THE EFFECT OF EXPECTATIONS ON SLOW OCULOMOTOR CONTROL—IV. ANTICIPATORY SMOOTH EYE MOVEMENTS DEPEND ON PRIOR TARGET MOTIONS

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Abstract—Prior work had shown that smooth eye movements depend both on the motion of the target on the retina and on the subject's expectations about future target motion (Kowler and Steinman, 1979a, b). Effects of expectation cannot be eliminated by making target motions unpredictable (Kowler and Steinman, 1981). The experiment reported here shows that effects of expectations on smooth eye movement depend in a lawful way on the history of prior target motions. Anticipatory smooth eye movements (involuntary drifts in the direction of future target motion) were measured while subjects fixated a stationary target that was expected to step in an unpredictable direction (right or left). Anticipatory smooth eye movement velocity depended on the sequence of steps in prior trials, e.g. velocity was faster to the right when the prior steps were to the right. The influence of prior steps diminished the further back into the past the step occurred. Sequential dependencies were also observed for the saccades used to track the target steps. Anticipatory smooth eye movement velocity was predicted by a two-state Markov model developed by Falmagne *et al.* (1975) for similar sequential dependencies observed in a manual reaction-time task (button-pressing). The model uses the prior sequence of target motions to predict the subject's expectation, and assumes that the expectation determines anticipatory smooth eye movement velocity. The fit of the model to the data was good which shows that taking expectations into account is both necessary and feasible. Taking expectations into account, quantitatively, allows accurate predictions about smooth eye movement velocity when target motions are unpredictable.

INTRODUCTION

Smooth eye movements are important for vision because they are used to keep stationary and moving targets relatively stationary on the retina. Despite their importance and an extensive literature, smooth eye movements are not yet well understood. For example, the nature of the stimulus for smooth eye movements is controversial. Traditionally, modelers of smooth eye movements have proposed that the stimulus initiating and maintaining smooth eye movement is the motion of the target on the retina (see Carpenter, 1977, for a review). This proposal, however, cannot account for the observation, first made by Dodge *et al.* (1930), that the eye often turns around before the target during smooth pursuit of highly predictable, sinusoidal, target motion. Dodge *et al.*'s (1930) early observation was confirmed by Westheimer (1954), Stark *et al.* (1962), and Winterson and Steinman (1978).

The observation that smooth eye movements can predict future motions of the target means that there is a factor affecting smooth eye movements in addition to the motion of the target on the retina. Many investigators (e.g. Dallos and Jones, 1963) proposed that learning was this additional factor. Two assumptions underlie this proposal, specifically: (1) the smooth pursuit subsystem learns a repetitive pattern of target motion and uses what it learns to predict the future path of the target, and (2) the contribution of learning to smooth pursuit is restricted to periodic, predictable target motions (Stark *et al.*, 1962; Dallos and Jones, 1963; Young, 1971; Michael and Jones, 1966). These assumptions were attractive because they offered a way to separate the contribution of prediction from the contribution of the target motion on the retina to the operation of the smooth pursuit subsystem: namely, as long as aperiodic target motions were used, it was believed that effects of learning and prediction could be safely ignored. This approach was used by Dallos and Jones (1963) who presented a model in which smooth pursuit of aperiodic target motions (bandwidth-limited Gaussian noise) was assumed to be determined by retinal events. Only differences between smooth pursuit of periodic and aperiodic target motions were attributed to the operation of a predictor which learned the periodic pattern of motion. (See Kowler and Steinman, 1979a, b, 1981, for more extensive reviews of this material.)

Recent work has shown that such a parsing of the smooth pursuit response cannot lead to an accurate model because the ability of smooth eye movements to predict the future path of the target does not depend on learning and is not restricted to periodic, predictable target motions. Instead, Kowler and Steinman, (1979a, b, 1981) have shown that smooth eye movements are affected by the subject's expectations about future target motions. The effect of expectations on smooth eye movements cannot be eliminated by making target motions random.

Prior studies of the effect of expectations on smooth eye movement

The effect of expectations on smooth eye movement was first studied when subjects fixated stationary targets which were expected to move in directions and at times that were known to the subject in advance (Kowler and Steinman, 1979a). In that case the eye moved smoothly in the direction of the future target motion before the target motion began. These anticipatory smooth eye movements began about one-half second before the target began to move and their velocity was 5–100 times faster than the velocity of smooth eye movements observed when the target was stationary and no future target motion was expected.

Anticipatory smooth eye movements occurred whenever target motion was expected. Specifically, they occurred:

(1) before expected periodic target steps (square-wave motion) (Kowler and Steinman, 1979a);

(2) before an expected single target step (Kowler and Steinman, 1979b);

(3) before an expected single target ramp (Kowler and Steinman, 1979b);

(4) before expected target motion that was either toward or away from the primary position (Kowler and Steinman, 1979a);

(5) during slow control when the target was stationary before expected motion (Kowler and Steinman, 1979a);

(6) during smooth pursuit when the target was already in motion (ramp) before an expected step (Kowler and Steinman, 1979b); N.B. the expectation of a step in the same direction as the ramp motion increased smooth pursuit gain (eye velocity/target velocity) to as much as 2. The expectation of a step in the opposite direction decreased gain to as little as 0 and often caused high velocity smooth pursuit in the wrong direction;

(7) in the direction of expected horizontal, expected vertical, or expected oblique target motion (Kowler and Steinman, 1979a, 1981);

(8) while subjects voluntarily tried to suppress the anticipatory smooth eye movements (Kowler and Steinman, 1979a);

(9) on the first trial with no effect of further practice on the velocity of anticipatory smooth eye movements (Kowler and Steinman, 1979a);

(10) before expected target motion occurring at randomly chosen times (Kowler and Steinman, 1979b);

(11) before expected target motion in as many as 12 randomly chosen directions, with anticipatory smooth eye movements occurring in the direction of the subject's guess about the direction of future target motion (Kowler and Steinman, 1981); and

(12) before expected target motion in as many as 12 randomly chosen directions when the subjects were distracted from paying close attention to their guess by solving mental arithmetic problems while waiting for the expected target motion (Kowler and Steinman, 1981).

Anticipatory smooth eye movements have been observed in all subjects who have been tested. These include:

(1) two highly experienced eye movement subjects (Kowler and Steinman, 1979a);

(2) three naive, inexperienced eye movement subjects (Kowler and Steinman, 1979a);

(3) three naive, inexperienced eye movement subjects, including two 10-yr-old children (Kowler and Facchiano, 1982);

(4) many subjects (including rhesus monkeys) studied by other investigators, who noticed anticipatory smooth eye movements in the course of other research, but did not systematically investigate or report them (see Kowler and Steinman, 1981, for a list of references and personal communications from these investigators).

Anticipatory smooth eye movements require only two things, namely:

(1) the presence of a visible target—anticipatory smooth eye movements do not occur in total darkness (Kowler and Steinman, 1979b);

(2) the expectation that the target will move—anticipatory smooth eye movements do not occur when saccades are made to look between stationary targets (Kowler and Steinman, 1979a).

Taken together, these studies show that expectations about the future motion of a target always influence smooth eye movements. A complete model of smooth eye movements must, therefore, incorporate the subject's expectations about future target motion.

