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THE EFFECT OF EXPECTATIONS ON SLOW OCULOMOTOR CONTROL—III. GUESSING UNPREDICTABLE TARGET DISPLACEMENTS

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Abstract—Previously, we had shown that expectations about the direction of future target motion produce involuntary anticipatory smooth eye movements in the direction of the expected target motion (Kowler and Steinman, 1979a, b). The present experiments extend these results to expected target motions in unpredictable directions.

Subjects showed anticipatory smooth eye movements while tracking an unfamiliar pattern of right- and left-going target steps while they were guessing the direction of the expected steps. Eye velocity increased when subjects became certain that they knew what the pattern was. Guesses also produced anticipatory smooth eye movements for both expected target steps and ramps in one of 12 unknown directions. Anticipatory smooth eye movements produced by guesses and by certain knowledge of target direction were not affected when subjects performed a distracting task (mental arithmetic).

These results show that the effect of expectations on slow eye movements cannot be removed simply by making target motions unpredictable. Models of the slow oculomotor subsystems, to be complete, require development of techniques to predict the direction and certainty of human expectations about unpredictable patterns of target motion. A technique, which may serve this purpose, is described.

INTRODUCTION

Recently, we reported that expectations of future target motion produce involuntary drifts of the eye in the direction of the future target motion (Kowler and Steinman, 1979a, b). We called such drifts anticipatory smooth eye movements. These eye movements were found to be a pervasive and general property of the slow oculomotor subsystem. Anticipatory smooth eye movements were found in knowledgeable, experienced eye movement subjects and also in naive inexperienced eye movement subjects. They were found before different types of target motion (steps and ramps) and they were found both during maintained fixation of a stationary target and during smooth pursuit when the target and eye were already moving smoothly before the target made a step-displacement. In all of these instances the expected target displacement was highly predictable in the sense that the direction of its future motion was known to the subject in advance. We now ask whether the effects of expectations are limited to predictable target motions. Specifically, do expectations affect slow eye movements when future target motion is highly unpredictable and the subject can only guess the direction in which the target will move?

We already knew from our prior work that the time of an expected target step need not be predictable in order for anticipatory smooth eye movements to occur (Kowler and Steinman, 1979b, Table 1). There were also suggestions in our prior work that direction need not be predictable. Namely, when the direction of a future target step was unpredictable, the line of sight was not as stable as it was when the target remained stationary and the subject knew that the target would remain stationary. Subjects drifted in idiosyncratic directions when they expected an unpredictable target step. They did not show such drifts when the target remained stationary and they knew that it would remain stationary (Kowler and Steinman, 1979b, Figs 1 and 2 and Table 1). It seemed plausible to us that these idiosyncratic drifts were actually anticipatory smooth eye movements in the direction of the subject's guess about the direction of the future target motion. This possibility could not be evaluated in the prior experiments because the subjects had not been asked to report their guesses about target step direction.

The present experiments examined the effect of guessing on anticipatory smooth eye movements. We found that the velocity of slow eye movements before unpredictable target motions depends on the subject's guess about the direction of the future target motion. We also found that subjects cannot be distracted from making guesses about the direction of future target motions even when these motions are highly unpredictable. These results mean that anticipatory smooth eye movements cannot be eliminated. They occur whenever a subject is required to track an object that he expects to move in the visual field.

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METHOD

Eye movement recording

Eye movements 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. Movements of the right eye on either the horizontal or on both the horizontal and vertical meridans were recorded. The left eye was closed and covered and the head was stabilized by an acrylic dental biteboard.

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

Subjects

The authors served as subjects. Both were experienced in eye movement experiments and knew the purpose of the present research.

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 for the initial experiments was a single diffraction-limited point whose motion was controlled by the computer. On any trial, a sequence of 12 right- and left-going 99′ target steps occurred, one step occurring every 2 sec. The point, whose intensity was 1 log unit above foveal threshold, jumped against a dark background. 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. 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.

Procedure

Before trials the point was located at the primary position. Trials, which lasted 25 sec, were started 100 msec after the subject pressed a button which began data acquisition. Two seconds after the start of the trial, the first target step occurred, and steps continued to occur at 2 sec intervals.

The sequence of steps followed a predetermined pattern subject to the following constraint. Whenever the point was in the center (primary) position, it could either jump to the right or to the left. But whenever the point was in 1 of the 2 eccentric positions, it always jumped back to the center. Thus, on any trial the direction of half of the steps (those that returned to the center) was always predictable, and the direction of the other half of the steps (those that took the point away from the center) was unpredictable in that steps could either be to the right or to the left.

The sequence of the directions of steps away from center was chosen randomly before each trial from one of 10 simple patterns. A typical pattern of directions for the 6 steps away from center might consist, for example, of 2 steps to the right, one step to the left, 2 steps to the right, and 1 step to the left.

Two consecutive trials of the same pattern were presented. On some trials, the subjects were told the pattern before the start of the trial. On the other trials, they were not told the pattern and, therefore, had to figure out what it was. During these trials, in which the pattern was unknown, the subjects signalled 2 different things by throwing switches: (1) their guess about step direction (right or left) before each step away from center, and (2) when they were certain that they knew the pattern of steps.

An approximately equal number of trials was run in which the point remained stationary throughout the trial. During these trials, the subjects expected the point to remain stationary and were instructed to use slow control to maintain the line of sight on the point throughout the trial.

Data analysis

The procedures for analyzing data have been described previously (Kowler and Steinman, 1979a). 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 350 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 a small number of 50 msec samples (1%) were discarded for this reason.

RESULTS

Anticipatory smooth eye movements are produced by guesses about the direction of a step-displacement

The stimulus used in the initial experiment was a simple pattern of right-and left-going target steps. The pattern presented on any trial was initially unknown to the subject, but could be determined by the subject after tracking the target for about one trial. This kind of stimulus was chosen because it permitted a comparison of eye velocity when the pattern of step directions was guessed at the beginning of the experimental sequence with eye velocity when the same pattern of step directions was known after a brief period of tracking.

