

COGNITIVE EXPECTATIONS, NOT HABITS, CONTROL ANTICIPATORY SMOOTH OCULOMOTOR PURSUIT

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Abstract—Human smooth pursuit eye movements anticipate the future path of moving targets. Anticipatory pursuit is sometimes attributed to cognitive expectations about future motion and other times to the habitual repetition of previous pursuit responses. Expectations and habits were separated by having subjects smoothly pursue a target moving along a randomly-selected path that was either undisclosed to the subject before each trial or disclosed by means of auditory or visual cues. When the path was undisclosed, the direction of anticipatory smooth eye movements was determined by the direction of target motion in the previous trial. In the presence of cues—the critical condition for separating habits and expectations—effects of previous trials diminished and anticipatory smooth eye movements were primarily determined by the direction of motion the subject was told to expect. These results show a strong contribution of cognitive expectations which overrides persevering smooth oculomotor habits. Smooth pursuit eye movements are driven by a signal that combines the present target motion with the target motion expected to occur several hundred milliseconds into the future. The expected motion is based on a genuine cognitive prediction, not lower-level sensory or motor memories of past events.

Eye movement Oculomotor system Smooth pursuit Learning Expectations Prediction
Habit

INTRODUCTION

It has been known since the work of Raymond Dodge (Dodge, 1931; Dodge, Travis & Fox, 1930) that smooth pursuit eye movements anticipate the future path of a moving target. Figure 1 shows representative examples in which anticipatory pursuit can be seen to begin at least one-half second before the target begins to move. We still do not understand what produces anticipatory pursuit, despite numerous observations of the eye beginning to move before the start of target motion, or the eye changing direction ahead of the target during pursuit of sinusoidal motion (e.g. Westheimer, 1954; Stark, Vossius & Young, 1962; Dallos & Jones, 1963; Wintersson & Steinman, 1978; Kowler & Steinman, 1979a, b, 1981; Kowler, Martins & Pavel, 1984; Collewijn & Tamminga, 1984; Becker & Fuchs, 1985; Boman & Hotson, 1988). Anticipatory pursuit can be as fast as 50 deg/sec (Collewijn, Steinman & van der Steen, 1985).

Developing an explanation for anticipatory pursuit requires abandoning two assumptions that underly most models of smooth eye movement (see Kowler & Steinman, 1979a; Kowler et al., 1984; and Steinman, 1986; for detailed re-

views). The first assumption is that the stimulus for smooth eye movement is a sensory signal representing the motion of the target in either retinal or in orbital coordinates. The second assumption is that the "goal" of smooth eye movement is to use sensory signals to fashion a response that reduces the existing, momentary retinal image velocity. Anticipatory pursuit cannot be explained by these assumptions because: (1) there are no identifiable sensory signals to initiate pursuit before the visual target starts moving; and (2) the anticipatory pursuit takes the eye away from a stationary target, thereby increasing, rather than reducing, retinal image velocity. Anticipatory pursuit shows that the stimulus for smooth eye movement and the "goal" of smooth eye movement are more complex than often assumed. If we knew what was responsible for the initiation and control of anticipatory pursuit, we might have a better general understanding of how smooth eye movements work.

This paper is concerned with the origin of anticipatory pursuit. Anticipatory pursuit might arise in two different ways, each with different theoretical implications.

Anticipatory pursuit could be provoked by cognitive expectations about the future path of

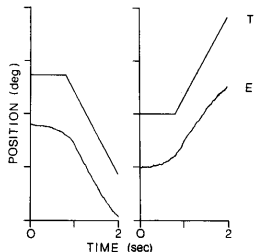


Fig. 1. Horizontal eye position (bottom traces) as a function of time during smooth pursuit of constant velocity motion (top traces) to the left (lefthand graph) and to the right (righthand graph). The data are from subject JW when the visible "barrier" provided the cue to the direction of future motion (see the Methods Section for an explanation of the visible barrier).

target motion. These expectations might take the form of an internally-generated motion signal whose effects on smooth eye movements would be indistinguishable from the effects of a genuinely moving target.