How expectations can be incorporated into models of smooth eye movements

Incorporating expectations into models of smooth eye movement requires a way of determining the relative contributions of expectations *and* of target motion on the retina to the observed smooth eye movement. The following illustrates the importance of determining the relative contribution of each factor.

Suppose that smooth pursuit of relatively complex patterns of target motion is found to be poor. Such a result might lead to conclusions about limitations in the information processing capabilities of the smooth oculomotor subsystem (e.g. St. Cyr and Fender, 1969). This interpretation is reasonable, but there is an alternative. Smooth pursuit of target motions can be poor because the subject's expectations about the direction of future target motions are often incorrect when target motion is com-

plex. Incorrect expectations can cause the eye to pursue either very slowly or in the wrong direction (Kowler and Steinman, 1979b).

Evaluating these two interpretations boils down to the following question: how much of the smooth pursuit response depends on the ability to analyze and follow the motion of the target and how much depends on the specific expectations that the subject develops about the motion of the target? An answer to this question requires measurements of smooth eye movements when the direction in which a subject expects a target to move is known.

The direction in which a subject expects a target to move is known when target motions are predictable. But general conclusions about the smooth oculomotor subsystem based only on performance with predictable target motions are not desirable for at least two reasons. First, the set of stimuli are restricted. Second, extensive practice increases smooth pursuit gain when predictable target motions are tracked (Dodge et al., 1930; Westheimer, 1954; Kowler et al., 1978). So, if predictable target motions are used, practice, as well as expectations and target image motion, will all be operating together, making it more difficult to analyze their relative contributions. Thus, unpredictable target motions must be studied. The problem when studying unpredictable target motions is to find a way of determining the subject's guess about the direction in which the target will move. This paper reports a technique which can solve this problem.

The rationale behind the approach is as follows. Human beings use what they know about prior events to formulate guesses about future events. Baseball batters, for example, use what they know about prior pitches to guess the kind of pitch they are likely to receive next. Similarly, a subject who is tracking a target moving in unpredictable directions may use knowledge about the directions of previous target motions to guess the direction of future target motion. If this is true, then anticipatory smooth eye movements produced by guesses should depend on the directions of prior target motions.

The experiment reported in this paper was designed to find out whether the past history of target motions affects anticipatory smooth eye movements when the direction of target motions are random. The experiment was adapted from a study of two-choice manual reaction time by Falmagne et al. (1975) in which effects of prior stimuli on reaction time were prominent. In their experiment, one of two possible stimuli could appear—a form whose orientation was either to the right or to the left. The subject's task was to press a button corresponding to the orientation of the form. Falmagne et al. (1975) found that reaction time depended on the sequence of orientations presented on previous trials. They developed a finite-state Markov model which predicted mean manual reaction time from the sequence of orientations of stimuli presented on previous trials.

The present experiment examined anticipatory smooth eye movements in an analogous two-choice situation. The stimulus was a single target step, randomly chosen to be either to the right or to the left. The subject did not know the direction of the target step in advance. His task was simply to use a saccade to track the step. This stimulus and task were chosen for two reasons. First, it is easy to characterize effects of prior target motion on anticipatory smooth eye movements by measuring eye velocity when the target is stationary before expected future motion. Prior work had already shown that any appreciable drifts of the eye away from the stationary target are anticipatory smooth eye movements. These drifts are produced exclusively by the expectations of future target motion and not by other factors, such as an inability to maintain the line of sight on a stationary target or by a voluntary decision to make a smooth eye movement (Kowler and Steinman, 1979a). The interpretation of eye velocity when targets are already in motion before an expected step is more complex because characteristics of smooth pursuit (e.g. gain) are determined by factors in addition to expectation, such as the speed (Puckett and Steinman, 1969) or direction of the target motion (Dubois and Collewijn, 1979), or by voluntary decisions to pursue at fractions of target velocity (Steinman et al., 1969). Incorporation of these additional factors is necessary, but it was felt that this could be accomplished more easily in future experiments, after the effect of prior target motions on expectations had been characterized in the simple step-tracking task described in this paper. The second reason that this stimulus was chosen was that the latency of the saccade used to track the target steps could be measured. This is a useful measure because if prior stimuli affect expectations about future target motion, as we propose, then both anticipatory smooth eye movements and saccadic latency should be affected in similar ways by the prior stimuli. Specifically, saccadic latency to steps in a particular direction should be shortened if the subject expects a step in that direction, just as smooth eye movements reflect the expected direction of the step. Such an outcome would be consistent with prior evidence that factors, such as expectations, which affect manual reaction time (cf. Falmagne et al., 1975; Miller and Anbar, 1981), also affect saccadic latency (Steinman et al., 1973).

We found that anticipatory smooth eye movements before expected target steps, and the latency of saccades used to track the target steps, were affected by the direction of target steps in the prior trials. This result made it possible to use Falmagne et al's (1975) manual reaction time model to predict the velocity of anticipatory smooth eye movements when unpredictable target motions were tracked. The success of Falmagne et al.'s (1975) model in predicting the velocity of anticipatory smooth eye movements will be described after the experimental method and results are reported.

METHOD

Eye movement recording

Horizontal movements of the right eye were recorded by a Generation III *SRI* Double Purkinje Image Eyetracker (Cornsweet and Crane, 1973). The left eye was closed and covered and the head was stabilized by dental biteboard.

The voltage output of the tracker 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. The digitized voltages were stored and analyzed later.

Tracker noise level on the horizontal meridian was measured with an artificial eye after the tracker had been adjusted so as to have the same 1st and 4th image reflections as the average subject's eye. Filtering and sampling rate were the same as those used in the experiment. Noise level, expressed as a standard deviation of horizontal position samples, was 0.65 min arc.

Subjects

Two subjects (Steinman and W.L.) were tested. They were both naive about the purpose of the experiment.

Steinman is a highly experienced eye movement subject. He was chosen to be a subject in this experiment because quantitative characteristics of his anticipatory smooth eye movements had been extensively studied previously (Kowler and Steinman, 1979a, b, 1981). Thus, anticipatory smooth eye movements observed in the present experiment could be compared to prior results obtained in the same subject under different experimental conditions.

W.L. was a naive and an inexperienced eye movement subject. His prior participation in eye movement experiments was limited to a single, brief recording session in which he served as a naive subject while his anticipatory smooth eye movements were measured during tracking of squarewave target motion (Kowler and Steinman, 1979a).

Stimuli

Stimuli were generated on a display monitor (Tektronix 604, P4 phosphor) located at optical infinity 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 was a single well-focused point target whose motion was controlled by the computer. The intensity of the point, which moved against a dark background, was 1 log unit above light-adapted absolute foveal threshold. The output of the computer's digital-to-analog converter was not only sent to the display monitor but was also fed to a channel of the ADC. This allowed the eye and stimulus channels to be sampled at the same time so that a digital sample of target position was obtained for each digital sample of eye position.

Trials

Before trials the target was located at the center (primary) position. Trials, which lasted 2 sec, started 100 msec after the subject pressed a button. Nine hundred msec later, the target stepped 123 min arc. Step direction was chosen randomly to be either right or left. The subject never knew the direction of the target step in advance. A second target step occurred 900 msec after the first step. Its purpose was to return the target to the center position.