Anticipatory smooth eye movements were present when the unfamiliar pattern of steps was tracked, i.e. during the period the subjects were guessing the direc-

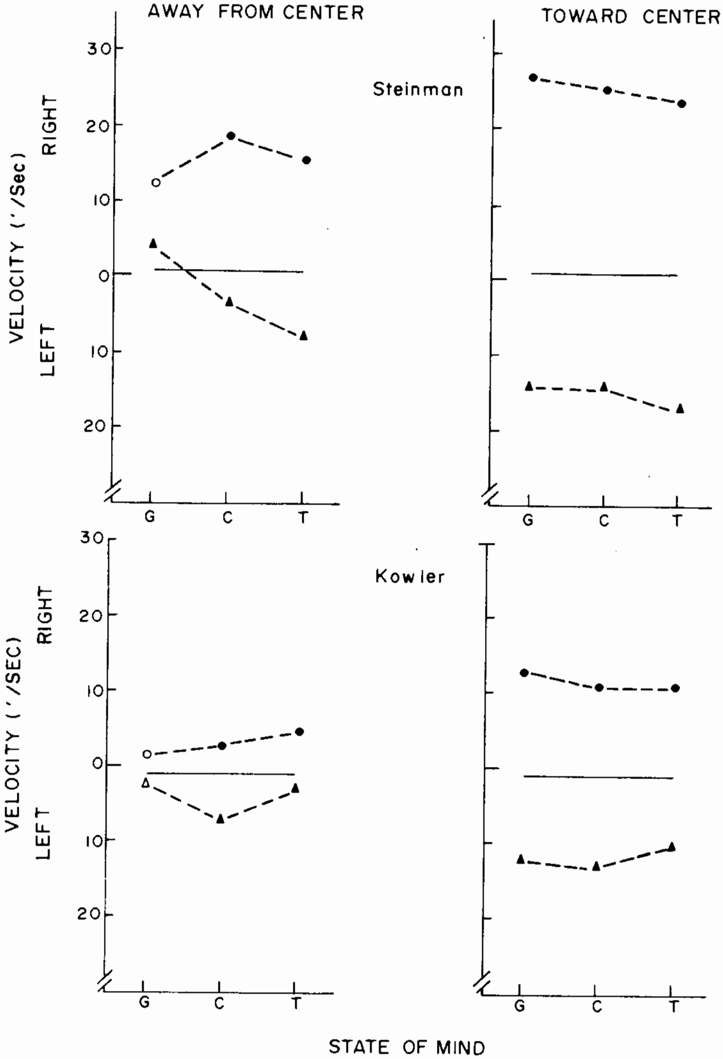

Fig. 1. Mean 50 msec eye velocities for expected patterns of steps. Mean velocities for steps away from center are shown separately for the different states of mind: while step directions were guessed before subjects determined the pattern (G), after they became certain of the pattern (C), and when they were told the pattern in advance (T). Mean velocities for the interleaved steps returning towards center are shown separately for the different states of mind about the steps away from the center. Mean velocities for expected rightward steps are shown by circles, expected leftward steps by triangles, and no expected steps by the horizontal lines. Each datum point for expected steps is based on about 700 observations. The mean velocity for no steps is based on 2000 observations. Standard errors are about the size of the datum point.

tion of each of the steps. Guesses produced different kinds of anticipatory smooth eye movements in each subject. Steinman tended to drift to the right when he was guessing step direction. But his drifts were affected by the direction of his guesses because he drifted faster to the right when he guessed that the step would go to the right than when he guessed that it would go to the left. Kowler, on the other hand, drifted in the direction of her guess. Right when she guessed "right" and left when she guessed "left." These results are summarized in Fig. 1 which plots mean 50 msec eye velocities for rightward and leftward expectations for 3 different states of mind about the steps, i.e. when the subjects were guessing step direction before they had figured out what the pattern was, when they were certain that they knew what the pattern was and when the pattern was described to them before they started to track it.

Note that anticipatory smooth eye movements were faster and always in the direction of the expectation when subjects became certain that they knew what the pattern was. Their anticipatory smooth eye movements, when they were certain, were similar to their anticipatory smooth eye movements when the pattern was described to them in advance.

To summarize, the anticipatory smooth eye movements found before the steps going away from center show two things. First, guesses produce anticipatory smooth eye movements whose direction or velocity depends on the direction of the guess. Second, anticipatory smooth eye movements are faster when subjects become certain about step direction.

This effect of certainty on the velocity of anticipatory smooth eye movements is shown more vividly by comparing the eye velocity before the expected steps away from center with eye velocity before expected steps going towards center. Recall that the direction of steps going towards center was always completely predictable because the subjects knew that targets in eccentric positions always step back to the center. This means that there could never be any doubt about the direction of steps from eccentric positions—they always went back to the center. It was not even necessary to keep track of an already deciphered pattern of steps to recall which direction should be expected next. Anticipatory smooth eye movements were fastest for the steps towards center as is shown in Fig. 1. It can also be seen that anticipatory smooth eye movements for steps towards center were not appreciably affected by the state of mind about interleaved steps which were going away from center.

We believe that the higher anticipatory smooth eye movement velocities for steps going towards center was caused by the increased certainty of their direction and not by the position of the eye in the orbit because we have already shown that the velocity of anticipatory smooth eye movements with highly predictable periodic steps is the same when expected steps are towards the primary position as when they are away from the primary position (Kowler and Steinman, 1979a).

Anticipatory smooth eye movements are produced by guesses about the direction of step displacements in one of 12 unpredictable directions

The previous demonstration that the velocity of anticipatory smooth eye movement increases with the certainty of the expectation raises the possibility that the effect of guesses on slow eye movements might be eliminated by reducing the certainty that the guess would be correct. In the first experiment the target could step either to the right or to the left, so the probability that any guess about step direction would be correct on any trial was 1/2. Would the effect of guesses on slow eye movements still be observed when certainty is reduced by having the target step in any one of many unpredictable directions?

To find out, we looked at anticipatory smooth eye movements with a target that was expected to step in any one of 12 different directions. The directions used were defined by the positions of the 12 hr on the clockface. Trials consisted of 2 target steps. They were run as follows: The point stepped 60′ one and 1/2 sec after the subject started the trial. One and 1/2 sec later it stepped back to the center. This allowed a comparison of anticipatory smooth eye movements for steps in highly unpredictable directions (those which took the point away from the center) with anticipatory smooth eye movements for steps in predictable directions (those which returned the point to the center).

On some trials subjects were told the direction of the step in advance. On other trials they were not told the direction of the step and thus could only guess the direction of the step. In this experiment subjects did not report the direction of their guess. The report was omitted to be sure that anticipatory smooth eye movements produced by guesses were not limited to situations in which a guess was encouraged by the need to report its direction before each trial.

Omitting the requirement to report the guess meant that we could no longer plot the velocity of anticipatory smooth eye movements as a function of the direction of the subject's guess as we had done in the prior experiment. Therefore, an alternative way of determining whether anticipatory smooth eye movements occurred was required.

