THE EFFECT OF EXPECTATIONS ON SLOW OCULOMOTOR CONTROL—II. SINGLE TARGET DISPLACEMENTS

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Abstract—It had previously been reported that when periodic target steps are tracked, the eye moves smoothly in the expected direction of the target step before the step occurs. Here we report anticipatory smooth eye movements with single target steps, with single ramps, and during smooth pursuit when a single target step is expected following a ramp. The direction and latency of anticipatory smooth eye movements depended on the expected direction and time of the step, but steps in unpredictable directions or at unpredictable times also influenced smooth eye movements. Anticipatory smooth eye movements require retinal error signals. They were not found in the absence of visual targets.

Our demonstration that expected target motion need not be predictable nor periodic in order for anticipatory smooth eye movements to occur suggests that expectations about the future position of targets always influence slow eye movements.

INTRODUCTION

In the previous paper (this issue, p. 619) we showed that expectations have powerful effects on slow oculomotor control. Namely, when subjects use saccades to track periodic target steps, the eye moves smoothly in the direction of the expected target step well before the step occurs. We will now show that the effects of expectation are not restricted to periodic target steps.

METHODS

Eye movement recording

Horizontal eye movements of the right eye were recorded 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. 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 four 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 made a single 99' step along the horizontal meridian, its motion controlled by the computer. The point, whose intensity was 1 log unit above foveal threshold, jumped against a dark background. The digital-to-analog output of the computer 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

Subjects were Steinman and Kowler. Both were experienced in eye movement experiments and knew the purpose of the present research.

Procedure

The initial experiments examined the response to a single target step in the following way. Trials, which lasted 3 sec, started 100 msec after the subject pressed a button which began data acquisition. One second after the subject started a trial the centered point jumped 99' either to the right or to the left and remained there for the rest of the trial. Target step directions were either predictable or unpredictable—the conditions changing every 10 trials. 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.

An approximately equal number of blocks of trials were run during which the target did not step. The subject knew that it would remain in place and, therefore, had no expectation that its position would change.

Data analysis

The procedures for analyzing data have been described previously (Kowler and Steinman, 1979). Briefly, 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. Only

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a small number of 50 msec samples (1%) were discarded for this reason.

The latency of the first saccade made in response to each target step was also measured. 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.

RESULTS

Anticipatory smooth eye movements before a target step in a predictable and an unpredictable direction. If the expectation of a predictable single target step produces the same effects as the expectation of periodic step displacements, then the eye would drift in the direction of the target step before the step. Unpredictable step directions might not lead to anticipatory smooth eye movements because knowledge that the sequence of target step directions is random might prevent the development of expectations. If there are no expectations, anticipatory smooth eye movements should not be seen and drifts should resemble drifts observed while the subjects maintain the line of sight without any expectation of a target step. Alternatively, if the subject expects the target to step in a particular direction on a given trial, anticipatory smooth eye movements should appear in the direction of the expectation but not necessarily in the true direction of the target step because its direction is unpredictable. Such drifts would reflect guesses about the direction of the target step and would be anticipatory smooth eye movements, but in the long run their direction would not correlate with the actual direction of the target steps which is random.

When step direction was predictable, both subjects made anticipatory smooth eye movements—they drifted in the direction of the expected target step. These results are illustrated by the representative eye movement records reproduced in Fig. 1 and summarized in Fig. 2 and Table 1.

Drift velocities before expected steps in unpredictable directions were different from velocities when no step was expected. Such performance, when step direction was unpredictable, could mean that the drifts observed were anticipatory smooth eye movements in the direction that the subject expected the target to move. This expectation could only be a guess about target step direction because the direction was unpredictable. It is not clear that the drifts reflected guesses because high velocity drifts appeared only in one direction—to the right for Steinman and to the left for Kowler. The reason that drifts in one direction were faster than drifts in the other, when steps were in unpredictable directions, is unknown. But note that neither subject showed this kind of strong directional bias when no step was expected, so it is clear that the expectation that a target will step, even though its direction is not known, affects slow eye movements in a different way than the expectation that no step will occur.

This result raises a problem for those wishing to study the oculomotor system's response to stimulus motion without *any* influence of expectation. This is usually done by moving targets unpredictably—the strategy used by investigators who make the assump-

tion that if motion is unpredictable, then attempts to predict motion will be abandoned because they would be futile (Stark, 1968). However, we have just seen that this assumption can be dangerous. The knowledge that a target will step, even though its direction is unknown, is sufficient to influence smooth eye movements. This raises the possibility that expectations always contribute to oculomotor performance. For example, the stability seen during slow control depends not only on the presence of a stationary target but also on the expectation that the target will remain stationary.

Expectations about time and their effect on anticipatory smooth eye movements

Anticipatory smooth eye movements are present before a target step at an unpredictable time. Is the advanced knowledge of when to expect a step necessary to produce the anticipatory smooth eye move-
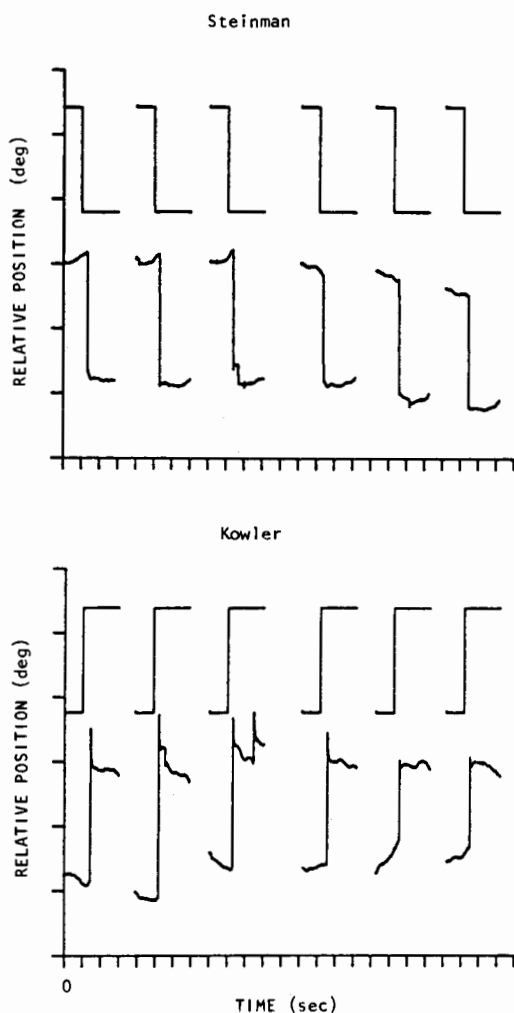

