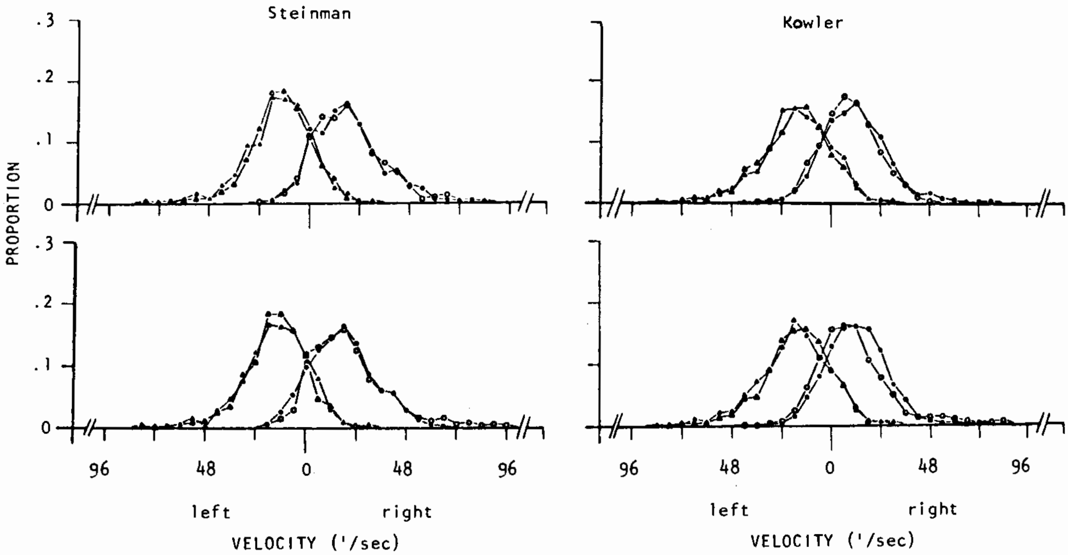

Fig. 5. Comparison of first with second halves of trials (top) and first with second halves of experimental sessions (bottom). Open symbols signify first halves and closed symbols second halves. Circles signify rightward steps and triangles leftward steps. Target step frequency was 0.50 Hz. Histograms contain 50 msec velocity samples beginning 350 msec before and continuing to 150 msec after the target stepped. Each histogram contains about 700 samples.

petitive steps are tracked, the eye drifts in the expected direction of each step before the step occurs. Anticipatory smooth eye movements begin as early as 350 msec before the step and become faster as the time of the step approaches, attaining velocities much higher than those seen when a target step is not expected. This phenomenon occurs on both horizontal and vertical meridians. It is not learned and does not change with practice.

Anticipatory smooth eye movements are caused by the expectation of a target step and not by the expectation that a saccade will be made

In the experiments just described, two events are expected. One is that the target being fixated is about to jump in a known direction. The other is that a saccade will be made in a known direction. Which of these expectations produces anticipatory smooth eye movement? To find out, each of these expectations was removed separately. The expectation of the target step proved to be critical.

First, the instruction to make a saccade in response to the step was removed. Instead, the subject was required to stay in place at one of the target locations (either the center or the eccentric location) while the target stepped back and forth. The stimuli and analyses were identical to those of the previous experiment with one exception. Only steps in which the target jumped away from the position of the subject's line of sight were analyzed because steps in which the target jumped back to the line of sight never occurred in the original experiment.

Both subjects continued to show anticipatory smooth eye movements; only the velocity of the movements was reduced as can be seen in Fig. 6. So, anticipatory smooth eye movements do occur before expected target steps when the expectation to make a saccade is removed.

This result suggests that the expectation of the target step is more important than the expectation that a saccade will be made. This was confirmed in the next experiment where the target step was removed but the instruction to make a saccade was reinstated. Here, the stimulus was two stationary points, one located at the primary position and the other at one of the eccentric positions (99′ to the right or left). The subject began each trial by looking at one of the points. An auditory signal every 1.5 sec told the subject to make a saccade to the other point. The results of this experiment are summarized in Fig. 7. Clearly, the effect of expectation on smooth eye movement was abolished. Thus, anticipatory smooth eye movements are caused by the expectation that a target will step and not by the expectation that a saccade will be made.