We adopted the following procedure. Trials were run in which the target did not step and the subjects knew that it would not step. These trials provided the baseline velocities against which we could determine whether anticipatory smooth eye movements were made when the target stepped in one of 12 unpredictable directions. If anticipatory smooth eye movements were abolished by the high degree of uncertainty introduced in this experiment, then mean eye velocity before expected steps in one of 12 unpredictable directions should not differ from mean eye velocity on the trials when the target did not step and the subjects knew that it would not step.

Anticipatory smooth eye movements were not abolished when certainty was reduced. Both subjects drifted faster and in a different direction when they expected steps than when they did not expect steps. This result is summarized in the center graph in Fig. 2. This graph shows mean 50 msec eye velocities before expected steps whose directions were not known to the subjects in advance. Mean 50 msec eye velocities are shown as vectors whose lengths are proportional to mean eye speed and whose directions represent the mean directions of drifts of the line of sight. Mean eye velocities are plotted as a function of the actual direction of the target step (step direction is indicated by the clockface numbers on the vectors). Mean eye velocities are also shown for trials in which steps were not expected (the vector labelled NS). Note that the average direction of the line of sight did not depend on the actual direction of the step. This result is not surprising because the subjects did not know the direction of the step in advance. The fact that anticipatory smooth eye movements did occur, when step directions were unknown, can most easily be seen in the right-most graph in Fig. 2. Here, mean eye velocity before expected steps is shown averaged over all step directions. Clearly, the eye drifted faster and in a different direction before expected steps in unknown directions than it did when the target did not step and the subject knew that it would not step.

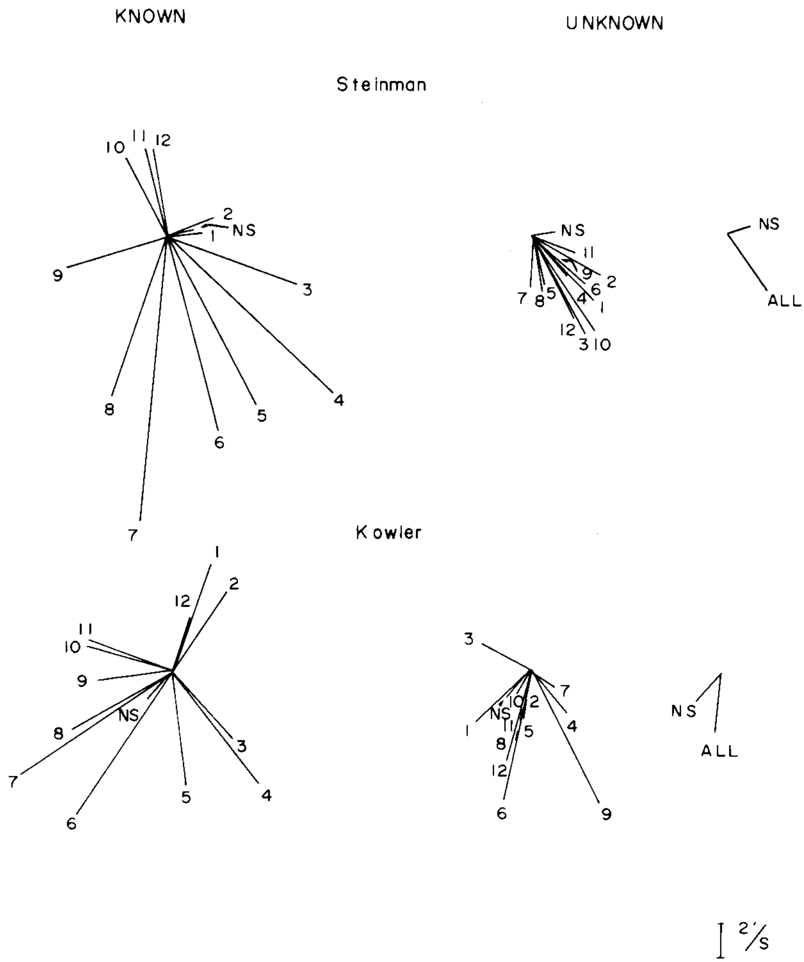

Fig. 2. Mean 50 msec eye velocity vectors for expected steps away from center in the direction of the hours on the clockface. Mean velocities when step directions were *Known* to the subject in advance and when directions were *Unknown* are shown separately for expected steps away from center in each of the 12 directions (numbered vectors) and for no expected steps (NS). Mean velocity averaged over all 12 directions when step directions were unknown is also shown (ALL). Each vector for expected steps is based on approximately 150 observations and the vector for no expected steps on approximately 2000 observations.

Anticipatory smooth eye movements in the actual direction of the target step were also obtained, as expected from the results of the first experiment, when the subjects knew the step direction in advance. This is shown by the graphs on the left side of Fig. 2. Also, as in the first experiment, increasing certainty increased drift velocity. This is shown by the higher velocities obtained for steps that were expected to return towards center (see Fig. 3).

The higher velocities obtained for the steps returning towards center require further comment because at first glance it is not obvious why subjects would be more certain about the direction of a single step returning toward center than they would be about the direction of a single step going away from center to a known location. The center location was a more familiar and more easily remembered location for at least two reasons. First, there was only one endpoint for steps toward center and it was the same on each trial. There were 12 possible endpoints for steps away from center and the endpoint changed from trial to trial. Second, the target and the line of sight had just been at the center less than 2 sec earlier. Thus, there should be greater certainty in estimating where one had just been looking than in estimating the location of a particular hour on the clockface.

Anticipatory smooth eye movements produced by guesses are not abolished by a distracting task

Anticipatory smooth eye movements produced by guesses might be eliminated if subjects were encouraged not to guess. The prior experiment showed that removing the requirement to report the guess did not abolish anticipatory smooth eye movements. But, most likely, the guesses were not abolished either. Both subjects noticed that it was difficult to suppress the tendency to speculate about where the next step might go. Instructing subjects to avoid such specu-