Fig. 1. Horizontal eye movements (bottom traces in each graph) with single target steps (top traces in each graph) in an unpredictable direction (left 3 trials) and in a predictable direction (right 3 trials). The time scales show 1 sec intervals. The position scales show 1° distances. Time is read from left to right. Upward displacements of the traces signify movements to the right.
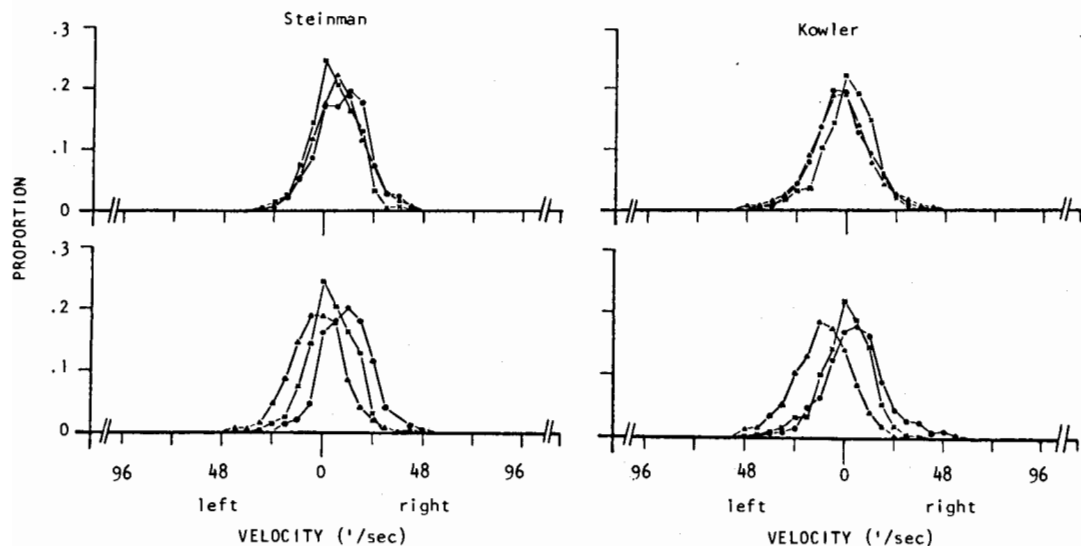
Fig. 2. Velocity histograms when single target steps were expected in a predictable (bottom) and unpredictable (top) direction and when steps were not expected. Circles signify rightward steps, triangles leftward steps, and crosses no steps. Histograms for target steps contain 50 msec velocity samples beginning 350 msec before and continuing to 150 msec after the target stepped. Histograms, when no step was expected, are based on the same portion of the trial. Each histogram, when no step was expected, contains about 600 samples.

Table 1. Mean 50 msec eye velocities (*MV*) when subjects Steinman and Kowler expected single target steps (*Step*) in predictable (*PD*) and in unpredictable (*UD*) directions, single target steps at predictable (*PT*) and at unpredictable (*UT*) times, single ramps (*Ramp*) in predictable (*PD*) and in unpredictable (*UD*) directions, and no steps or ramps (*NSR*). Velocities before rightward (*R*) and leftward (*L*) displacements are shown separately

	Steinman MV ('/sec)	N	Kowler MV ('/sec)	N
Step—PD				
R	11.6 (0.42)	765	5.7 (0.65)	675
L	−2.7 (0.45)	779	−11.2 (0.51)	852
Step—UD				
R	8.5 (0.47)	639	−2.1 (0.59)	530
L	7.0 (0.41)	821	−3.4 (0.50)	832
Step—PT				
R	14.4 (0.51)	590	8.8 (0.76)	476
L	−2.8 (0.45)	649	−10.3 (0.72)	470
Step—UT				
R	14.4 (0.50)	590	5.7 (0.74)	452
L	−1.5 (0.48)	655	−7.4 (0.62)	476
Ramp—PD				
R	11.9 (0.69)	368	6.2 (0.57)	356
L	−6.8 (0.64)	373	−9.2 (0.66)	357
Ramp—UD				
R	1.1 (0.61)	338	−1.7 (0.59)	350
L	2.0 (0.53)	430	−0.2 (0.60)	408
NSR	3.1 (0.39)	773	0.0 (0.52)	596

Standard errors are given in parentheses and the number (*N*) of 50 msec samples is also shown. Means for target steps and ramps are based on samples beginning 350 msec before and continuing to 150 msec after the target displacement. Means, when no displacements were expected, are based on the same portion of the trial. Negative signs indicate leftward direction.

ments? To find out, steps in a predictable direction occurred either at a predictable time (1.5 sec after trial onset) or at a random time between 1 and 2 sec after trial onset. Table 1 shows that anticipatory smooth eye movements were present when time was predictable and also when it was not predictable. Velocities were reduced slightly when time was unpredictable but only for one subject (Kowler).

How long does it take an expectation to produce an anticipatory smooth eye movement? Previous experiments could not answer this question because in all cases the direction of the target step was known before the trial began. Thus, the motor commands to control anticipatory smooth eye movements could have been programmed before the trial began. The following experiment was done to overcome this problem and answer this question. The subject started the trial. At a random time between 1 and 2 sec after the trial began, an auditory signal (1 or 2 "beeps") revealed whether the target step (99') would be to the right or to the left. The target step always occurred 2 sec after the beeps. Eye velocities were calculated beginning 100 msec after beep-offset to allow time for the significance of the auditory signal to be processed. The examination of the time course of anticipatory smooth eye movements shows that the eye traveled at a relatively constant velocity for about 1 sec after the direction of the step was signaled and then began to accelerate (see Fig. 3).

Is the latency of the anticipatory smooth movement always 1 sec regardless of when the step occurs? The experiment was repeated with one difference. The step

occurred 1 sec instead of 2 sec after the beeps. The result is also shown in Fig. 3. The sooner the step was expected the sooner the anticipatory smooth eye movement began. For a 1 sec delay anticipatory smooth eye movements began about 0.6 sec after the beeps. Latency was about half of the latency observed when the delay before the step was twice as long. Also, note that these graphs show that the sooner the step was expected the higher the acceleration. Furthermore, in both cases average anticipatory smooth eye velocity was about the same at the time of the step.

These results indicate that the expectation of when a target will step is critical. It determines the latency and acceleration of anticipatory smooth eye movement.

Anticipatory smooth eye movements before and during a ramp displacement

Up to now anticipatory smooth eye movements have been described for a number of different stimulus configurations but in all cases the expected target displacement was a step. The next experiment shows that expected ramp displacements also produce anticipatory smooth eye movements.

Anticipatory smooth eye movements before a ramp in a predictable and an unpredictable direction. One second after the subject started a 5 sec trial, a centered point began moving smoothly either to the right or to the left. The point traveled at constant velocity (41'/sec) for 2 sec at which time it stopped and remained stationary during the last 2 sec of the trial.
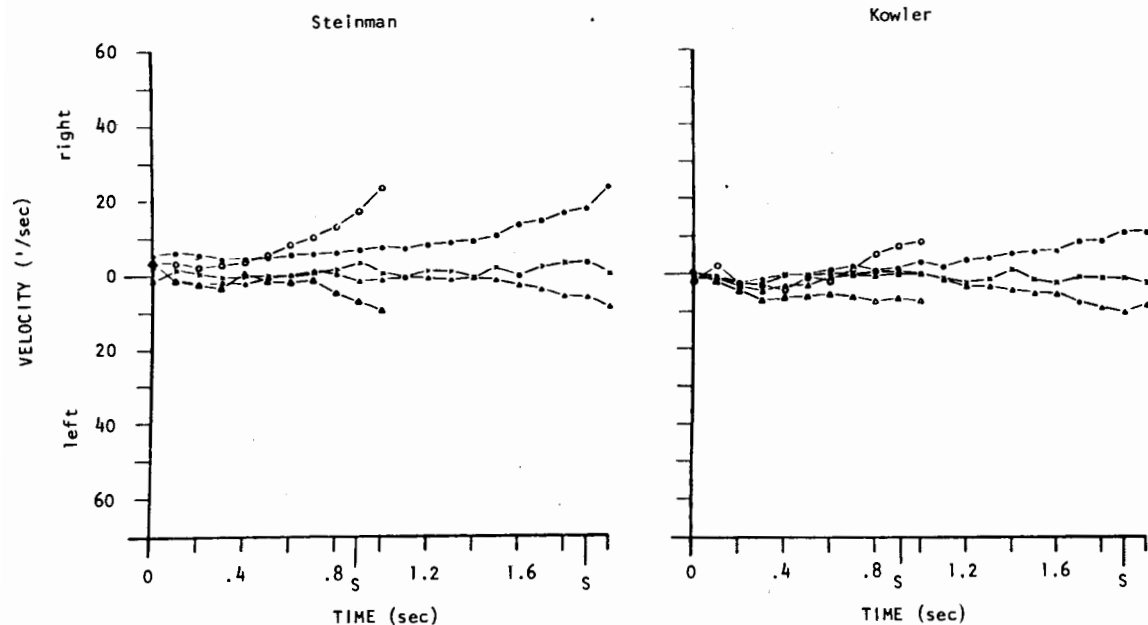