Sessions

The probability that the first target step, away from the center position, would be to the right or to the left depended on the experimental session. For about half of the sessions rightward steps were more probable ($P = 0.65$). For the other sessions, leftward steps were more probable ($P = 0.65$). The subject was never told what the stimulus probabilities were, nor that stimulus probability had been manipulated.

Each experimental session consisted of 385 trials. During the first 25 trials of each session the target remained stationary throughout the trial. For these trials the subject expected the target to remain stationary and was instructed to use slow control to maintain the line of sight on the target throughout the trial. The first 35 trials containing target steps were practice trials and not analyzed. These were followed by 325 experimental trials. Sixteen experimental sessions (i.e. 5200 experimental trials) were run for each subject.

Instructions

The subject was instructed to make a single saccade to track each target step. He was told to make the saccade promptly after the step and to sacrifice the accuracy of the saccade in order to achieve the shortest possible latency. (See Steinman *et al.*, 1973, for evidence that saccadic latency and accuracy can be traded off during step-tracking.) The subject was also told to run trials at a brisk, yet comfortable, pace. These instructions were given to increase the likelihood that anticipatory smooth eye movements would reflect the first guess a subject formulated about the direction of an expected step. It seemed likely that the effects of prior stimuli on guesses would be more reliable for the first guess than for guesses formulated after many seconds of contemplation.

Data analyses

Digitized eye position samples were analyzed by computer programs which calculated average eye velocity before expected steps. This was done by measuring the change in eye position over the 500 msec interval immediately preceding target steps. Occasional intervals (14% for Steinman and 6% for

W.L.) contained a small saccade (about 5–10 min arc). These saccades were removed from the measure of eye velocity in the following way. The saccades were detected and their directed magnitudes measured (see Kowler and Steinman, 1979a, for a description of the algorithm used to detect saccades). The directed magnitudes were then subtracted from the measured change in the position of the eye over the 500 msec interval. Trials in which small saccades occurred during the initial or final 100 msec of the 500 msec interval before the target step (12% for Steinman, and 9% for W.L.) were not included because the small saccades prevented accurate measure of the change in eye position before the target step.

The size and latency of the large saccade made to track the target step was also measured. Trials in which saccades occurred before target steps (2% for Steinman, and less than 1% for W.L.) were omitted so that all measures of eye velocity before target steps could be based on 500-msec intervals. These trials, as well as those trials (described above) which were eliminated from analyses of eye velocity, were also omitted from analyses of saccade latency and size so that all data would be based on the same trials. N.B. Very little data were discarded for the reasons described above. Results reported are based on 86% of the total number of trials run for Steinman, and 90% for W.L.

RESULTS

Anticipatory smooth eye movements were prominent

Mean eye velocity before expected steps, averaged over all trials, was 4.91 min arc/sec (SE = 0.12, $N = 4486$) for Steinman, and −3.16 min arc/sec (SE = 0.11, $N = 4706$) for W.L. (negative eye velocity indicates movements to the left). Steinman's anticipatory eye velocity was faster by about a factor of 20 than his mean velocity when no steps were expected (mean eye velocity = 0.25 min arc/sec, SE = 0.31, $N = 338$), and W.L.'s was faster by about a factor of 2 than his mean eye velocity when no steps were expected (mean = −1.70 min arc/sec, SE = 0.29, $N = 378$).

The average velocity of Steinman's anticipatory smooth eye movements was similar to that observed in a prior study in which he guessed the direction of future target motions (Kowler and Steinman, 1981). In that experiment, his anticipatory smooth eye movements were rightward on the average, regardless of the direction of his guess, but were faster to the right when he guessed that the steps would be to the right. In this experiment, W.L.'s anticipatory smooth eye movements were, on the average, to the left. W.L. does drift to the right when he is certain that future target motion will be to the right, and Steinman to the left when he is certain that future target motion will be to the left (Kowler and Steinman, 1979a).

The reason for the tendency of anticipatory smooth eye movements produced by guesses to be in idiosyncratic directions is not known. However, we do know that similar phenomena have been observed before. For example, subjects have small but reliable drifts in idiosyncratic directions during slow control when no future target motion is expected (see mean eye velocities when no steps were expected, given above, and also Nachmias, 1959, and Kowler and Steinman, 1979a). Also, the open-loop gain of smooth pursuit varies in idiosyncratic ways with the direction of target motion (Dubois and Collewijn, 1979). All of these phenomena suggest that idiosyncratic directional asymmetry is inherent in the operation of the smooth oculomotor subsystem.

Effect of stimulus probability on anticipatory smooth eye movements

If anticipatory smooth eye movements are affected by the direction of steps in prior trials, then their velocity may differ as a function of the relative frequency of rightward and leftward steps that occurred in the prior trials. The frequency of occurrence of rightward and leftward steps did affect Steinman's anticipatory smooth eye movements. His anticipatory smooth eye movements were, on the average, faster to the right for sessions in which rightward target steps were more probable than for sessions in which leftward target steps were more probable. This is shown in Fig. 1, in which the rightmost point of each graph shows eye velocity averaged over all trials for each type of session. W.L.'s anticipatory smooth eye movements were not affected by stimulus probability. His eye velocity averaged over all trials was about the same for each type of session (see Fig. 2).

The next section will show that despite these individual differences in the effect of stimulus probability, each subject's anticipatory smooth eye movements within each type of session were determined by the direction of target steps in the immediately prior trials.

Anticipatory smooth eye movements depended on the direction of target steps in the immediately prior trials (sequential effects)

The effect of the direction of target steps in immediately prior trials will be described first for Steinman's sessions in which leftward steps were more probable. The effect of the immediately prior trial (trial n-1) was determined in the following way. Trials were divided into two groups: those in which the stimulus in trial n-1 was a rightward step and those in which the stimulus in trial n-1 was a leftward step. Mean eye velocity was then calculated for each group. Anticipatory smooth eye movements were faster to the right when trial n-1 contained a rightward step. This result is shown in Fig. 1.

Steps occurring further back into the past had similar effects. The effect of the direction of the step in trial n-2 was determined by dividing the trials in
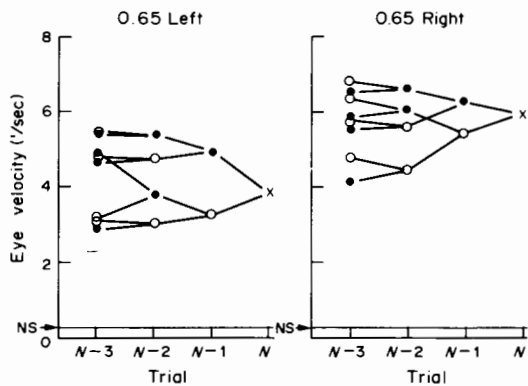
Fig. 1. Mean anticipatory smooth eye movement velocity as a function of the direction of steps in prior trials for subject Steinman for sessions in which the probability of a leftward step was 0.65 (0.65L) and the probability of a rightward step was 0.65 (0.65R). All mean velocities are rightward. The rightmost datum point in each graph (trial n) shows eye velocity averaged over all trials for the given type of session. Moving to the left across the graph, each datum point continues to branch into two more points to show the effect of the direction of the step in successively earlier trials on mean eye velocity. Thus, the pair of data points at trial n-1 shows mean eye velocity as a function of the direction of the step in the immediately preceding trial (solid symbols indicate rightward steps, open symbols, leftward steps). The 4 data points at trial n-2 show mean eye velocity as a function of the direction of the steps in the two preceding trials. The 8 data points at trial n-3 show mean eye velocity as a function of the direction of the steps in the three preceding trials. Mean eye velocity when no steps were expected (NS) is also shown. Eye velocity averaged over all trials for 0.65L sessions was based on 2167 observations (SE = 0.17), and for 0.65R sessions on 2319 observations (SE = 0.15). The number of observations per datum point decreases by about a factor of 0.65, and standard errors increase by about a factor of 1.2, as steps in successively earlier trials in the more frequently presented direction are taken into account. The number of observations per datum point decreases by about a factor of 0.35 and standard errors increase by about a factor of 1.7 as steps in successively earlier trials in the less frequently presented direction are taken into account.
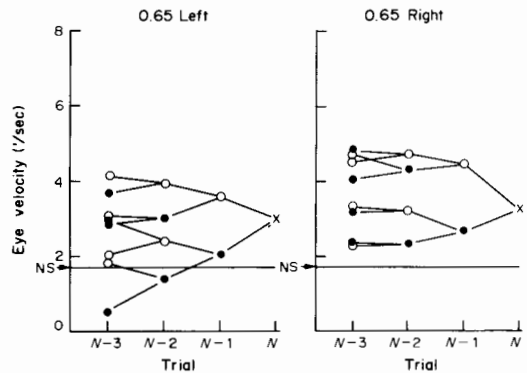