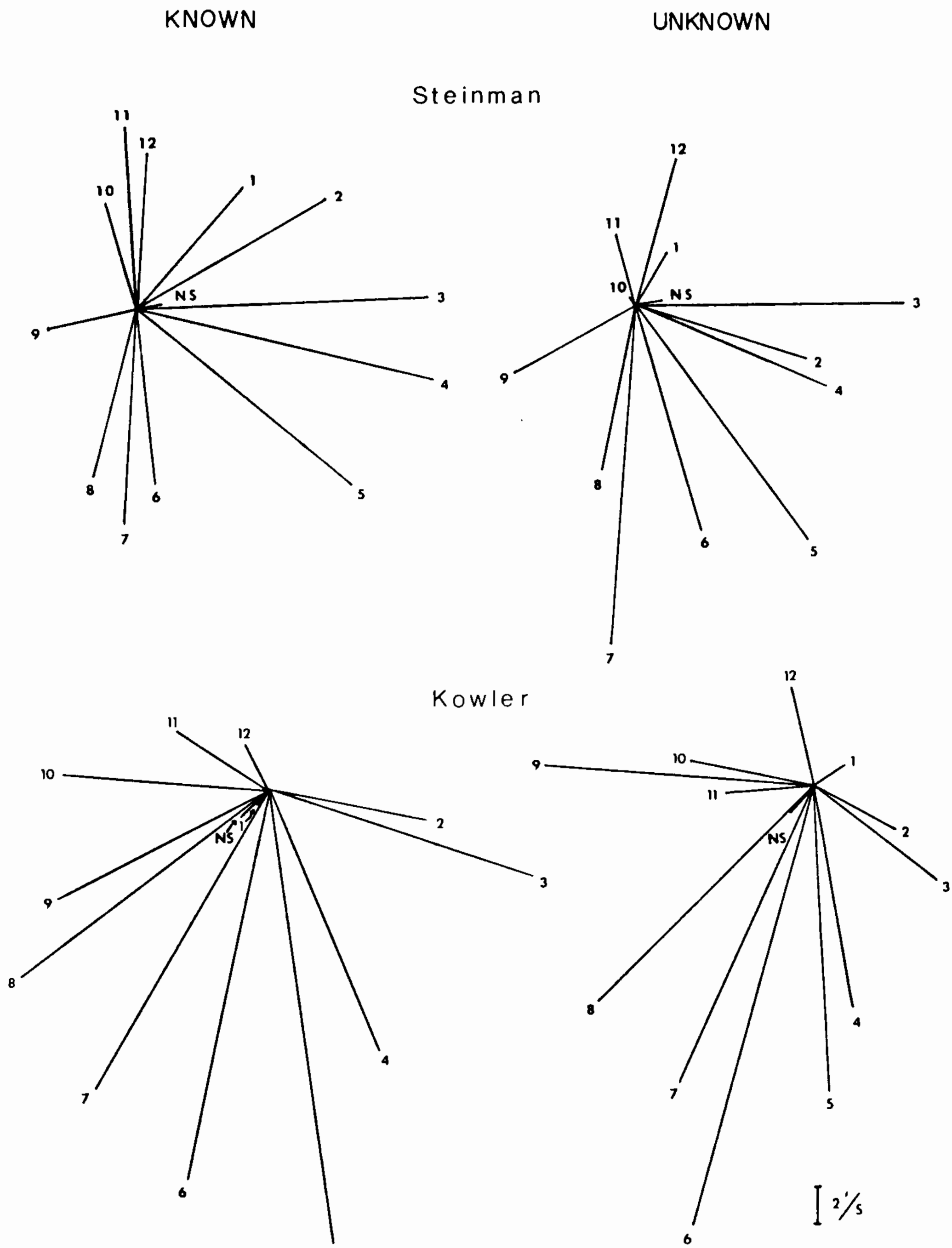

Fig. 3. Mean 50 msec eye velocity vectors for expected steps returning toward center from the hours on the clockface. Mean velocities when the directions of steps away from center were *Known* to the subject in advance and when directions were *Unknown* are shown separately for expected steps toward center in each of the 12 directions (numbered vectors) and for no expected steps (NS). Each vector for expected steps is based on approximately 150 observations and the vector for no expected steps on approximately 2000 observations.

lations would probably not be successful in preventing guesses. Even if such an instruction would be successful, there is no obvious objective way of monitoring how well the instruction had been followed.

Such considerations led to the next experiment in which a distracting task (mental arithmetic) was used in the attempt to discourage guessing. The experiment was identical to the previous experiment except for the inclusion of the mental arithmetic task. The experiment was run as follows: A series of 3 numbers was read aloud to the subject during each trial. The subject was required to report their sum at the end of