These results suggest that anticipatory smooth eye movements are not produced by the saccadic subsystem when it is preparing to make a saccade to a predictable location. It seems more likely that the expectation phenomenon originates in neural structures that are concerned with changes in retinal stimulation or with changes in the perceived location of an object. These results also suggest that anticipatory smooth eye movements are not produced by shifts of attention towards the periphery of the visual field. If this were the case, then anticipatory smooth eye movements would have occurred when saccades were made between the two stationary points because attention surely shifted in the direction of the intended saccade to the periphery when the signal sounded. Anticipatory smooth eye movements did not occur under this condition.

Anticipatory smooth eye movements are hard to abolish

We have just seen that anticipatory smooth eye movements require the expectation that a target will step. But, given such an expectation, do anticipatory smooth eye movements always occur? Can they be

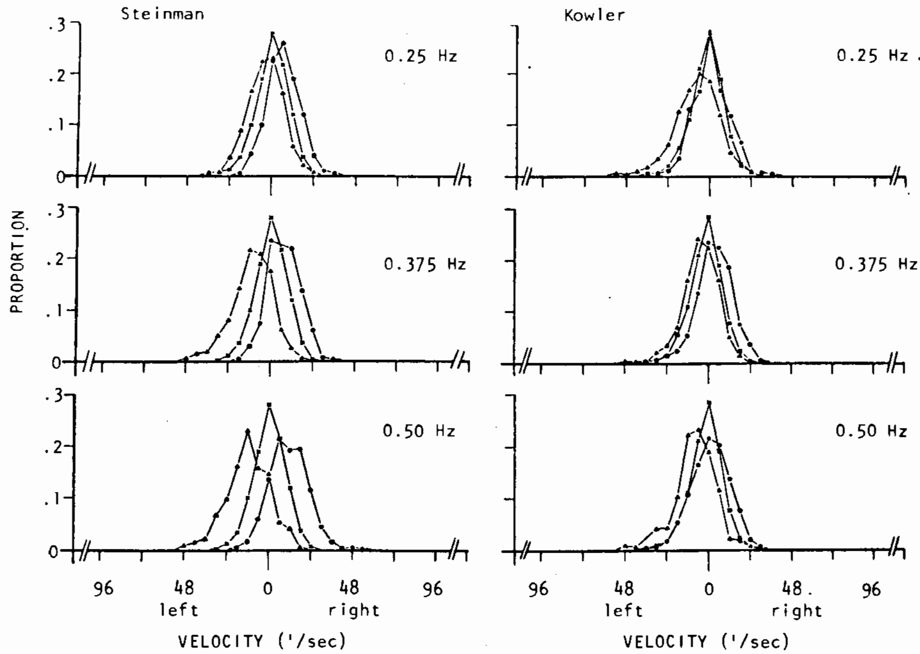

Fig. 6. Velocity histograms when saccades were not made to expected periodic target steps and when steps were not expected. Circles signify rightward steps, triangles leftward steps, and crosses no steps. Histograms for target steps contain 50 msec velocity samples beginning 350 msec before and continuing to 150 msec after the target stepped. Histograms when no step was expected are based on entire 25 sec trials when the target was located at primary, 99′ to the right, or 99′ to the left. Each histogram for target steps contains about 500 samples. Each histogram, when no step was expected, contains about 4000 samples.

abolished by changes in the stimulus or instructions? Four likely changes were tried. None abolished the effect of expectations.

Target step size had little influence. Given that the expectation that a target will step causes anticipatory smooth eye movements, it is reasonable to suspect that reducing the size of the expected step might reduce the velocity of the drifts. This was examined by asking subjects to track target steps of four sizes (99′, 50′, 25′, and 10′) at one step frequency (0.375 Hz). Step size was always known in advance. Anticipatory smooth eye movements were present at all step sizes, but there was no consistent relationship between step size and drift velocity. Steinman's velocities were reduced at smaller sizes but reductions were small and not proportional to the reductions in step size. Kowler's velocities were reduced only for rightward steps. Thus, the expected direction of the target step has a larger effect on the velocity of anticipatory smooth eye movements than the expected size of the target step. These results are summarized in Table 2.

