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Cogito Ergo Moveo: Cognitive Control of Eye Movement

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ABSTRACT

Eye movements serve the needs of vision. They are used to bring images of eccentric targets to the central fovea, where visual acuity is best, and to keep images sufficiently stable on the retina to allow accurate visual processing. Most models assume that eye movements are driven by low-level sensory signals, such as retinal image position or retinal motion. This chapter shows that eye movements are driven by a higher-level signal, incorporating cognitive states, such as selective attention and expectations. By relying on high-level signals, eye movements become inextricably tied to concurrent cognitive activities, helping ensure that the eye will be directed to objects of current interest with little or no additional effort on the part of the observer. Cognitive control of eye movements, which is so prominent in human beings, may also be a useful principle to apply to the design of robots.

2.1   Introduction

The task of recognizing objects in natural visual environments is made enormously difficult by the existence of the fovea: the small (1.5 deg diameter), central, retinal region where visual acuity is best. The visual limitations created by the existence of the fovea make an effective pattern of eye movements essential if we are to be able to process visual information over extended regions of space. Eye movements are needed both to shift gaze to objects of interest, bringing the selected portion of the retinal image to the fovea, and to maintain stable gaze on selected targets as they, or as we, move about. Mobile artificial visual systems similarly plagued with a limited area of high-quality vision must also have appropriate means of controlling the movements of sensors in order to recognize objects in the surrounding visual environment.

Research on human eye movements over the past 40 years or so — going back to the beginning of the modern era of accurate instrumentation for eye movement recording — has documented an impressive array of oculomotor skills, which at

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first glance, would seem to be more than adequate to accomplish the tasks confronting us when we inspect the visual world. For example, when we try to maintain a stable line of sight on a stationary target, the standard deviation of eye position is only 2-3′ when the head is artificially supported, and increases to about 30′ when head movements are permitted (Steinman, Cushman & Martins, 1982). These values are small enough to keep the target image well within the foveal floor. If the target is set in motion at a constant velocity, smooth eye movements can follow along quite accurately, with eye velocity reaching values that can be as high as 90% or more of the velocity of the target (Collewijn & Tamminga, 1984; Kowler, Murphy & Steinman, 1978). If the target should change its position abruptly, or if we should take an interest in another object, a single saccadic eye movement can take the line of sight to the new position of the target with considerable accuracy (Collewijn, Erkelens & Steinman, 1988; Kowler & Blaser, 1995; Lemij & Collewijn, 1990). Saccades are not only accurate, but are also precise: Standard deviations of saccade offset error are only about 5% of the size of the saccade (Aitsebaomo & Bedell, 1992; Kowler & Blaser, 1995).

The oculomotor skills described above have been demonstrated in laboratory environments, usually containing a simple target (often a point of light) seen against a dark, or otherwise homogeneous, visual background while the head is stabilized by a biteboard or a chinrest. (Head support is required by most oculomotor instrumentation with sensitivity better than about 0.5 degree; for an exception to the general rule, see Steinman, this volume, Chapter 1.) Despite the obviously unnatural aspects of these testing conditions, the high degree of oculomotor skill that has been demonstrated would seem to be adequate, if not optimal, in more natural settings for providing a stable retinal platform for the subsequent analysis needed to recognize visual patterns. I say "subsequent analysis" because, according to most popular oculomotor models, oculomotor skill does not depend on high-level visual analysis, but instead precedes it. The control of eye movements is assumed to be a reflexive process based on fairly primitive signals — such as retinal position, retinal velocity, or vestibular signals — that are coded by low-level sensory mechanisms and transformed, more or less automatically, into the appropriate oculomotor commands (for a review of such approaches, see Carpenter, 1991; Hallett, 1986; Kowler, 1990). These commands are designed to minimize the putative "error" signals (e.g., retinal slip velocity or retinal position error) and create the retinal image conditions that are presumably ideal for vision. This is an attractive and popular story, but problems arise as soon as we begin to ask whether these mechanisms would be able to explain the performance of intelligent, mobile beings exploring richly patterned visual environments. When we ask such questions, we discover that effective oculomotor performance is not achieved by reflexive responses to sensory "error" signals. Instead, effective oculomotor responses require the involvement of cognitive processes, most notably, selective attention and expectations about the future motion or position of targets.

This chapter considers four examples of the cognitive control of eye movements. The first is the selection of the target for smooth eye movements from a crowded visual environment. The second is the effect of cognitive expectations about the

future motion of targets on smooth eye movements. The third is the role of cognitive planning in the programming of sequences of saccadic eye movements. The fourth is the selection of the target for saccades. These examples will all show that cognitive processes play important and unavoidable roles in the control of eye movements, both in the selection of the input and in the formulation of the oculomotor command. Their contribution is not tangential or ephemeral — that is, cognitive processes do not simply make minor adjustments to already-formed reflexive responses. If anything, the story is the reverse: sensory cues operate on a system that, to use Lashley's (1951) expression, is already "actively excited and organized" to respond in particular ways.

2.2   Example 1: Selection of the Target for Smooth Eye Movements

2.2.1   Smooth eye movements in the presence of visual backgrounds

Smooth eye movements are not under voluntary control. By this I mean that in the presence of nothing but stationary objects, observers (with the exception of a few very rare individuals) are not able to move the eye smoothly across the visual field. Similarly, if the visual field contains nothing but smoothly moving objects, the observer cannot keep the eye stationary. It is dragged along smoothly in the direction of the stimulus motion. This observation implies that whether the eye is relatively stationary or moving smoothly in one or another direction depends not on voluntary choice, but rather on what sort of stimulus motion is present in the visual field. This is consistent with traditional reflexive models of smooth eye movement in which stimulus motion is detected, coded, and automatically transformed into the appropriate smooth following commands.

How would such reflexive, smooth-following mechanisms behave in the typical visual environment, in which a variety of stationary and smoothly moving targets are present at the same time? There are several possibilities. One is that the stimulus motion signals originating from the most intense target, or from the target that happens to fall on the fovea, might dominate and constitute the effective stimulus for smooth eye movements. Alternatively, all the available motion signals might be pooled, causing the eye to track at a direction and speed determined by the average of all the signals. Both of these schemes are consistent with models, described above, in which stimulus motion is coded and automatically transformed into the smooth oculomotor command because for both schemes the smooth response of the eye is determined by nothing but the properties of the stimulus.

Neither of these schemes is correct. Observers do not track the motion of the strongest target, nor do they track the average of the available motions. They track the target they select.

Selective capacity was studied by Kowler, van der Steen, Tamminga and Collewijn (1984b). In this experiment subjects were confronted with two identical, full-field patterns of randomly positioned dots. One field was stationary and the other moved to the left at 1 deg/sec. The subjects were asked to maintain a steady line of sight on either one of the two fields while ignoring the other, superimposed field. The two fields were the same intensity and density (either 1 or 8 dots/deg^2) so that one field would not constitute a stronger stimulus than the other. The rest of the stimulus attributes were chosen to make the task as difficult as possible and, therefore, provide a good test of selective capacity. For example, cues, such as differences in depth planes of the fields, which might have aided the selection process, were absent. Also, the velocity of the moving field was set low enough so that dots would be seen clearly (Murphy, 1978; Westheimer & McKee, 1975). And, the denser field used (8 dot/deg^2) was sufficiently dense so that subjects could not isolate a single dot moving against a blank portion of the background. In the dense stimulus, dots from one field were continually passing across dots from the other.

Fig. 2.1(A) shows that smooth eye movements were as effective in maintaining the line of sight on the chosen field regardless of whether the field was presented alone (left-hand eye movement records) or with the superimposed background field (right-hand records). These records are representative of overall performance. The overall effect of the background on eye velocity amounted only to about 2–4% of the velocity of the moving field (Fig. 2.1(B–C)). Similar results were recently reported by Niemann, Ilg and Hoffman (1994).