Fig. 2. Mean anticipatory smooth eye movement velocity as a function of the direction of steps in prior trials for subject W.L. for sessions in which the probability of a leftward step was 0.65 (0.65L) and the probability of a rightward step was 0.65 (0.65R). All mean eye velocities are leftward. Meaning of the symbols and the abscissa is the same as in Fig. 1. Eye velocity averaged over all trials for 0.65L sessions was based on 2351 observations (SE = 0.13), and for 0.65R sessions on 2355 observations (SE = 0.14). The number of observations per datum point decreases by about a factor of 0.65, and standard errors increase by about a factor of 1.2, as steps in successively earlier trials in the more frequently presented direction are taken into account. The number of observations per datum point decreases by about a factor of 0.35 and standard errors increase by about a factor of 1.7 as steps in successively earlier trials in the less frequently presented direction are taken into account.

each of the two groups, based on the direction of the step in trial n-1, into two more groups, this time based on the direction of the step in trial n-2. This procedure created one group for each of the possible two-trial sequences (i.e. two consecutive rightward steps, a leftward step followed by a rightward step, a rightward step followed by a leftward step, and two consecutive leftward steps). The occurrence of a rightward step on trial n-2 resulted in faster anticipatory smooth eye movements to the right than did the occurrence of a leftward step (see Fig. 1).

The direction of the step in trial n-2 did not have as much influence as the direction of the step in trial n-1. Mean eye velocity was always faster to the right when the step in trial n-1 was to the right, regardless of the direction of the step in trial n-2.

The direction of the step in trial n-3 had almost no effect on eye velocity. Only in one case, when the step in trial n-1 was to the left and the step in trial n-2 was to the right, did the direction of the step in trial n-3

matter. Here, once again, drifts were faster to the right when a rightward step had occurred.

These effects of prior stimuli on anticipatory smooth eye movements mean that either (1) prior stimuli affect expectations, or (2) practice tracking a sequence of steps affects the velocity of anticipatory smooth eye movements without changing the expectations. The former explanation is favored because prior work has shown that the velocity of anticipatory smooth eye movements is unaffected by practice when sequences of predictable steps are tracked (Kowler and Steinman, 1979a).

To summarize, two effects of prior step direction are apparent. First, anticipatory smooth eye movements were faster to the right when prior steps were to the right. Second, the influence of prior step direction diminished the further back into the past the step had occurred.

The sequential effects were similar for Steinman's sessions in which rightward steps were more probable (see Fig. 1). But some characteristics of the sequential effects differed. First, in one case, the direction of the step in trial n-2 had a slightly larger effect than the direction of the step in trial n-1. Mean eye velocity was faster to the right when a rightward step was followed by a leftward step than when a leftward step was followed by a rightward step. Second, the effects of the stimulus in trial n-3 were opposite to the general trend for the 1- and 2-trial sequences. There, drifts were faster to the right when the step in trial n-3 was to the left.
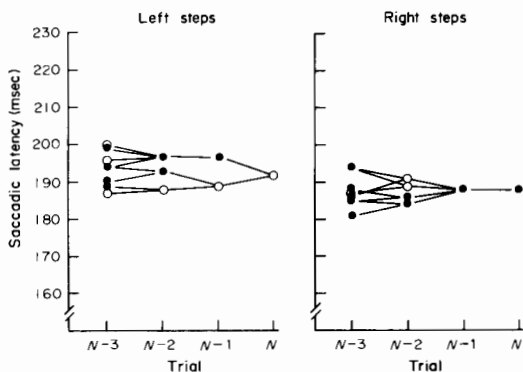
Fig. 3. Mean saccadic latency to *Left*ward and *Right*ward target steps as a function of the direction of steps in prior trials for subject W.L. for sessions in which the probability of a leftward step was 0.65. Meaning of the symbols and abscissa is the same as in Fig. 1. Saccadic latency averaged over all trials for leftward steps was based on 1485 observations (SE = 0.80), and for rightward steps on 866 observations (SE = 0.86). The number of observations per datum point decreases by about a factor of 0.65, and standard errors increase by about a factor of 1.2, as steps in successively earlier trials in the more frequently presented direction are taken into account. The number of observations per datum point decreases by about a factor of 0.35 and standard errors increase by about a factor of 1.7 as steps in successively earlier trials in the less frequently presented direction are taken into account.

The effect of target steps in prior trials on anticipatory smooth eye movements observed for both types of sessions for W.L. were similar to those observed for Steinman's sessions in which leftward steps were more probable. The main difference was that, on the average, W.L.'s anticipatory smooth eye movements were leftward, whereas Steinman's were rightward. Otherwise, characteristics of W.L.'s results were the same, that is, W.L.'s anticipatory smooth eye movements were faster to the left when prior steps were to the left, and the influence of the direction of a prior step diminished the further back into the past the step had occurred.* These sequential effects are analogous to those reported for manual reaction time (button-pressing) experiments (cf. Falmagne et al., 1975) and for psychophysical experiments (cf. Collier and Verplanck, 1958).

Effects of prior stimuli on saccades

The effect of prior stimuli on saccades was anal-

*Statistical analyses confirm that the direction of the step as far back into the past as trial n-2 had a reliable effect on mean eye velocity. Specifically, mean eye velocities for all 8 pairs of 2-trial sequences were in the predicted direction, i.e. faster to the right when prior steps were to the right for Steinman, and faster to the left when prior steps were to the left for W.L. (see Figs 1 and 2). A binomial test (1-tailed) shows that the probability of this result occurring by chance is 0.004. The effect of the direction of the step in trial n-3 was not reliable. Mean eye velocity for only 6 of the 16 pairs of 3-trial sequences were in the predicted direction. A binomial test (1-tailed) shows that the probability of this result occurring by chance is 0.227.

ogous to the effect of prior stimuli on anticipatory smooth eye movements. This result supports the view that prior stimuli affected the expectations, which in turn, affected the eye movements.

