Eye movements and their role in visual and cognitive processes
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CHAPTER 1

The role of visual and cognitive processes in the control of eye movement

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1. Introduction

1.1. Theme

The understanding of human eye movement has always seemed a natural prerequisite to the understanding of many visual, perceptual and cognitive processes. This is because eye movements determine the position and the velocity of the retinal image. An accurate interpretation of performance on any visual task requires that we either know what the eye is doing or make some reasonable assumptions based on known oculomotor characteristics. So, the better we understand the processes that determine human eye movement, the better will we be able to predict the state of the retinal image in a wide variety of circumstances.

This chapter examines some of the visual and cognitive processes that determine human eye movements. This is an ambitious goal considering that we lack a comprehensive explanation of human oculomotor performance. A major obstacle has been the difficulty of finding invariant relationships between characteristics of the visual stimulus, such as the position or the velocity of the retinal image, and the movements of the eye. Many different eye movement patterns can be observed with the same visual stimulus. Similarly, large changes in the visual stimulus often have no systematic effect on the eye movements. Obscuring these sought-for invariant stimulus-response relationships are the 'cognitive' factors – choice, effort, selective attention, expectations and memory.

To appreciate how serious a challenge cognitive factors present for the development of theories, consider what has happened in the study of visual perception. The most complete theories have been those which account for the relationships consistently observed between a psychophysical report (the detection of the bars of a grating, for example) and the characteristics of the stimulus (the contrast and the spatial frequency of the grating). But as soon as investigators begin to consider the aspects of perception more susceptible to cognitive activity, such as the role of selective attention or past experience in the recognition of an alphanumeric character, consensus about theories disappears. Moreover, the prospect of relating the psychophysical observations to currently available physiological data becomes remote.

Those who study human eye movements, like those who study visual recognition, are confronted with the problem of incorporating the influence of both stimulus variables and cognitive factors. Unfortunately, the solution to this problem that has been adopted too often in oculomotor research has been not to deny cognitive influences, but rather to ignore, minimize or postpone their consideration in an attempt to develop models of the supposedly simpler lower-level processes, namely, sensorimotor relationships and their underlying physiology. I will argue in this chapter that such approaches will

not work. We will not succeed in understanding eye movements unless cognitive factors are incorporated from the outset. Selective attention, expectations and memory play essential and inescapable roles in the programming of eye movements. Their contribution will be shown to be pervasive and effortless, becoming more apparent the closer the laboratory situation approaches that of the natural world. No special procedures are needed to elicit cognitive contributions: indeed, if anything, special procedures are often devised in the hope of keeping them at bay. Even the types of eye movement that are insensitive to willful, deliberate control (smooth pursuit, for example) are nevertheless unavoidably tied to what we expect and to what we attend.

Pervasive, effortless, cognitive influences make trouble for the prevailing models, which typically envision eye movements as under the control of passive, mechanistic processes, producing automatic reactions to external events. The picture to be painted here is that of an active oculomotor system, which creates a purposeful pattern of action based on the internal states of the organism. The 'internal states' might include representations of selected portions of the immediate visual environment, as well as representations of relevant memories, plans and beliefs. The central thesis of the chapter is that we have to understand the role of cognitive processes in order to devise theories of oculomotor control that capture the essence of how eye movements work in the natural world.

1.2. Organization of the chapter

This chapter will describe some of the visual and cognitive processes which determine three kinds of eye movement: eye movements of maintained fixation, smooth eye movements, and saccades. Vergence is reviewed in the chapters by Collewijn and Erkelens, and certain phenomena related to vestibularly driven eye movements in the chapter by Steinman and Levinson. The chapters by O'Regan, Pavel, Skavenski and Viviani also contain material relevant to the programming of saccades and smooth eye movements. This chapter deals mainly with human oculomotor performance, and with attempts to relate the performance to the properties of the visual stimulus, and to what the subject perceives, knows, wants, expects, attends to and remembers. Performance of other species and neurophysiological results, with a few exceptions, will not be described.

I have tried in many places to take a somewhat historical perspective, in which the background, as well as the contemporary status, of various lines of research is presented. This was done in an attempt to portray present work in the context of how we got to where we are today, and to show that many contemporary ideas (including ideas about cognitive influences) are, in fact, revivals of themes developed by oculomotor pioneers – Dodge and Ter Braak, in particular – during the first half of the century.

There have been several recent discussions of the relative contributions of cognitive and stimulus factors to eye movement control. See Berthoz and Melvill Jones (1985) and Collewijn (1989) for discussions of vestibularly driven eye movements, Erkelens et al. (1989a,b) for discussion of vergence, and Robinson (1986), Steinman (1986a) and Steinman et al. (1990) for different views of the contribution of the 'systems' approach to oculomotor research. There are also classical treatments of the role of cognitive processes in motor activity in general, rather than eye movements in particular. Dodge (1931), Craik (1947) and Lashley (1951) are particularly interesting, thoughtful and influential treatments of motor control, all of which, for a variety of different reasons, reject mechanistic approaches in favor of central control and organization.

2. Maintaining stable gaze

This section discusses the eye movements made while we attempt to look steadily at a stationary target. This is often referred to in the oculomotor literature as 'maintained fixation'. I am starting out with a discussion of fixation for two reasons. First, it is useful to know the characteristics of these eye

movements in order to specify the retinal image conditions that typically confront our visual and cognitive systems. Second, the studies of fixation offer a relatively simple situation in which to search for, and model, invariant relationships between the retinal stimulus and the oculomotor response. The lessons learned from the studies of fixation may prove quite valuable when we come to the task of understanding the eye movements used to look about or to follow moving targets. These tasks, however, demand attentional resources and sophisticated decisions, and so, clearly, performance becomes harder to interpret. So let us start with something which seems to be relatively simple, namely, the eye movements made to look at a single stationary target.

2.1. Maintained fixation of stationary targets is extremely stable when the head is firmly supported

Studies of the eye movements during maintained fixation of stationary targets, the first eye movement studies to employ highly accurate recording techniques, began in the early 1950s. These studies were inspired by a prediction of the 'dynamic theories' of visual acuity (e.g., Jones and Higgins, 1947; Marshall and Talbot, 1942). The dynamic theories proposed that high-frequency oscillations of the retinal image provide the basis for a neural sharpening process, which computes the average position of a single visual feature with a precision better than the width of a single cone. Before 1950 there were long-standing disagreements about the true characteristics of fixational eye movements, so no one knew whether the image actually moved around enough to provide the kind of rapidly changing visual input that the averaging process needed. (See Steinman and Levinson's chapter for further discussion of the dynamic theories; and Ratliff and Riggs (1950) for a review of the disagreements in the early studies of fixational eye movements.)

To resolve these disagreements a technique for making accurate measurements of eye movements was developed independently by Ratliff and Riggs (1950) and by Ditchburn and Ginsborg (1953) (see also Yarbus, 1967). They made cinematographic records of a small spot of light reflected from a plane mirror mounted on the surface of a custom-fitted scleral contact lens. This method, known as the 'contact lens optical lever', could detect eye rotations of well under a minute of arc. By virtue of the use of a plane mirror, the recordings were insensitive to translational movements. Insensitivity to translations is important and deserves brief discussion here. Contamination of recordings by translational movements, a property of corneal reflection or diffuse reflection monitors, limits the accuracy with which one can estimate the true motion of the retinal image from the eye recordings. This is because translations and rotations have different effects on the retinal image. For example, consider an extreme case: only eye rotations change the position of the retinal image of a very distant target; translations do not. The size of the eye rotation is equivalent to the angular motion of the retinal image when targets are very far away, and approximately equivalent (within 5%) when targets are as close as 0.1 m (see Ratliff and Riggs, 1950; Steinman et al., 1982; Ferman et al., 1987; and the footnote on p. 10 for discussion of the sources of error in estimating retinal image motion from measurements of eye rotation.) Accurate inferences about the motion of the retinal image from recordings of eye movements can be made when recordings show pure rotational movements, uncontaminated by translations. It might seem that one way to remove translations, regardless of the type of eye monitor used, is to hold the head firmly in place. This technique will be only partially successful because translations cannot be prevented completely, even with firm head support (see Skavenski and Steinman, 1970; Cornsweet, 1976, for further discussion). The contact lens optical lever method of recording eye movements offers a better solution because its output is insensitive to translations. Moreover, by using a distant target any translations that might occur will not change the position of the retinal image. Other eye movement monitors, developed more recently, have adopted different solutions to minimizing or eliminating translations from the

measurements (see, for example, Cornsweet and Crane, 1973; Skavenski et al., 1979; Steinman and Collewijn, 1980; Ferman et al., 1987; and Steinman and Levinson's chapter).

The contact lens optical lever requires the head to be firmly supported in order to keep the eye within the very limited recording range of the instrument (± 5′). The consequences of head support for interpreting the visual significance of the stability of gaze did not become apparent until well after the pioneering studies of maintained fixation had been done, and will be discussed in section 2.3.

The studies of maintained fixation in the 1950s described a fairly stereotypical, and by now well-known, pattern of eye movements when subjects fixated small, stationary targets, such as points of light, or thin lines or cross-hairs. The eye movement pattern consisted of a high-frequency (30–80 Hz), small-amplitude (15 sec arc) tremor, which was superimposed on low-frequency (2–5 Hz) slow oscillations whose amplitude was about 1′–3′. Interrupting these movements at intervals ranging from 0.2 to several seconds were small (5′–10′) saccades (microsaccades). An example of this 'typical' fixation pattern is shown in Fig. 1a. The immediate significance of these findings was that the amplitude of the high-frequency tremor, less than the width of a single cone, was clearly too small to play any important role in visual acuity, in contrast with the proposals of the dynamic theorists.

The most striking characteristic of maintained fixation was its remarkable stability. Ratliff and Riggs (1950) estimated that the "total movement (of the eye) over a period of 3 to 4 seconds is 10 to 20 min of arc". A similar conclusion was reached by Ditchburn and Ginsborg (1953). To appreciate how small a region this is, realize that the 'bouquet of central cones', the central retinal area described by Polyak (1941) as containing the 'most delicate', slenderest cones, is 20′ in diameter.