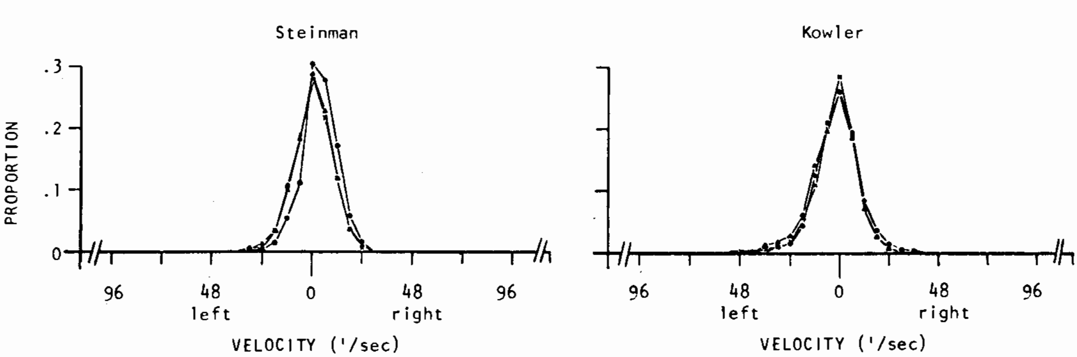

Fig. 7. Velocity histograms when saccades were made between two stationary points in time with an auditory signal (0.375 Hz) and when the line of sight was maintained on a single stationary point. Circles signify rightward saccades between the two points, triangles leftward saccades between the two points, and crosses no saccades with the single point. Histograms for the two points contain 50 msec velocity samples beginning 350 msec before and continuing to 150 msec after the auditory signal. Histograms for the single point are based on entire 25 sec trials when the target was located at primary, 99′ to the right, or 99′ to the left. Each histogram for the two points contains about 700 samples. Each histogram for the single point contains about 4000 samples.

Anticipatory smooth eye movements cannot be abolished voluntarily. Subjects tried to use an effort of the will to suppress anticipatory smooth eye movements while tracking steps at 0.375 Hz. Only Kowler was successful, and she only partially. She reduced the anticipatory smooth eye movements but only in one direction—the right (mean 50 msec drift velocity before rightward steps = 1.7′/sec, S.E. = 0.47, $N = 737$). Her anticipatory smooth eye movements while expecting leftward steps were still clearly present (mean 50 msec drift velocity before leftward steps = −9.8′/sec, S.E. = 0.56, $N = 634$). Steinman was completely unsuccessful. His anticipatory smooth eye movements were *faster* when he tried to suppress them (mean 50 msec drift velocity before rightward steps = 17.7′/sec, S.E. = 0.61, $N = 755$; mean 50 msec drift velocity before leftward steps = −10.8′/sec, S.E. = 0.51, $N = 780$) than when no specific effort was made to suppress them (see Fig. 4). These results indicate that anticipatory smooth eye movements are only marginally under voluntary control. They could be suppressed but only by one subject and, in this case, only in one direction.

Anticipatory smooth eye movements were not abolished when saccades were synchronized with the target steps. Subjects were instructed to make saccades in time with each step. This was done to see whether using saccades to anticipate steps would prevent slow eye movements from reflecting the expectations of the steps.

Both subjects followed the instruction. Steinman's mean saccade latency was 38 msec (S.D. = 96.4, $N = 176$). Kowler's was −17 msec (S.D. = 109.2, $N = 149$). These latencies were much shorter than those observed in the original experiment where the subjects were instructed to wait for each target step before making a saccade in response to it (Steinman's mean latency = 283 msec, S.D. = 60.1, $N = 204$; Kowler's mean latency = 309 msec, S.D. = 76.6, $N = 332$). Synchronizing saccades with target steps had little effect on the drifts. Steinman's mean 50 msec drift velocity before rightward steps = 12.4′/sec (S.E. = 0.63, $N = 549$) and his mean 50 msec drift velocity before leftward steps = −3.6′/sec (S.E. = 0.55, $N = 549$). Kowler's mean 50 msec drift velocity before rightward steps = 9.6′/sec (S.E. = 0.80, $N = 360$) and her mean 50 msec drift velocity before leftward steps = −12.3′/sec (S.E. = 0.63, $N = 359$).