In general the prior occurrence of a step in a particular direction resulted in shorter latencies for saccades to steps in that direction and longer latencies for saccades to steps in the opposite direction. This is illustrated in Figs 3 and 4 which show the effects of prior stimuli on W.L.'s latencies. Steinman's pattern of latencies were about the same. The effect of prior stimuli on saccadic latency was more variable than the effect of prior stimuli on anticipatory smooth eye movements (Figs 1 and 2). At least some of the increased variability came from the fact that the number of observations per point was smaller for the saccade data than for the anticipatory smooth eye movements, because saccades were examined separately for trials in which rightward and leftward steps occurred. Also, it is not surprising that saccadic latency was more variable than anticipatory smooth eye movement velocity for an additional reason. Saccades, unlike anticipatory smooth eye movements, are voluntary motor acts—their onset, size, and direction offer a wide variety of options to the subject. Any decisions about these options will affect saccadic latency and thus make overall saccadic performance more variable than anticipatory smooth eye movements, which are known not to be under voluntary control (Kowler and Steinman, 1979a). Despite this variability in saccadic latency, however, it is clear that saccadic latency reflects the effects of
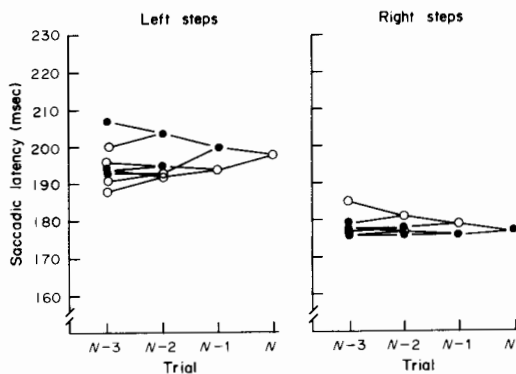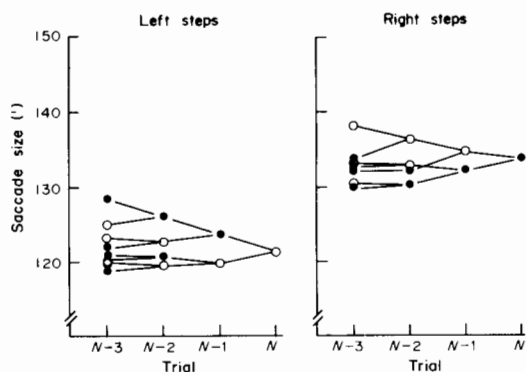

Fig. 4. Mean saccadic latency to *Left*ward and *Right*ward target steps as a function of the direction of steps in prior trials for subject W.L. for sessions in which the probability of a rightward step was 0.65. Meaning of the symbols and abscissa is the same as in Fig. 1. Saccadic latency averaged over all trials for leftward steps was based on 839 observations (SE = 0.90), and for rightward steps on 1516 observations (SE = 0.55). The number of observations per datum point decreases by about a factor of 0.65, and standard errors increase by about a factor of 1.2, as steps in successively earlier trials in the more frequently presented direction are taken into account. The number of observations per datum point decreases by about a factor of 0.35 and standard errors increase by about a factor of 1.7 as steps in successively earlier trials in the less frequently presented direction are taken into account.

Fig. 5. Mean saccade size to *Left*ward and *Right*ward target steps as a function of the direction of steps in prior trials for subject W.L. for sessions in which the probability of a leftward step was 0.65. Meaning of the symbols and abscissa is the same as in Fig. 1. Saccade size averaged over all trials for leftward steps was based on 1485 observations (SE = 0.36), and for rightward steps on 866 observations (SE = 0.65). The number of observations per datum point decreases by about a factor of 0.65, and standard errors increase by about a factor of 1.2, as steps in successively earlier trials in the more frequently presented direction are taken into account. The number of observations per datum point decreases by about a factor of 0.35 and standard errors increase by about a factor of 1.7 as steps in successively earlier trials in the less frequently presented direction are taken into account.

prior target motions on expectations in much the same manner that expectations are evidenced in anticipatory smooth eye movements.

The effects of prior stimuli observed for anticipatory smooth eye movements and saccades may be related to each other in the following way. The occurrence of, for example, a rightward step increased the probability that the subject expected a rightward step in the next trial. The expectation (1) produced faster anticipatory smooth eye movements to the right and (2) encouraged the subject to begin planning a saccade to the right, resulting in shorter saccadic latency to rightward steps and longer saccadic latency to leftward steps. In other words, the direction of prior steps affected the expectation about the direction of future steps, and the expectation in turn affected the eye movements.

Prior stimuli also affected the size of saccades, as shown for W.L. in Figs 5 and 6. (The sizes of Steinman's saccades were about the same.) The prior occurrence of steps in a particular direction generally resulted in shorter saccades to steps in that direction and longer saccades to steps in the opposite direction. The pattern of sequential effects for saccade size, like the sequential effects for saccadic latency, was variable.

The pattern of sequential effects observed for saccade size is consistent with what would be expected if the change in position of the eye before the target step, produced by the anticipatory smooth eye movements, was taken into account when planning the saccades. For example, W.L.'s shortest saccades to

leftward steps occurred after a sequence of leftward steps (Figs 5 and 6)—the same sequence of steps that produced the faster anticipatory smooth eye movements to the left (see Fig. 2). Similarly, his largest saccades to leftward steps occurred after a sequence of rightward steps—the same sequence that produced the slowest anticipatory smooth eye movements to the left (see Fig. 2). The same relationship between saccade size and anticipatory smooth eye movements also occurred for W.L.'s rightward saccades and for Steinman's saccades. It is possible, however, that the observed relationship between saccade size and anticipatory smooth eye movements was not due to anticipatory smooth eye movements being taken into account, but instead, to effects of the prior sequence of target steps on the sizes of saccades. The present experiment does not allow these two possibilities to be distinguished.

MODEL

Falmagne *et al.* (1975) found analogous sequential effects to those reported here for their two-choice manual reaction time (button-pressing) experiment. Specifically, they found that reaction time was faster to a stimulus when that stimulus had been presented in prior trials, and that the effect of a prior stimulus on reaction time diminished the further back into the past the stimulus had occurred. They proposed a finite-state Markov model which described their data well. The similarities between our two sets of data suggested that their model could provide a technique
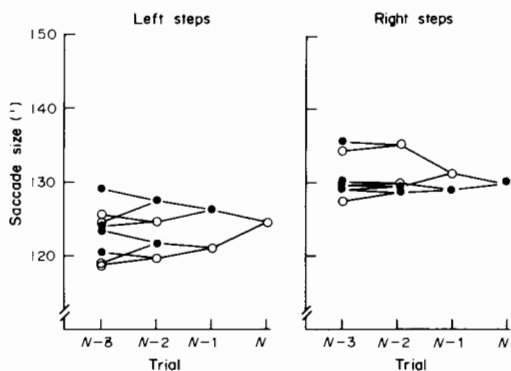

Fig. 6. Mean saccade size to *Left*ward and *Right*ward target steps as a function of the direction of steps in prior trials for subject W.L. for sessions in which the probability of a rightward step was 0.65. Meaning of the symbols and abscissa is the same as in Fig. 1. Saccade size averaged over all trials for leftward steps was based on 839 observations (SE = 0.51), and for rightward steps on 1516 observations (SE = 0.40). The number of observations per datum point decreases by about a factor of 0.65, and standard errors increase by about a factor of 1.2, as steps in successively earlier trials in the more frequently presented direction are taken into account. The number of observations per datum point decreases by about a factor of 0.35 and standard errors increase by about a factor of 1.7 as steps in successively earlier trials in the less frequently presented direction are taken into account.

for predicting the velocity of anticipatory smooth eye movements based on the direction of target steps in prior trials.