These early estimates of fixation stability were extended in later work. Nachmias (1959), for example, studied the 2-dimensional properties of fixational eye movements. This required mounting the plane mirror so as to be normal to a stalk on the contact lens that was parallel to the line of sight. The earlier method of resting the plane mirror on (or embedding it into) the surface of the contact lens (Ratliff and Riggs, 1950; Ditchburn and Ginsborg, 1953) was fine for horizontal movements, but confounded vertical eye rotations with torsions. Nachmias (1959) described the 2-dimensional stability of the line of sight by means of a bivariate contour ellipse area, which represented the area in which the line of sight would be located 68% of the time. The bivariate contour ellipse areas, determined from random samples of eye position taken during 30-s fixation trials, was about 60–100 min of arc^2. This would be equivalent to standard deviations of 3′–4′ on either the horizontal or vertical meridian, assuming no correlation between the horizontal and vertical eye movements.

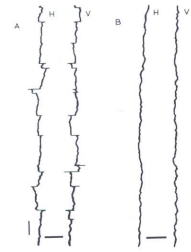

Fig. 1. (A) Horizontal (H) and vertical (V) eye movements of a subject fixating a point of light in darkness. Records were made with a contact lens–optical lever. The record begins at the top. The horizontal black bar at the bottom represents 15 min arc, the vertical bar a 1 s interval. The abrupt changes in eye position are saccades. (B) Same, except the subject has elected not to make saccades. (From Steinman et al., 1973)

There was also evidence that the stable fixation described above for relatively brief intervals (less than about 30 s) would also be maintained for far longer periods. Steinman (1965) found that the mean eye positions were almost the same across sets

of trials (the standard error of the trial mean eye positions was only 2′–3′), leading him to conclude that the fixation target was consistently placed within the same 10′ retinal region.

The estimates of fixation stability, described above, were remarkably similar to those obtained by Barlow (1952), who used a recording technique that was, in principle, sensitive to translations. Barlow photographed a droplet of mercury placed on the limbus. Translations of the head were minimized by having subjects lie on a stone slab with their heads wedged tightly inside a rigid iron frame. Barlow asked the subjects to indicate when they believed that they were actually looking at the target. The standard deviation of eye positions at the beginning of such intervals, corrected for the estimated contribution of head movements, was only about 5′.

The fixational eye movement pattern discovered by the scientists working with highly accurate eye movement monitors in the 1950s and 1960s had several implications:

First, stable fixation was a boon to psychophysical research. It meant that reliable placement of the retinal image could be achieved simply by asking subjects to look at a suitable fixation target. Even the choice of a suitable target proved to be easy. Neither the stability of fixation nor the mean position of the eye depended in any important way on the color of the target or on its luminance (Steinman, 1965; Boyce, 1967b), provided that luminance remained above absolute foveal threshold (Steinman and Cunitz, 1968). The size of the target (Steinman, 1965; Rattle, 1969) and its shape (Murphy et al., 1974) did not have much effect either, at least for targets confined to the fovea. Stability suffered, but only modestly, with targets as large as 30 deg in diameter (see Fig. 2) (Sansbury et al., 1973). Fixational eye movements were as stable for naive, inexperienced subjects as they were for the experienced subjects (Winterson and Collewijn, 1976). So, for all practical purposes, concern that sloppy eye position control would send a visual stimulus far from a small, central retinal position could be safely dismissed.

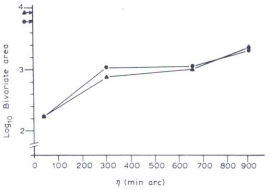

Fig. 2. Inverse fixation stability (log bivariate area) of two subjects who were instructed to maintain the line of sight in the center of target configurations of various sizes. Targets were either a single, homogeneous disc (1.3° diameter), or two of the same discs separated horizontally by 21.8°, or four of the same discs separated horizontally and vertically by 10, 21.8 and 29.5°. Data are plotted as a function of the distance between the target and the line of sight. The arrows on the ordinate show log bivariate area for each subject in complete darkness. (From Sansbury et al., 1972)

The second implication of the studies of fixational eye movements was that the eye, although quite stable, was obviously not completely stationary. The small amount of wandering of the image proved to have profound visual consequences. Abolishing all image motion, by moving the stimulus in the same spatiotemporal pattern as the eye, led to the fading of the stimulus within a few seconds (Ditchburn and Ginsborg, 1952; Ratliff et al., 1953). The fading of stablized images and more generally the role of retinal image motion in vision is discussed extensively in Steinman and Levinson's chapter.

The third implication of the studies of fixation in the 1950s was methodological. These studies introduced into eye movement research the highly accurate and precise recording techniques and the procedures for testing performance under the rigorous conditions that had been established in the visual psychophysical laboratory; that is, intensive investigation of a few committed observers trying to do the task as well as they could. The virtues of this approach became more apparent when the statistical properties of fixational eye movements were examined in attempts to discover how the eye remained so stable.

2.2. Stable fixation is accomplished by smooth eye movements, not by saccades

Cornsweet (1956) was probably the first to take a serious interest in the role of the saccades and smooth movements in the control of eye position during fixation. He recorded horizontal eye movements with the contact lens optical lever technique while subjects fixated a narrow vertical line. He found that neither the saccades nor the slow oscillations were correlated with the amount of fading of a retinally stabilized target, suggesting that neither type of movement functioned specifically for the purpose of providing the retinal motion needed to keep images visible. This led Cornsweet to investigate the role of saccades and slow movements in maintaining stable fixation. Cornsweet found that the further the eye was from its mean position, the more likely a saccade was to occur. Moreover, the saccades were corrective: they returned the eye to within 1′–2′ of its mean position. The velocities of the slow, intersaccadic drift movements, on the other hand, were not correlated with the distance of the eye from the mean position. Cornsweet suggested that the slow movements were oculomotor instabilities, which produced fixation errors. The errors then triggered the appropriate corrective saccades.

Cornsweet (1956) also made a suggestion that has since appeared frequently in the oculomotor literature (e.g., Becker and Jurgens, 1979), namely, that the size and direction of saccades are programmed independently. He made this suggestion based on analysis of the average saccade direction and average saccade size as a function of eye position before the start of saccades. Recall that he found that the direction and the size of saccades were both appropriate to return the eye approximately to its mean position. This implies that any saccades which might occur when the eye was already at its mean position should be very small and be equally likely to be directed to the right or to the left. But this turned out to be only partly true. The average size of the saccades was smallest (3′) when the eye was 1′ to the left of its mean position before the start of the saccade. Direction was a different story. The proportion of rightward and leftward saccades was equal when the eye was located 1.5′ to the right of its mean position before the start of the saccade. Cornsweet reconciled this discrepancy between size and direction by suggesting that there are separate 'size' and 'direction' mechanisms, which select different goal positions for the line of sight.

Cornsweet's (1956) model got things off to a good start. It proposed a clear, quantitative relationship between eye movement and retinal input signals. But as others began detailed analyses of fixation it soon became apparent that the 'drift away–saccade back' pattern that Cornsweet had described was by no means universal. Nachmias (1959), who recorded two-dimensional eye movements and analysed the components of eye movements along 8 meridians, was able to confirm Cornsweet's result for some meridians but found that the slow 'drift' movements could be corrective along others. He concluded that the compensatory 'drifts' were really smooth pursuit of a stationary target, much as the eye smoothly pursues moving targets (see section 3). Fiorentini and Ercoles (1966) and St. Cyr and Fender (1969a) also found that the drifts could be corrective. Others found that the velocity of drift increases in total darkness, supporting the idea that drifts were not 'instabilities' (Cornsweet, 1956) but were controlled by visual input (Ditchburn and Ginsborg, 1953; Nachmias, 1961; Proskuryakova and Shakhnovich, 1968; Matin et al., 1970; Skavenski and Steinman, 1970; Sansbury et al., 1973; Becker and Klein, 1973). Fig. 3 shows a comparison of fixational eye movements in the light and in the dark.

Saccades, like the drifts, did not follow the pattern expected from Cornsweet's data. Saccades were supposed to correct fixation errors, but several investigators reported that saccades would create fixation errors as well (Glezer, 1959; Proskuryakova and Shakhnovich, 1968; Barlow, 1952; Boyce, 1967a). An analysis of the movements of both eyes during fixation supports the same conclusion. Krauskopf et al. (1960) found no correlation between the drifts in the two eyes (determined from

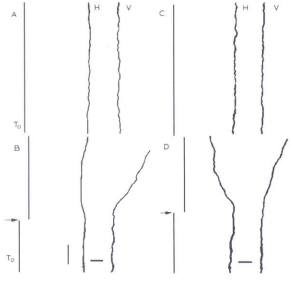

Fig. 3. (A) A two-dimensional record of the eye movement pattern during maintained fixation of a point located directly in front of the subject's right eye. The record begins at the bottom (T_O). (B) A record made under similar conditions except that the target was removed from view in the 2nd second at the time indicated by the black arrow. (The vertical black bar shows a 1 s interval.) Four seconds later the eye had drifted down (the vertical trace (V) went to the right) and had reached the recording limits of the apparatus. The size of the drift can be estimated from the black bar at the bottom of the record which shows 15 minutes of arc. (C) A record made under the same conditions as (A) except that the target was located about 30 degrees to the right of the subject. (D) A record made with the target in the same position shown in (C) except that the target was removed from view at the time indicated by the black arrow. The eye drifted toward the straight-ahead position when the target was removed (left in the horizontal trace (H)). It also drifted downward (to the right in the vertical (V) trace). (From Steinman et al., 1973)

eye positions taken from 2-s saccade-free drift samples), but a near perfect correlation of the occurrence, direction and size of saccades in each eye. The discrepant correlations implied that saccades were likely to be producing a fixation error in at least one of the two eyes.

There were other reasons to believe that saccades were not position-correcting fixation reflexes. Barlow (1952) found that saccades began to drop out of the fixation pattern the longer the subject kept looking at the target. He thought that saccades had more to do with the interest in the task than with basic mechanisms of oculomotor control. Barlow also speculated that saccade rates could be controlled voluntarily. His speculation was confirmed by Steinman et al. (1967). They found that the simple instruction to concentrate on keeping the eye still, rather than on 'fixating' the target, brought saccade rates down from about 1 to 2 each second, to 1 saccade every 2 or 3 seconds. The ability to reduce saccade rates in compliance with simple instructions has since been demonstrated often, including with naive, inexperienced eye movement subjects (Steinman et al., 1973; Winterson and Collewijn, 1976; Schor and Hallmark, 1978; Ciuffreda et al., 1979), and is consistent with the early reports of occasional long periods (many consecutive seconds) of saccade-free fixation (e.g., Barlow, 1952; Ditchburn and Ginsborg, 1953; Fiorentini and Ercoles, 1966; Proskuryakova and Shakhnovich, 1968; Ratliff and Riggs, 1950; Yarbus, 1967).