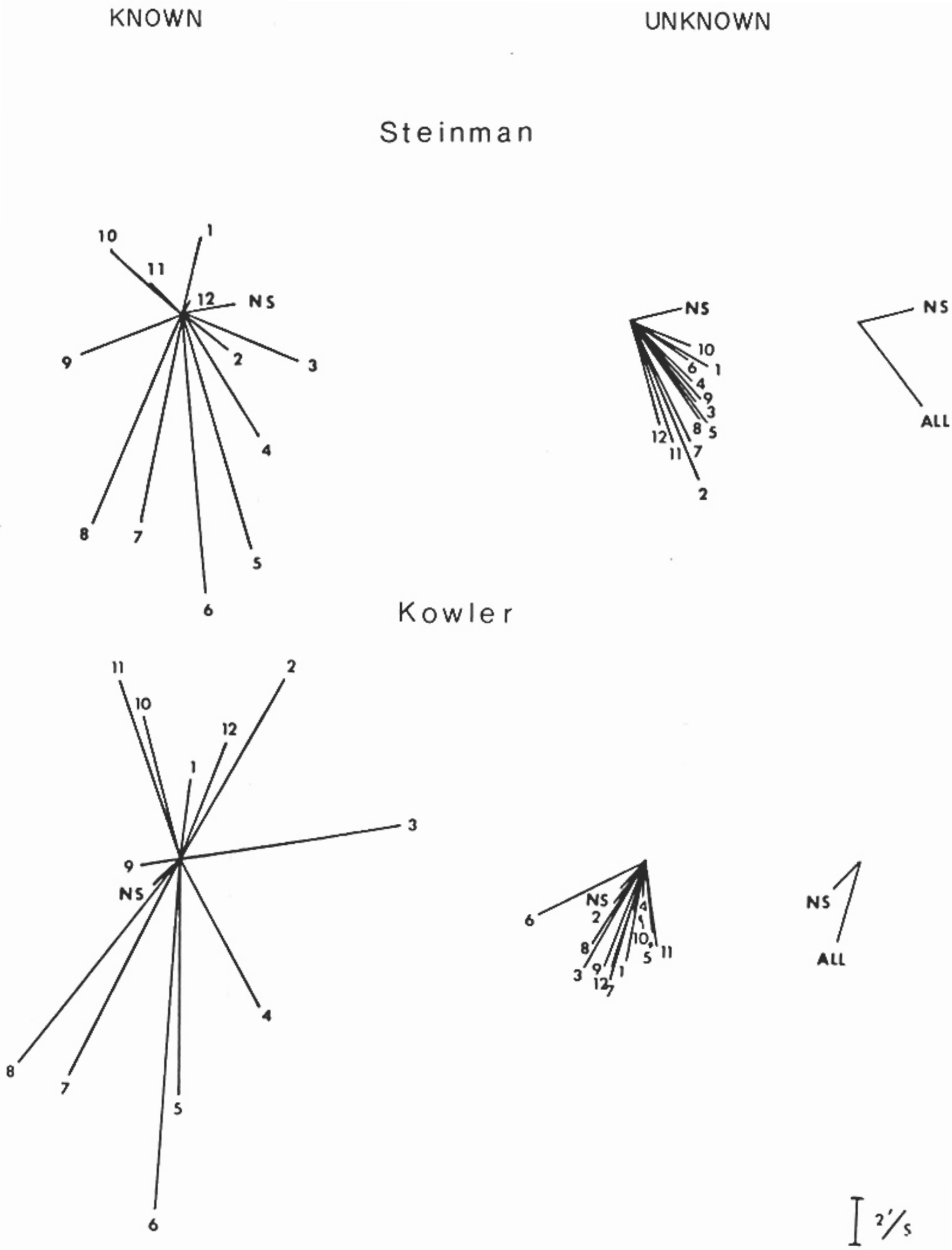

Fig. 4. Mean 50 msec eye velocity vectors when mental arithmetic was performed while expecting steps away from center in the direction of the hours on the clockface. Mean velocities when step directions were *Known* to the subject in advance and when directions were *Unknown* are shown separately for expected steps away from center in each of 12 directions (numbered vectors) and for no expected steps (NS). Mean velocity over all 12 directions when step directions were unknown is also shown (ALL). Each vector for expected steps is based on approximately 150 observations and the vector for no expected steps on approximately 2000 observations.

each trial. Subjects were instructed to pay close attention to the numbers and to try to get all the sums correct.

The mental arithmetic proved to be a good distractor. Subjects reported that they were not aware of attempts to guess step direction. Their arithmetic scores supported their introspections in that they were able to perform the task with reasonable accuracy (both scored 98% correct). However, the mental arithmetic task did not abolish the anticipatory smooth eye movements. In fact, mean eye velocities for steps away from center, shown in Fig. 4, and for

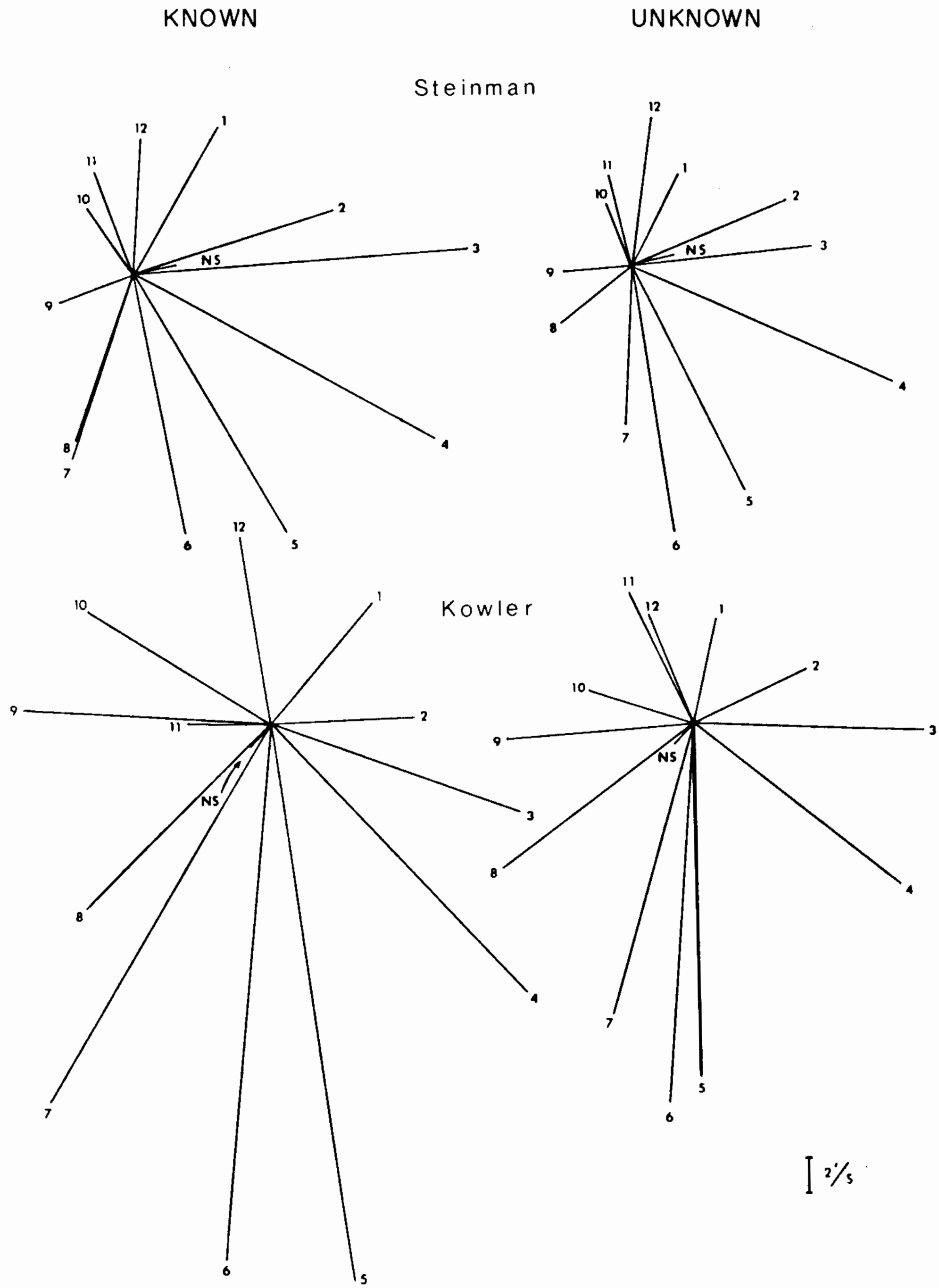

Fig. 5. Mean 50 msec eye velocity vectors when mental arithmetic was performed while expecting steps returning toward center from the hours on the clockface. Mean velocities when the directions of steps away from center were *Known* to the subject in advance and when directions were *Unknown* are shown separately for expected steps toward center in each of the 12 directions (numbered vectors) and for no expected steps (NS). Each vector for expected steps is based on approximately 150 observations and the vector for no expected steps on approximately 2000 observations.

steps toward center, shown in Fig. 5, were almost identical to mean eye velocities in the prior experiment when mental arithmetic was not being performed (see Figs. 2 and 3). Thus, the distracting task did not reduce anticipatory smooth eye movement velocity when expectations were guesses nor when expectations were based on certain knowledge of step direction. Kowler, in fact, tended to drift slightly faster while she was doing mental arithmetic and expecting steps at the same time.