A richly textured visual background reduces but does not abolish anticipatory smooth eye movements. A visual background was provided by placing a graticule on the face of the display and turning on the room lights. Figure 8 shows that the drifts were reduced but not abolished. The largest effect of visual frames was found in Steinman's response to leftward steps at the 2 lowest frequencies (0.25 Hz and 0.375 Hz). The effects of visual frames were less striking in Kowler's response. She showed anticipatory smooth eye movements in both directions at all 3 frequencies.

Thus, anticipatory smooth eye movements cannot be abolished by reductions in step size, a richly textured visual background, voluntary attempts to turn them off, or synchronizing saccades with target steps. Anticipatory smooth eye movements are robust. They

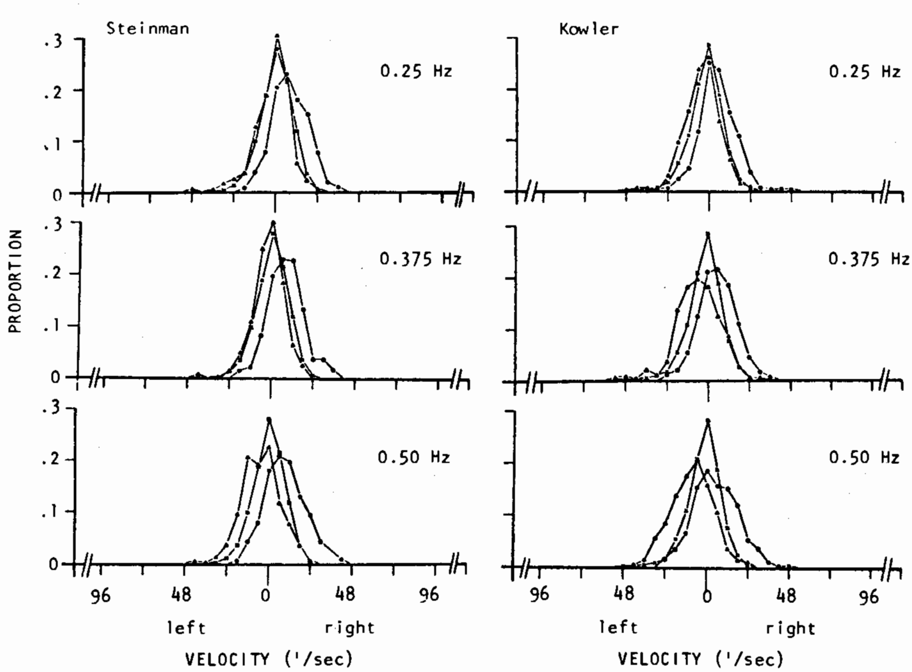

Fig. 8. Velocity histograms when expected periodic target steps were superimposed on a richly textured visual background and when steps were not expected. Circles signify rightward steps, triangles leftward steps, and crosses no steps. Histograms for target steps contain 50 msec velocity samples beginning 350 msec before and continuing to 150 msec after the target stepped Each histogram, when no step was expected, is based on entire 25 sec trials when the target was located at primary, 99′ to the right, or 99′ to the left. Each histogram for target steps contains about 300 samples. Each histogram when no step was expected contains about 4000 samples.