Fig. 3. Time course of anticipatory smooth eye movement velocity with single target steps and when steps were not expected. Single target steps occurred 1 sec (open symbols) or 2 sec (filled symbols) after an auditory signal indicated the direction of the target step. $T = 0$ signified when the auditory signal occurred. The steps occurred at the long lines (S). Circles signify rightward steps, triangles leftward steps, and crosses no steps. Each datum point, when steps occurred after 1 sec, is the mean of about 250 100-msec velocity samples. Each datum point, when steps occurred after 2 sec, is the mean of about 500 100-msec velocity samples. Each datum point, when no step was expected, is the mean of about 100 100-msec samples.
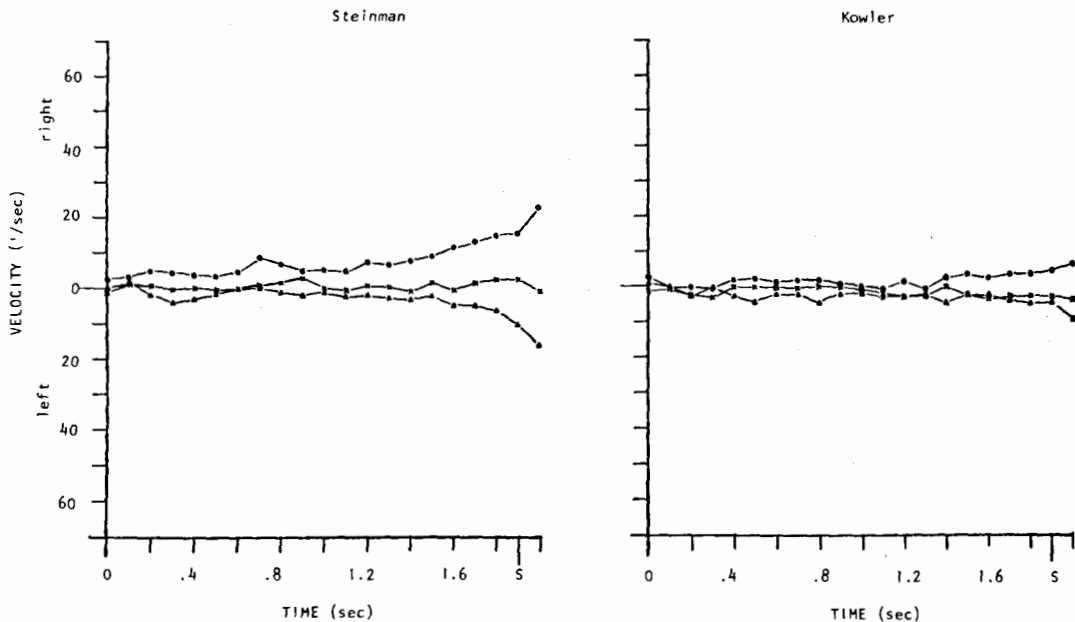
Fig. 4. Time course of anticipatory smooth eye movement velocity with single ramps and when ramps were not expected. $T = 0$ signifies when an auditory signal indicated the direction of the ramp. The ramp occurred at the long line (S). Circles signify rightwards ramps, triangles leftward ramps, and crosses no ramps. Each datum point for ramps is the mean of about 150 100-msec velocity samples. Each datum point, when no ramp was expected, is the mean of about 100 100-msec velocity samples.

As in the experiment with single target steps, ramp direction was either predictable or unpredictable, the conditions changing every 10 trials.

The anticipatory smooth eye movements before expected ramps in predictable directions shown in Table 1 are about the same velocity as those found before single target steps in predictable directions. However, the result with unpredictable ramps was different than the result with unpredictable steps. When ramp direction was unpredictable, drifts resembled drifts when the point was stationary and no displacement was expected. The directional bias in drifts found for unpredictable step directions was not observed while expecting ramps in unpredictable directions. The reasons for the difference in unpredictable ramps and steps is obscure and cannot be explained at this time.

The time course of anticipatory smooth eye movements before expected ramps. Time course measurements were made in the same way that they were made for single target steps. Namely, at a random time between 1 and 2 sec after the trial began an auditory signal (1 or 2 beeps) indicated whether the ramp would move to the right or to the left. The ramp motion always began 2 sec after the beeps. The time course curves for ramps shown in Fig. 4 are similar to those found for expected steps that occurred 2 sec after the auditory signal (Fig. 3). The eye began to accelerate about 1 sec after the direction of the ramp was signaled. The only difference is that Kowler showed slower anticipatory smooth eye movements before expected ramps than she did before expected steps.

Expectations influence the velocity of ramp tracking.

We have just seen that expectations of a ramp displacement cause the eye to move smoothly in the expected direction of the ramp before the ramp begins. These expectations also lead to higher tracking velocity when the eye follows the moving target. This result is shown in Fig. 5. This figure shows two things. First, anticipatory smooth eye movements occurred when the direction of the ramp was predictable. Second, pursuit velocity was higher for ramps in predictable directions than for ramps in unpredictable directions until 0.5–0.7 sec after the ramp began to move. During this time peak pursuit velocity was higher (10%) than the velocity of the target in both predictable and unpredictable trials. After this brief initial period of high gain, the difference between predictable and unpredictable slow eye movements, which began long before the target started to move, disappeared and both predictable and unpredictable pursuit velocities hovered near target velocity. This period of approximate velocity matching lasted until about 1 sec after the target began to move at which time pursuit velocity began to decrease. One exception can be seen; that is, Kowler's velocity for leftward ramps remained high while she pursued.