Steinman et al.'s (1967) demonstration that saccades could be easily suppressed at will made the saccades less like reflexes and more like voluntary behaviors, and, more importantly, showed that saccades were not necessary to achieve stable fixation. The slow movements, which had come to be called 'slow control' instead of drifts (Steinman et al., 1973), were sufficient to keep the eye in place. Figs. 1b and 3a,c show examples of slow control. Slow control has since been demonstrated in young children (Kowler and Martins, 1982), as well as in several species, such as cat (Winterson and Robinson, 1975), rabbit (Collewijn and Van der Mark, 1972), and monkey (Skavenski et al., 1975; Snodderly, 1987). So far, no useful function (either oculomotor or visual) for small saccades has been found, despite many attempts to unearth their role (Kowler and Steinman, 1977, 1979a, 1980; Winterson and Collewijn, 1976; Bridgeman and Palca, 1980). (See section 4.3 for further discussion of the characteristics and utility of small saccades.)

The rejection of Cornsweet's model, featuring noisy drifts and corrective saccades, simplified things because the number of different types of eye

movement that had to be accounted for was reduced. There was no longer good reason to believe that the small saccades during fixation were different from the large, voluntary saccades we use to scan a visual scene (Cunitz and Steinman, 1969). To use Dodge's (1927) criteria for voluntary behavior, it had been established that small saccades could be 'voluntarily inhibited and arbitrarily initiated', the latter property demonstrated by Haddad and Steinman (1973), who showed that subjects could make 5′ saccades away from a single stationary target in specified directions.

The number of different types of smooth movement to be accounted for had also been reduced. The smooth eye movements during fixation of a stationary target could now be regarded as essentially the same as the smooth eye movements made to follow moving targets (Nachmias, 1961), as Dodge had assumed in 1903 (see also Walls, 1962). So, one implication of the discovery of slow control was that the smooth pursuit of intrinsically produced retinal image motion may not operate on principles fundamentally different from those involved in the smooth pursuit of targets that are truly in motion.

How did slow control work? Did it correct retinal position errors in order to maintain the image at some optimal place, or did it correct velocity errors in order to keep the image stable? This issue is still not clearly resolved, but at this point velocity correction seems more plausible. For one thing, the line of sight does not drift toward single targets at eccentricities greater (Whittaker et al., 1988) or less than 5° (Kowler et al., 1990a). Other reasons that position correction is unlikely are based on examining what happens when subjects fixate targets other than the small points or lines or cross-hairs used in most studies. Murphy et al. (1974) asked subjects to try to maintain a stable line of sight at some designated position, either along the boundary or inside outline drawings of small (<80′) simple forms. (Fig. 4 shows their stimuli.) They found that the stability of fixation was the same with the forms as with the traditional single point target. Fixation stability, as well as the mean position of the line of

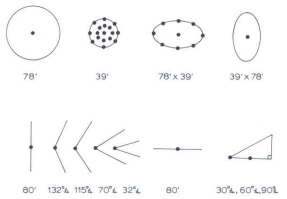

Fig. 4. The stimuli used in the Murphy et al. (1974) study of the effect of stimulus shape on fixation. The superimposed points show the different fixation positions studied. These points were not present during the experimental trials. Subjects were able to maintain a stable line of sight on any of the fixation positions. (From Murphy et al., 1974)

sight, was independent of the shape of the fixation target and independent of where, within the form or on the boundary, the subject was told to look. The same results were obtained regardless of whether subjects made small saccades while they fixated, or whether they refrained from making saccades, maintaining the line of sight exclusively with slow control.

Murphy et al.'s (1974) experiment showed that there was no simple one-to-one relationship between position error signals and the slow control movements of the eye. In their experiment, position error signals of assorted sizes and directions were present when a location within a form was fixated. Yet the eye was never dragged over to a boundary. It would seem to be simpler to account for the stability Murphy et al. (1974) observed by a fixation system designed to keep images stationary rather than one designed to bring images to a particular location. This is because Murphy et al.'s results show that any position-correcting system would have to be under the subject's, rather than under stimulus control. To appreciate the greater complexity that would be introduced by a subject-controlled position system, consider the position-correcting system based on stimulus control described by Steinman (1965) in an attempt to explain how fixation stability and

mean fixation position were about the same for small point targets and for 87′ discs. He proposed that position error signals are determined by averaging the location of each element on the target's boundary with respect to the location of the line of sight. The resulting error signal would be zero when fixation was maintained at one location inside the target (presumably, the center). This model was consistent with Steinman's (1965) data, but could not explain Murphy et al.'s finding of equally stable fixation at a variety of places on or inside the contour of a form. To explain Murphy et al.'s results with a position-correcting model, it would be necessary for the position-error signal to be defined with respect to an invisible reference position determined by the subject based on information in the contour of the target. Such a process cannot be ruled out based on current evidence, and if confirmed it would show a far greater control over fixational error signals by voluntary processes than has been envisioned in all prior work.

Murphy et al.'s (1974) results also led to a reinterpretation of Kaufman and Richards's (1969) and Richards and Kaufman's (1969) finding that subjects tended to fixate near the center of simple shapes. They had tried to relate the centering tendencies to Blum's (1973) theory of shape coding, in which a shape is represented according to its symmetric axis. Richards and Kaufman speculated that symmetric axis transformations might be occurring in the visual system to produce the effective stimulus for eye movements. But Murphy et al.'s demonstration of the independence of eye movements from the shape of the target, in an experiment in which subjects were told where to look, showed that Kaufman and Richards had actually measured their subject's preferences rather than inviolate oculomotor tendencies. (The role of centering tendencies will come up again in the discussion of saccadic eye movements to eccentric targets in section 4.7.1.)

The story of fixational eye movements told so far may be summarized by saying that the line of sight is maintained on a chosen target, or at a chosen location within a target, by means of slow eye movements which appear to be designed to keep images stable on the retina. The question of how stable images have to be in order to ensure clear vision is discussed in the next section, which will show that fixational characteristics change considerably when the head is not artificially supported.

2.3. Fixation stability diminishes when the head is free to move

The studies of fixation up through the 1970s employed accurate and precise eye movement monitors which, as noted earlier, required stable placement of the subject's head. It seemed reasonable to expect that the same excellent control of fixational eye movements described in the earlier sections would be found even when the head was not artificially supported. This is because both the vestibulo-ocular response and the visually activated slow control mechanism should be able to compensate for any additional retinal image motion caused by motions of the unsupported head.

Techniques to measure eye movements while the head is unsupported were developed in the 1970s. These methods employed a magnetic field sensor coil technique and will be briefly described here. (See Ferman et al., 1987, for a recent detailed treatment.) The magnetic field sensor coil method, developed initially by Robinson (1963), is based on the principle that the voltage induced in a coil of wire located inside an a.c. magnetic field is proportional to the sine of the angle between the coil and the field. In the sensor coil technique, eye movements are recorded while the subject sits inside a magnetic field generated by passing alternating current through Helmholtz coils. The sensor coil is attached to the eye by means of a contact lens, or, for better adherence of the coil to the eye, by means of a silicone annulus (Collewijn et al., 1975). Translations of the eye will have no effect on the eye recordings, provided that the eye remains confined to the small, homogeneous central region of the magnetic field. So, the extent to which head motions can be permitted without introducing contamination by translations depends on the size of

this homogeneous region. In conventional sensor coil instruments, with magnetic fields generated by 60 or 90 cm diameter round Helmholtz field coils, the homogeneous region is too small to dispense with head supports.

Skavenski et al. (1979) built a sensor-coil monitor using a set of square Helmholtz field coils, 2 m on a side, which generated magnetic fields large enough to permit head translations of up to ± 1 cm without introduction of translational artifacts of more than 1 minute of arc into the recordings. They measured eye movements of subjects instructed to sit or stand as still as possible while looking at a single point target located at optical infinity. Asking subjects to sit or stand as still as possible should make only minimal demands on systems which compensate for head motions and provide an estimate of the best possible fixation stability achievable without the use of head support.

Skavenski et al. found that movements of the unsupported head were appreciable and were not compensated fully by eye rotations, even when subjects tried to hold the head as still as possible. Fig. 5 shows examples of the head and eye movements made while trying to sit or stand as still as possible. (Note that both the head and eye traces show movements with respect to earth-fixed coordinates, which means that the eye traces represent motion of the retinal image*.) The 2-dimensional dispersion of the line of sight (bivariate contour ellipse area) was about 1.5 – 3-times greater when the head was not artifically supported. Eye speed increased from about ¼°/s with artificial head support to about ½°/s when the head was free. Clearly, the compensation for head motion was incomplete.

If the stability of gaze suffers without artificial head support, even when subjects try to keep as still as possible, what would happen with the sorts of head motion we normally make when going about ordinary activities? This problem was investigated with new instrumentation developed by Collewijn and co-workers – the revolving magnetic field sensor coil monitor used with a cube-surface, rather than Helmholtz, field coil arrangement. This instrument allowed greater freedom of head movement without sacrificing the precision of measurement or introducing translational artifacts. It also provided linear indications of eye orientation and absolute calibration of rotations. Briefly, this instrument employed a rotating magnetic field so that the measure of eye position was based on the phase (not the amplitude) of the voltage induced in the sensor coil mounted on the eye or head. With suitably large, homogeneous regions of the field, eye movements of less than 1′ could be recorded accurately while the head was in motion. Head translations can be quite large (>60 cm) when large cube-surface coils are used without introducing artifacts into the recordings (see Erkelens et al., 1989a). (See Collewijn, 1977; Steinman and Collewijn, 1980; and Collewijn et al., 1983, for more detailed descriptions of this device, and Steinman, 1986b, for a history of the development of the instrumentation currently in use for measuring eye movements in subjects whose heads are free to move naturally.)

The studies of eye fixation using the revolving field monitor showed that the dispersion of eye position and the mean eye speed both increased when subjects attempted active head motion while looking at a small, distant target. Eye rotations compensated for about 95–98% of the head rotations. Although this sounds like very good compensation (indeed, it may be unrealistic to expect better performance of biological systems), it nevertheless led

* Eye rotation in space is not always exactly equivalent to retinal image motion. This is because: (1) the center of rotation of the eye is not coincident with the nodal point of the eye (see Ratliff and Riggs, 1950; Steinman et al., 1982; and Collewijn and Erkelens, this volume, for further discussion), (2) the center of rotation of the head is not coincident with the center of rotation of the eye, requiring the eye to rotate through a slightly greater angle than the head to fully compensate for head rotation, and (3) eye rotations made to compensate for translations of the head will not result in motion of the retinal image. It can be shown than none of these three factors is large enough to warrant consideration for targets at optical infinity, which were used in the experiments described in the text. Mis-estimates of retinal image motion will be well under 1% (Steinman et al., 1982). See Collewijn et al. (1990) and Kowler et al. (1990b) for studies in which retinal image motion was measured accurately for near targets.