The second way for anticipatory pursuit to arise is by means of oculomotor learning. By oculomotor learning I mean an automatic tendency to remember previously-seen target motions or previously-issued smooth oculomotor commands and re-issue the commands at the appropriate time. Attributing anticipatory pursuit to learning is an old idea (Dodge et al., 1930; Westheimer, 1954; Dallos & Jones, 1963).

It remains attractive because it offers the possibility of accounting for anticipatory pursuit by low-level learning or adaptive processes, without the need for high-level cognitive involvement.

Previous oculomotor research, using either predictable or random target motions, did not distinguish these two sources of anticipatory pursuit—cognitive expectations vs oculomotor learning—because the expectation about the future path of motion was always derived from the pattern of motion tracked in previous experimental trials. Expectations were distinguished from learning in the present experiment by putting the expected future path of the target in conflict with the path of the target in the recent past. This was done by providing symbolic cues about the future direction of randomly-selected target motion.

I found that the expectation about the direction of future target motion, derived from the symbolic cues, was much more important than tendencies to repeat previous pursuit responses. This shows that low-level learning or adaptive processes are insufficient explanations of anticipatory responses. Cognitive expectations about future motion can drive smooth pursuit.

A portion of these results was reported in Kowler (1988).

METHOD

Stimulus

The target was a thin annulus (20 min dia.) that moved inside an outline drawing of an inverted Y-shaped tube (width = 40 min) (Fig. 2). The stimulus was "painted" on a CRT

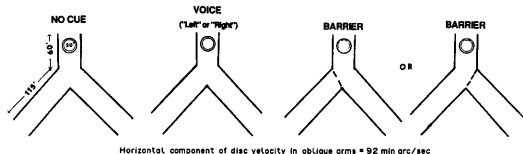


Fig. 2. The stimulus display, consisting of a stationary inverted Y-shaped tube and an annulus which served as the moving target. The velocity of the target was 130 min/sec. The target moved down the tube and continued at the same velocity down either the righthand or lefthand oblique branch of the Y (horizontal component of velocity when the target was in either branch of the Y was 92 min/sec). The target was equally-likely to travel down either branch. The 4 drawings show the different experimental conditions in which the branch to be traveled by the target was either: undisclosed before each trial (*No Cue*), disclosed by a *Voice* cue, or disclosed by a visible *Barrier* cue blocking access to either the lefthand or righthand branch.

screen (Tektronix 608; P4 phosphor) once every 10 msec, a rate high enough to prevent any visible flicker. The display, located at optical infinity, appeared medium-bright (luminous directional energy/painting = 0.06 cd-microsec; Sperling, 1971) and was seen against a dim (0.3 cd/m^2) homogeneous background field produced on a second CRT located at right angles to the first. Views of the two CRT displays were combined by a pellicle beam splitter.

Subjects

Subjects were the author (EK) and a naive eye movement subject (JW) who had served in a previous study dealing only with saccades (Zin-gale & Kowler, 1987).

Eye movement recording

Horizontal movements of the right eye were recorded by a Generation IV SRI Double Purkinje Image Tracker (Crane & Steele, 1978). The left eye was covered and the head was stabilized on a dental biteboard.

The voltage output of the Tracker was fed on-line through a low pass 50 Hz filter to a 12-bit analog to digital converter (ADC). The ADC, under control of a computer (LSI 11/24), sampled eye position every 10 msec. The digitized voltages were stored for subsequent analysis.

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 first and fourth Purkinje image reflections as the average subject's eye. Filtering and sampling rates were the same as those used in the experiment. Noise-level, expressed as a standard deviation of horizontal samples, was 0.4 min on the horizontal and 0.7 min on the vertical meridian. Both the auto-stage and focus-servo of the Tracker were disabled (a necessary procedure with the Generation IV) to prevent the introduction of artifactual deviations into the Tracker output. See Kowler and McKee (1987) for further details.

Procedure

A trial began with the annulus at the top of the tube. The subject started a trial by means of a button press and 300 msec later the annulus began moving downward at a constant velocity of 130 min/sec. The motion of the target was produced in a conventional manner, namely, by moving the point in a series of jumps which were sufficiently small and frequent (1.3 min/0.01 sec)

so that the individual jumps could not be discerned and the target appeared to be moving smoothly.