How was the influence of the background field prevented? It was not done by the subjects choosing to track the dots at a particular location in the visual field because dots from each display were everywhere. (Too bad: This would have been an easy selection rule to incorporate into oculomotor models because sensory velocity signals could be tagged according to retinal location.) The influence of the background field could not have been prevented by selecting one or another stimulus velocity because the velocity the subjects perceived was very different from the velocity of the eye. Subjects perceived vivid induced motion of the stationary field when the moving background was present, but induced motion had no effect on the smooth eye movements, as can be seen in the upper right-hand graph of Fig. 2.1(A) (see also Mack, Fendrich & Wong, 1982). The remaining alternative is that the subjects chose what to track, and not how fast to move the eye. For such a selection process to work, the two fields must first be segregated into distinct "objects" (a process not yet understood with transparent fields such as these that move in the same apparent depth plane). Then, after the segregation occurs, motion signals from each field must be appropriately tagged so that only the selected set is permitted to reach the smooth oculomotor circuitry.

Understanding segregation and selection will not prove to be an easy task. To appreciate only one of the challenges, realize that the voluntary component of the selection process, the one that decides which object to track, is doing so based on motion information that is highly sensitive to the relative motion of the different fields (recall the strong impression of induced motion noted above). At the same
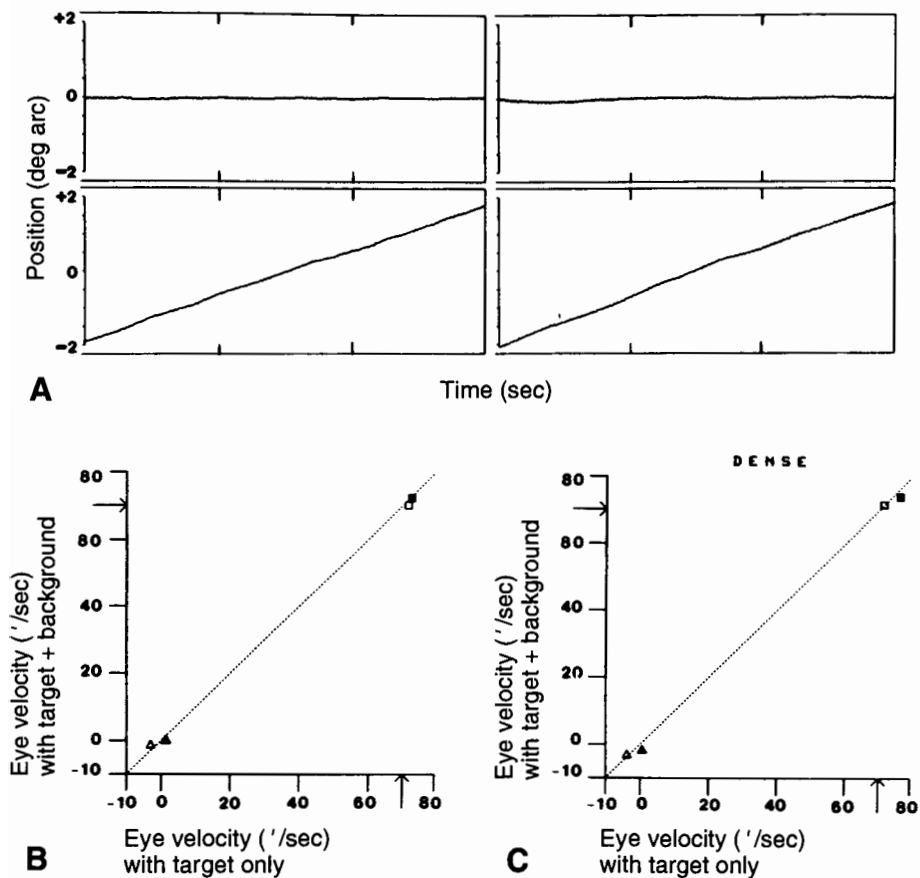
FIGURE 2.1. (A) Representative records of horizontal eye movements for subject RS under instructions to maintain the line of sight on the stationary (top 2 graphs) or moving (bottom 2 graphs) field of random dots. In the left-hand graphs, only one field was present; in the right-hand graphs, both were presented superimposed. Tic marks on the x-axis separate 1 sec intervals. Upward deflections of the eye trace indicate movements to the left. (B) Mean 21 msec eye velocities for subjects HC (open symbols) and RS (solid symbols) under the instruction to maintain the line of sight on the random dot field presented either alone (abscissa) or with the superimposed background field (ordinate). Triangles show eye velocity when the stationary field was the target, squares when the moving field was the target. The density of the dots was 1 dot/deg^2. Standard errors were smaller than the plotting symbols. Negative values on the axes indicate rightward velocities. The arrow indicates the velocity of the moving field. Velocities falling on the dotted diagonal line indicate no effect of the background. Velocities falling above the line, when the stationary field was the target, indicate smooth eye movements in the direction of the moving background. Velocities below the line, when the moving field was the target, indicate smooth eye movements slowed by the stationary background. (C) Same as (B) except that the density of the dots was increased to 8 dots/deg^2 (from Kowler et al., 1984b).

time, the smooth oculomotor system, which determines how fast the eye is to travel, is exposed to the same motion signals, but is blind to relative motion and instead uses velocity signals in retinal or in orbital coordinates. The remarkable thing is that two such very different processes, each using motion signals in different ways, work together so effectively to keep the line of sight on the chosen target.

2.2.2   The role of selective attention

Voluntary selection of the target for smooth eye movements is accomplished by allocating perceptual attention to the target. This was shown by Khurana and Kowler (1987), who asked subjects to make a perceptual judgment about the target being tracked, as well as about other, untracked stimuli. The stimulus display is shown in Fig. 2.2(A) (top). It consisted of 4 rows of letters, each moving to the right, with the velocity of the top and third rows twice that of the velocity of the 2nd and 4th rows. The subject's task was to keep the line of sight in the vertical gap between rows 2 and 3 while matching horizontal eye velocity to either the slower or the faster pair of rows. When the eye was near the middle of the display, the letters briefly (200 msec) changed to the kind of display shown in the bottom of Fig. 2.2(A), in which one numeral appears in the tracked, and another in the untracked, pair of rows. The subject had to identify and locate both numerals.

Fig. 2.2(B) shows the performance on the perceptual task. Each datum point shows the percent correct reports of identity and location for both the faster and the slower pair of rows. The filled circle shows performance when the faster pair was the tracked target, the open circle when the slower pair was the tracked target. Clearly, subjects were much better able to identify and locate the numerals appearing in the tracked target rows than in the untracked, background rows. The superior performance for the tracked target rows was not due to their lower retinal image velocity. Performance on the tracked target rows was better than performance on the untracked background rows even when retinal image speeds of target and background were equal (see Fig. 2.1(C)).

Finding superior perceptual performance for the tracked target meant that the same selective attentional decision serves both perceptual and motor systems. Even strenuous effort proved unable to dissociate two "attentions", one perceptual and the other motor. When the subjects — both experienced and highly-motivated — tried as best they could to track one set of rows and attend to the other, perceptual performance for the untracked rows did improve slightly, but at the cost of a shift in eye velocity toward the velocity of the untracked rows. In other words, they could not track one thing and attend to another. The best they could do in response to the instructions was to shift a bit of attention over to the untracked rows. Recently, links analogous to those Khurana and Kowler (1987) found between smooth pursuit and attention have been found to hold for saccades and attention (Kowler, Anderson, Dosher & Blaser, 1995).