There are a number of indications that expectations are important in determining the eye movement before and during smooth pursuit. Namely, the expectation of impending ramp motion influences smooth eye movements before a predictable ramp starts to move. This influence continues into the first phase of smooth pursuit. The expectation of sustained uniform target motion influences the middle phase of smooth pursuit with both predictable and unpredictable ramps, and the expectation of cessation of target
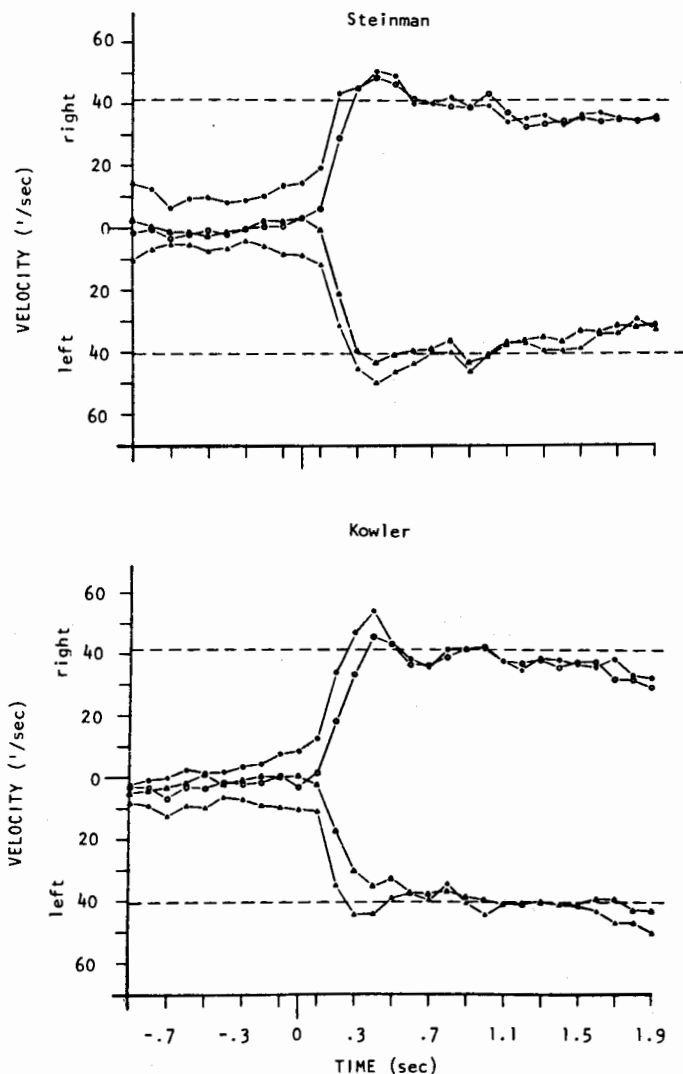
Fig. 5. Time course of smooth eye movement velocity before and during ramps (41'/sec) in a predictable (filled symbols) and unpredictable (open symbols) direction. The horizontal dashed lines indicate ramp velocities. $T = 0$ signifies ramp onset. Circles signify rightward steps and triangles leftward steps. Each datum point is the mean of about 70 100-msec samples.

motion influences the last phase of smooth pursuit. The next experiment shows additional indication of the extent to which expectations influence smooth pursuit.

Expectations of target steps slow down or speed up smooth pursuit depending on the direction of the step relative to the direction of the smooth pursuit. Each trial began with a ramp that was followed by a step. Two ramp velocities were used. Velocity on any given trial was known to the subject. One velocity (8'/sec) was within the distribution of eye velocities seen during slow control. The other was 5 times faster (41'/sec). It was chosen because it is known to produce brisk smooth pursuit (Murphy *et al.,* 1975). When the subject started a 3 sec trial, the target began to move (8'/sec or 41'/sec) to the right or to the left. The ramp continued to move for 2 sec at which time

the target stepped 99' to the right or to the left. Target step directions were either predictable or unpredictable—the conditions changing every 10 trials. Trials without steps were also run. During these trials the ramp was pursued for 5 sec and the subject knew that the target would not step.

When steps in the same direction as the ramp were expected, pursuit velocity was higher than when no step was expected. Pursuit velocity exceeded target velocity more frequently (67%) when steps in the direction of the ramp were expected than when steps were not expected (43%). When steps in the direction opposite to the ramp were expected, smooth pursuit slowed down and frequently (40%) turned around before the step. In other words the subjects smoothly pursued in the direction opposite to the direction the target was moving.
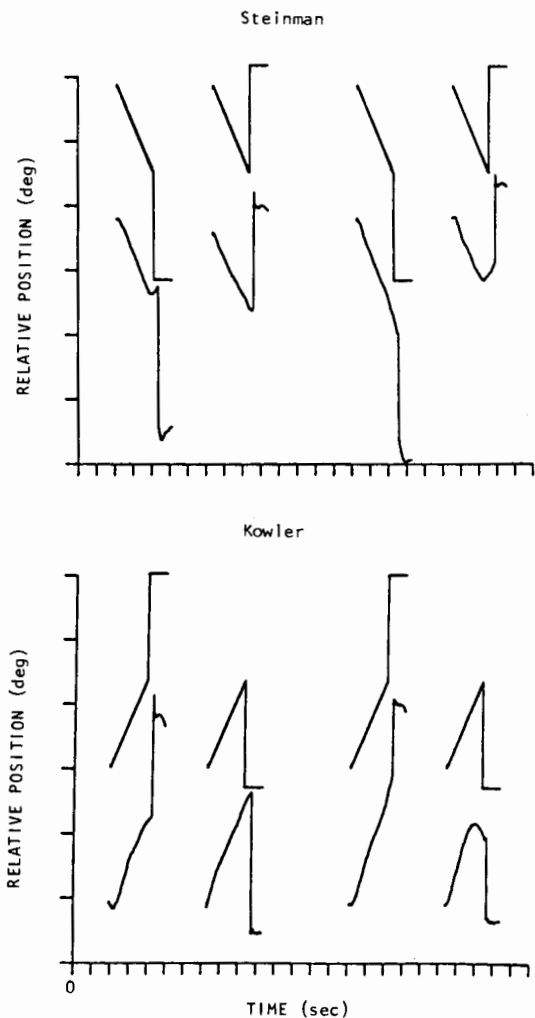
Steinman

Kowler

Fig. 6. Horizontal eye movements (bottom traces in each graph) while tracking ramps (41'/sec) followed by single target steps (top traces in each graph) in an unpredictable direction (left two trials) and in a predictable direction (right two trials). The time scales show 1 sec intervals. The position scales show 1° distances. Time is read from left to right. Upward displacements of the traces signify movements to the right.

These effects for expected steps that followed the higher velocity ramps are illustrated by the analog records reproduced in Fig. 6 and summarized by the histograms in Figs 7 and 8. The effects of expected steps that followed the lower velocity ramps were similar but space does not permit a graphic representation. These effects, however, are summarized in Table 2 along with summary statistics for the higher velocities. The main conclusion to be drawn from these data is that expectations of a target step, operating when the line of sight is smoothly pursuing a moving target, operate in much the same way as expectations of a step operate during slow control when the line of sight is maintained by smooth eye movements on a stationary target. In both cases expectations of a target step in a predictable direction

cause the eye to move smoothly in the direction of the expected step. Also, in both cases, expectations of a target step in an unpredictable direction influence the velocity of slow eye movements, as can be seen in Table 2. When ramps were followed by steps in unpredictable directions, pursuit velocities were different from velocities when steps were not expected.

The time course of anticipatory smooth eye movements during smooth pursuit. The technique for measuring the time course of expectations during smooth pursuit was the same as the technique used for measuring expectations while maintaining the line of sight on a stationary target. Namely, at an unpredictable time between 1 and 2 sec after the ramp began to move, an auditory signal indicated the direction of the target step. The target step occurred 2 sec after the auditory signal. The time course curves shown in Figs 9 through 12 are similar to those seen when the point was stationary before the step (Fig. 3) in that the eye generally began to move in the direction of the target step before the step occurred. However, other features of the time course of anticipatory smooth eye movements during smooth pursuit are different from those seen when the point remained stationary before the step. First, anticipatory smooth eye movements did not begin 1 sec after the auditory signal, as they did when the point was stationary before the step and the step occurred 2 sec after the auditory signal. Rather, anticipatory smooth eye movements began at different times for each subject and ramp velocity. They tended to begin more than 1 sec after the auditory signal and it is difficult to estimate precisely when they started. They could begin as soon as 1.1 sec (Kowler, 41'/sec, left ramp, right step) or as late as 1.4 sec (Kowler, 8'/sec, right ramp, right step). There is even one case where expectation effects are not in the correct direction (Kowler, 41'/sec, left ramp, left step). Eye acceleration was also variable and different from that seen when the point remained stationary before the step. Acceleration, as well as latency, depended on the subject and ramp velocity. Acceleration was highest with the higher velocity ramp when the expected step was opposite to the direction of the ramp. This effect of expectations on pursuit, when expected steps were opposite to ramp direction, is not particularly surprising. It could have been due to the well-known ability of subjects to voluntarily reduce smooth pursuit velocity (Steinman *et al.*, 1969). Note, however, that these authors have also shown that it is not possible to voluntarily adjust smooth pursuit velocity such as to exceed target velocity. So, the other effects of expectation—speeding up and turning around during smooth pursuit—cannot be explained by voluntary control of smooth pursuit. Control experiments were performed to be certain of this. Both subjects tried to exceed target velocity voluntarily. They were not able to do so, nor were they able to make voluntary smooth pursuits opposite in direction to the motion of the target. This confirms the earlier report and shows that the effects of expectations of steps during smooth pursuit cannot simply arise from the ability to make voluntary adjustments in smooth pursuit.