In summary, the effect of expectations on slow eye movements is not easy to remove. Even a distracting task which prevents, or at least reduces, attention to the expectations does not affect the drifts of the eye. These results suggest that expectations, even when they are guesses, need not be actively attended to in order for anticipatory smooth eye movements to be produced.

Anticipatory smooth eye movements are produced by guesses about the direction of expected ramp displacements in one of 12 unpredictable directions

The previous experiments have shown that anticipatory smooth movement is a robust phenomenon. These eye movements occur before target steps, whose direction is guessed, even when the probability that the guess will be correct is low (0.08) and even when guessing is discouraged by a distracting task.

However, our results, thus far, only apply to expectations of target steps. In the next experiment we found the same effects of expectations on slow eye movements with expected ramps moving in one of 12 unpredictable directions.

The experiment was run in essentially the same way as the previous experiments except that a ramp displacement of the target was used instead of a step displacement of the target. The subject started each trial and $1\frac{1}{2}$ sec later the target moved smoothly at 60′/sec to one of the positions of the 12 hr on the clockface. The total displacement produced by the ramp was 60′—the same as the size of the displacement produced by the steps in the prior experiment. One and $\frac{1}{2}$ sec after the ramp stopped, the target moved smoothly back to the center position at 60′/sec (the same velocity).

There was one other major change in this experiment besides the type of target motion. Subjects were required to report the direction of their guesses. Given that the previous experiment showed that guessing is difficult to discourage, it seemed useful to record the direction of the subject's guess about future target motion. This allowed anticipatory smooth eye movements to be examined as a function of the guessed direction of the ramp, rather than as a function of the actual direction of the ramp which was not known to the subject while he waited for the target to move. Subjects indicated the direction of their guess verbally before each trial.

Guesses about the expected direction of a ramp produced anticipatory smooth eye movements in the directions of the guesses. This is shown by the mean eye velocities before expected ramps moving away from center in unknown directions plotted in Fig. 6. Keep in mind that the graphs showing anticipatory smooth eye movements before expected ramps in unknown directions plot eye velocity as a function of the guessed direction and not as a function of the actual direction of the ramp. Most of the time guesses were wrong so the actual directions of the ramps differed from the directions of the guesses.

A comparison of anticipatory smooth eye movements produced by guesses with the two types of displacements, steps and ramps, shows that the subjects performed differently. This can be seen by looking at the velocity of anticipatory smooth eye movements averaged over all trials in which direction was unknown (the right-most graphs in Fig. 2 for steps and Fig. 6 for ramps). For Steinman the average direction of the drift was the same for steps as for ramps. For Kowler, on the other hand, the average direction of the drift was different for these 2 kinds of displacements. Why steps and ramps produced different effects in the one subject when their directions were unknown is presently obscure. It is clear, however, that anticipatory smooth eye movements were present in both subjects with both types of displacements.

Anticipatory smooth eye movements also occurred before expected ramps in known directions. This is shown in the left-most graphs in Fig. 6. These graphs plot eye velocity as a function of the actual direction of the ramp, which was the same as the direction of the expectation, because ramp direction was always known to the subject during these trials.

The direction and speed of drifts before ramps in known and guessed directions were about the same for one of the subjects (Steinman). This result shows that guesses can be as effective as certain knowledge in producing anticipatory smooth eye movements. Kowler's velocities, however, were slightly higher when she knew ramp direction. This result suggests that knowing is more effective than guessing. The reason for these individual differences is not clear but some speculation about their cause is possible. Results of the previous experiments have indicated that the certainty of an expectation affects eye velocity. Perhaps Steinman drifted faster than Kowler because he was surer of his guesses. This kind of psychological speculation, although not testable in the present experiment because confidence judgements were not obtained, does point to the major message of all of our results: namely, a complete understanding of the activities of the slow oculomotor subsystem requires the development of techniques to specify psychological inputs to this subsystem.

The anticipatory smooth eye movements for ramps moving towards center (shown in Fig. 7) were generally faster than anticipatory smooth eye movements for ramps moving away from center. This result is similar to the results obtained with target steps. Target movements towards center were always highly predictable and certainty increases anticipatory smooth eye movement velocity. However, there is one case in the ramp experiment in which anticipatory smooth eye movement velocity with ramps moving towards center was relatively slow. Kowler did this with ramps that had gone away from the center in unknown directions. In this case we also found marked differences between the mean direction of the line of sight and the actual direction of the ramp. Kowler's pattern of anticipatory smooth eye movements in this condition agreed with her perceptual observations. She noted that it was difficult to be sure