These results have two consequences for the role of selective attention in active vision: First, it is known from numerous studies done over the past few years that instructions to attend to one or another location in the visual field can improve
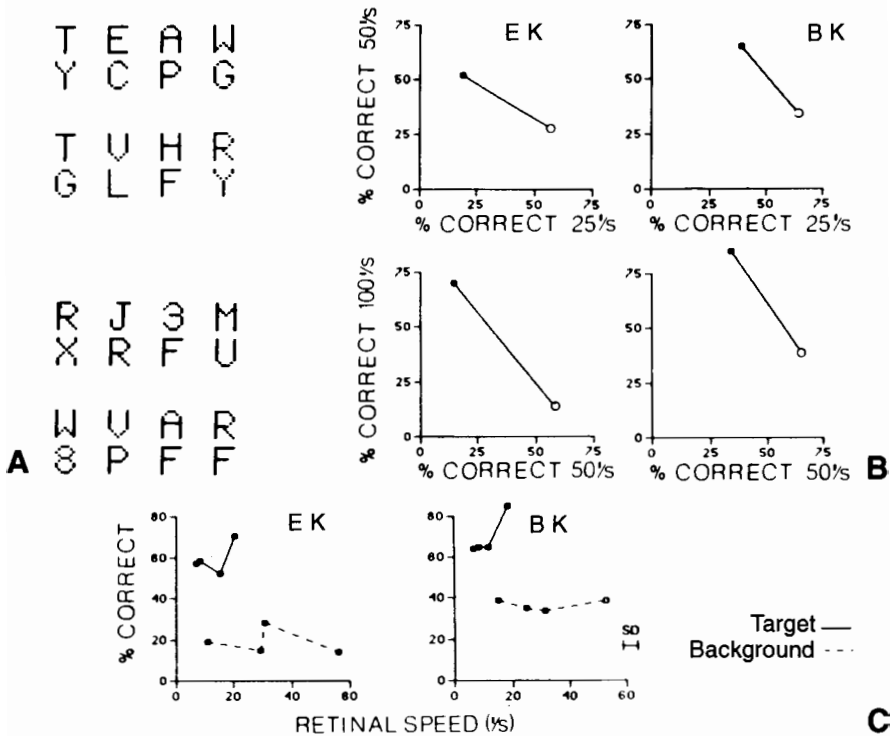
FIGURE 2.2. (A) The stimulus used in an experiment that measured smooth eye movements and selective perceptual attention at the same time. An array of 16 characters began moving horizontally at the beginning of the trial. The velocity of the characters in row 1 (top row) was the same as the velocity of characters in row 3. Similarly, the velocity of row 2 matched that of row 4. (Velocities were as follows: When one pair moved at 25′/sec, the other moved at 50′/sec; when one pair moved at 50′/sec, the other moved at 100′/sec.) The subject kept her line of sight in the vertical gap between rows 2 and 3 and tried to match horizontal eye velocity to one of the row-pairs (called the "target" pair). When the line of sight reached the approximate center of the display, the characters were replaced briefly (200 msec) by an array such as that shown in the bottom portion of (A). Note that one numeral is present in each pair of rows. In this example, a "3" is in row 1 and an "8" in row 4. Subjects had to identify both numerals and report the row in which they were located. (B) Visual search performance. Percent correct reports for the slower pair of rows is shown on the abscissa, for the faster pair on the ordinate. The open symbol shows performance when the slower pair was the target, the filled symbol when the faster pair was the target. Performance was always better for the target rows. (C) The same data points in (B) plotted as a function of measured retinal speed. Performance was always better for the target rows and retinal speed was largely irrelevant (from Khurana & Kowler, 1987).

the perceptibility of objects at that location at the expense of other locations — an example of just such an improvement was illustrated above. But the improvements are limited in degree. Attention, by itself, does not have large effects on visual thresholds or visual resolution. The data in Fig. 2.2(B–C), for example,

show that performance in the unattended, background rows was still substantially above chance levels. On the other hand, the effect of allocating attention to one or another moving stimulus on smooth eye movements can have quite profound visual consequences. In natural visual environments (as opposed to the laboratory, where we deliberately used slowly-moving targets so as to avoid degrading acuity) the retinal velocity of the unattended, hence, untracked, objects will often be quite high — tens or even hundreds of degrees per second — and, as a result, detectability and resolution of untracked stimuli will be poor. This means that the main consequence of selective attention on active vision will not be its direct effects on stimulus perceptibility, but rather its indirect effects on visibility, exerted through the attentional selection of the target for smooth eye movements.

The second implication of the results linking oculomotor selection to selective attention is a solution to the problem that perturbed Ernst Mach (1906/1959). Mach was fascinated by how he was able to walk forward, keeping his eye steadfastly fixed on his goal ahead of him, without the eye being dragged off by the flow of the retinal image motion on either side. We now know that Mach did this simply by paying attention to his goal. No special effort was needed to control the movements of the eye. It was sufficient to take an interest in what was before him.

2.3   Example 2: Predicting the Future Position of Targets

2.3.1   The effect of expectations on smooth eye movements

As described at the beginning of Section 2.2.1, the traditional view of smooth eye movements is that they are evoked by the smooth motion of the target across the retina. According to this traditional view, the retinal velocity of the selected target is encoded by the visual system and used to compute a smooth pursuit response that allows the eye to move at a velocity nearly matching that of the target, thus reducing retinal image motion to values low enough to support clear vision. Let us now turn to the processes that use the retinal velocity signals to determine the smooth oculomotor command.

In recent years it has been popular to revive an idea of Rashbass (1961), which was suggested earlier by Craik (1947), that the signal driving smooth eye movements is not retinal velocity by itself, but includes a signal representing the current velocity of the eye in the orbit. The combination of retinal image velocity and orbital eye velocity produces a signal that represents the velocity of the eye with respect to the head. This model has been popular because it can account for several oculomotor phenomena, most notably, the ability of some subjects to generate directed smooth eye movements with retinally-stabilized stimuli, such as an afterimage. (The pursuit of stabilized targets is actually more complex because smooth eye movements with afterimages and other retinally-stabilized targets are subject

to large individual differences that are not explained simply by the addition of a positive feedback signal; see Cushman, Tangney, Steinman & Ferguson, 1984.)

Are these reflexive models of smooth eye movement, in which responses are determined by the motion of targets in retinal or in orbital coordinates, adequate to guarantee retinal image velocities low enough to support clear vision, once the target has been selected? The research to be described below shows that they are not. Smooth pursuit eye movements follow the target accurately, but only if the target is moving in a simple, repetitive pattern, or moves in some pattern that can be predicted by the subject with reasonable accuracy. This suggests that knowledge of the upcoming target motion, and not simply the presence of a moving stimulus, is necessary to obtain an accurate response.

A vivid example of how smooth pursuit eye movements take advantage of knowledge of future target motion is contained in Fig. 2.3. This record was made while a subject was tracking a light-emitting diode moved by the experimenter. The top trace shows the target and the bottom trace the motion of the eye. The figure shows that the eye started moving smoothly several hundred milliseconds before the target began to move. The eye reached a velocity of about 50 deg/sec by the time the target started to move.

We have called the pursuit response observed before the onset of expected target motion "anticipatory smooth eye movement" (Kowler & Steinman, 1979a,b). Anticipatory smooth eye movements, such as those shown in Fig. 2.3, were observed
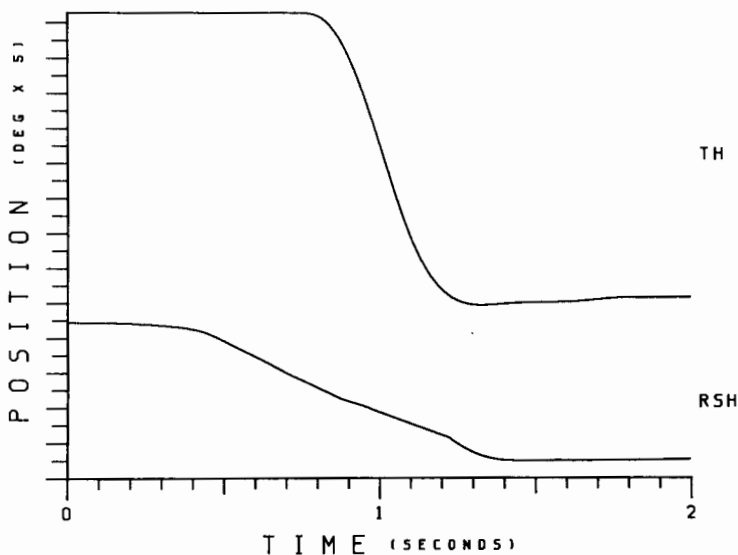

FIGURE 2.3. Movements of the right eye (RSH) of a subject tracking a single point target (TH) moved by an experimenter across the subject's visual field. The subject knew the direction of target motion but did not know when the target was to begin moving relative to the onset of the trial.

in the classical work of Raymond Dodge and colleagues more than 50 years ago (see Dodge, Travis & Fox, 1930). More recent investigators, confirming another one of Dodge's observations, noticed "anticipatory reversals" (Dodge's term) during the tracking of sinusoidal motion. These were episodes in which the eye would change direction ahead of the target (e.g., Stark, Vossius & Young, 1962; Westheimer, 1954; Winterson & Steinman, 1978). There were also several reports that pursuit of repetitive, predictable motions was far more accurate than pursuit of random motions, a result that not only implicated predictive processes in the control of pursuit, but also showed that linear systems models, in which responses to complex patterns of motion can be predicted from the response to sinusoidal motion, could not successfully explain pursuit (Collewijn & Tamminga, 1984; Dallos & Jones, 1963; Pavel, 1990; Stark et al., 1962).