These results have implications for determining how expectations influence oculomotor control. One
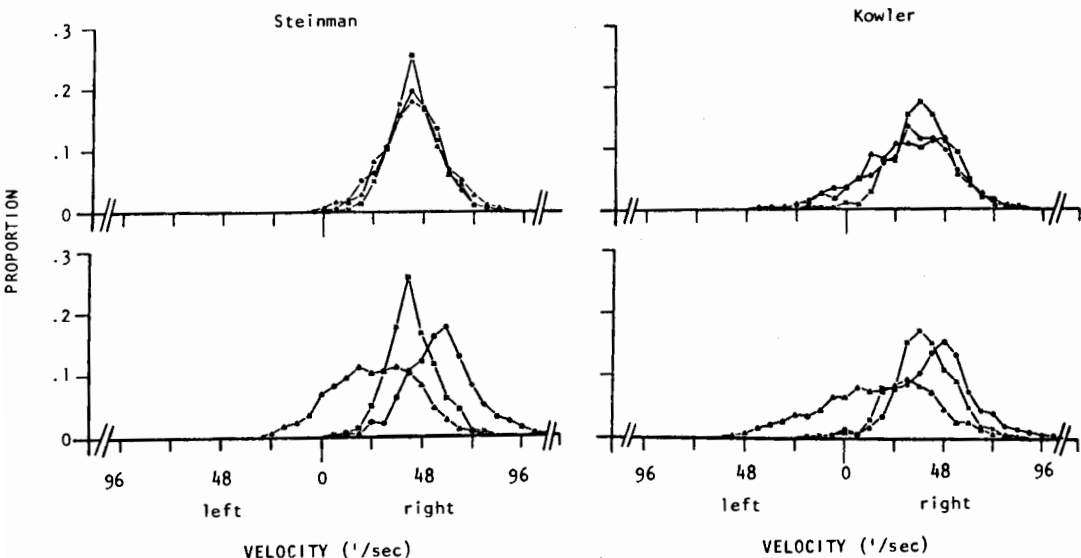
Fig. 7. Velocity histograms when 41'/sec rightward ramps were followed by expected single target steps in a predictable (bottom) and unpredictable (top) direction and when steps were not expected following the ramp. Circles signify rightward steps, triangles leftward steps, and crosses no steps. Histograms 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 the same portion of the trial. Each histogram for target steps contains about 500 samples. Each histogram, when no step was expected, contains about 200 samples.
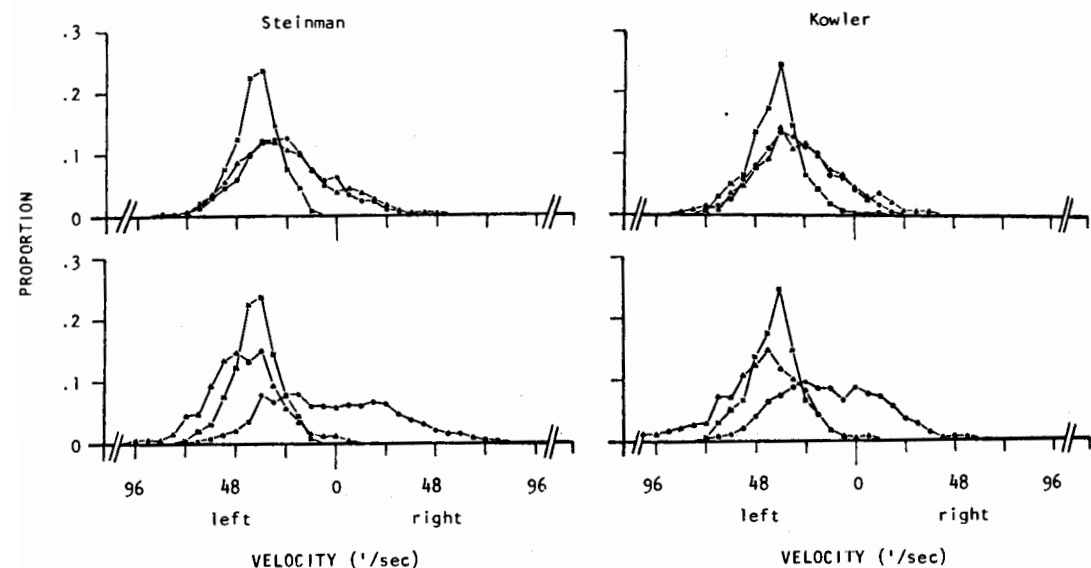

Fig. 8. Velocity histograms when 41'/sec leftward ramps were followed by expected single target steps in a predictable (bottom) and unpredictable (top) direction and when steps were not expected following the ramp. Circles signify rightward steps, triangles leftward steps, and crosses no steps. Histograms 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 the same portion of the trial. Each histogram for target steps contains about 900 samples. Each histogram, when no step was expected, contains about 400 samples.

Table 2. Mean 50 msec eye velocities (MV) when subjects Steinman and Kowler
expected ramps moving at each of four target velocities (TV) to be followed by
a single target step in a predictable (PD) and in unpredictable (UD) direction,
and when no steps were expected (NS). Velocities before rightward (R) and leftward
(L) steps are shown separately

TV	Steinman MV ('/sec)	N	Kowler MV ('/sec)	N
8'/sec				
PD - R	20.6 (0.47)	791	17.4 (0.61)	879
PD - L	3.3 (0.42)	939	−1.9 (0.53)	739
UD - R	12.5 (0.42)	787	7.1 (0.41)	947
UD—L	12.8 (0.39)	943	8.2 (0.54)	679
NS	10.1 (0.56)	323	6.7 (0.50)	362
−8'/sec				
PD - R	9.5 (0.80)	432	3.3 (0.69)	651
PD—L	−12.1 (0.54)	504	−14.4 (0.53)	486
UD—R	1.6 (0.59)	515	−4.1 (0.64)	528
UD—L	−1.2 (0.62)	445	−6.8 (0.56)	650
NS	−6.7 (0.57)	238	−8.0 (0.74)	167
41'/sec				
PD—R	57.3 (0.57)	780	44.7 (0.73)	645
PD—L	25.1 (0.68)	809	14.7 (0.87)	955
UD—R	42.0 (0.49)	723	29.9 (0.84)	655
UD—L	42.1 (0.51)	873	30.1 (0.78)	771
NS	43.3 (0.58)	382	37.7 (0.80)	378
−41'/sec				
PD—R	−1.8 (0.97)	915	−12.1 (0.76)	1047
PD—L	−44.8 (0.61)	787	−47.3 (0.76)	799
UD—R	−25.0 (0.70)	814	−28.3 (0.64)	958
UD—L	−25.3 (0.76)	836	−26.8 (0.76)	782
NS	−39.5 (0.73)	369	−38.7 (0.66)	374