In the model, the velocity of anticipatory smooth eye movements is assumed to depend on the subject's expectation about the direction of future target motion, e.g. the eye moves smoothly to the right when the subject expects a rightward step, and moves smoothly to the left when the subject expects a leftward step. The subject's expectation changes from trial to trial based on the following strategy: whenever his expectation about the direction of a step is correct, the same expectation is maintained on the next trial. But whenever his expectation is wrong, there is some probability that the subject changes his expectation on the next trial. By applying these assumptions, a prediction for the velocity of anticipatory smooth eye movements as a function of the direction of the target steps in prior trials is obtained.

A brief description of the model will be presented here. A more complete description and formal derivations from the model can be found in Falmagne *et al.* (1975).

We will confine our attention to application of Falmagne *et al.*'s (1975) model to anticipatory smooth eye movements. However, the general similarity of effects of prior stimuli on manual reaction time (Falmagne *et al.*, 1975), on anticipatory smooth eye movements (Figs 1 and 2) and on saccades (Figs 3–6) suggests that the model would also account for the effects of prior stimuli on saccades. However, as noted earlier, the effects of prior stimuli on saccades are sufficiently noisy to make a test of the model on the saccade data difficult to interpret. A test of the model's fit to the saccade data was not undertaken for this reason.

Stimulus

The stimulus presented on the nth trial will be denoted by a discrete random variable, S_n, which can take on one of two values: $S_n = R$ whenever a rightward step occurs and $S_n = L$ whenever a leftward step occurs. Also, q_R will denote the probability that $S_n = R$, and q_L the probability that $S_n = L$.

States

On each trial the subject is assumed to be in one of two states: expecting a rightward step or expecting a leftward step. Stated formally, the state of a subject on the nth trial is represented by the discrete random variable, X_n, which can take on one of two values: $X_n = R$, which represents the subject's expectation of a rightward step and $X_n = L$, which represents the subject's expectation of a leftward step.

Eye velocity

The velocity of anticipatory smooth eye movements on the nth trial, A_n, depends on the state. The velocity of anticipatory smooth eye movements is represented by the continuous random variables, V_R

and V_L. Whenever $X_n = R$, the velocity of anticipatory smooth eye movements is drawn from the distribution of velocities corresponding to the subject's expectation of a rightward step, $\text{Prob}(V_R < v) = P(V_R < v)$. Whenever $X_n = L$, the velocity is drawn from the distribution of velocities corresponding to the subject's expectation of a leftward step, $\text{Prob}(V_L < v) = P(V_L < v)$.

The distribution of eye velocity for the nth trial, $P(A_n < v)$, is determined by: (1) the probability that $X_n = R$ and the probability that $X_n = L$, and (2) the velocity distributions. That is

$$P(A_n < v) = P(X_n = R)P(V_R < v)$$
$$+ P(X_n = L)P(V_L < v). \quad (1)$$

We will confine our attention to predictions of mean eye velocity rather than predictions of the entire distribution. The mean eye velocity on the nth trial, $E(A_n)$, is

$$E(A_n) = P(X_n = R)\bar{v}_R + P(X_n = L)\bar{v}_L \quad (2)$$

where $\bar{v}_R$ and $\bar{v}_L$ are the means of the velocity distributions corresponding to the two states. These means are parameters of the model which will be estimated later.

Transitions between states

In the model the state, X_n, depends on the state and stimulus of the prior trial (X_{n-1}, S_{n-1}). In the experiment the distribution of S_n was constant within any session and independent of trial number. Thus, the sequence of pairs (X_n, S_n) is a Markov process.

Transitions between states are determined by the following assumptions

$$P(X_n = R \mid X_{n-1} = R, S_{n-1} = R) = 1 \quad (3)$$

$$P(X_n = R \mid X_{n-1} = L, S_{n-1} = R) = a_R. \quad (4)$$

Similarly,

$$P(X_n = L \mid X_{n-1} = L, S_{n-1} = L) = 1 \quad (5)$$

$$P(X_n = L \mid X_{n-1} = R, S_{n-1} = L) = a_L. \quad (6)$$

Where a_R and a_L are two of the model parameters $(0 < a_R \leq 1, \ 0 < a_L \leq 1)$. These transitions between states are illustrated in Fig. 7.

These transitions may be interpreted in terms of the subject's expectations. Whenever the subject's expectation is correct, the expectation always remains the same in the next trial [see equations (3) and (5)]. But whenever the subject's expectation is wrong, either his expectation changes (with probability a_R or a_L) or remains the same in the next trial [see equations (4) and (6)].

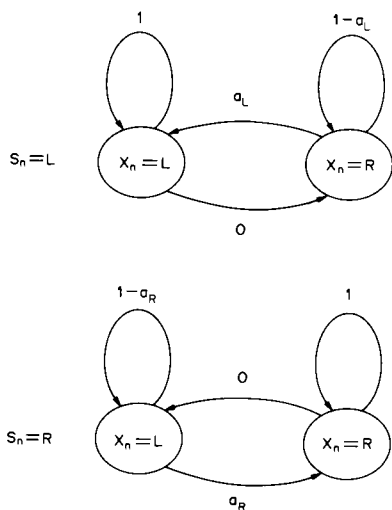After many trials of moving back and forth between the states, the process becomes stationary and

Fig. 7. Transitions between states of expecting a leftward step ($X_n = L$) and a rightward step ($X_n = R$) when the target step on the nth trial was to the left ($S_n = L$) or to the right ($S_n = R$). Arrows show transitions and are labelled with transition probabilities: $1 =$ the probability that a correct expectation is maintained on the next trial; $a_L =$ the probability that an incorrect expectation of a rightward step is changed to an expectation of a leftward step on the next trial; $a_R =$ the probability that an incorrect expectation of a leftward step is changed to an expectation of a rightward step on the next trial.

independent of the initial state. This means that the probabilities of being in each of the two states approach asymptotic values and will not depend on trial number. The effect of recently presented sequences of stimuli on these asymptotic probabilities can then be examined without the need to take into account when a particular sequence occurred during the session.

For this model the asymptotic probabilities of being in the two states (P_R and P_L) can be shown to depend both on the stimulus probabilities (q_R and q_L) and on the parameters a_R and a_L. Specifically

$$P_R = \lim_{n \to \infty} P(X_n = R) = \frac{q_R a_R}{q_R a_R + q_L a_L} \quad (7)$$

and

$$P_L = \lim_{n \to \infty} P(X_n = L) = \frac{q_L a_L}{q_R a_R + q_L a_L}. \quad (8)$$

Henceforth, we will deal with the process after it has become stationary and the probabilities of being in each of the 2 states have reached asymptotic levels [see equations (7) and (8)].