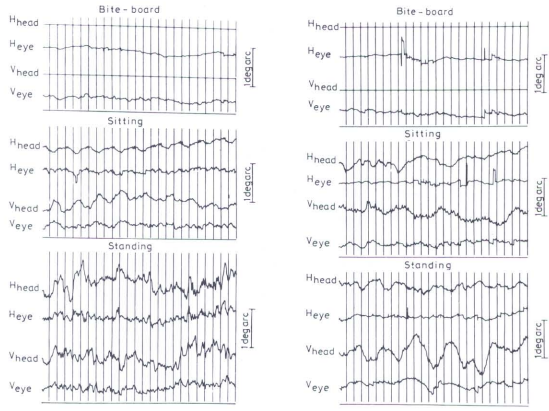

Fig. 5. Representative records of the horizontal (H) and vertical (V) positions of the head and eye in space of two subjects, AS (left) and RS (right), fixating a target at optical infinity, while their heads were supported by a bite-board or while sitting or standing as still as possible without artificial support. Time began on the right and repetitive vertical stripes indicate 1-s intervals. The length of the vertical bars on the right corresponds to a 1° arc rotation on either meridian. Upward changes in head and image traces signify rightward movements in (H) and upward movements in (V). (From Skavenski et al., 1979)

to residual retinal image speeds of about 1–2°/s for modest head rotations (frequency < 1 Hz, amplitude 10–15°). Image motion frequently exceeded 5°/s for more vigorous rotations. Fig. 6 shows several examples of eye movements during both modest and vigorous rotations of the head, and Fig. 7 shows distributions of 100-ms retinal image velocities. The sorts of head motion shown are typical of those we make in daily life, and the subjects in these experiments were under the impression, as we typically are, that the world appears stable and continues to be seen clearly. (Several chapters in this volume discuss different aspects of vision while the head is mobile. See Wallach's and Skavenski's chapters for discussion of perceptual stability, Steinman and Levinson's chapter for discussion of contrast detection and visual resolution, and Collewijn and Erkelens' chapter for discussion of stereovision during head motion.)

Ferman et al. (1987) recently confirmed and extended the initial measurements of fixational stability in subjects whose heads were not artificially supported. The important new feature of their study was the use of experimental and analytical techniques to eliminate possible sources of measurement artifacts that might have contributed in the prior work. Measurement artifacts might have come from misalignment of the annulus on the eye or from cross-coupling of the head movements. Ferman et al. replicated the results of the prior studies,

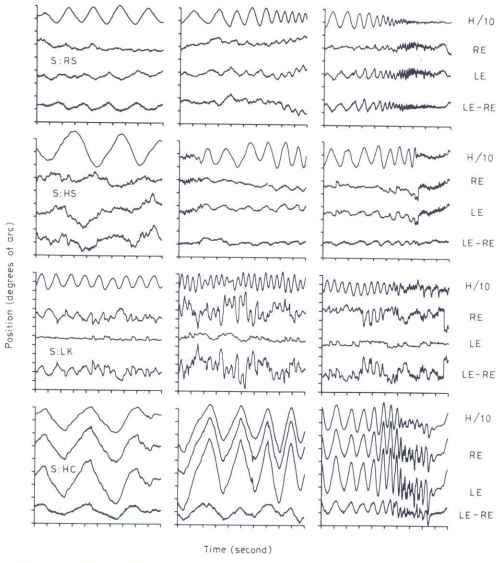

Fig. 6. Representative records of horizontal head and eye movements of four subjects (RS, HS, LK and HC) while they fixated a distant object as they moved their heads. Each record begins on the left. The time-scale marks signify 1-s intervals. The ordinate in each record shows the position of the head and eyes in space. The position scale-marks signify 1° distances. The head position trace (H/10) shows the position of the head scaled to 1/10 of its actual value. The position of the retinal image in the right eye (RE) is shown just below the head, the position of the retinal image in the left eye (LE) just below the right eye, and the vergence of the eyes (LE-RE) is shown at the bottom of each record. Position changes upwards in the head and eye records signify rightward movements. Upwards changes in the vergence trace signify convergence. (From Steinman and Collewijn, 1980)

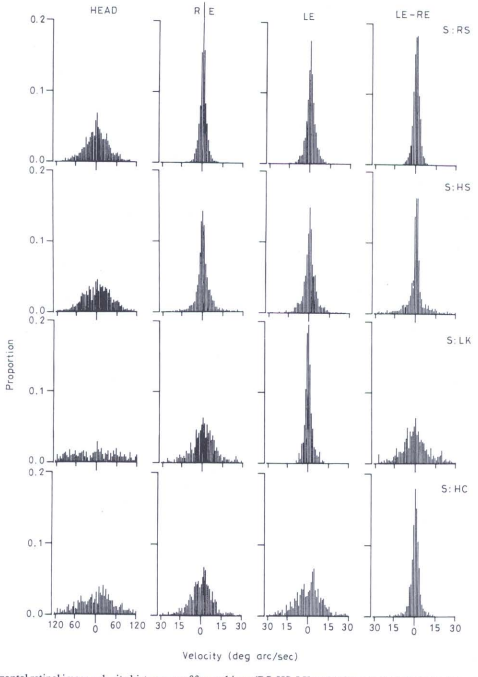

Fig. 7. Horizontal retinal image velocity histograms of four subjects (RS, HS, LK and HC) while they fixated a distant object as they moved their heads. The histograms plot proportions of velocities. Leftward velocities are plotted to the left of zero and rightward velocities to the right of zero. Head velocities (HEAD) are grouped in 4°/s bins. Right eye (RE), left eye (LE) and vergence (LE-RE) velocities are grouped in 1°/s bins. Vergence velocities to the right of zero signify convergence. Vergence velocities to the left of zero signify divergence. (From Steinman and Collewijn, 1980)

described above, and showed that any misalignment of the annulus or cross-coupling of the head motions was too small to be of significance.

The relatively large amounts of eye motion, when normal freedom of head movement is allowed, need not imply that visual or vestibular compensatory systems are too poor or imprecise to serve the needs of vision. Skavenski et al. (1979) suggested that the imperfect compensation may represent the operation of finely-tuned processes whose goal is not to abolish as much retinal image motion as possible, but to maintain the retinal image motion at a value that may be optimal for clear vision.

The suggestion that a briskly oscillating retinal image is useful for vision, made 30 years after the beginning of the modern studies of fixational eye movements, challenges the fundamental assumption that the goal of eye movements is to achieve the stable placement of the retinal image in a central retinal location whose size is but a few minutes of arc in diameter. A complete description of the pattern of retinal image motion that eye movements are trying to achieve cannot be made now because the appropriate concurrent oculomotor and visual experiments to address this fundamental question have yet to be done.

2.4. Overview

We have seen that stable gaze is accomplished by smooth eye movements, not by saccades. The stability most commonly observed in the oculomotor or psychophysical laboratory is indeed impressive, but is rarely achieved in natural environments where the head is not supported artificially. The velocity of the retinal image when the head is free to move ranges from about ½ to several degrees per second.

The oculomotor performance described in this section is presumably controlled by low-level sensorimotor circuitry, perhaps involving systems that sense retinal image motion and then program the appropriate compensatory eye movements. The next section deals with the smooth eye movements made to track moving targets, a task which makes greater demands on the attention, interest and knowledge of the observer.

3. Smooth tracking eye movements

3.1. Human beings cannot voluntarily initiate smooth tracking eye movements in the absence of a moving stimulus

Smooth tracking eye movements cannot be initiated at will in the absence of a smoothly moving stimulus. Efforts to voluntarily initiate smooth eye movements within a stationary visual field result in a sequence of saccades. This event has always seemed curious because it contradicts subjective impressions. Dodge (1931), for example, felt as if his eyes were gliding smoothly across the line of text as he was reading. He proved that his subjective impression of smooth eye motion was wrong by observing the successive jumps of an afterimage as he read a line of text. His subjective impression of smooth eye motion might have reflected the continuous acquisition of information from the text, and not the actual movements of the eye.

The inability to voluntarily initiate smooth tracking eye movements in the absence of a smoothly moving target, and the corresponding inability to completely suppress them in the absence of a stationary target (e.g., Murphy et al., 1975), has made it seem quite sensible to regard smooth eye movements as a sensorimotor reflex, operating under the control of the stimulus rather than free will*. I will begin the discussion of smooth tracking eye movements by reviewing reflexive approaches, which are

* Voluntary initiation of pursuit in some individuals has been noted, although this is rare (e.g. Westheimer and Conover, 1954; Heywood, 1972). The interpretation of these rare instances is not clear. For example, I know of individuals who can voluntarily initiate pursuit on the horizontal meridian, but not on the vertical. This argues that the rare instances of horizontal voluntary pursuit are idiosyncratic phenomena (perhaps related to vergence; Gertz, 1916, cited in Heywood, 1973) rather than a result of subjects' mastery of particular strategies or tricks that can be used by anyone to control smooth eye movement once they know how.

centered on attempts to discover and interpret invariant stimulus-response relationships. I will then describe several phenomena which are inconsistent with many of the basic tenets of these reflexive approaches. These phenomena demonstrate the crucial role of central and subjective factors, such as selective attention and expectations, in the programming of smooth eye movements.

Most of the research to be described will deal with the way in which alert and attentive subjects track small, smoothly moving targets. Some oculomotor researchers might take this to mean that I will be describing an active 'smooth pursuit' response rather than a more primitive 'optokinetic nystagmus' (OKN). OKN usually refers to the smooth eye movements evoked by the motion of a large pattern, typically a pattern of stripes painted on the inner surface of a moving cylinder that surrounds a stationary subject (cf. Collewijn, 1985). This large moving pattern is assumed to represent the image motion of the natural, stationary world as the subject rotates the head and the eyes (Ter Braak, 1936; Walls, 1962). In this sense the 'OKN' is assumed to represent the eye movements made to stabilize stationary environments, rather than to track smoothly moving objects. Recall that the stabilization of stationary environments was also supposed to be the function of the slow control movements, described in section 2. Slow control, however, is a smooth response to the retinal motion of a genuinely stationary environment produced by the observer's own eye movements, and it is studied in the laboratory just that way: with stationary targets viewed by observers whose heads are either stabilized or free to move, and who actively attend to the visual target. By contrast, the observer in an OKN experiment is often told to stare straight ahead at a large moving pattern and to let the eye be dragged along with the stimulus motion, rather than actively trying to track it (Ter Braak, 1936; Ter Braak and Buis, 1970). Sometimes investigators will also talk about 'OKN' when they study the smooth eye movements made while the observer is rotated within a stationary, patterned cylinder. 'Smooth pursuit', in contrast to 'OKN' or 'slow control', traditionally refers to the smooth tracking of fairly small, smoothly moving targets.