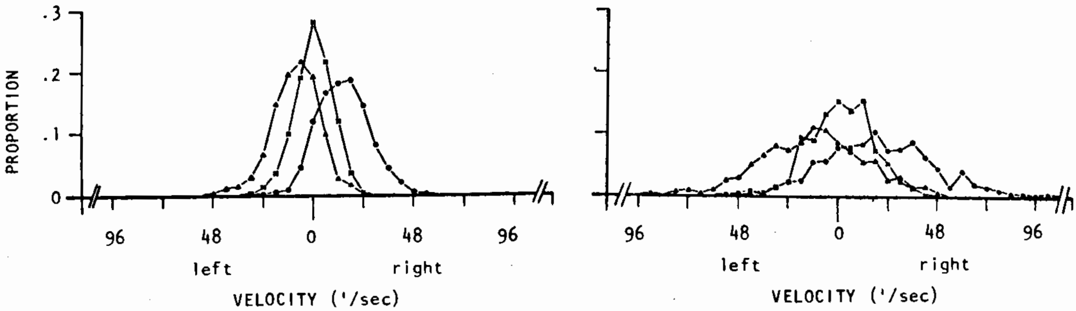

Fig. 9. Velocity histograms for Steinman when periodic target steps at 0.375 Hz were expected and when steps were not expected. Recordings on the left were made with the optical lever, on the right with the Double Purkinje Image Tracker. Circles signify rightward steps, triangles leftward steps, and crosses no steps. Histograms for target steps contain velocity samples beginning 350 msec before and continuing to 150 msec after the target stepped. Histograms when no step was expected are based on entire 25 sec trials when the target was located at primary, 99′ to the right, or 99′ to the left. Optical lever histograms are based on 50 msec velocity samples. Tracker histograms are based on 100 msec velocity samples. Each histogram for target steps contains about 1400 samples for the optical lever and 550 samples for the tracker. Each histogram, when no step was expected, contains about 4000 samples for the optical lever and 650 samples for the tracker.

do not depend on particular stimulus configurations or instructions. Rather, they appear whenever target steps are expected.

Anticipatory smooth eye movements within large visual fields

The next experiments show that anticipatory smooth eye movements: (1) occur for larger steps than had been studied up to this point, (2) occur when a sequence of target steps in the same direction is tracked, and (3) do not occur when saccades are made across a row of stationary points in response to an auditory signal.

Eye movements for these and all subsequent experiments were recorded with an SRI Double Purkinje Image Tracker (Cornsweet and Crane, 1973). Briefly, this instrument records eye rotations free from head or eye translations by measuring the distance between infrared reflections from the front surface of the cornea (the first Purkinje image) and the rear surface of the crystalline lens (the fourth Purkinje image). This method is effective because the relative position of these two images changes only when the eye rotates and not when the eye or head translates. The RMS noise level of this instrument was 1.1′, seven times higher than the noise level of the optical lever. However, the tracker, despite the high noise level, has certain advantages that made its use necessary for the remaining experiments. Namely, its recording field is large ($\pm 20^\circ$) and it requires no attachments to the eye (a biteboard is required). These features allowed recording from naive subjects, the study of large eye rotations, and long recording sessions (a contact lens cannot be worn for longer than 40 min). The tracker, unfortunately, can only be used easily with emmetropes which meant that only one of the experienced subjects (Steinman) could be studied. Kowler could not because she is myopic. This presented no problem with the optical lever because her spectacle correction was incorporated into her scleral contact lens. Contact lenses, however, cannot be worn with the tracker.

Figure 9 acquaints the reader with the contributions of relatively high levels of Gaussian noise to quantitative analyses based on recordings made with the Double Purkinje Image Tracker. This figure shows velocity histograms measured with the optical lever and the tracker. The data were obtained under the same experimental conditions and the analyses were the same with one exception. Tracker histograms plot 100 msec velocity samples while optical lever histograms, as usual, plot 50 msec samples. The longer intervals were used for tracker data in order to prevent its noise level from obscuring the phenomenon.

Anticipatory smooth eye movements with large target steps. Steinman's response to large target steps were studied with the Tektronix 604 display located at optical infinity. The optical arrangements used permitted the display to subtend 21°. Periodic target step displacements of 99′, 199′ and 426′ from the primary position to the right and from the primary position to the left were tracked within this large field. Step frequency was 0.375 Hz. Anticipatory smooth eye movements were present for all three step sizes and, as was the case with small periodic steps, drift velocities increased as step size increased. The effect of step size on drift velocity depended on step direction. The mean 100 msec drift velocity for the largest (426′) rightward step (23.7′/sec, S.E. = 1.39, $N = 372$) was only slightly greater than mean 100 msec drift velocity with both the middle (199′) rightward step (21.5′/sec, S.E. = 1.50, $N = 361$), and the smallest (99′) rightward step (20.7′/sec, S.E. = 1.12, $N = 401$). Leftward steps were affected more by changes in target step size. The mean 100 msec drift velocity for the largest (426′) leftward step (−16.5′/sec, S.E. = 2.07, $N = 423$) was almost twice as great as the mean 100 msec drift velocity for the middle (199′) leftward step (−8.3′/sec, S.E. = 1.63, $N = 354$). But velocity was reduced by only about 25% when step size was reduced again by a factor of two. Mean 100 msec velocity for the 99′ leftward step was −6.5′/sec (S.E. = 1.17, $N = 431$). This result is similar to what was found for this subject when small steps were studied in (see Table 2) in that the reduction in mean drift velocity was not proportional to the reduction in step size.