Effects of stimuli in immediately prior trials

Once the asymptotic probabilities of being in each state are obtained, the probability of being in either of the two states after the presentation of a specified sequence of stimuli can be determined by applying the assumptions about transitions between states described in the previous section [see equations

(3)–(6)]. An example of how such probabilities are determined is shown in Fig. 8. This figure shows how the probabilities of being in either state in trial n are obtained for one sequence, namely, the stimuli in each of the two previous trials (trials n-1 and n-2) were rightward steps.

Figure 8 shows that the subject may be in either state on trial n-2 ($X_{n-2} = R$ or $X_{n-2} = L$). The probabilities of being in either state in trial n-2 are given by the asymptotic probabilities [equations (7) and (8)]. There are 4 possible paths that lead from the state on trial n-2 to a state on trial n when the stimuli in each of the two previous trials were rightward steps.

In the first path, shown at the top of Fig. 8, the subject's state in trial n-2 is $X_{n-2} = R$. A rightward step occurs, thus, the state is not changed on the next trial, i.e. $X_{n-1} = R$. A rightward step again occurs in trial n-1, so that the state is again not changed in trial n. The probability that this path occurs is obtained by multiplying the asymptotic probability that $X_{n-2} = R$ by the probabilities of all the other events in the path

$$P(X_{n-2} = R, S_{n-2} = R, X_{n-1} = R, S_{n-1} = R,$$
$$X_n = R) = P_R q_R^2. \quad (9)$$

The second path leading from a state on trial n-2 to a state on trial n begins with the subject in the state corresponding to the expectation of a leftward step ($X_{n-2} = L$). This expectation will be wrong. Thus, either the state will change with probability a_R, or the state will remain the same with probability $1 - a_R$. If the state changes, so that $X_{n-1} = R$, then the rest of the second path will be identical to the first path, described above. The probability of this second path is determined by multiplying the asymptotic probability that $X_{n-2} = L$ by the probability of all the events in the path

$$P(X_{n-2} = L, S_{n-2} = R, X_{n-1} = R, S_{n-1} = R,$$
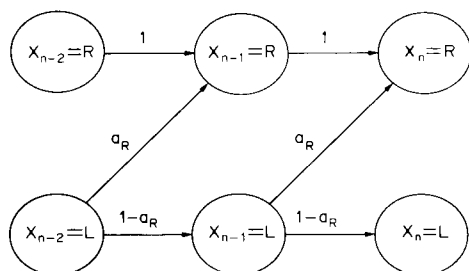$$X_n = R) = P_L q_R^2 a_R. \quad (10)$$

Fig. 8. Transitions from a state on trial n-2 (expecting a rightward step, $X_{n-2} = R$, or expecting a leftward step, $X_{n-2} = L$) to a state on trial n ($X_n = R$ or $X_n = L$) when the target steps on trials n-2 and n-1 were to the right. Arrows show transitions and are labelled with transition probabilities: $1 =$ the probability that a correct expectation is maintained on the next trial; $a_R =$ the probability that an incorrect expectation of a leftward step is changed to an expectation of a rightward step on the next trial.
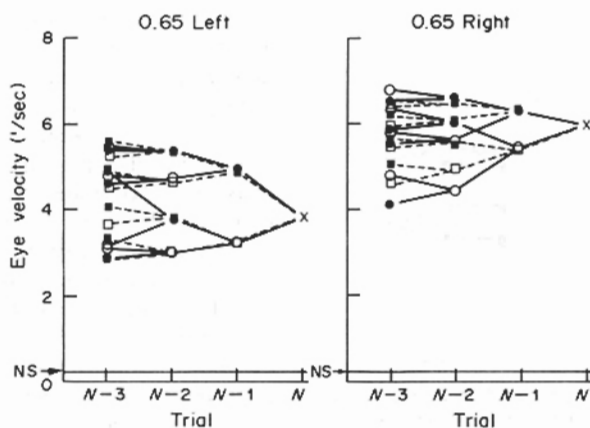
Fig. 9. Observed (circles, reproduced from Fig. 1) and predicted (squares) mean anticipatory smooth eye movement velocity as a function of the direction of steps in prior trials for subject Steinman for sessions in which the probability of a leftward step was 0.65 (0.65L) and the probability of a rightward step was 0.65 (0.65R). All mean velocities are rightward. Meaning of the symbols and the abscissa is the same as in Fig. 1.

The third and fourth paths begin with the subject in the state corresponding to the expectation of a leftward step ($X_{n-2} = L$) and remaining in this state on trial n-1. The subject's expectation will be incorrect on trial n-1, and thus, he either changes state on the next trial ($X_n = R$), completing the third path, or remains in the same state ($X_n = L$), completing the fourth path. The probability of each of these two paths is determined, once again, by multiplying the asymptotic probability that $X_{n-2} = L$ by the probability of all the events in the path.

The probability that $X_n = R$, given that the two previous steps were to the right, is the sum of the probabilities of the three paths leading to $X_n = R$, conditional on the presentation of two rightward steps. Thus

$$P(X_n = R \,|\, S_{n-1} = R, S_{n-2} = R) = P_R + P_L a_R$$
$$+ P_L a_R (1 - a_R) = 1 - P_L(1 - a_R)^2. \quad (11)$$

Similarly, the probability that $X_n = L$, given that the two previous steps were to the right, is the probability of the single path leading to $X_n = L$, conditional on the presentation of two rightward steps. Thus

$$P(X_n = L \,|\, S_{n-1} = R, S_{n-2} = R) = P_L(1 - a_R)^2. \quad (12)$$

The conditional mean eye velocity can be computed from these expressions. Thus

$$E(A_n \,|\, S_{n-1} = R, S_{n-2} = R) = [1 - P_L(1 - a_R)^2]\bar{v}_R$$
$$+ [P_L(1 - a_R)^2]\bar{v}_L. \quad (13)$$

The means of the two velocity distributions [$\bar{v}_R$ and $\bar{v}_L$; see equation (2)] are model parameters which must be estimated.

Expressions for the mean eye velocities for all other possible stimulus sequences are obtained by similar derivations.

Estimation of parameters and evaluation of fit

Estimates of the four model parameters ($a_R, a_L, \bar{v}_R, \bar{v}_L$) were chosen to be those which minimized, by a least squares criterion, the difference between observed and predicted mean eye velocities. (Parameters were estimated by the computerized search procedure STEPIT, Chandler, 1969.) Parameters were estimated using the mean velocities for all the eight possible 3-trial sequences (i.e. the mean velocities shown for trial n-3 in Figs 1 and 2). Each session was fit separately, but within each session parameters were estimated simultaneously using the eight mean velocities. The parameter values obtained (see Table 1) were used to generate predicted eye velocities for the 1- and 2-trial sequences, and for the mean eye velocity averaged over all trials.

The model provided a good fit to Steinman's eye velocities when leftward steps were more probable. The only noticeable departures occurred for the 3-trial sequences. Departures were more frequent when rightward steps were more probable. These occurred primarily because the model could not account for two features of these data which were noted earlier in the description of the results, namely, (1) the influence of the direction of the step in trial n-2 was greater than the influence of the direction of the step in trial n-1 for two stimulus sequences (a rightward step followed by a leftward step and a leftward step followed by a rightward step), and (2) eye velocity was faster to the right when the step in trial n-3 was to the left. These results are shown in Fig. 9.

The model also provided a good fit to W.L.'s data for both types of sessions. Departures were generally less frequent than in Steinman's data (see Fig. 10).