Standard errors 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 displacement. Means, when
no step was expected, are based on the same portion of the trial. Negative signs
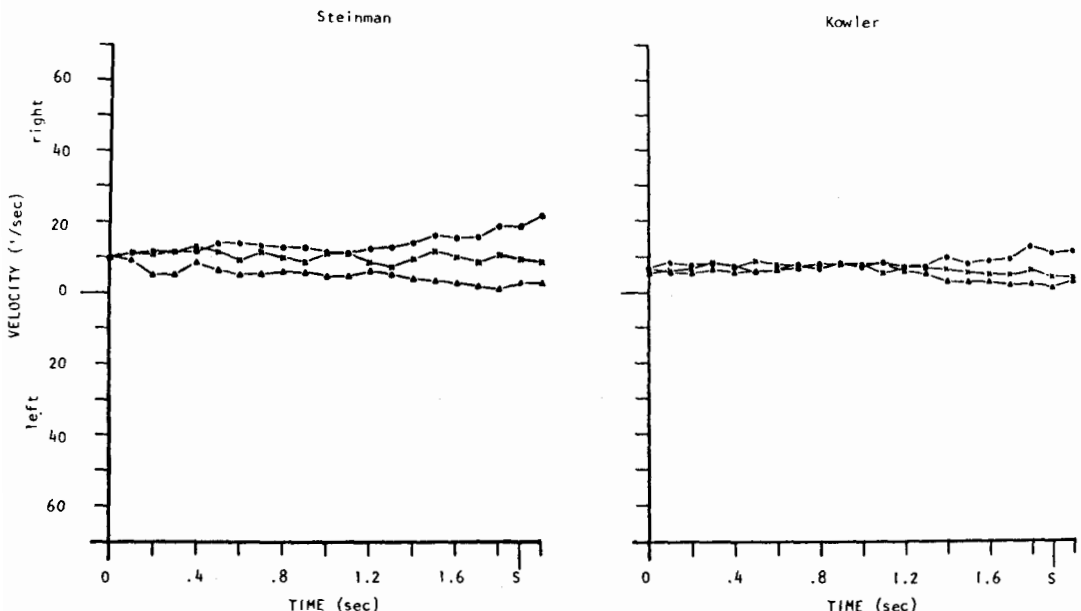indicate leftward direction.

Fig. 9. Time course of anticipatory smooth eye movement velocity when 8'/sec rightward ramps were
followed by single target steps and when steps were not expected following the ramp. $T = 0$ signifies
when an auditory signal indicated the direction of the target step. The step occurred at the long
line (S). Circles signify rightward steps, triangles leftward steps, and crosses no steps. Each datum
point for target steps is the mean of about 150 100-msec velocity samples. Each datum point, when
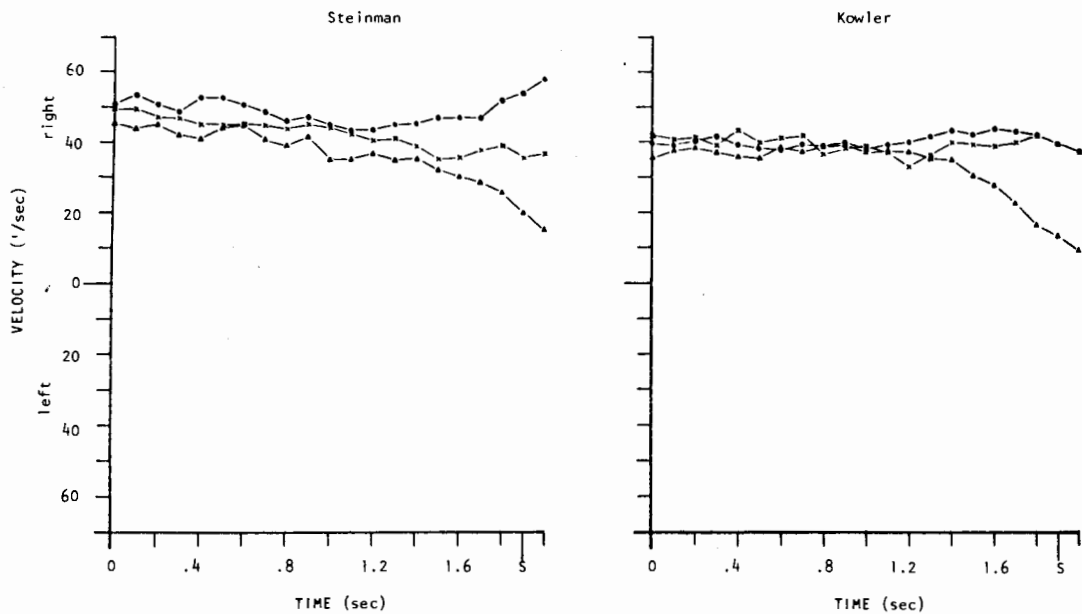no step was expected, is the mean of about 75 100-msec velocity samples.

Fig. 10. Time course of anticipatory smooth eye movement velocity when 41'/sec rightward ramps were followed by single target steps and when steps were not expected following the ramp. $T = 0$ signifies when an auditory signal indicated the direction of the target step. The step occurred at the long line (S). Circles signify rightward steps, triangles leftward steps, and crosses no steps. Each datum point for target steps is the mean of about 150 100-msec velocity samples. Each datum point, when no step was expected, is the mean of about 75 100-msec velocity samples.
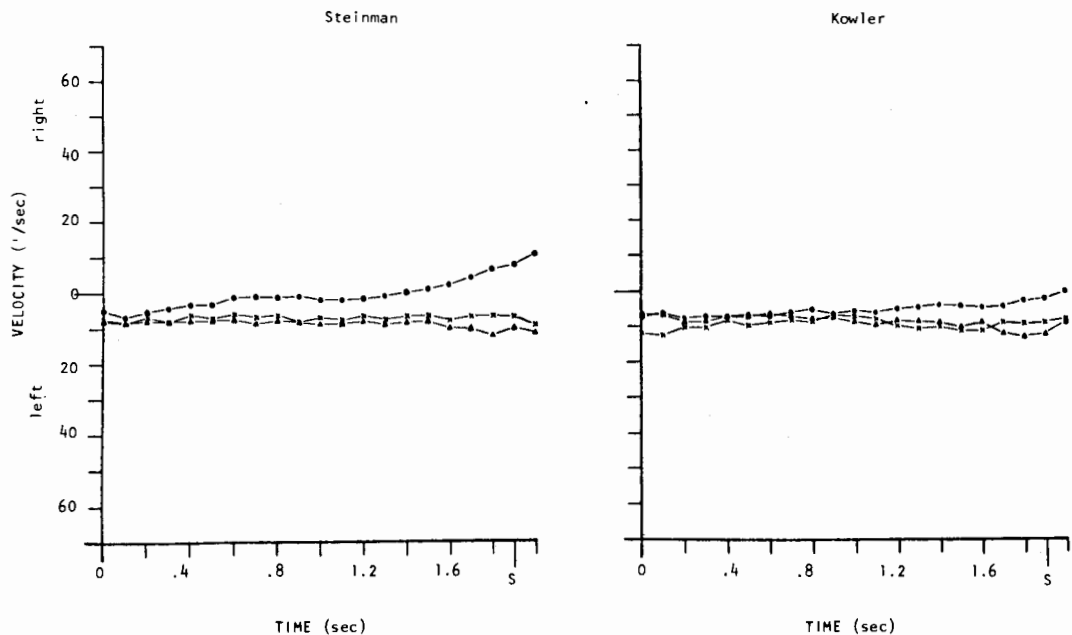