Oculomotorists continually talk about whether any of these distinctions, made on the basis of the type of stimulus used in the laboratory (large vs. small; stationary vs. moving), or on the basis of the presumed functions of eye movements, actually reflect the operation of distinct and independent smooth oculomotor subsystems. So far, the attempt to separate smooth subsystems has led to quite a muddle. A clear separation cannot be made based on the choice of stimulus – large moving pattern vs. small moving point – because the main characteristics of the smooth eye movements are essentially the same for both. For example, the differences between the pursuit of patterns and points are relatively modest (e.g., larger aftereffects following prolonged stimulation with large moving patterns than with moving points (Muratore and Zee, 1979), or higher maximal eye velocities with large moving patterns than with moving points (Van den Berg and Collewijn, 1986)), and could well be due to differences in the way a single, smooth subsystem responds to large and small stimuli. Certainly, resorting to separate mechanisms seems to be an option to be taken only after this simpler alternative has been eliminated (and so far it has not).

Anatomical distinctions between 'smooth pursuit' and 'OKN' are also obscure. In the late 1970s and early 1980s several investigators proposed that smooth pursuit is controlled by a special, fast 'direct' pathway that operates in parallel with a slower 'OKN' pathway (Cohen et al., 1977; Lisberger et al., 1981a; Robinson, 1981). The evidence offered to support such a proposal is the finding that lesions to this 'direct' pathway reduce the velocity of smooth pursuit of point targets in humans or in monkeys while producing little impairment of the steady-state velocity of the pursuit of large patterns (e.g., Zee et al., 1976, 1981; Westheimer and Blair, 1973). Such results might suggest parallel pathways, but there are several reasons why they do not distinguish 'OKN' from 'smooth pursuit'. One is that the smooth pursuit of small targets might be more vulnerable to the effects of lesions simply because

the task is harder. For example, falling behind a point target leads to potentially harmful displacements of the target from the fovea and to subjective uncertainty about where the target actually is. On the other hand, there is no such thing as falling behind the large striped pattern because the stripes are everywhere. Complicating the comparison of points and patterns even further has been a tendency to use different kinds of motion pattern in studies of the two kinds of stimulus, i.e., points are often moved back and forth, and stripes in a single direction. Finally, it turns out that two parallel pathways, one fast and another slow, were proposed several years before the two pathways were proposed for primates, in order to explain the dynamic properties of the optokinetic response of the rabbit (Collewijn, 1972, 1981, 1985) – an animal which is often said to lack genuine 'smooth pursuit'. (The rabbit is discussed in section 3.3.)

The important point for the purposes of the present chapter is that the present evidence does not allow us to attribute some characteristics of smooth eye movements in human beings to a 'smooth pursuit subsystem' and others to an 'optokinetic subsystem' solely on the basis of the type of stimulus, waveform of the target motion, or the enthusiasm of the subject. I will not, therefore, presuppose the existence of two distinct smooth subsystems, but instead try to describe smooth oculomotor capacities of human beings who try to maintain the line of sight on a smoothly moving target. Active tracking seems to be more representative of how we use eye movements in natural viewing than letting the eye be dragged off by whatever motion happens to come along. (Indeed, we may never engage in the sort of passive following of full-field visual scenes described in the studies of OKN; passive following may be no more than a voluntary reduction in the velocity of smooth eye tracking (Steinman et al., 1969).) The existence or nature of any smooth oculomotor subdivisions remains to be worked out once we better understand the sensory, motor, attentional and predictive processes which are involved in the tracking of moving targets. It may turn out that smooth oculomotor performance in human beings is best viewed as under the control of a single subsystem whose input is selected by the observer from among the various stationary or moving patterns in the visual field at any given time.

3.2. Smooth eye movements may reduce, but do not abolish, the motion of a target on the retina

A relatively early and well-known attempt to find out how smooth eye movements are initiated and maintained was Rashbass's (1961) study of smooth pursuit of constant-velocity target motions. He found that smooth eye movements in the direction of the target motion began about 150 ms after the onset of the target motion. Rashbass (1961) wanted to find out whether the smooth response was evoked by the change in the target position or by the smooth motion itself. To distinguish between the effects of these two kinds of stimulus error signals – position error and velocity error – Rashbass measured pursuit with a target that jumped in one direction and immediately began to move smoothly in the opposite direction. If smooth pursuit eye movements were driven by position errors, then the eye should start off by drifting toward the eccentric target, opposite to the direction of smooth motion, but in the direction that would bring the line of sight closer to the position of the target. Rashbass found that the eye moved smoothly in the direction of the smooth target motion, just as if the jump had not occurred (see Fig. 8). Rashbass's observation confirmed the earlier suggestion by Dodge and Fox (1928) that smooth eye movements function to keep retinal images stable, not to bring them to a central retinal location. Recall that a case for the importance of velocity errors, rather than position errors, was made earlier in the discussion of slow control movements with stationary targets (section 2.2).

The question of whether smooth pursuit is sensitive to position error reappears periodically and requires brief discussion here. Smooth responses to abrupt target displacements (target 'steps' in the conventional jargon) are seen occasionally. For ex-

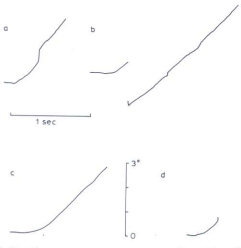

Fig. 8. Tracking responses to a target moving with uniform velocity preceded by a variety of displacements: (a) no displacement; (b) 3° displacement in a direction opposite to the velocity; (c) 1° displacement in a direction opposite to the velocity; (d) 1° displacement in the same direction as the velocity. (From Rashbass, 1961)

ample, Wyman and Steinman (1973a) found instances of smooth correction, but only for very small (7′) steps; larger steps had no effect on smooth eye movements. Carl and Gellman (1987) found smooth responses to 2° steps, but only when the steps were presented in the context of an experimental session containing mostly ramp motions. This result shows that the expectation of encountering smooth motion, or recent past experience tracking smooth motion, was needed to provoke the smooth response to the steps. Carl and Gellman also observed smooth responses to 2° steps imposed on ongoing smooth target motion while pursuit was under way. But the dominant response to the steps larger than 2° was a reduction in eye velocity, regardless of the direction of the steps. Reductions in eye velocity that are independent of step direction do not suggest sensitivity to position, because subjects are known to be able to reduce pursuit velocity voluntarily (Steinman et al., 1969) and might have chosen to do so in Carl and Gellman's experiment in response to the sudden, unexpected disappearance of the moving target from the central fovea. Wyatt and Pola (1981) claimed to find smooth responses to steps, but they used an unusual stimulus. They presented an eccentric target that jumped once, at the beginning of the trial. Subsequent jumps were triggered by saccades, that is, whenever a saccade occurred the size and direction of the jump was the same as the measured size and direction of the saccade. As a result, saccades should not have affected the target's retinal eccentricity, at least within the limits imposed by the speed, accuracy and precision of their image-stabilization system. They found no response to the initial target step, which occurred independently of the saccade. Smooth responses did occur to the subsequent target steps, which were triggered by the saccades. Results obtained with such 'open-loop' stimuli (called open-loop because the normal effects of eye movements on the position of the retinal image are prevented, i.e., retinal feedback signals are removed) do not necessarily support a role for position sensitivity. This is because open-loop stimuli can produce strong subjective impressions of smooth motion. Also, open-loop performance is characterized by a variety of oculomotor idiosyncrasies (described in sections 3.4 and 3.5), and therefore tends not to produce performance which can be directly related to the stimulus conditions, or to performance under normal, 'closed-loop', conditions. On balance, the best that might be said, in agreement with Carl and Gellman's (1987) conclusion, is that certain abrupt displacements of the target may provide adequate stimuli for smooth motion detectors (e.g., Burt and Sperling, 1976) and, in that way, allow smooth oculomotor responses. Unambiguous support for the sensitivity of smooth eye movements to pure position errors is still lacking (Kowler et al., 1990a).

Given the evidence that velocity errors appear to be more important than position errors, let us return to the consideration of the characteristics of pursuit of constant velocity motion. Rashbass (1961) reported that eye velocity reached target velocity by about 400 ms after the onset of target motion, at least for target velocities up to 10°/s. He claimed that any mismatch between the velocity of the eye and the velocity of the target was negligible,

about the same magnitude as the typical oscillations of the eye observed during maintained fixation (see section 2.1). Rashbass suggested that the close match of eye and target velocity meant that continual motion of the retinal image is not needed to maintain pursuit. He suggested that pursuit is initiated by the initial sweep of the target across the retina, which causes the eye to accelerate in the direction of the smooth target motion until it reaches the velocity of the target. Pursuit is then maintained at target velocity because the eye is able to remember and continually re-program smooth movements at its current velocity. The re-programming of the same response continues until a change in the motion of the target initiates acceleration of the eye to a new maintained velocity.

Rashbass's model of pursuit was the same model that Craik had proposed some years earlier (1947) for smooth manual tracking in one of the earliest papers to apply Control Theory to human motor performance. Craik believed that an ongoing motor response would be maintained by means of a positive feedback signal, which he suggested might be produced by reverberating circuits, to allow the system to 'go on doing whatever it was doing at the moment' (p. 59) until a change in stimulation was detected. It was a predictive process of sorts, in which the standard prediction was that things would always stay as they are.

Things did not stay as they were. Rashbass's (1961) observation that eye velocity matched target velocity after 400 ms of pursuit was not confirmed by Puckett and Steinman (1969). They found that the eye always lagged behind the target. Eye velocity during the final half-second of target motion, when performance was expected to be at its best, was 70–90% of the velocity of the target. The finding that the eye lagged behind the target meant that retinal image motion would be available all the time to stimulate pursuit, and the automatic maintenance of eye velocity suggested in the Craik-Rashbass model would not be needed.