The estimated parameter values were different in each type of session (see Table 1). This result is troublesome for the model because one of its assump-
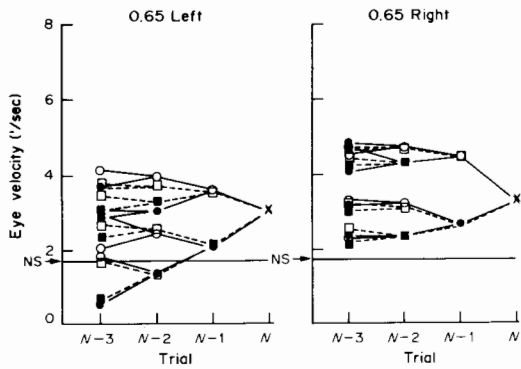
Fig. 10. Observed (circles, reproduced from Fig. 2) and predicted (squares) mean anticipatory smooth eye movement velocity as a function of the direction of steps in prior trials for subject W.L. for sessions in which the probability of a leftward step was 0.65 (0.65L) and the probability of a rightward step was 0.65 (0.65R). All mean velocities are leftward. Meaning of the symbols and the abscissa is the same as in Fig. 1.

tions is that parameter values are independent of stimulus probability. According to the model, stimulus probability should only affect the proportion of trials the subject spends in each state (see equations 7 and 8). The effect of stimulus probabilities on parameter values is not, however, restricted to anticipatory smooth eye movements. Falmagne *et al.* (1975) also found that parameter values depended on stimulus probability for their manual reaction time task. These results mean that modification of the model will be required for it to provide a complete characterization of the effect of prior stimuli on anticipatory smooth eye movements, as it had previously been known to be required for Falmagne *et al.*'s (1975) results of experiments on manual reaction time.

DISCUSSION

Previous research has shown that expectations about the direction of future target motion always affect smooth eye movements (Kowler and Steinman, 1979a, 1979b, 1981). These effects cannot be abolished by making target motions unpredictable (Kowler and Steinman, 1981). These results mean that a complete understanding of the response of the smooth oculomotor subsystem to any pattern of target motion must incorporate expectations. That is, characteristics of smooth eye movements (e.g. eye velocity) must be determined both as a function of the present target motion, and also as a function of the subject's expectation of future target motion. Such a determination requires that the subject's expectation be known. Our finding that anticipatory smooth eye movements depend in a lawful way on prior target motions shows that expectations may be inferred from the pattern of target motions presented in the past.

Falmagne *et al.*'s (1975) finite-state Markov model can be used to make inferences about a subject's

expectations based on the pattern of target motions presented in the past. The model assumes that subjects employ a relatively simple guessing rule—namely, keep the same expectation as long as it is correct, but either keep or change the expectation if it is wrong. By applying such assumptions, predictions can be generated about the probability that a subject will expect a particular stimulus after presentation of any specified sequence of stimuli. We found that the model provided a reasonable prediction of anticipatory smooth eye movement velocity as a function of prior stimuli, suggesting that the guessing rules assumed by the model approximate the rules employed by the subjects.

The model, however, could not account for all characteristics of the effects of prior stimuli (see Steinman's data when rightward steps were more probable, Fig. 9), nor could it account for the finding that parameter values varied as a function of stimulus probability (Table 1). Further research will be required to determine how the fit of the model to the data can be improved. One possible modification to the model, for example, is to increase to four the number of states permitted. Two of these states may represent the expectation of a rightward step, one state corresponding to an expectation with a high degree of certainty, and the other corresponding to an expectation with a low degree of certainty. The other two states may represent the expectation of a leftward step under both degrees of certainty. This modification of the model is attractive because prior work has shown that anticipatory smooth eye movement velocity varies as a function of the certainty of the expectation (Kowler and Steinman, 1981).

Implications of the effect of prior stimuli on saccades

Our finding that saccadic latency is affected by prior stimuli does not agree with Saslow's (1967b)

Table 1. Estimated parameter values that gave best fits by a least squares criterion for sessions in which leftward steps were more probable (0.65L) and rightward steps were more probable (0.65R) for subjects Steinman and W.L.

	Parameters			
	a_R	a_L	$\bar{v}_R$	$\bar{v}_L$
Steinman				
0.65L	0.54	0.47	5.76	2.64
0.65R	0.63	0.33	6.54	3.98
W.L.				
0.65L	0.15	0.72	3.16	−3.75
0.65R	0.56	0.80	−2.11	−4.76

Note—a_R = the probability that an incorrect expectation of a leftward step is changed to an expectation of a rightward step on the next trial; a_L = the probability than an incorrect expectation of a rightward step is changed to an expectation of a leftward step on the next trial; $\bar{v}_R$ = the mean of the velocity distribution corresponding to the expectation of a rightward step; $\bar{v}_L$ = the mean of the velocity distribution corresponding to the expectation of a leftward step.

report that saccadic latency is not affected by the direction of the target step on the immediately prior trial. Based on this result, as well as his other observations that saccades are not affected by factors which affect manual reaction time, such as the probability of occurrence of a given stimulus, Saslow (1967a, b) implied that saccades and manual responses are controlled by very different kinds of processes.

We do not know why we found that saccadic latency is affected by prior stimuli and Saslow (1967b) did not. However, we are not the first to fail to confirm Saslow's (1967b) results. For example, Norcia *et al.* (1979) and Viviani and Swensson (1982) reported that, contrary to Saslow (1967b), the probability of occurrence of a given stimulus does affect saccadic latency. Such results, along with our present finding that saccadic latency, like manual reaction time, is affected by prior stimuli, show that, contrary to Saslow's suggestion, saccadic latency and manual reaction time are controlled by very similar processes. This is not the first time such a suggestion was made. Steinman *et al.* (1973) also concluded that saccades and manual responses are controlled by similar processes based on their experiments showing that saccades are under voluntary, and not reflexive control, and that saccadic latency, like manual reaction time, can be adjusted according to instructions to stress the speed or the accuracy of the response. (See also Viviani and Swensson, 1982, for discussion of this point.)

Implications for anticipatory smooth eye movements during smooth pursuit

Experiments similar to the one described in this paper can be performed to study effects of prior stimuli on anticipatory smooth eye movements that occur during smooth pursuit when a target is already in motion before an unpredictable change in its path. For example, the stimulus might be a ramp motion followed by a step, either in the same direction or in the opposite direction as the ramp. The effect of the direction of steps in prior trials on the velocity of smooth pursuit can then be determined. (Variations in this experiment are, of course, possible, e.g. two ramps rather than a ramp followed by a step.)

The finite-state Markov model could then be used to estimate the means of the eye velocity distributions corresponding to the expectation of a step in the same direction and in the opposite direction as the ramp. The estimated means will depend on both the expectation and on the velocity of the ramp before the step. Thus, examination of how these estimated means vary as a function of target velocity and as a function of the expectation effectively separates the contribution of target velocity from the contribution of expectations to smooth eye movements. Our demonstration that anticipatory smooth eye movements depend on the sequence of prior stimuli, and

the good fit of the model to these sequential dependencies, show that taking expectations into account is both necessary and feasible. We have shown that accurate predictions about smooth eye movement velocity can be made even when target motions are unpredictable, and subjects have expectations about future target motions which contribute to the smooth eye movement velocities observed.

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