Fig. 11. Time course of anticipatory smooth eye movement velocity when 8'/sec leftward ramps were followed by single target steps and when steps were not expected following the ramp. $T = 0$ signifies when an auditory signal indicated the direction of the target step. The step occurred at the long line (S). Circles signify rightward steps, triangles leftward steps, and crosses no steps. Each datum point for target steps is the mean of about 150 100-msec velocity samples. Each datum point, when no step was expected, is the mean of about 75 100-msec velocity samples.
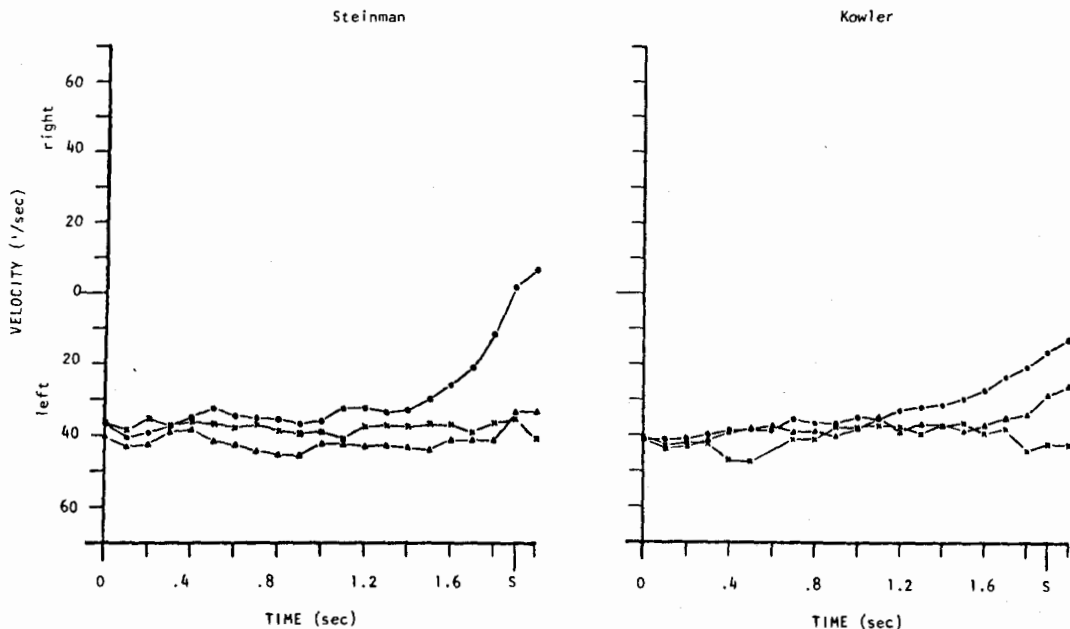
Fig. 12. Time course of anticipatory smooth eye movement velocity when 41'/sec leftward ramps were followed by single target steps and when steps were not expected following the ramp. $T = 0$ signifies when an auditory signal indicated the direction of the target step. The step occurred at the long line (S). Circles signify rightward steps, triangles leftward steps, and crosses, no steps. Each datum point for target steps is the mean of about 150 100-msec velocity samples. Each datum point, when no step was expected, is the mean of about 75 100-msec velocity samples.

possible explanation for anticipatory smooth eye movements, viable when targets are stationary before the steps, is that anticipatory smooth eye movements occur because expectations of future target motions turn off slow control causing the line of sight to drift away from the visual stimulus. There is a situation in which slow control is known to be turned off—the eye drifts in the dark (Skavenski and Steinman, 1970). If this were the kind of thing that were happening before expected target steps, then expectations need only control the direction of drift but need not initiate drift. This scheme can be rejected for expectations during smooth pursuit for the following reason. If smooth pursuit were turned off before expected target steps, then the eye would drift in the direction of the expected step at a velocity independent of the velocity of the pursuit stimulus. This was not what happened. Expectations added to the ongoing pursuit velocity. So it does not seem plausible that expectations operate by turning off smooth pursuit and substituting a directed drift.

Now that we see that this notion is not plausible for expectations during smooth pursuit, it becomes interesting to find out whether this notion is plausible for expectations operating during slow control—the situation in which the line of sight is maintained on a stationary target while expecting the target to step. If expectations produced anticipatory smooth eye movements by turning off slow control before expected target steps, then the eye would drift in the direction of the expected step at the same velocity regardless of whether the point was visible or absent

during the period preceding the step. The next experiment showed that this is not the case.

Anticipatory smooth eye movements require a visible target. Subjects began each 4 sec trial while fixating a centered point. At an unpredictable time between 1 and 2 sec after the trial began, an auditory signal indicated where the point would be located 2 sec later. Immediately after the auditory signal the centered point disappeared and the subject maintained his line of sight in complete darkness for 2 sec. The point then either, (1) reappeared in its original position, or (2) reappeared displaced (99') to the right or to the left.

Anticipatory smooth eye movements were not observed (see Fig. 13). Slow control was, as expected, turned off in the dark. A comparison of the functions in Fig. 13 with those in Fig. 2 show two things. First, that there is no expectation effect in the dark. Second, that drifts in the dark are different from drifts when a stationary point is visible. In the dark Steinman drifts to the right. Kowler drifts to the left under the same conditions. Individual differences in the dominant direction of drift in the dark have been reported before (Skavenski and Steinman, 1970). Both subjects, however, show very little asymmetry in their drifts when the target is visible. So, slow control was turned off when the target was removed, and drifts in the dark when slow control was turned off, do not show effects of expectation. This experiment shows that the notion that expectations produce anticipatory smooth eye movements by first turning off slow control and then replacing it with a directed drift is not tenable.
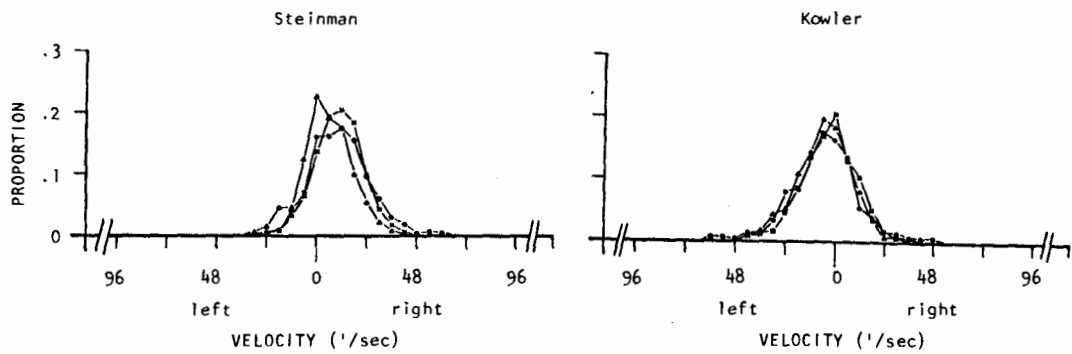
Fig. 13. Velocity histograms when a target disappeared and reappeared 2 sec later in a predictable displaced position or reappeared in the same position. Circles signify rightward displacements, triangles leftward displacements, and crosses the same position. Histograms contain 50 msec samples beginning 350 msec before and continuing to 150 msec after the target reappeared. Each histogram contains about 600 samples.

The fact than anticipatory smooth eye movements require a visible target makes anticipatory smooth eye movements similar to slow control and smooth pursuit in that both of these types of smooth eye movements are also responses to target motion on the retina. This demonstrated similarity raises a new question that will have to be examined in future research. Namely, do anticipatory smooth eye movements arise from the activity of a separate oculomotor subsystem, or do anticipatory smooth eye movements arise because of modifications of the way in which smooth pursuit and/or slow control subsystems respond to retinal image motion?