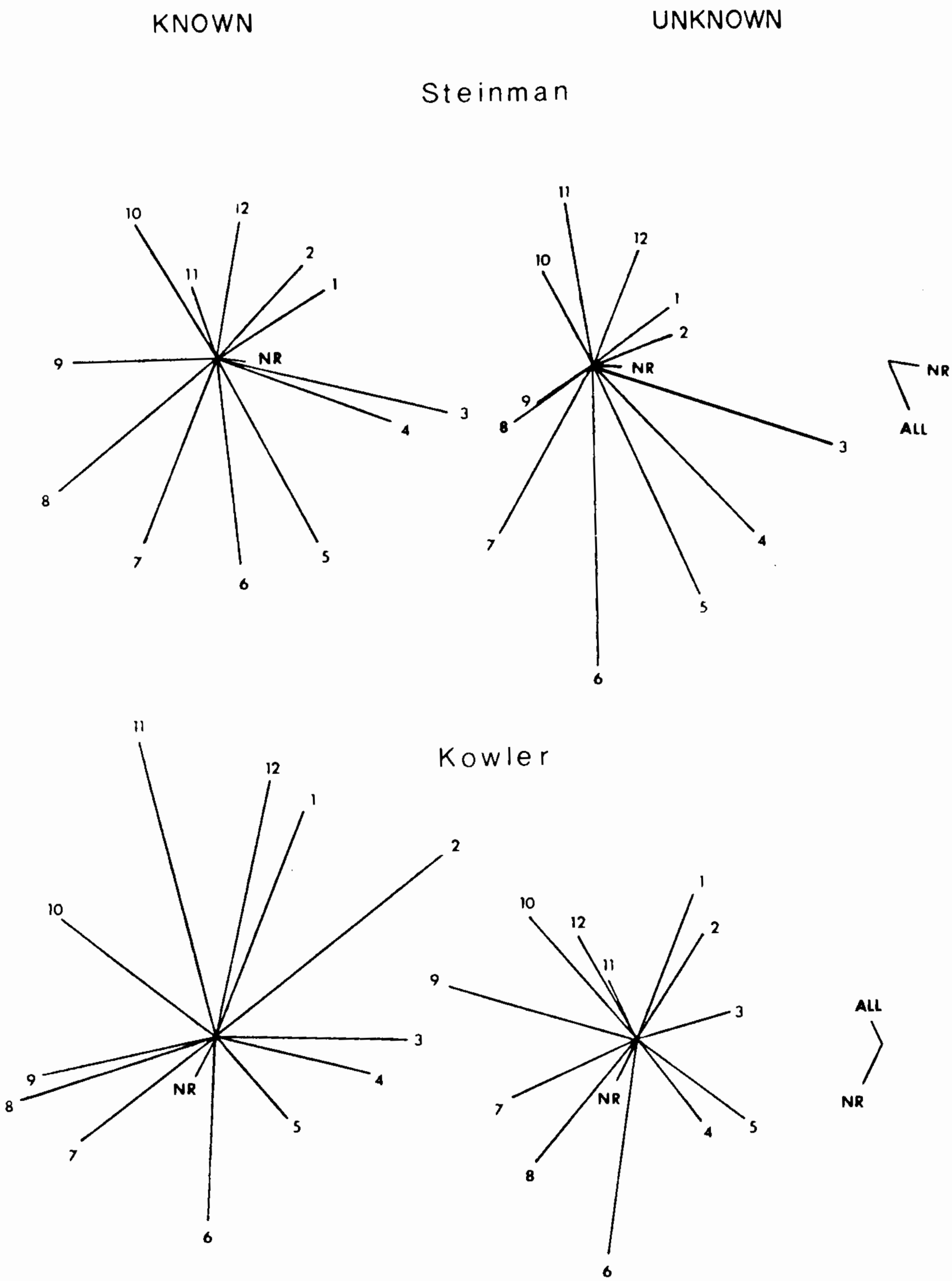

Fig. 6. Mean 50 msec eye velocity vectors for expected ramps away from center in the direction of the hours on the clockface. Mean velocities when ramp directions were *Known* to the subject in advance are shown separately for expected ramps in each of the 12 directions (numbered vectors). Mean velocities when ramp directions were *Unknown* are shown separately for each guessed ramp direction (numbered vectors) and averaged over all 12 guessed directions (ALL). Mean velocity for no expected ramps is also shown (NR). Each vector for expected ramps is based on approximately 150 observations and the vector for no expected ramps on approximately 1000 observations.

of the actual direction of the ramp, even after it had begun moving, when its direction had not been described in advance. Sometimes, in fact, the moving target appeared stationary. When Kowler did not see the target move, she could not determine when it had stopped, when it was ready to turn around, and in which direction it would go next. Her occasional inability to formulate an expectation about ramp motion was reflected in her anticipatory smooth eye movements which were occasionally slow and in the wrong direction.

DISCUSSION

We have shown that knowledge about the direction of future target motion is not required in order for expectations to affect slow oculomotor control.