The disagreement over velocity-matching encouraged precise quantitative evaluation of eye velocity in subsequent work in order to detect even

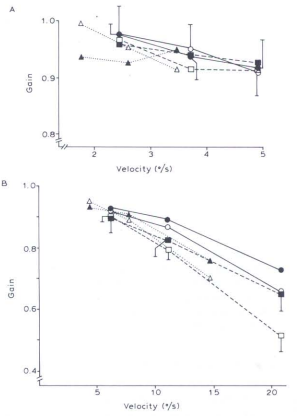

Fig. 9. Gain (eye velocity/target velocity) of horizontal (filled symbols) and vertical (open symbols) smooth eye movement responses to triangular-wave stimuli moving in one dimension with an amplitude of 10° (continuous lines), or in two dimensions simultaneously with an amplitude of 7.07° (dotted lines) or 10° (dashed lines). Means ± S.D. for five subjects for low (A) and high (B) target velocities. (From Collewijn and Tamminga, 1984)

small mismatches. Subsequent studies confirmed that the eye lagged behind the target, on average (Murphy, 1978; Kowler and McKee, 1987; Collewijn and Tamminga, 1984, 1986; Van den Berg and Collewijn, 1986). These studies showed that the average ratio of eye velocity to target velocity (sometimes referred to as pursuit 'gain') tends to decrease as target velocity increases (see Fig. 9 (from Collewijn and Tamminga, 1984)). Sustained pursuit at target velocity was found only in special cases, namely after considerable practice tracking

low-velocity (2°/s) periodic target motions (Kowler et al., 1978).

These studies of pursuit implied that retinal image motion is necessary to maintain pursuit, unless extensive practice tracking simple, slow periodic motions was provided. The significance of retinal motion for models of smooth pursuit is described in the next section, where performance of the rabbit is described briefly.

3.3. Smooth eye movements of human beings are similar in several (but not all) respects to smooth eye movements of rabbits

Comparisons of smooth eye movements in the human with smooth eye movements in the rabbit have been popular since the classic work of Ter Braak (1936). The rabbit has provided us with the prototypical smooth-following system, whose basic principles appear to be fairly well understood, and despite many differences between the smooth eye movements of humans and rabbits, which I will discuss later, the models developed for the rabbit (discussed below) form the core of many of the models developed to account for performance of primates. It is, therefore, instructive to consider the rabbit at this point in the chapter to understand the sort of basic smooth sensorimotor tracking mechanism one might hope to find in humans, and to provide a context for the discussion, in later sections, of the contributions of central and subjective factors to human performance.

Rabbits readily pursue high-contrast textured patterns that occupy the large central 'visual streak' of their retina (the region where the density of ganglion cells is highest) (Dubois and Collewijn, 1979a). Rabbits will also pursue small targets, but will not pursue targets moving against stationary, structured visual backgrounds (Collewijn, 1981). (This result demonstrates that the rabbit lacks selective capacity (see section 3.6), not that it lacks a 'smooth pursuit' subsystem.) Like the human being, the rabbit tracks constant velocity motion with an average eye velocity that is less than target velocity, and the ratio of eye velocity to target velocity falls off as target velocity increases (Collewijn, 1969).

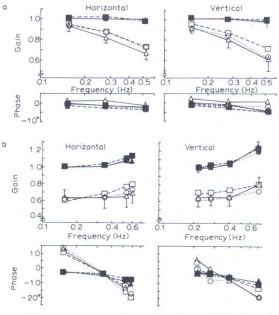

Fig. 10. (a) Gain and phase of the tracking of one-dimensional sinusoidal motion with an amplitude of 10° (continuous lines), or a two-dimensional stimulus with an amplitude of 7.07° (dashed lines) or 10° (dotted lines). Filled symbols show performance including saccades, open symbols show the pure smooth component after the contribution of saccades was removed from the eye traces. Means ± S.D. for five subjects. (b) Same, for pseudo-random target motion (sums of sinusoids). (From Collewijn and Tamminga, 1984)

Performance in human and rabbit is also similar in that the gain of pursuit of sinusoidal target motion (expressed as eye amplitude/target amplitude) decreases as either the frequency or the amplitude of the motion increases (Fig. 10a shows this relation for human smooth eye movement). Collewijn (1969, for rabbit) and Collewijn and Tamminga (1984, for human) argued that effects of both frequency and amplitude on the pursuit of sinusoidal motion represents the dependence of pursuit on the peak velocity of the target. This conclusion may hold for target frequencies below 0.5 Hz. Higher-frequency target motions, however, are harder for humans to track even when a reduction in amplitude makes the peak velocity slow enough so that near perfect pursuit would be expected (Martins et

al., 1985). High target frequencies are detrimental for rabbit as well (Collewijn, 1981).

The gain of the rabbits' pursuit of sinusoidal motions and the gain and time course of pursuit of constant velocity motions were predicted by a linear systems model in which retinal slip signals (the difference between eye velocity and target velocity) were integrated by two parallel pathways to produce the smooth oculomotor command (Collewijn, 1972). One pathway had a short time constant and low gain and simulated the initial increase in eye velocity that occurred 100 ms after the onset of constant-velocity stimulus motion. The other pathway contained a 'leaky' integrator, was characterized by high gain and a long time constant, and simulated the more gradual rise in eye velocity to its maximal value. This model predicted the rabbit's response more accurately than alternatives, such as a single pathway with one or two integrators placed in series.

Additional information about the sensory input to smooth eye movement in rabbit was obtained by means of open-loop experiments. Recall that in such experiments special techniques are used so that the motion of the retinal image remains unaffected by the eye movements. This effectively opens the feedback loop containing the eye-motion signal, which normally combines with the target motion to produce the retinal slip. Open-loop measurements make it possible to discover the response to experimentally controlled amounts of retinal image motion.

Open-loop conditions were established in Collewijn's (1969) experiments by allowing the rabbit to view the moving stimulus through an immobilized eye, while movements of the other, occluded eye were recorded. An interesting aspect of the open-loop results was that the pattern of variation in eye velocity as a function of target velocity turned out to be remarkably close to the pattern of variation in the firing rate of retinal ganglion cells as a function of target velocity (Oyster et al., 1972). This similarity pointed to the ganglion cells as the likely source of the image motion signals used to drive the smooth eye movement. It also suggested that the eye velocity command is computed in a relatively simple way, namely, by summation of the firing rates of the active neurons. More elaborate schemes, such as those based on relationships between the outputs of different types of velocity-sensitive cell, did not appear to be necessary. A temporal-coding scheme comparable to that proposed for rabbit has also been suggested for the monkey, except that the relevant velocity-sensitive cells were assumed to be located in extrastriate cortical regions (Lisberger et al., 1987).

Later work caused some of the confidence in the simple temporal-coding scheme for rabbit to be lost. The shape of the velocity-tuning curves for neurons in the rabbit's central motion pathways was different from the shape of the velocity-tuning curves of the ganglion cells, and, therefore, different from the shape of the function relating eye velocity to stimulus velocity (Collewijn, 1975, 1981). Another complication was the surprising dependence of open-loop gain on the method used to control the retinal motion of the target. Gain fell off less steeply with increasing stimulus velocity when the movements of the viewing eye were compensated electronically, by feeding back the recorded eye motion into the stimulus motion, than when the movements of the viewing eye were prevented by immobilization of the eye (Dubois and Collewijn, 1979a). This result suggested that non-visual signals (proprioception or efferent copy), available when the viewing eye was free to move, had contributed to the pursuit. So, there are clearly unsolved problems even with the rabbit – the animal that has been introduced here as providing a well-understood, prototypical smooth tracking machine.

Despite these complications, there has clearly been a good deal of significant progress in developing models of smooth eye tracking in the rabbit, and in relating performance to the underlying physiology. So, to the extent that the stimulus-response relationships in primate and rabbit are similar, we may be able to gain useful insight into the primate by using what we know about the rabbit to guide the research. For example, we have already seen attempts to draw parallels between the primate and

the rabbit in the previous discussions of the role of retinal slip in maintaining pursuit (section 3.2), the interpretation of the velocity-tuning curves in monkey extrastriate cortex (this section, see above), and the proposed contribution of separate fast and slow pathways to smooth eye movement (section 3.1).

The strategy of taking advantage of what has been learned about a simpler animal to tackle problems of human performance has worked exceedingly well in the study of motion perception. Reichardt's (1961) models of motion detection, developed originally to account for the optomotor response of the beetle, embodies general principles of motion detection which can also account for some aspects of motion perception in humans (Van Santen and Sperling, 1984, 1985). (In his influential book, Marr (1982) assumed that Reichardt's model of the fly's optomotor response would also apply to human smooth pursuit. This view, we shall soon see, is not correct.)

Will the same good fortune that has befallen investigators of motion perception, who learned something about humans from studies of insects, also fall on the oculomotorists hoping to understand human eye movement from observations of a simpler species? Not necessarily. The models of motion-processing developed for insects are most useful in accounting for phenomena at relatively early levels of processing, such as the detection of motion, or the discrimination of its direction. Incorporation of higher-level perceptual phenomena, such as perceptual illusions derived from the relative motion of different objects in the visual field, can legitimately be delayed until more basic processes are better understood. Those who study eye movements, in contrast with those who study motion perception, do not necessarily have the luxury of studying more primitive (rabbit-like?) aspects of the response in isolation from higher-level processes, such as selective attention, learning, memory and expectations. In studies of motion perception, investigators will attempt to control the contribution of these higher-level processes by making the stimulus and task fairly simple (i.e., detection or discrimination) and by relying on well-established psychophysical techniques to make sure that the contribution of expectations, decision criteria and other sorts of response bias are distinguished in the experimental design and analyses from the contribution of the lower-level sensory processes. But eye movement research is at a much more primitive stage. We are still in the midst of finding out what the higher-level factors are, whether they can be removed, or whether their effects can somehow be taken into account, or even whether trying to bypass higher-level processes is a good research strategy. After all, in perceptual research, the internal experience is the main issue, and extraneous factors which affect the report of the experience can legitimately be regarded as nuisances, to be circumvented as cleanly as possible. But in eye movement research, the responses themselves are the issue, and in trying to side-step what are assumed to be nuisances one can end up distorting the very processes under study.

The next several sections will discuss a variety of influences on smooth tracking eye movements, and evaluate the attempts to isolate the supposedly more primitive sensorimotor mechanisms from the contribution of cognitive processes. I will attempt to show that a complete understanding of smooth eye tracking requires incorporating cognitive factors into models, rather than delaying their appearance in the hope that more primitive and low-level processes will be understood first.