Anticipatory smooth eye movements show that the motion of the target cannot be the only thing that drives the motion of the eye. In the past, modelers have tried to avoid the contribution of anticipation by assuming that anticipatory smooth eye movements were no more than learned habits formed after many cycles of tracking the same, periodic motion (e.g., Dallos & Jones, 1963; Westheimer, 1954). This attractive idea was not supported by several observations, including Dallos and Jones' (1963) own report of anticipatory reversals during the very first cycle of tracking — hardly leaving much time for learning. More recently, the habit hypothesis was contradicted by observations of anticipatory smooth eye movements preceding aperiodic (Kowler & Steinman, 1979a,b) and even randomly selected target motions (Kowler, Martins & Pavel, 1984a; Kowler & Steinman, 1981). When targets move in randomly selected directions, the eye moves in the direction determined by the subject's guess about the future direction of the target motion (Kowler & Steinman, 1981). The guess is determined by which target motions were seen or tracked in the recent past (Kowler et al., 1984a).

An example of anticipatory pursuit when targets move at randomly selected velocities is shown in Fig. 2.4, taken from Kowler and McKee (1987). Each graph shows average eye velocity as a function of time, with target motion starting at time 0 on the abscissa. There were 5 possible target velocities in each set, indicated by the horizontal lines on the graphs, and the subject did not know ahead of time which would be presented on any given trial. The target began to move at time "0" on the abscissa and stopped moving 1 second later. Notice that the eye started to move before the target and reached the approximate velocity of the target quite quickly (in about 250 msec). The interesting thing is that the initial pursuit responses were almost the same for all the targets in each set, regardless of which target velocity had actually been presented. These initial responses tended to be biased towards the mean velocity of the target set, that is, responses to the slower target velocities in the set were too fast, and responses to the faster target velocities were too slow. The eye velocity traces did not fully sort themselves out until several hundred milliseconds after the target started to move. (In this example, target direction was always leftward, but the outcome was the same when direction was selected randomly.)
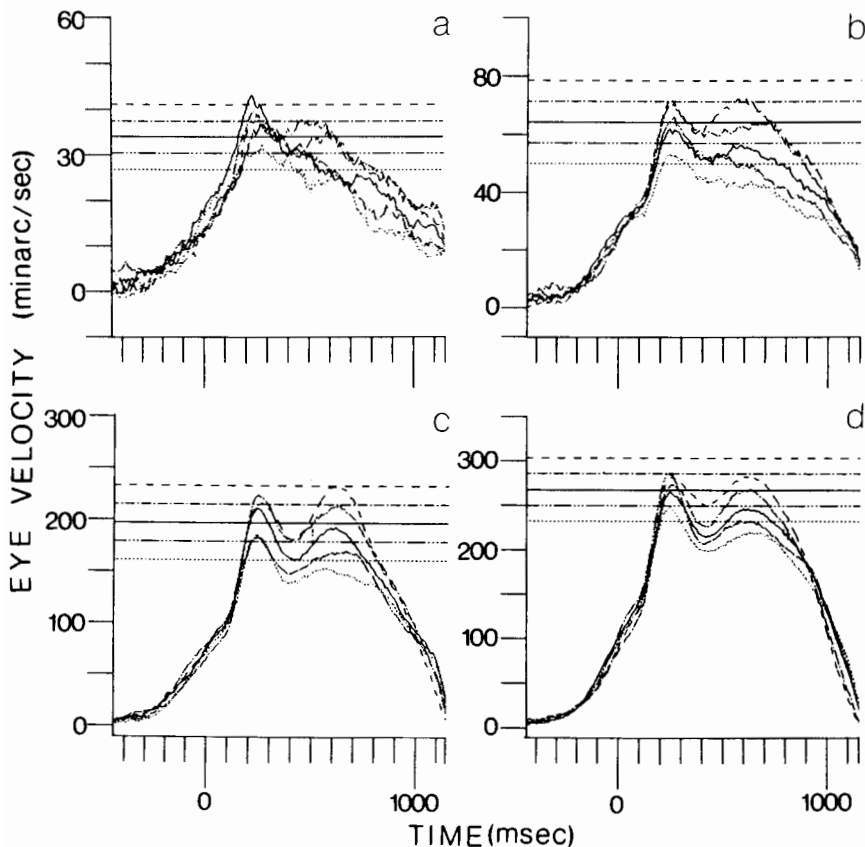
FIGURE 2.4. Mean 100 msec eye velocity for subject EK pursuing leftward target motions in 4 different sets of constant velocity target motion (A–D). Eye velocity is shown as a function of the midpoint of successive 100 msec intervals whose onsets are separated by 10 msec. Target motion began at 0 msec and ended at 1000 msec. Velocities less that 0'/sec indicate rightward motion. Scales are different on the ordinate of each graph. The horizontal lines indicate the velocities of the targets (from Kowler & McKee, 1987).

This example shows that the initial few hundred milliseconds of pursuit of randomly chosen stimuli is based primarily on the set of stimuli presented during previous trials of the experimental session. The contribution of the immediate stimulus motion to the initial pursuit is, by contrast, relatively modest. The modest contribution of the immediate stimulus motion to pursuit is not due to any deficiencies in sensory motion systems. Human beings can distinguish differences in target velocity of only about 5% with very brief (100–200 msec) exposures (Kowler & McKee, 1987; McKee, 1981), showing that precise information about stimulus motion is available in the brain after only about 100 msec. Smooth pursuit does not reach this level of precise discrimination until 600 or 700 msec after the
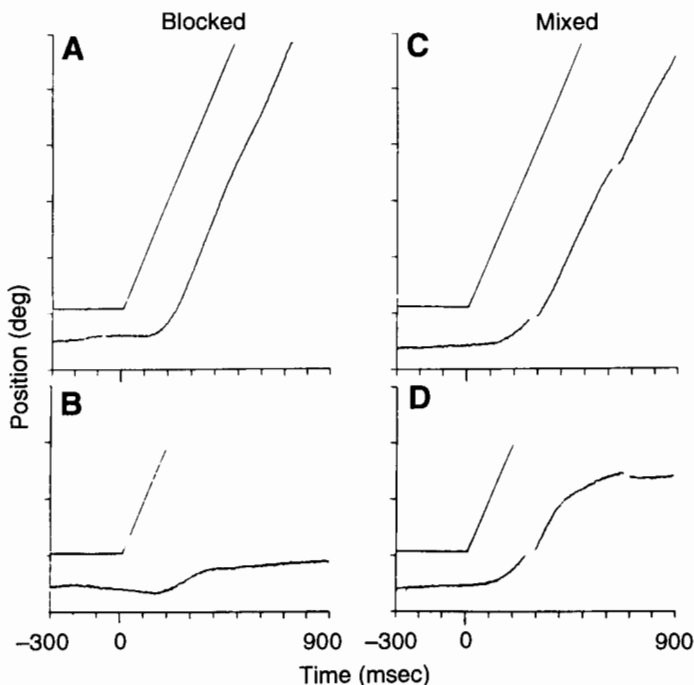
FIGURE 2.5. Representative eye movements (bottom traces) during smooth pursuit of 9.5 deg/sec target motion (top traces). On the left (Blocked) the duration was set to a constant value of either 1 sec (top graph) or 200 msec (bottom graph). On the right (Mixed) duration was selected randomly to be either 1 sec or 200 msec on each trial. Note the brisk initial pursuit of the longer duration and the poor initial pursuit of the shorter duration in the Blocked condition. The initial response took on a value roughly in between these 2 extremes when durations were randomly mixed. The gaps in the eye traces indicate when saccades occurred; the eye traces were shifted by amounts about equal to the size of these saccades.

target starts to move (Kowler & McKee, 1987) — well after pursuit reaches the approximate velocity of the target. Evidently, smooth eye movements do not rely on precise information about the immediate target motion to launch the brisk initial pursuit response. The initial response depends primarily on the expected velocity of the target, which is determined by the target motions tracked in the recent past.