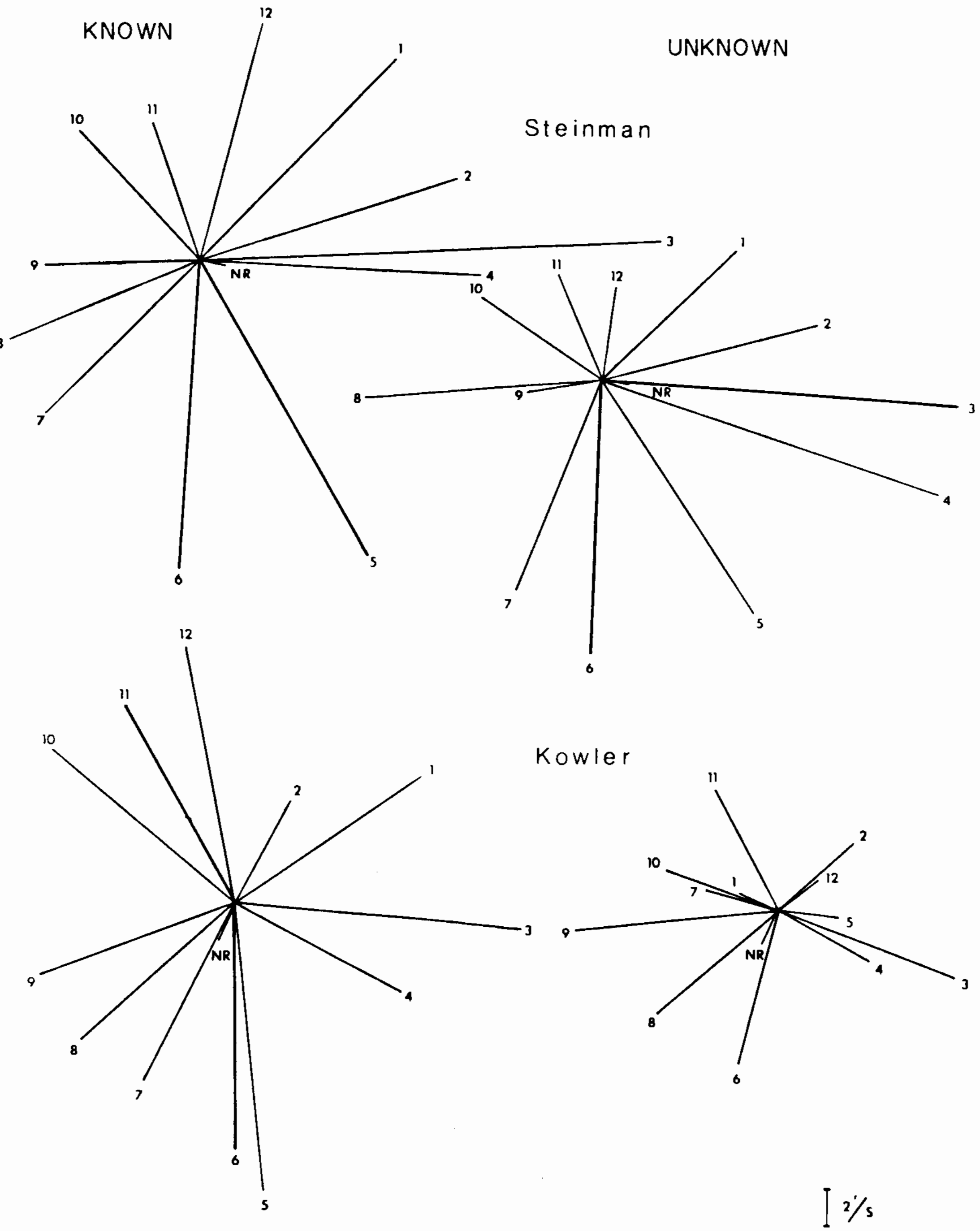

Fig. 7. Mean 50 msec eye velocity vectors for expected ramps returning toward center from the hours on the clockface. Mean velocities when the directions of ramps away from center were *Known* to the subject in advance and when directions were *Unknown* are shown separately for expected ramps toward center in each of the 12 directions (numbered vectors) and for no expected ramps (NR). Each vector for expected ramps is based on approximately 150 observations and the vector for no expected ramps on approximately 1000 observations.

Expectations, based on guesses about the direction of future target motion, produce anticipatory smooth eye movements.

This is news because the role of expectations in the control of smooth eye movement has been neglected previously*. Prior workers did not discuss expectations when they observed what has been called "predictive tracking". This term was used to describe the high smooth pursuit gains, short phase lags and phase leads that were observed during smooth pursuit of sinusoidal target motions (e.g. Dodge *et al.*, 1930; Westheimer, 1954; Stark *et al.*, 1962; Dallos and Jones, 1963; Michael and Melvill Jones, 1966). Such predictive tracking was not ascribed to the influence of expectations on smooth eye movements. Rather, it was ascribed to the ability of the smooth pursuit subsystem to learn a repetitive pattern of target motion and use what it had learned to predict the path of the target. Predictive tracking of unpredictable, aperiodic motions (e.g. sums of sinusoids or bandwidth-limited Gaussian noise) was either explicitly rejected (Stark *et al.*, 1962; Dallos and Jones, 1963) or believed to decline as the bandwidth of the motion increased (Michael and Melvill Jones, 1966). The assumption that predictive tracking is a learned response to periodic predictable target motions was incorporated into Dallos and Jones' (1963) model of the smooth pursuit subsystem. They attributed characteristics of pursuit with aperiodic motions exclusively to the influence of retinal events. Only differences between pursuit of sinusoidal and aperiodic target motions were attributed to the effects of prediction.

However attractive such a parsing of the smooth pursuit response may be, our results have shown that it is not easily achieved. We had already shown that neither practice nor a periodic stimulus is required for anticipatory smooth eye movements to occur (Kowler and Steinman, 1979a, b). The present results go further. They show that even a predictable stimulus is not required. Expectations influence slow eye movements when the direction of target motion is not predictable and expectations are, therefore, only guesses. Furthermore, we found that the influence of guessed step direction could be as great as the influence of known step direction when subjects felt certain that their guess was correct.

Although the effect of guesses on slow eye movements, which we have shown, may seem at first glance to make oculomotor modeling more complicated, more serious consideration suggests quite the opposite. Namely, the slow oculomotor subsystem is simpler than had been supposed because no decision-making mechanism is required to determine when expectations should and should not be permitted to influence slow eye movements. Instead, expectations are now known to contribute to slow eye movements all of the time. We now know that the problem for modeling the slow oculomotor subsystem is to devise ways of incorporating, rather than eliminating, the effects of expectations.

One way of incorporating the effect of expectations into models of the slow oculomotor subsystem is to use only predictable target motions. The advantage of this method is that the subjects' expectations are always known. There are, however, problems with this method. First, it restricts the type of target motions which can be studied. Second, it is known that extensive tracking practice with predictable periodic target motions increases smooth pursuit gain (Kowler *et al.*, 1978). Such practice effects might obscure the effects of expectations when predictable target motions are used.

A better way to proceed is to develop a model which predicts the subjects' expectations about the direction of target motion when direction is unpredictable. Models which can do this may, in fact, already be available because a similar problem has been encountered in studies of other motor responses. Falmagne *et al.* (1975), for example, found that two-choice manual reaction time to the appearance of a triangle oriented either to the right or to the left depended on the sequence of orientations presented on previous trials. They developed a finite-state Markov model which predicted mean reaction time from the sequence of stimuli that were presented on up to 4 previous trials. The notion underlying their approach was that the subject chooses to respond right or left by sequentially comparing the form that had been presented to an internal memory representation of each of the two forms. The subject responds as soon as a comparison produces a match, thus, the order of the comparisons determines the reaction time. Their model assumed that the probability that one of the two comparisons occurs first depends on the sequence of stimuli that had been previously presented.

To the extent that the order of the two comparisons is analogous to the strength of the expectation that

* Consultation with other investigators has shown that a number noticed anticipatory smooth eye movements during tracking of predictable target displacements. They did not systematically investigate or report these effects either because the effects were tangential to the purpose of their experiments or because of concern about possible extraneous sources of the eye movements, e.g. drifts toward primary position or contact lens slippage (Brown, personal communication; Hallett, personal communication; Matin *et al.*, 1970; Robinson, personal communication; Timberlake *et al.*, 1972; Winterson and Steinman, 1978). In a prior paper we ruled out such extraneous sources of anticipatory smooth eye movements (Kowler and Steinman, 1979a).

Karpov (1976) observed, but misinterpreted, anticipatory smooth eye movements in his experiments. Karpov shows eye movement records in which smooth eye movements in the direction of future target motion were prominent during tracking of both periodic, squareware motions and periodic motions containing both steps and ramps. He hypothesized that such movements are produced by the extraction and learning of the fundamental (sinusoidal) frequency component of the periodic waveforms. Such an interpretation, although original and interesting, clearly cannot explain anticipatory smooth eye movements because we have shown in these and prior experiments that neither practice, nor periodic and predictable motion are required for anticipatory smooth eye movements to appear.

one of the forms will appear next, their model may also be able to predict the direction and speed of anticipatory smooth eye movements when subjects track sequences of unpredictable right- and left-going target steps. Sequences of directions which produced faster reaction times in Falmagne *et al.*'s (1975) manual reaction time task would be expected to produce higher velocity anticipatory smooth eye movements for the expected steps. If such an approach works well with a relatively simple stimulus (an expected step when the target is stationary before the step), then it may also be possible to apply similar techniques and develop models to predict eye velocity when subjects smoothly pursue complex patterns of unpredictable motions. Experiments to test this technique are underway (Kowler and Martins, 1980).

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