I begin by reviewing the research on human eye movements measured under open-loop conditions, a situation which has proven to be invaluable for understanding stimulus-response relationships in the rabbit, but has so far proven intractable for the human.

3.4. When the normal relationship between eye movements and retinal image motion is disrupted, smooth eye movements are no longer related to the pattern of stimulus motion in a systematic way

3.4.1. The role of orbital signals

Measurement of open-loop performance permits the testing of a straightforward hypothesis. If retinal-slip velocity signals are the main effective input for maintenance of smooth eye movements, as has been proposed for human (Puckett and Steinman, 1969) and rabbit (Collewijn, 1969), then removing slip by stabilizing the image on the retina should make the smooth eye movement mechanism blind to the target. The eye should drift, just as it does in darkness. This is in fact what happens in rabbit: stability is lost and the eye drifts about its mean position, resembling the drifts the rabbit makes in the dark (Collewijn and Van der Mark, 1972).

In human the story is different. Performance with a retinally stabilized visual stimulus (an afterimage, for example) does not resemble smooth eye movements in the dark. Recall that in the dark the eye tends to drift in idiosyncratic directions (Fig. 3) (Skavenski and Steinman, 1970; Matin et al., 1970; Hansen and Skavenski, 1977). But with an afterimage a variety of different types of smooth eye movement pattern have been observed. For example, some subjects can voluntarily initiate certain patterns of directed smooth eye motions (Heywood and Churcher, 1971; Heywood, 1972; Steinbach and Pearce, 1972; Cushman et al., 1984; Kommerell and Klein, 1971; Mach and Bachant, 1969). This is a surprising result, because voluntary initiation of smooth eye movements is normally not possible in darkness, or in a visual field containing nothing but stationary targets (see footnote on p. 14). Subjects can voluntarily reduce eye velocity to specified fractions of target velocity (Steinman et al., 1969). They cannot voluntarily track faster than the target (Steinman et al., 1969) or voluntarily change direction (Kowler and Steinman, 1979b).

The observation that smooth eye movements observed with afterimages are different from the smooth eye movements observed in total darkness means that some signal, other than retinal slip, must be contributing to the smooth oculomotor command. A complete model of pursuit would have to specify this signal. One well-known response to this challenge has been a revival of the Craik-Rashbass model. In the revival, eye velocity was once again said to be maintained in the absence of retinal slip. Maintenance of eye velocity was accomplished by adding a positive feedback signal, representing the velocity of the eye in the orbit, to the usual retinal slip (Young, 1971; Robinson, 1971; Yasui and Young, 1975; Lisberger et al., 1981b). This combination represents the velocity of the target in orbital coordinates, which then becomes the effective stimulus for pursuit. The revival of the Craik-Rashbass model differed from the original in that the pathway carrying the copy of the eye velocity was given a gain of less than 1 to prevent instabilities (Yasui and Young, 1975). As a result, the new version of the Craik-Rashbass model, unlike Rashbass's (1961) version, did not predict that the eye would match the velocity of the target.

Yasui and Young (1975) argued that their model would account for the pursuit of an afterimage in the following way. The sum of retinal velocity and eye velocity was said to represent the 'perceived' velocity of the target, which is the signal they believed drives the smooth pursuit. In the case of the afterimage, for which the retinal velocity is zero, the 'perceived' velocity would be equal to (or slightly less than, given the reduced gain of the positive feedback) the velocity of the smooth motion of the eye. Once pursuit of the afterimage gets going, the 'perceived' velocity signal would continue to generate new pursuit movements. To support this model, Yasui and Young (1975) noticed that the eye movements compensating for sinusoidal rotation of the head in darkness could be enhanced by providing the subject with an afterimage. They argued that the perceived motion of the afterimage was the stimulus responsible for the enhanced smooth eye movements. Note that it was not necessary to call the combination of retinal velocity and eye velocity the 'perceived velocity' of the target. 'Orbital ve-

locity' would have been more appropriate, as will be shown in the next section.

The suggestion that a positive feedback signal carrying a copy of eye velocity contributes to smooth pursuit has appeared frequently and has been justified on a variety of grounds. For example, the positive feedback signal has been proposed in order to better account for dynamic properties of pursuit (Robinson et al., 1986), to account for similarities between the precision of pursuit and velocity perception (Kowler and McKee, 1987) and to account for the firing patterns of neurons in the cerebellum (Miles and Fuller, 1975). There has also been a suggestion that the signal contributes to smooth tracking in rabbit (Collewijn, 1985). The observations that pursuit occasionally 'runs on' for a brief period following the removal of the moving target (Whittaker and Eaholtz, 1982; Van den Berg, 1988; for human; Eckmiller and Mackeben, 1978, for monkey; Collewijn, 1985, for rabbit), or following a brief period of retinal stabilization of a moving target (Van den Berg, 1988), have also been attributed to the contribution of a positive feedback signal representing eye velocity. (A timely and accurate copy of the eye *position* signal also plays a role in perceptual and in motor (arm) localization, an idea that goes back to Helmholtz and that undoubtedly contributed to the attraction of using such a signal to control smooth eye tracking; see Skavenski's chapter.) Yet the one thing that the positive feedback signal does not adequately explain is the pattern of smooth eye movements observed with retinally stabilized targets, the mystery which had prompted its appearance in smooth pursuit models in the first place. Smooth eye movements with retinally stabilized targets are described in greater detail in the next section.

3.4.2. Performance idiosyncrasies

Inclusion of a positive feedback signal predicts that smooth eye movement with a retinally stabilized target should be different from smooth eye movements in darkness. But the positive feedback signal, by itself, does not explain the characteristics of the smooth eye movements with stabilized targets. For example, as already noted, one unexplained phenomenon is the emergence of some voluntary control over eye speed or direction. More disturbing, however, the positive feedback signal does not explain the observation, described below, that pursuit of stabilized targets is subject to large individual differences.

Individual differences were demonstrated by Cushman et al. (1984), who asked subjects to try to smoothly pursue an afterimage so as to mimic a variety of simple constant-velocity or periodic target motions. They found a remarkable range of variation in the performance. Some subjects could initiate smooth eye movements in only one direction. Others could make smooth eye movements in either direction but could not control the speed. Fig. 11 illustrates the limited voluntary control over smooth eye movements with stabilized targets. Performance is shown for the two subjects who, of the four tested, had the most voluntary control. The figure shows that each could smoothly pursue a target moving under normal, closed-loop conditions (top graphs in Fig. 11a and b) but that neither could accurately mimic the same patterns of motion with either an electronically stabilized target (middle graphs) or an afterimage (bottom graphs).

Individual differences in smooth eye movements with eccentric afterimages were also prominent. Previous workers had reported that the eye drifts in the direction of eccentric afterimages (e.g., Steinbach and Pearce, 1972). But Cushman et al. (1984) found that the eye would drift toward eccentric afterimages only in some of their subjects. Other subjects could just as easily drift away from as towards the afterimage, and others could not drift at all. The individual differences seen with afterimages, which were the same with electronically stabilized targets, disappeared when very small amounts of image slip were permitted (i.e., compensation for 94%, rather than 100%, of eye motion; Cushman et al., 1980). This last result has an important methodological implication. It shows that highly precise stabilization is essential in order to draw correct conclusions about performance un-

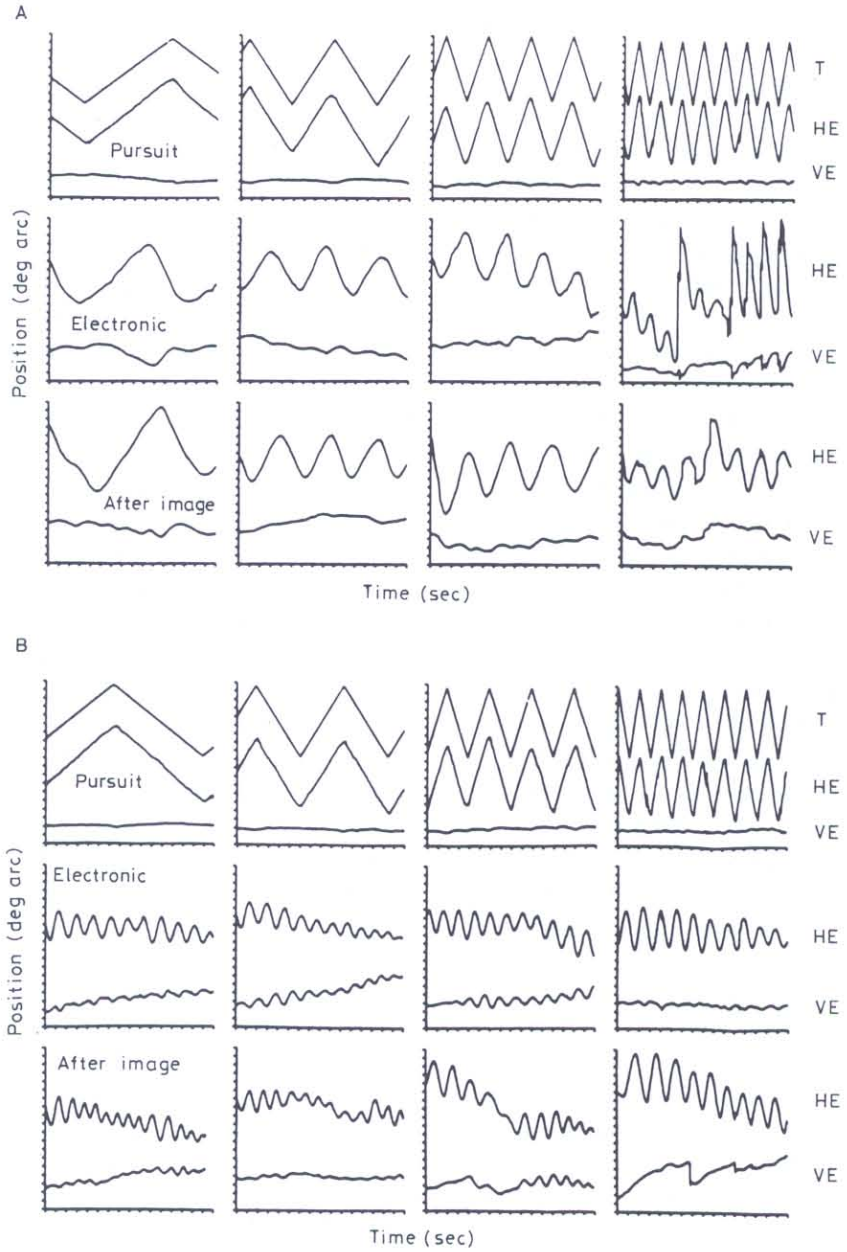

Fig. 11. Best-case analog records of subject JT (A) and subject WC (B) pursuing a triangular target motion (top four graphs in (A) and (B)), attempting to make the same eye movement pattern with an electronically stabilized target (middle four graphs in (A) and (B)) and with an afterimage (bottom four graphs in (A) and (B)). Target velocities were 1, 2, 4 and 8°/s. Traces are reproduced for the target (T), the horizontal position of the eye (HE) and the vertical position of the eye (VE). The time scale shows 1-s intervals. The position scale shows 1° distances. Upward displacements of the traces signify eye movements to the right or upward. (From Cushman et al., 1984)