Fig. 2.5 shows another example of anticipatory eye movements with randomly selected target motions. This figure contains representative records showing how pursuit velocity near the onset of target motion depends on how long the target is expected to continue moving (Kowler & McKee, 1987; Kowler, Steinman, He & Pizlo, 1989). In the left-hand graphs, the duration of target motion was known in advance. Brief durations (200 msec) led to a slow initial pursuit response (lower-left), while long (1 sec) durations led to a fairly brisk initial response (upper-left). This result, illustrating the effect of expected duration, shows that pursuit is not launched solely by the initial sweep of the target across the retina, but requires the expectation that target motion will continue into the future.

In the graphs on the right of Fig. 2.5, the short- and long-duration target motions were randomly mixed. This led to higher pursuit velocities for the brief motions and lower pursuit velocities for the long duration motions. So, randomizing duration did not remove the effect of expectations. It simply encouraged the development of a response intermediate between the one deemed most appropriate for each of the 2 durations in the stimulus set — a compromise that took past history into account in an attempt to avoid large errors during the initial part of pursuit.

These studies of pursuit with randomly chosen velocities and randomly chosen durations show that smooth eye velocity near the onset of pursuit depends on information derived from the past history of target motions. This appears to be a useful state of affairs because, left to itself, the smooth oculomotor subsystem evidently cannot incorporate new information about target motion fast enough to program an accurate, timely response that would bring the line of sight to the target before the target has moved to a very different location.

2.3.2 Past history vs. cognitive expectations of future target motion

It seems reasonable to use the past history of target motions to generate predictive smooth eye movements because there is little else on which to base predictions, at least in the laboratory. In the laboratory, where target motions are selected at random and any cues about the likely pattern of target motion are carefully removed, there is no information allowing prediction of future motion other than the pattern of motions presented in the past. The dependence on past history makes smooth eye movements prime candidates for adaptive models, in which various parameters of the smooth oculomotor system are continually adjusted on the basis of past stimuli or past performance to produce an optimal future response (Pavel, 1990).

Despite the value of taking past history into account, there may be more involved in the generation of smooth eye movements than just the adaptive responses made on the basis of prior events. The natural world, in contrast to the laboratory, presents a host of cues about the likely future motion of targets. For example, we can easily predict the motion of targets we control ourselves, such as the motion of objects we hold in our hands, or the motion of stationary objects in the environment relative to ourselves as we move about. In natural environments, the motion of objects we do not control often can be predicted on the basis of situational cues. For example, it is easy to predict the future motion of an animal based on the direction it is facing. Are smooth eye movements able to take advantage of such cues? In other words, are smooth eye movements generated on the basis of genuinely intelligent processes that take into account various sorts of symbolic cues about future motion? Or, are smooth eye movements blind to such cues and instead constrained to repeat successful pursuit responses made in the immediate past, even in the face of new information signaling that the pattern of target motion is about to change?

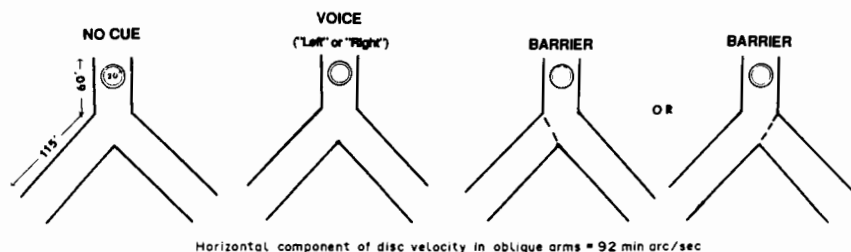Horizontal component of disc velocity in oblique arms = 92 min arc/sec

FIGURE 2.6. The stimulus display in an experiment comparing habits to cognitive expectations. It consisted of a stationary, inverted Y-shaped tube and an annulus which served as the moving target. The velocity of the target was 130'/sec. The target moved down the tube and continued at the same velocity down either the right-hand or left-hand oblique branch of the Y (horizontal component of velocity when the target was in either branch of the Y was 92'/sec). The target was equally likely to travel down either branch. The branch in which the target moved 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 left-hand or the right-hand branch (from Kowler, 1989).

To answer this question, target motions of the recent past were put in conflict with cues signaling a new pattern of motion in the future. The conflict was created by using the stimulus shown in Fig. 2.6, taken from Kowler (1989). It consists of a disc that moved downward inside an inverted Y-shaped tube. When the disc reached the junction of the oblique branches of the Y, it could travel down either the right-hand or the left-hand branch. The branch was chosen at random before each trial. In one experimental condition ("no cue"), the branch was not disclosed to the subject before the trial. In other conditions the branch was disclosed before each trial, either by a speech-synthesized voice saying "right" or "left", or by a visual barrier blocking access to one branch. What is of most interest is the velocity of the horizontal anticipatory smooth eye movements measured just before the target entered either branch.

Fig. 2.7 shows the average velocity of the eye as a function of time when there was no cue, a voice cue, or a barrier cue. The moving target-disc entered the oblique branch at time-0 on the abscissa of each graph. When there was no cue (Fig. 2.7(A)), anticipatory smooth eye movements depended on the motion in the prior trial — they were rightward when prior motion was to the right and leftward when prior motion was to the left.

Effects of the past on smooth eye movements were overridden by the symbolic cues (Fig. 2.7(B–C)). The eye began to travel in the direction of the expected motion at least 300 msec before the target entered either branch of the Y. Anticipatory smooth eye velocity was about 1/3 of the velocity of the disc by the time the disc entered the oblique branch.