About 0.5 sec after the start of target motion the annulus reached the intersection of the left and right branches of the Y. It continued travelling without interruption at the same speed down either branch. The branches formed an angle of 45 deg with the horizontal meridian so that the horizontal and vertical components of the annulus's velocity were each 92 min/sec.

Conventional instructions were used to elicit smooth pursuit, namely, pay attention to the moving target and try to match the velocity of the eye to the velocity of the target.

Cues about the path of motion

In 4 of the 12 experimental sessions, the branch to be travelled by the annulus was not disclosed before each trial (Fig. 2A); in 4 sessions, the branch was disclosed before each trial by an auditory cue (a computer-controlled synthesized voice saying "left" or "right"; Fig. 2B); and in 4 sessions, it was disclosed by a visual barrier (a dashed line) blocking access to the untraveled branch (Fig. 2C, D). The branch to be traveled by the annulus was selected randomly and independently on each trial, with the probability of the annulus entering either branch equal to 0.5. This meant that a random sequence of leftward and rightward target motions was presented during each experimental session. Sessions with voice or barrier cues differed from sessions with no cue only in that the subject knew the direction in which the target would move before each trial.

Data analysis

Horizontal eye velocity was calculated from the digitized records of eye position. Eye velocity was measured within 100 msec intervals. (Intervals containing saccades or portions of saccades were discarded.) Eye velocity for each 100 msec interval was taken as the slope of the straight line fit by a least-squares criterion to 10 consecutive eye position samples. A "sliding-window" techniques was used (see Kowler & McKee, 1987; Collewijn & Tamminga, 1984) in which the onsets of successively measured 100 msec velocity samples was separated by 10 msec.

The duration of the velocity samples was set to 100 msec in order to: (1) reduce the contribution of high frequency noise to the measured eye velocities; and (2) facilitate comparison with

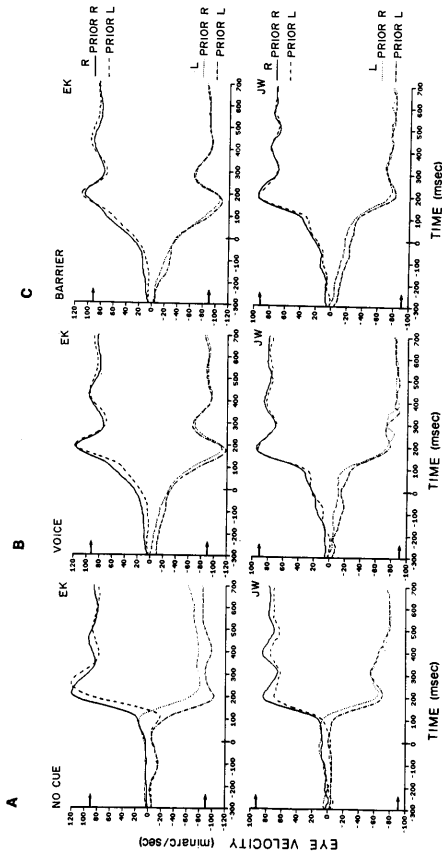


Fig. 3. Mean horizontal eye velocity during successive 100 msec intervals (offsets 10 msec apart) as a function of the midpoint of the interval when either: (A) No Cue; (B) Voice Cue; or (C) Barrier Cue about the direction of future horizontal target motion was given. Top graphs, EK; bottom, JW. Time 0 is the start of horizontal target motion (the first entry of the moving target into the oblique branch of the Y-shaped tube). Arrows on the ordinate show horizontal target velocity; negative values denote leftward motion. The top pair of functions in each graph show eye velocity when the target moved down the righthand branch; the bottom pair when it moved down the lefthand branch. One function in each pair shows eye velocity when the target motion in the prior trial was to the right; the other when the target motion in the prior trial was to the left. Each mean is based on 80-100 observations. Standard errors were 1-2 min/sec and as high as 3 min/sec (5 min/sec with No Cue) only during the interval (0-200 msec) of most rapid eye acceleration.

prior work using the same sample duration (e.g. Kowler & McKee, 1987).