Table 2. Mean 50 msec eye velocities (*MV*) when periodic target steps of different sizes were expected for subjects Steinman and Kowler. Velocities before rightward (*R*) and leftward (*L*) steps are shown separately.

Step size	Steinman *MV* (′/sec)	*N*	Kowler *MV* (′/sec)	*N*
99′				
R	15.7 (0.71)	345	8.1 (0.90)	326
L	−13.1 (0.71)	363	−13.8 (0.91)	214
50′				
R	13.1 (0.56)	535	4.1 (0.55)	613
L	−8.1 (0.43)	612	−16.2 (0.59)	576
25′				
R	10.6 (0.48)	551	3.2 (0.65)	591
L	−8.2 (0.40)	569	−13.4 (0.52)	555
10′				
R	9.9 (0.44)	649	−1.6 (0.88)	646
L	−7.7 (0.43)	636	−14.5 (0.70)	615

S.E. are given in parentheses and the number (*N*) of 50 msec samples is also shown. Means are based on samples beginning 350 msec before and continuing to 150 msec after the target stepped. Negative signs indicate leftward direction.

Anticipatory smooth eye movements with a sequence of target steps in the same direction. For this experiment two kinds of 5 sec trials were run. In one kind target steps were tracked. Before each of these trials the point was located at an eccentric position either 198′ to the right of the primary position or 198′ to the left of the primary position. When Steinman started a trial, the target stepped 99′ toward primary and then continued to make 99′ steps at 1 sec intervals until four steps had occurred. In the other kind of trial saccades were made when an auditory signal sounded each second. The display consisted of five stationary targets located in the positions occupied by the target when it stepped. Steinman was looking at one of the extreme points when he started each trial. He then saccaded to the next point in the sequence every time the auditory signal sounded. A Tektronix 603 Storage monitor was used for these experiments.

Anticipatory smooth eye movements were found when target steps were tracked (mean 100 msec velocity before rightward steps = 18.2′/sec, S.E. = 1.22, $N = 581$; before leftward steps = −9.02′/sec, S.E. = 1.17, $N = 511$). Anticipatory smooth eye movements were not found when saccades were made across the stationary display (mean 100 msec velocity before rightward saccades = 1.5′/sec, S.E. = 1.15, $N = 239$; before leftward saccades = 5.6′/sec, S.E. = 1.06, $N = 231$). This result confirms and extends the earlier experiment in which it was found that expectations of target steps, rather than expectations that saccades will be made, produce anticipatory smooth eye movements (see Figs 6 and 7). These results suggest that when saccades are used for inspecting stationary visual scenes, anticipatory smooth eye movements are not likely to occur. Note, however, that these results do suggest that anticipatory smooth eye movements are likely to occur whenever an object moves predictably in a visual scene.

Anticipatory smooth eye movements are made by naive subjects

So far, we know that anticipatory smooth eye movements are made by experienced subjects who