The stronger influence of the symbolic cues, relative to the influence of prior trials, is also shown in Fig. 2.8. It shows the average velocity of the purely anticipatory portion of the pursuit response measured during the 200 msec interval before the start of horizontal motion. The cues produced a change in anticipatory
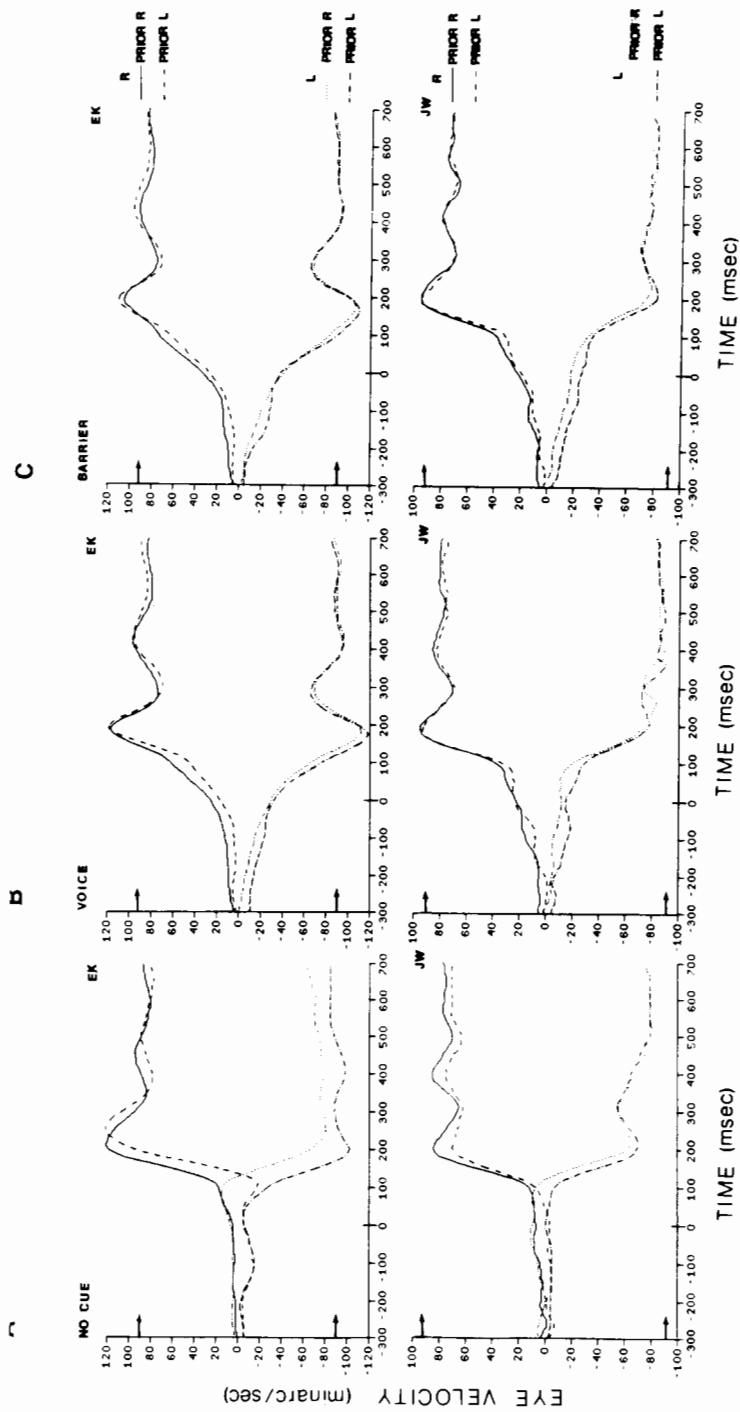
FIGURE 2.7. Mean horizontal eye velocity during successive 100 msec intervals (onsets 10 msec apart) as a function of the midpoint of the interval when either (A) No Cue, (B) a Voice Cue, or (C) a Barrier Cue about the direction of future horizontal target motion was given. Top graphs, EK; bottom graphs, naive subject 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 eye moved down the left-hand branch. One function in each pair shows eye velocity when the target motion in the prior trial was to the right; the other when motion in the prior trial was to the left. Each mean is based on 80–100 observations. Standard errors were 1-2′/sec and as high as 3′/sec (5′/sec with No Cue) only during the interval (0–200 msec) of most rapid eye acceleration (from Kowler, 1989).
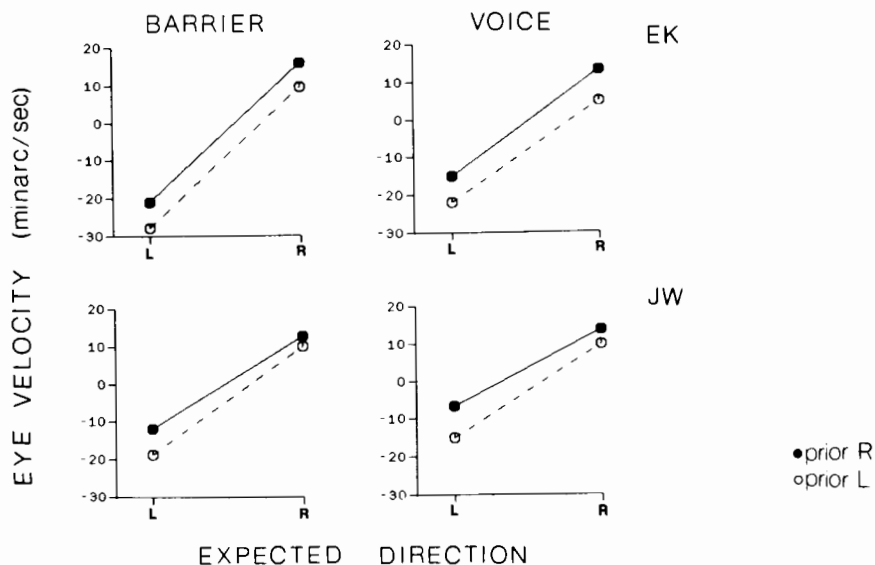
FIGURE 2.8. Mean horizontal eye velocity during the 200 msec interval before the start of horizontal target motion (first entry of the moving target into the oblique branch of the Y-shaped tube) for expected motion to the left and to the right with the Barrier and Voice cues. Top, subject EK; bottom, subject 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 (from Kowler, 1989).

eye velocity of as much as 40′/sec while the past produced changes of only about 5′/sec.

These results show that cognitive expectations drive anticipatory pursuit. How might expectations exert their influence? It seems implausible that cognitive expectations should operate by means of a separate neural pathway, existing alongside, and in continual conflict with, the "reflexive" pathways that carry the immediate retinal motion signals. A better arrangement would have smooth eye movements driven by a single representation of target motion. This representation would include not only the current motion of the target, but its motion path projected several hundred milliseconds into the future. A representation of this sort is ideal for motor control because it removes potential conflicts between retinal signals and expectations. It does, on the other hand, present interesting problems for those trying to understand the neural coding of visual motion. Not only is it necessary to study neural responses to motion that hasn't yet occurred, but it is, once again, necessary to distinguish the effect of motion signals on perception from the effects of motion signals on oculomotor responses. This distinction is compelled by this experiment because the eye began to travel in the direction of expected motion well in advance, but the subjects, nevertheless, perceived the path of the moving target accurately.

The research summarized here, as well as many prior experiments (see Kowler, 1990, & Pavel, 1990, for reviews), show that the contribution of expectations that accurately reflect the state of affairs in the physical world is essential for accurate pursuit. Pursuit of random motions is notoriously poor. Pursuit is best when the subject knows what sort of target motion to expect, either by means of appropriate environmental cues or by having enough time to figure out the future path of the target based on its motion in the recent past. If smooth eye movements are to confine retinal image velocities to levels that allow clear vision in the natural world, then the contribution of expectations is essential. The results summarized here show that our knowledge about the likely future motion of a target is sufficient to evoke the appropriate predictive response. No special types of target motions, or elaborate repetitive learning experiences are required. Cognitive expectations are an important component of the normal operation of pursuit. There is no evidence to support a separate, low-level, purely reflexive, smooth oculomotor subsystem in human beings.

The next 2 examples of the cognitive control of eye movement deal with saccades: the rapid, voluntary, eye movements we make to shift gaze between stationary targets.

2.4   Example 3: Planning Sequences of Saccades

Inspection of the visual world requires saccadic eye movements to bring eccentric visual details to the fovea, where visual acuity is best. Intuitively, we all have an idea about how this sort of thing proceeds, namely, we select something of interest to look at and move the line of sight (sometimes, rotating the head as well as the eyes) to the chosen target.

Oculomotor researchers studying this process have concentrated on a simple and convenient laboratory version of the natural task. In the laboratory version, a target point jumps from one location to another and the subject's task is to make a saccade to follow the target when it jumps. Most models of saccades have concentrated on the way that the assumed error signal — the eccentric position of the target on the retina — is used to program a saccade of the appropriate size and direction to bring the line of sight to the target. Natural scanning, however, involves processes that are not revealed by this conventional laboratory target "step-tracking" task.

In natural scanning, targets are stationary objects presented in the midst of irrelevant visual backgrounds. Instead of a single saccade to a target, natural scanning consists of continual sequences of saccades made to look from one stationary target to the next.