Eye velocity was also measured for the single, 200 msec interval beginning 200 msec before the onset of the horizontal component of target motion and ending at the onset of the horizontal component of target motion. The eye velocity for this 200 msec interval was taken as the slope of the straight line, fit by a least-squares criterion, to 20 consecutive eye position samples. Samples containing saccades or portions of saccades were discarded.

Saccades were detected from the original digitized records of eye position by a computer program that used an acceleration criterion. The criterion was determined by comparing the analog records of the eye position to the output of the program. Saccades as small as the microsaccades which may be observed during maintained fixation could be reliably detected by the algorithm.

RESULTS

In the absence of cues about the path of the moving target, the horizontal anticipatory smooth eye movements depended on the direction of the motion in the previous trial. Graphs of the mean horizontal eye velocity as a function of time (Fig. 3A) show that, before the horizontal component of target motion began, the eye moved smoothly to the right when the target motion in the previous trial was rightward and to the left when the previous target motion was leftward. The influence of the previous target motion persisted well after the horizontal component of target motion began. Eye velocity after the horizontal component of the target motion began was generally higher when the direction of the previous target motion was the same as the direction of the current target motion. This shows that the influence of the prior target motion was not restricted to the purely anticipatory epoch of the smooth response, but continued even after the target motion began.

If anticipatory pursuit resulted exclusively from a tendency to re-program the eye movements used in the previous trial, then the same pattern of eye velocities observed when no cue was available (Fig. 3A) should be observed in the presence of cues. This did not happen. Eye velocity depended on the availability of cues. With either the voice (Fig. 3B) or the barrier cue (Fig. 3C), anticipatory smooth eye movements

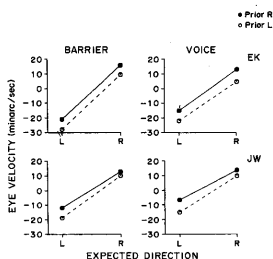


Fig. 4. Mean horizontal eye velocity during the 200 msec interval before the start of horizontal target motion (first entry of the moving target into the oblique branch of the Y-shaped tube) for expected motion to the left and to the right with *Barrier* and *Voice* cues. Top, EK. Bottom, JW. Solid symbols show eye velocity when the prior target motion was to the right; open symbols when it was to the left. Means are based on 80-100 observations. Standard errors are smaller than the plotting symbols.

in the direction of the expected future motion were underway 300 msec before the onset of horizontal target motion and became faster over time. There was little effect of the direction of motion in the previous trial. Performance was determined primarily by the current verbal or visual cue.

An estimate of the relative influence of the direction of motion in the previous trial and the direction of expected motion signaled by the cue was obtained by measuring eye velocity during a single interval beginning 200 msec before the onset of horizontal target motion and ending at the onset of the target motion (Fig. 4). The difference between mean eye velocity for the rightward and leftward cues was 20 to 37 min/sec. The visible barrier was more effective than the voice. In contrast to the strong influence of the cues, the effect of the direction of target motion in the previous trial was only 4-8 min/sec.

The trial before the immediately preceding trial also influenced anticipatory eye velocity, but not enough to overcome the effect of the cues. The effect of prior trials is shown in Fig. 5, which illustrates such "sequential effects" in the conventional manner (see: Falmagne et al., 1975; Luce, 1986). In these graphs eye velocity during the 200 msec interval before the start of horizontal target motion is shown for different

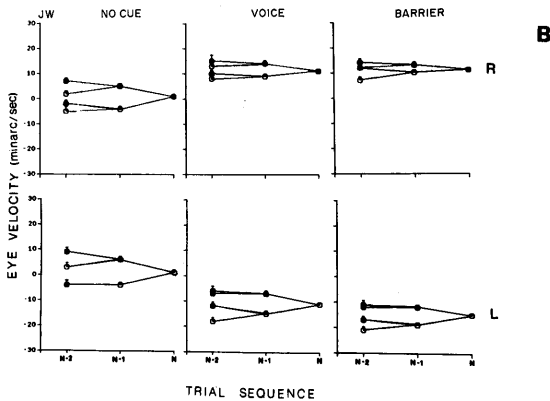
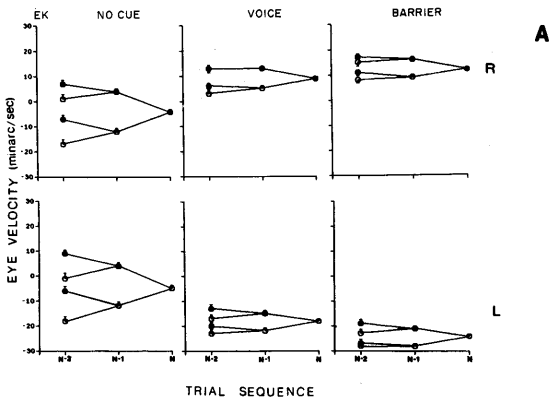