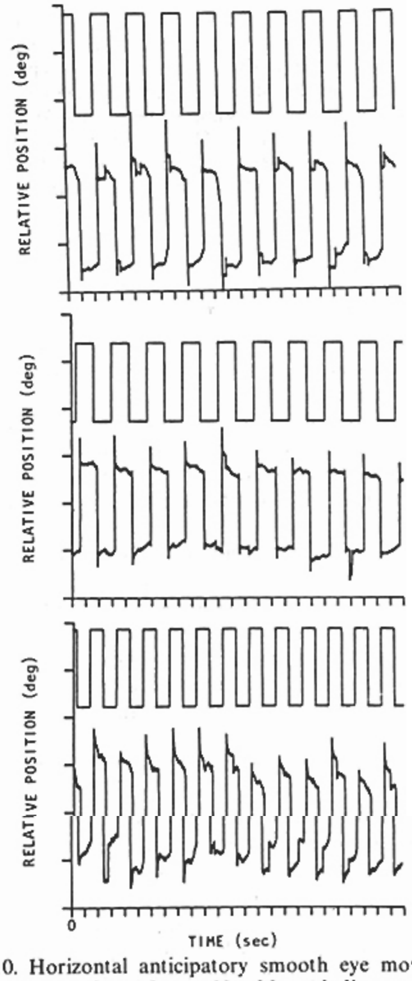

Fig. 10. Horizontal anticipatory smooth eye movements (bottom traces in each graph) with periodic target steps (top traces in each graph) of naive subjects WL (top graph) and MW (middle graph) tracking 0.375 Hz target steps and AK (bottom graph) tracking 0.50 Hz target steps. The time scales show 1 sec intervals. The position scales show 1° distances. The records begin at the left at $T = 0$. Upward displacements of the traces signify movements to the right.

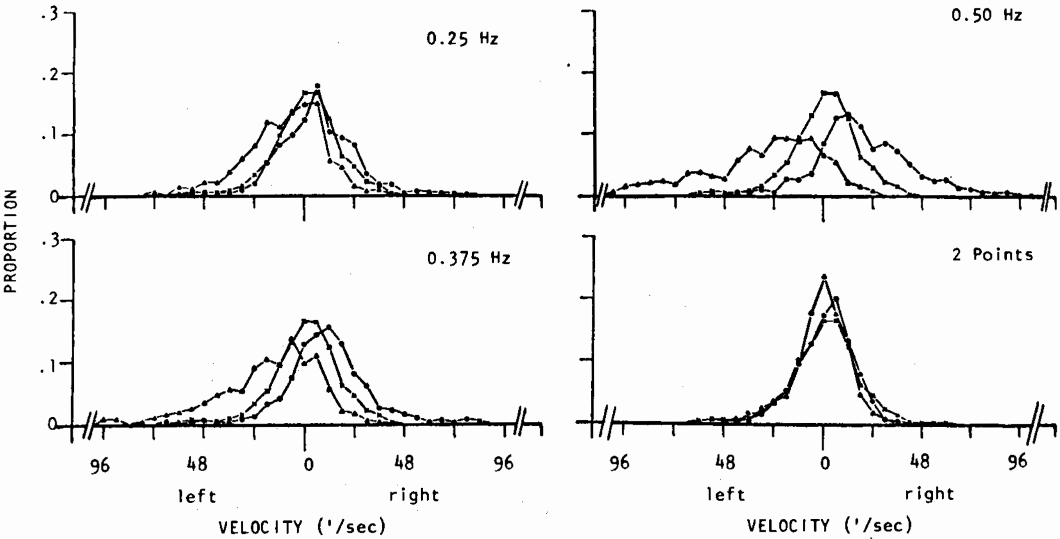

Fig. 11. Velocity histograms for a naive subject (WL) when periodic target steps were expected and when saccades were made between two stationary points in time with an auditory signal (0.375 Hz). Velocity histograms when the line of sight was maintained on a stationary point and no steps were expected are also shown in each graph. Circles signify rightward steps when steps occurred and rightward saccades when there were no steps. Triangles signify leftward steps or leftward saccades, and crosses neither steps nor saccades. Histograms for the target steps and the two stationary points contain 100 msec velocity samples beginning 350 msec before and continuing to 150 msec after the step or the auditory signal. The histograms, when neither steps or saccades occurred, are based on entire 25 sec trials when the target was located at primary, 99′ to the right, or 99′ to the left. Each histogram for the steps and two stationary points contains about 400 samples. The histogram, when neither step nor saccades occurred, contains about 1000 samples.

knew about the phenomenon and the purpose of the experiments. It will be shown that neither experience as an eye movement subject nor knowledge that there are anticipatory smooth eye movements are necessary to produce them.

Three naive subjects were asked to track periodic target steps for 25 sec at three frequencies (0.25, 0.375 and 0.5 Hz). Step size was 99′ for two of the subjects (MW and AK) and slightly larger (125′) for the third subject (WL).

All three naive subjects showed anticipatory smooth eye movements. Representative eye movement records are reproduced in Fig. 10. One of the subjects (WL) was studied extensively. His velocity histograms at each of the three frequencies and his performance when he made saccades between two stationary points in response to an auditory signal are shown in Fig. 11. His performance was similar in all respects to the performance of the experienced subjects.