Zingale and Kowler (1987) studied the properties of patterns of saccadic sequences. Their stimulus was a 2-dimensional array of single points located at the vertices of a small (90' on a side) imaginary pentagon. On each trial, anywhere from 2 to 5 points would be presented. Subjects had to look at one of the points
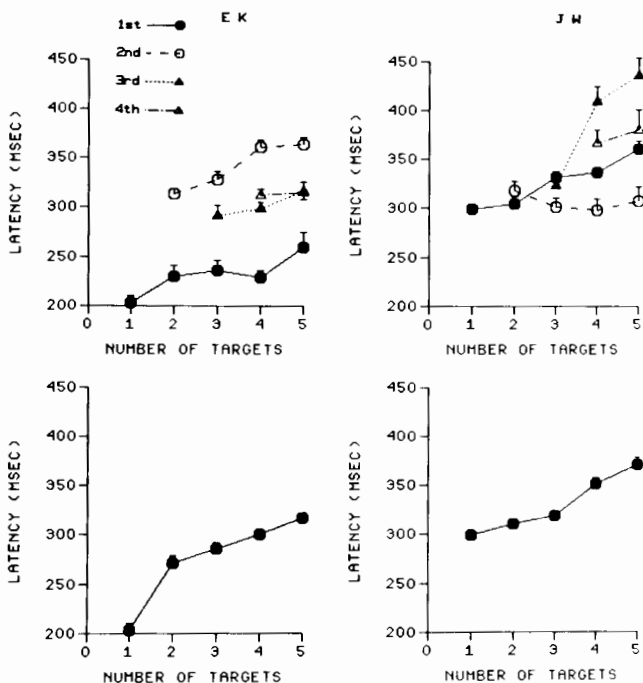
FIGURE 2.9. Top: Mean latency of the first through fourth saccades in the sequence as a function of the number of targets in a sequence for subject EK and naive subject JW. Bottom: Mean latency averaged over all saccades in the sequence as a function of the number of targets in the sequence. Vertical bars represent 1 SE (from Zingale & Kowler, 1987).

to start and, at a signal, begin to make a sequence of saccades to look from one visible target point to the next.

Fig. 2.9 shows that the latency of the first saccade of the sequence, and the time between subsequent saccades, depended on how many targets the subject was going to have to scan. This sort of pattern is by no means unique to saccades. Typewriter keypresses and spoken syllables have the same characteristic, as was demonstrated by Sternberg and colleagues (1978a, 1978b) in a study that provoked our study of saccadic sequences. We also found that the time between successive saccades in the sequence depended on the ordinal position of the target in the sequence (Fig. 2.10) — a property once again shared with typing and speech.

These results show that the timing patterns of saccadic sequences depend not only on the movement that is about to be programmed, but on the entire sequence of movements to be made. Sternberg and colleagues suggested that the increase in latency and in inter-response times with sequence length implies that motor programs for the entire sequence are prepared in advance, stored, and retrieved, as needed, during the execution of the sequence. They developed this model for typewriting and speech, but it could apply to saccades as well.
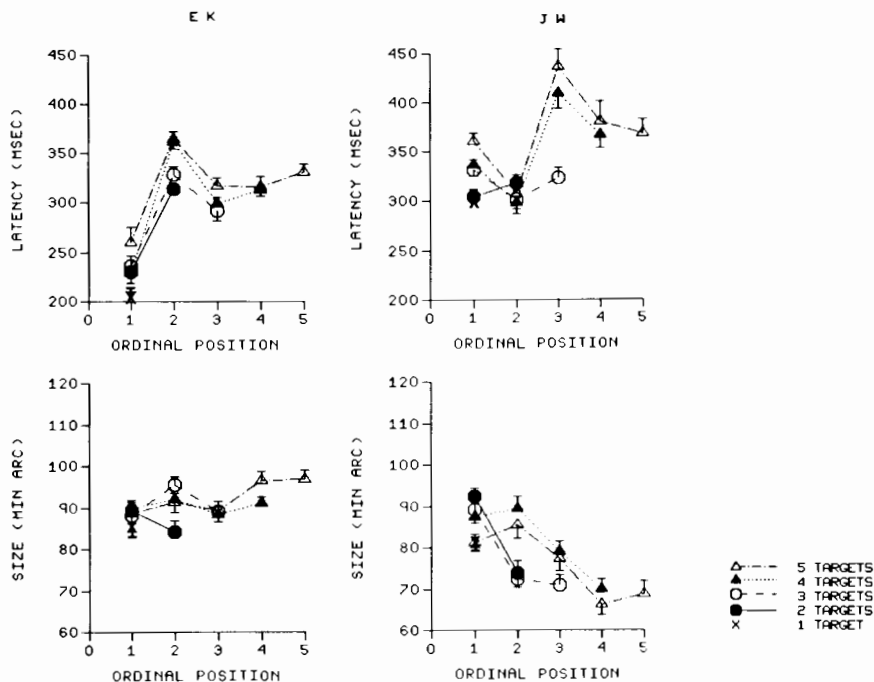
FIGURE 2.10. Mean latency (top) and mean size (bottom) as a function of the ordinal position of the saccade in the sequence for each of 5 sequence lengths. Vertical bars represent 1 SE. The distance between successive targets was 90' (from Zingale & Kowler, 1987).

Stored programs for saccades can be modified during the execution of the sequence. Zingale and Kowler showed this by removing all the target points just as the signal to begin execution of the sequence was given. Under these conditions, in which performance was based solely on remembered saccadic programs and remembered target positions, sequence length and ordinal position continued to determine the timing of saccades. Saccades sizes, however, were 20% larger than the separation of the targets. This shows that the visible targets do play a role in fine-tuning saccade size during sequence execution, perhaps by modifying parameters of pre-determined saccadic programs (see Rosenbaum, Inhoff & Gordon, 1984, who discuss the modification of pre-planned programs for a finger-tapping task).

What are the advantages of pre-planning sequences of saccades? The answer to this question is not obvious, given that visual targets are always available and it would seem reasonable to plan saccades only as needed, rather than in advance. Zingale and Kowler (1987) made two suggestions.

The first was that pre-planned sequences might be of value in freeing processing resources from the need to continually program saccades. This would make processing resources available for other tasks, such as making decisions about the

visual targets that were being scanned. This suggestion has gained plausibility recently because of demonstrations that saccadic planning consumes processing resources, that is, subjects cannot program a saccade to one target while simultaneously making accurate judgments about a target located elsewhere (Kowler et al., 1995).

The second suggested advantage for pre-planned saccadic sequences calls upon an idea of Lashley (1951). Lashley, who was interested in how animals integrate concurrent motor actions into effective patterns of movement, proposed that integration would not be successful if each individual response was triggered independently by a different sensory error signal. Lashley proposed instead the existence of a single internal clock, and a single spatial map, to be shared by concurrent voluntary motor activities. The temporal patterning of sequences of saccades is sufficiently similar to the temporal patterns of other voluntary motor responses (Sternberg et al., 1978a,b) to suggest that the temporal patterns reflect the reliance of all these activities on the same internal clock.

The idea that concurrent motor activities share the same temporal clock becomes more reasonable when you realize that saccades are rarely programmed in isolation. Concurrent voluntary movements of the head are involved as well. Zingale and Kowler inferred the involvement of concurrent commands to move the head when they noticed that the attempt to execute a very rapid sequence of saccades around the points of the pentagon produced striking discomfort of the neck muscles, as the subject fought to keep the head on the biteboard while rapidly looking from one point to the next. This result agrees with other observations that electrical activity in the neck muscles occurs during saccades, even when the head is artificially supported (Andre-Deshays, Berthoz & Revel, 1988; Berthoz & Grantyn, 1986). Others have noticed that allowing head motions during scanning improves performance by decreasing intersaccadic intervals (Kowler et al., 1992) and by increasing the velocity of saccades (Collewijn et al., 1992). All of these results suggest that the instruction to "look at an eccentric target" is, in fact, a more general instruction to orient to the target, moving both head and eyes at the same time. Perhaps, the temporal structure of the saccadic sequences Zingale and Kowler observed are glimpses into the works of the internal clock that sets up the rhythmic patterns used to coordinate the concurrent motions of the head and eye made while we scan natural environments.