Fig. 5. *Caption on facing page.*

1- and 2-trial sequences. The graphs are read as follows: the rightmost point in each graph shows eye velocity averaged over all trials for a given cue (no cue, voice, or barrier) and direction of motion (right or left). Moving leftward across each graph, the trials are divided into 2 groups depending on the direction of target motion in successively earlier trials. The solid symbols denote that the direction of motion in the earlier trial was rightward, the open symbols denote leftward motion. So, for example, the 4 data points at the extreme left of each graph, moving from top to bottom, show the mean eye velocity averaged over all trials preceded by the sequence of: (1) two consecutive rightward target motions; (2) rightward target motion preceded by leftward target motion, (3) leftward target motion preceded by rightward target motion, and (4) two consecutive leftward target motions.

These graphs of sequential effects show that eye velocity was faster to the right when the previous motion was rightward, and faster to the left when the previous motion was leftward. Also, the graphs show that the effect of the motion in the previous trials weakened the further back into the past the motion occurred. Finally, the effect of the motion in the previous trials was weaker in the presence of the cues than when no cue was present—in other words, the bias to repeat the movement of the recent past was weaker when the cues allowed the programming of accurate anticipatory smooth eye movements in the actual direction of the future motion.

DISCUSSION

This study of pursuit of targets moving in randomly-selected, cued directions showed that anticipatory smooth eye movement depended on both the cognitive expectations about the direction of future target motion and on the recent past history of stimulus motions. Cognitive expectations were the more important of

these two influences because they overcame the influence of the immediate past and led to anticipatory smooth eye movements in the actual (cued) direction of the future target motion. I will first consider the implications of the effects of past history for theories of smooth eye movement. This will be followed by consideration of the implications of the effects of cognitive expectations.

The dependence of anticipatory smooth eye movements on the past history of target motions was shown in a previous study in which targets moved in uncued, randomly-selected directions (Kowler et al., 1984). The pattern of the sequential effects in the prior work was quite similar to the pattern observed in this study (Fig. 5). A major difference was that the velocity of the eye was slower in the prior study. Undoubtedly this was because target steps, rather than smooth target motions, were used in the prior study. The use of smooth target motions in the present study also made it possible to demonstrate that the effects of prior stimuli on smooth eye movement continued after the onset of smooth target motion.

The effect of the past history of target motions on smooth eye movements observed in the present experiment is consistent with several reports, beginning with Kowler and McKee (1984, 1987), which showed that smooth pursuit velocity is influenced by context, i.e. by the set of velocities that are presented during an experimental session (see also Lisberger & Westbrook, 1985; Tychsen & Lisberger, 1986; and Carl & Gellman, 1987). The effect of context is particularly prominent during the first few hundred milliseconds of pursuit when the velocity of the eye is biased toward the mean of the target velocities presented during the experimental session (Kowler and McKee, 1987). The effect of the past history of target motion, which was shown by the sequential dependencies observed in the present experiment and by the context effects observed previously, demonstrate that at least some aspects of pursuit are modified—and

Fig. 5. Mean horizontal eye velocity during the 200 msec interval before the start of horizontal target motion (the first entry of the moving target into the oblique branch of the Y-shaped tube) for different 1- and 2-trial directional sequences with either *No Cue, Voice Cues or Barrier Cues*. (A) Subject EK; (B) Subject JW. Negative eye velocities indicate leftward motion. The rightmost point of each graph shows eye velocity averaged over all trials for target motion to the right (top graphs in A and B) or to the left (bottom graphs in A and B). Moving leftward across each graph, trials are divided into 2 groups according to the direction of target motion on successively earlier trials; solid symbols denote prior rightward target motion; open symbols prior leftward target motion. Standard errors are smaller than the size of the plotting symbols unless shown by a vertical bar. The rightmost datum point in each graph is based on approx. 160–200 observations. Moving leftward across the graphs, the number of observations/point decreases by about a factor of 2 each time the trials are divided according to the direction of prior motion.

modified rapidly—to produce a smooth pursuit response that is appropriate for the target motion that is most likely to be encountered in the near future.