None of the naive subjects, like the experienced subjects, were able to make directed smooth eye movement voluntarily. When asked to smoothly pursue between two stationary points, all used saccades to shift the line of sight. But all showed anticipatory smooth eye movements when they expected the target to step. Thus, anticipatory smooth eye movements produced by expectations of target motions are general characteristics of the human oculomotor pattern.

DISCUSSION

Expectations of future target motion have profound effects on slow oculomotor control. They cause the eye to move smoothly in the direction of the expected step. These effects are both easy to elicit and difficult to abolish. They are easy to elicit in the sense that they do not require explicit effort or practice. They are difficult to abolish in the sense that changes in step size, the presence of a textured visual background, voluntary attempts to suppress them, synchronization of saccades with target steps, and failure to track target steps with saccades do not eliminate anticipatory smooth eye movements. The effects of expectations are not restricted to a particular pattern of target steps or to experienced eye movement subjects. They were prominent with square-wave target motions and also with a sequence of target steps in the same direction. All five subjects showed anticipatory smooth eye movements. Neither experience nor knowledge influenced the phenomenon. In short we have found that whenever target steps are expected, anticipatory smooth eye movements occur. This characteristic suggests that the slow oculomotor subsystem is as concerned with expectations about what a target will be doing in the future as it is concerned with the target's current activities.

Expectations are important. Why have anticipatory smooth eye movements not been reported before? There are two reasons. First, the type of eye movement monitor limits what can be observed. A particular instrument may not be sufficiently sensitive to demonstrate anticipatory smooth eye movements, or it may be subject to head and eye movement artifacts. In these situations they would not be seen or would be difficult to interpret with confidence. Second, anticipatory smooth eye movements have been seen but not been reported in man and rhesus monkey. Consultation with a number of investigators showed that the phenomenon was observed but not mentioned because it was tangential to the purpose of the experiments (Winterson and Steinman, 1978; Pola, personal communication; Timberlake *et al*., 1972; Robinson, personal communication) and because there was concern in some cases that anticipatory smooth eye movements were merely drifts toward primary position or artifacts arising from slippage of a contact lens after a large saccade. These possibilities were explicitly ruled out in the present series of experiments.

Even in published reports where expectations were implicated, there was a tendency to underestimate their influence. For example, Westheimer (1954) and Dallos and Jones (1963) attributed prediction during sinusoidal tracking to learning. Others, (Young, 1971) limited the effects of prediction by attributing improvements during sinusoidal tracking to the capacity of the smooth pursuit subsystem to calculate, remember, and extrapolate target velocity (p. 432). These limitations do not apply to the anticipatory smooth eye movements described in the present paper because these movements occurred without learning and also when no smoothly moving target was available for velocity extrapolation.

In short, this is the first report of anticipatory smooth eye movements, but these movements have been seen by other investigators. Their importance has been ignored or minimized despite the fact that expectations, as we have shown here, exercise considerable influence on slow eye movements.

However, questions about the generality of the effect of expectations on slow oculomotor control still remain because in all of the experiments described thus far only multiple target steps, whose time and direction were always predictable, were studied. Do anticipatory smooth eye movements occur with single target steps as well? Do they occur when either the time or direction of the target step is not known in advance? Are anticipatory smooth eye movements restricted to target steps, or do they occur before other kinds of target displacements, for example, ramps? Finally, are the effects of expectation limited to slow control or can expectations also affect smooth pursuit? In a second paper (Kowler and Steinman, 1979) we will show that all questions can be answered affirmatively. Expectations affect smooth eye movements in all of these situations, providing further evidence that expectations about a target's future position always act as powerful inputs to the slow oculomotor subsystem.

Acknowledgements—We thank Drs Nancy Anderson, Genevieve Haddad, Willard Larkin, John Z. Levinson, David A. Robinson, Ellin Scholnick, Alexander Skavenski, George Timberlake and Barbara Winterson for valuable suggestions and comments, and M. Warshaw, I. Nicholson, W. Cushman, M. Fritz and A. Kowler for technical assistance.

This research was supported by Grant 00325 from the National Eye Institute and by Grant BNS77-16474 from the National Science Foundation.

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