2.5   Example 4: Saccades to Selected Targets in the Presence of Irrelevant Visual Backgrounds

The capacity to maintain the line of sight on a chosen target with smooth eye movements, without influence of irrelevant, unattended background stimuli, was the first example of the cognitive control of eye movements illustrated in this chapter. Saccades need this capacity as well, if we are to succeed in aiming the line of sight at targets of interest.

There has been some controversy about the selective capacity of saccades in the oculomotor literature. This controversy is due to studies in which failures of selection were inferred from experiments that required subjects to make saccades as quickly as possible, even if this meant they had not yet ascertained the true location of the target. These studies showed that the line of sight would often be displaced in the direction of irrelevant background stimuli. This led to suggestions that there are automatic sensorimotor "averaging" processes that take the line of sight to the "center of gravity" of an entire stimulus configuration (Coeffe & O'Regan, 1987; Findlay, 1982; Ottes, van Gisbergen & Eggermont, 1985). He and Kowler (1989) questioned the existence of such "centering tendencies" by doing an experiment in which the probability of a target appearing in one or another location was varied. An irrelevant, nontarget stimulus always appeared in the other location. He and Kowler (1989) found that the endpoint of the short-latency saccades was displaced toward the more probable location (Fig. 2.11, top graphs), a result suggesting that observed "centering" tendencies do not represent automatic sensorimotor averaging, but instead represent a high-level search strategy used to program saccades when the true location of the target is still unknown.

Subsequently, He and Kowler (1991) found that subjects were able to aim saccades accurately to designated places within an eccentric target form (a triangle), provided that there was no uncertainty on the part of the subject about where he was supposed to look. Such saccades were as accurate and as precise as saccades directed to single points at the same eccentricities. Saccades that were directed toward the form as a whole, rather than to a particular place within it, did tend to land in the same location each time, which was near the center-of-gravity.

These results shed some light on the process by which a saccadic endpoint is computed when the stimulus is a spatially-extended form, rather than a single point of light. It would seem that "averaging" of sorts might occur, but not an automatic averaging of all the elements in the visual field, as prior workers (see above) have suggested. Rather, "averaging" would operate only on those visual signals that were selected (i.e., attended) by the observer. It would seem that the visual position signals reaching the saccadic circuitry, like those reaching the smooth oculomotor circuitry, must first be subjected to a relative weighting by means of selective attention. Perhaps the same attentional decision that serves perception and smooth eye movements also serves to determine the target region for saccades.

2.6   Summary and Conclusions

The research described in this chapter has shown that:

(1) The target for both smooth eye movements and saccades is determined by spatially-selective attention that decides which signals are to reach lower-level oculomotor circuitry. The selection operates on representations of objects in the environment, rather than on simpler, isolated sensory cues — that is, you choose
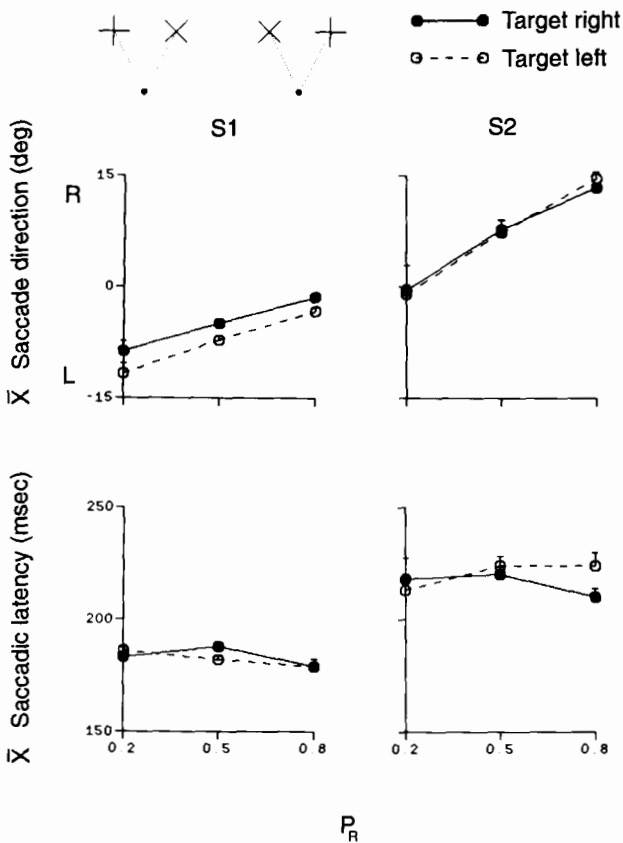
FIGURE 2.11. Mean saccadic direction (top) and latency (bottom) as a function of the probability (Pr) of the target appearing on the right for 2 naive subjects (S1 and S2). The target was either on the right (solid lines) or on the left (dotted lines). Standard errors were smaller than the plotting symbols except where noted by vertical bars (from He & Kowler, 1989).

what to track, not a particular stimulus velocity or eye velocity. How these representations of objects are then decomposed into the isolated velocity or position signals needed to compute the appropriate oculomotor commands is a major research problem, perhaps one as challenging as determining how the object representations were formed in the first place.

(2) The motion signals that guide smooth eye movements include projections of the expected target motion several hundred milliseconds into the future. In a somewhat analogous way, programs for saccadic eye movements also depend on an internal representation of future events, specifically, on a stored plan for an entire sequence of saccades. These phenomena show that effective oculomotor programs are based on representations of the visual world that encompass not only its current state, but its predicted state well into the future.

Each of these points shows that cognitive processes are inextricably tied to the oculomotor programming — they are not switched in and out, leaving the observer fluctuating between "reflexive" and "intelligent" modes of oculomotor control. The main advantage of cognitive control would appear to be the automatic and effortless linkage of oculomotor activity with other, concurrent visual, motor and cognitive events. For example, no special effort is required to select a target for smooth or saccadic eye movements. The line of sight will be drawn toward the target of current interest. Similarly, the knowledge we have about a target's future motion, or the plans we make about how we wish to move about in the environment, will find their way into the oculomotor circuitry without us having to activate any special mode of cognitive control to override low-level reflexes. This link between oculomotor commands and ongoing cognitive processes lets us avoid the need for special effort when we wish to choose targets and program appropriate eye movements. It also ensures that the line of sight is most likely to land on, and remain on, the target of interest.

Perhaps cognitive control will prove to be useful only in multi-purpose beings such as ourselves, who must see and think as we move eyes, head and limbs about in the environment, with all of these activities having to proceed in a coordinated fashion. I suspect, however, that the problem of coordinating diverse actions is as pressing in robots, who must, as we must, select targets of interest from cluttered backgrounds, and program motor responses early enough so that sensors or arms arrive at the selected targets before their location has changed. There are at least two lessons that may be learned from the way human beings accomplish these goals that may prove valuable in designing robots.

The first is that effective motor performance is not achieved by trying to expand sensory capacities or by trying to reduce motor programming time, but rather by taking advantage of the ongoing intelligent processes of selection and prediction — the same processes that are occurring as we (or the robots) are making decisions about the objects in the environment.

The second lesson is that it may be valuable to dissociate the visual representations that guide eye movements from those that determine percepts. We saw two examples of the dissociation in this chapter. One was the insensitivity of smooth eye movements to perceived induced motion. The second was the difference between the perceived path of a moving target and the predicted path that is used to guide the smooth eye movements. Similar dissociations between the visual representations used to organize perception and to guide eye movements have been reported before in the comparison of perceptual and motor localization of the position of a target (Hansen, 1979; Hansen & Skavenski, 1977; Skavenski, 1990; Sperling, 1990) and, also, in the comparison of the stimuli driving binocular vergence eye movements and the stimuli responsible for the perception of motion-in-depth (Collewijn & Erkelens, 1990; Erkelens & Collewijn, 1985). In both of these cases, percepts depended on the position or the motion of targets relative to visual backgrounds, while eye movements depended on the position or the motion of targets relative to the observer. Distinguishing two kinds of visual representations, one for perception and the other for motor control, perhaps at very early stages of processing,

may prove to be useful in designing a robot who, like us, must confront the dual challenge of controlling its own movements effectively while at the same time recognizing objects in the environment.

2.7   References

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