DISCUSSION

We have shown that periodic target motion is not necessary in order for expectations to influence slow oculomotor control. Anticipatory smooth eye movements occur before single target steps and before single ramps, as well as during smooth pursuit when single target steps are expected. Furthermore, although expected step direction determines the direction of the anticipatory smooth eye movement and expected step time determines the latency and acceleration of the anticipatory smooth eye movement, expectations also affect slow oculomotor control when neither step direction nor time is predictable. These findings do not agree with the conclusions of others, who, when they found evidence for prediction during smooth pursuit (e.g. Stark *et al.*, 1962; Dallos and Jones, 1963), emphasized the need for periodic and predictable stimulus motion. Our results indicate that the slow oculomotor subsystem responds to expectations of future target motion when target motion is neither periodic nor predictable.

The pervasive influence of expectations on slow eye movements have important psychological, physiological and oculomotor implications.

Psychological implications. The discovery of anticipatory smooth eye movements provides a potentially valuable way of objectively measuring expectations about changes in the position of objects in space. Expectations of this kind are not only of interest to

perceptionists and oculomotorists but to cognitive theorists as well (e.g. Michotte, 1954; Piaget, 1954) because the concept of causality is often studied by changing the position of objects in space.

There may be a number of advantages in using anticipatory smooth eye movements to measure expectations of this kind. First, it permits measurement of expectations that may not be accessible to consciousness, and second, it permits study of the presence and development of expectations in children and animals whose verbal and introspective skills are limited.

Given such possible advantages, what kind of questions might be asked? There are questions about expectations themselves. For example, how quickly does an expectation develop? Experimentally, if an observer is presented with a complex but repetitive pattern of target motions, how long does it take before anticipatory smooth eye movements are seen and how long does it take the eye movement pattern to change when the pattern of target motion is changed? Also, it becomes possible to examine the limits imposed by complexity of the pattern of motion on the observer's capacity to develop an expectation about what is likely to happen next. These questions can be addressed in psychophysical experiments but there may be an advantage in using the oculomotor response because it cannot be suppressed and can operate in the absence of any conscious awareness (none of the subjects, naive or experienced, were consciously aware of their anticipatory smooth eye movements).

There are also questions about cognitive development. For example, at what age do children develop realistic concepts about the forces that will be exerted by common objects when they move on collision courses? Experimentally, if a child is looking at a ball of yarn that is being approached from one direction by a crawling spider and from another direction by a rolling basketball, which direction is the yarn likely to move after the collision if the spider and the ball strike the yarn simultaneously? Questions of this type have been asked before and the child's expectations inferred from an emotional reaction to the collision

(Bower, 1974). Anticipatory smooth eye movements may prove useful in such experiments because the direction of anticipatory smooth eye movements will show the expected trajectory which can only be inferred from a series of experiments when the startle response is used.

Physiological implications. Currently, there is considerable interest in the physiological activities underlying and associated with the oculomotor system (Robinson, 1975; Aschoff, 1974; Wurtz, 1976). Finding that smooth eye movement is influenced by expectations about target motion is timely because there are recent hints about the location of the machinery that might be involved. Mohler and Wurtz (1976) reported cells in the intermediate layer of the superior colliculus that began to fire about 100 msec before predictable target steps that a monkey had been trained to track with saccades. Cells in this region that respond before saccades are not news, but cells that respond before target steps are. Mohler and Wurtz's data suggest that the anticipatory discharges were produced by the anticipated change in the position of the target and not by preparation to make a saccade before the target step because anticipatory discharges often occurred when saccadic latency was long. Mohler and Wurtz's (1976) EOG eye movement recordings, unfortunately, were not sufficiently sensitive (0.5°) to observe anticipatory smooth eye movements, so the relationship between activities in this region and such eye movements is speculative. If in subsequent research anticipatory smooth eye movement could be shown to correlate with such discharges, it would lend support to the suggestion made above that anticipatory smooth eye movements may not be smooth pursuits or slow control because it is known that units in this part of the superior colliculus do not fire during such activities (Lynch *et al.*, 1977). But there are reasons to doubt that a high correlation will be found between anticipatory discharges and anticipatory smooth eye movements. Namely, cells that discharged before target steps also discharged before saccades made in the dark, but anticipatory smooth eye movements did not occur in the dark. Also, anticipatory discharges began about 100 msec before the target step, but anticipatory smooth eye movements were underway 350 msec before the target step. This may simply prove to be a species difference, but it is clear that the relationship between unit activity in the superior colliculus and anticipatory smooth eye movements can only be suggestive until accurate eye movement recordings are obtained while these units discharge.

If the superior colliculus turns out not to be involved, one might look next in the parietal cortex because units that show enhanced firing rates before saccades to target steps have also been reported in this region (Lynch *et al.*, 1977).

Oculomotor implications. The question of whether anticipatory smooth eye movements arise from a separate oculomotor subsystem or arise because of modifications in the way either smooth pursuit or slow control respond to retinal image motion has already been raised. The present experiments, although they do not provide an answer to this question, do permit some consideration of the potential merit of the two alternatives.

Anticipatory smooth eye movements, like smooth pursuit and slow control, are responses to target motion on the retina. However, anticipatory smooth eye movements respond to retinal image motion differently than either smooth pursuit or slow control. Both smooth pursuit and slow control keep the line of sight near the attended visual target. This means that retinal image motions produced by motions of the target or drifts of the eye tend to be corrected by smooth eye movements. It has been suggested that a single slow oculomotor subsystem accomplishes this both for smooth pursuit and for slow control (Nachmias, 1961; Robinson, 1971; Murphy *et al.*, 1975).

Anticipatory smooth eye movements, however, do not respond to retinal motion in the same way as smooth pursuit and slow control. These smooth eye movements are not corrective. They introduce an error between target position on the retina and the line of sight. When targets are stationary before expected target displacements, the eye moves smoothly *away* from the target. Error increases. When targets are moving before expected target displacements, the eye frequently pursues faster than the target and even moves opposite in direction to the target motion. Both of these activities also do not correct position errors. They introduce them. Furthermore, the eye accelerates as the time of the expected target displacement approaches. This shows that not only do retinal position errors increase over time, but retinal slip velocity increases as well.

These properties of anticipatory smooth eye movements are radically different from the properties of the other smooth eye movements. This radical difference makes it plausible to suggest that anticipatory smooth eye movements might be controlled by a different oculomotor subsystem than that which controls smooth pursuit and slow control. However, a single subsystem may be sufficient if it is able to both reduce retinal error and increase retinal error.

These oculomotor implications are admittedly speculative. There is, however, one implication of this research that can be stated confidently. Doubts can no longer be raised about the slow oculomotor subsystem's ability to predict future target motions. Furthermore, no model of the slow oculomotor subsystem, which is based on data obtained when the subject is presented with a target that will move or whose motion will change, can be complete unless the effects of expectation are known and taken into account. There is no easy way of avoiding the effects of expectation. Unpredictable target motions are not sufficient to remove these effects. Both unpredictable time and unpredictable direction affect smooth eye movements differently than removing the expectation of target motion completely. A sign on the door of the oculomotor laboratory which states, "All expectation abandon ye who enter here" is not likely to help. Human beings have expectations and when expectations are present, they change the pattern of the oculomotor response. The best way to proceed might be to be aware of these effects, design experiments which permit evaluation of their contribution to performance, and then incorporate their contribution into models of the smooth oculomotor subsystem.

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