Important questions about the modification process remain. For example: (1) at what level, or levels, of information processing does it occur; (2) which signals, derived from the prior target motions or the prior oculomotor performance, are used to determine the appropriate modification; and (3) what is the optimal pursuit response sought by the modification process. One approach toward analyzing the modification process, which might ultimately help reveal the underlying mechanism, is illustrated by the stochastic model developed by Falmagne et al. (1975) to account for sequential effects in manual reaction time and fit to anticipatory smooth eye movements by Kowler et al. (1984). The model is based on the assumption of different preparatory states for each of the different possible stimuli. The state remains the same from one trial to the next whenever a response is correct; otherwise, the state may change. The model represents an adaptive process in the sense that effective responses are automatically maintained while ineffective responses tend to be modified. (See Luce, 1986, for a particularly clear and thoughtful review of the literature on sequential effects.)

Automatic adaptive processes, such as those described in the model of Falmagne et al. (1975), will be valuable for understanding smooth eye movements in the usual laboratory experiment, in which target motions are typically selected at random from some limited set of possible motions, and where any cues about the particular motion which had been selected are carefully removed. Under such conditions the past history of target motions is the only basis on which future motion can be predicted. By contrast, past history is far less important in the natural world, which is replete with all sorts of visual cues about the impending future motion of targets. For example, a standing animal is more likely to move forward than backward.

*There is one special case in which cognitive expectations might not override the effects of the past. This is the case in which a subject tracks the same target motion repeatedly, for a long period of time. In that situation over-trained responses might develop that are resistant to cues signalling a change in the pattern of motion. Pursuit is sensitive to practice (Kowler, Murphy & Steinman, 1978), but not enough is known about effects of long term training to predict how easily such responses could be overridden by expectations.

So, provided that you can determine the direction the animal is facing, it is very likely you will also know his direction of motion, when and if he moves. In natural situations, unlike the laboratory, an irreversible tendency to repeat the pursuit responses of the recent past would be dangerous because the past need not, and often does not, repeat itself. Patterns of target motion may change abruptly, or a new moving target may capture one's interest. Control by cognitive expectations allows anticipatory pursuit to deal with abrupt changes in target motion because abrupt changes can often be anticipated correctly by an observer who understands his environment and the significance of the cues it contains.*

The demonstration that anticipatory smooth eye movements depend on cognitive expectations shows that knowledge about the future path of target motion can be used to program an appropriate anticipatory response. The puzzle is to figure out how the observer's knowledge manages to influence a response that (unlike the smooth movements of the head or the limbs) cannot be initiated simply by an act of the will. A potentially useful way to view the influence of expectations is to suppose that the expectations combine with currently available sensory signals at a relatively high level of processing to create a single internal representation of target motion which provides the effective stimulus for smooth eye movement.

The suggestion that smooth eye movements are driven by a single representation of motion, combining sensory signals and expectations, portrays smooth eye movement as resulting from the operation of a single mechanism, working according to a single set of principles, rather than as a composite of separate and independent "anticipatory" and "reflexive" subdivisions. This view is consistent with recent treatments of the vestibulo-ocular response (Collewijn, 1989), vergence eye movements (Erkelens, Steinman & Collewijn, 1989) and saccades (He & Kowler, 1989), all of which offer evidence and arguments in favor of limiting, rather than expanding, the number of independent oculomotor subsystems. The control of all smooth eye movements by a single subsystem, whose input is a combination of sensory signals and expectations, avoids the need to resolve potentially conflicting outputs of different subdivisions with different goals.

In summary, by putting expectations about future motion in conflict with target motions of

the recent past I have shown that anticipatory smooth eye movements are not simply the result of tendencies to repeat previous smooth responses. Anticipatory smooth eye movements arise from true cognitive predictions about the future path of target motion.

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