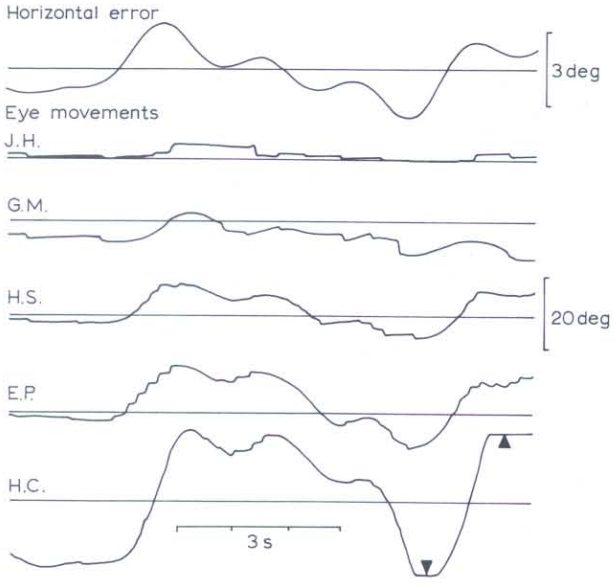

Fig. 12. Horizontal eye movements of five subjects who were asked to smoothly pursue stabilized targets with the same pattern of pseudo-random motion superimposed. The upper calibration bar applies to the retinal stimulus position; the lower one applies to the eye movements. The arrows in the lower trace mark saturations of the recording range. (From Collewijn and Tamminga, 1986)

der open-loop conditions.

Individual differences, comparable to those observed with stabilized targets, are equally striking when experimentally controlled patterns of retinal image motion are imposed on the stabilized target. Pursuit of controlled patterns of retinal image motion has been studied as part of attempts to discover the human 'open-loop' response. Dubois and Collewijn (1979b) found that some subjects vigorously pursued imposed retinal image motion in certain directions, while other directions were not pursued at all. The preferred directions differed among the subjects. (The idiosyncrasies were observed only for large (15 deg) stimuli centered on the fovea; eccentric stimuli were always tracked faster when they moved away from, rather than toward, the fovea.) Large individual differences in both the speed and the direction of pursuit have also been found under 'open-loop' conditions when pseudo-random image motions (sums of sinusoids) were imposed on stabilized targets (see Fig. 12) (Collewijn and Tamminga, 1986).

This section has shown two things so far. First, there are good reasons to believe that the effective stimulus for pursuit includes a positive feedback signal, representing eye velocity. This means that the effective stimulus for pursuit is defined in an orbital, rather than in a retinal, frame of reference. Second, the inclusion of such a signal will not explain pursuit under open-loop conditions. The large individual differences observed under open-loop conditions show that the open-loop technique is useless for discovering invariant, lawful relationships between retinal motion and eye motion in human smooth pursuit, thus depriving investigators of a potentially valuable analytic tool. Open-loop conditions open the way for all kinds of processes, their nature still unknown, to influence and control human smooth eye movements.

3.4.3. An alternative proposal for measuring 'open-loop' performance: the initial pursuit response

We have just seen how difficult it is to interpret smooth tracking under conventional open-loop conditions, in which controlled patterns of image motion are imposed on stabilized targets. An alternative method which has been tried is the study of the initial portion of pursuit. The initial portion of pursuit is taken to be a good estimate of the open-loop performance because, given that the eye is relatively stationary before the target starts to move, the pattern of the target motion in space should be about the same as the pattern of motion on the retina. So, measurements of the initial pursuit should allow the relationship between retinal motion and eye motion to be determined without the need for special techniques to experimentally control the retinal motion. (Actually, the eye does drift before the onset of target motion. These anticipatory smooth movements will be ignored for the present, and discussed later in section 3.7.2.)

Reasonably strong claims about the significance of initial pursuit have been made. For example, the initial response has been said to be a "direct reflection of visual processing in the input pathways of

pursuit" (Tychsen and Lisberger, 1986, p. 956). The question of whether such a strong claim is justified will be discussed later in this section after a few properties of initial pursuit have been described.

Tychsen and Lisberger (1986) studied the dependence of the initial pursuit response on several stimulus variables, in particular the velocity, intensity and retinal eccentricity of the moving target. They found that the average acceleration of the initial pursuit, measured over the first 100 ms following the onset of the pursuit response, was highest for targets that moved horizontally toward the fovea, starting from an eccentricity of about 3 deg. Eye acceleration fell off steadily as the starting position was shifted to locations farther from, or closer to, the approximate position of the line of sight. Vertical pursuit showed a different pattern. Eye acceleration was higher for targets located in the lower portion of the visual field than for targets located in the upper portion, regardless of whether the motion was toward or away from the fovea. Reducing the intensity of the target from about 2.8 to 0.8 log units above a psychophysically determined detection threshold caused eye acceleration to decrease, but only for targets moving 45°/s or faster. Pursuit of lower target velocities was unaffected by intensity. Thus, it seems that the initial pursuit response, at least on the horizontal meridian, is fastest when the target's initial motion crosses the fovea. In addition, fast-moving, dim targets do not produce a brisk initial response.

Do any or all of these effects of stimulus variables on initial pursuit derive exclusively from the status of signals in the afferent pathways to pursuit, as has been claimed? Perhaps. For example, afferent signals from the fovea may be stronger (e.g., more contributing neurons) than extrafoveal signals, thus accounting for the faster pursuit of foveal targets. By the same token, signals from dim, fast-moving targets may be relatively weak. These proposed relationships between neural signals and smooth pursuit must be viewed carefully, however, because they do not imply that the status of afferent signals is the only, or even the principal, determinant of pursuit velocity, nor that the straightforward transformation of sensory signals to the oculomotor command, described for the rabbit (section 3.3), necessarily applies to human beings. Smooth eye tracking is a complex phenomenon, and the tight links between stimulus variables and responses which characterize smooth eye movements in the rabbit are hard to nail down in human beings. For example, in human beings, pursuit velocity declines when the subject's focus of attention does not correspond to the position of the moving target (see section 3.6), in much the same way that the initial reponse velocity was found to decline with increasing eccentricity or decreasing stimulus intensity. This implies that attentional, not sensory, factors can account for, or at least contribute to, the decline in pursuit velocity with increasing eccentricity or decreasing intensity. The velocity of initial pursuit is also sensitive to the past history of stimulus motions, and to the length of time the target is expected to remain in motion (section 3.7). These effects often outweigh those of sensory variables. It seems, then, that we are far from being able to distill the precise contribution of afferent signals to pursuit, and, more importantly, far from a theory of *how* afferent (and other) signals determine the pursuit response. Achieving these goals will require a better appreciation of the way in which central and subjective factors determine pursuit. Consideration of these factors begins next with a discussion of the relationship between perceived motion and pursuit. Following this, the role of selective attention and expectations will be reviewed*.

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* In a recent paper Van den Berg (1988) took advantage of the influence of past history on pursuit in an attempt to characterize the open-loop response. He stabilized the image briefly (1.5 s) during ongoing pursuit of either sinusoidal or pseudo-random motions. He found that individual differences between the five subjects he tested were small, at least during the first 0.7 s of stabilization, and that pursuit characteristics were determined largely by the pattern of prior target motion, much as if subjects were trying to continue to mimic the motion they had been tracking (see section 3.7 on predictive eye movements). The extent to which this technique of brief image stabilization during ongoing pursuit proves to be successful in untangling the role of sensory processes, learning and expectations on smooth eye movement remains to be determined in future applications.

3.5. We pursue a highly organized motion signal, but we do not 'pursue what we perceive'

Section 3.4.1 introduced the suggestion that perceived motion is the effective stimulus for pursuit (Yasui and Young, 1975) but pointed out that, given the available evidence, it is not necessary to label the stimulus for pursuit 'perceived velocity'. 'Orbital velocity' (retinal velocity + eye velocity with respect to the head) is the better choice, as becomes clear by considering what happens when orbital motion is in conflict with perceived motion. The conflict will occur whenever the distance between the target and the observer is changed. Changes in the distance of the moving target will, of course, change the orbital velocity, but will not affect perceived velocity, at least within the limits of velocity constancy (cf. Mack, 1986). Smooth eye movements, unlike percepts of motion, must ignore distance cues, and other cues that promote velocity constancy, and try to match the orbital velocity, at least if accurate tracking is to be maintained. (For additional discussion of the implication of taking distance cues into account in the evaluation of oculomotor theories, see Steinman, 1986b.)

The dissociation between 'perceived' and 'orbital' motion allows us to quickly move from the question of whether perceived motion drives pursuit to the more precise question of the extent to which perceived motion and pursuit depend on the same motion analysers.

One reason to believe that pursuit and perception share motion analysers, at least at some level of processing, comes from studies of the smooth pursuit of targets moving in a sequence of small jumps (Westheimer, 1954), a stimulus that produces the percept of 'optimal' apparent motion (Wertheimer, 1912). This was studied in a clever experiment by Morgan and Turnbull (1978), who measured both perceived motion and smooth pursuit in an attempt to discover whether both varied in the same way as a function of the spatiotemporal pattern of the jumps. Their stimulus display consisted of a row of points, with each point illuminated briefly in succession. The trick to their measurement of the apparent smoothness of the motion was that each point was presented to one eye slightly before the other. As a result, the observer perceived the target as moving smoothly in depth whenever the intervals between the presentation of the adjacent points was sufficiently short. Morgan and Turnbull (1978) used the proportion of correct judgments of depth (i.e., whether the motion was towards or away from the observer) to represent the perceived smoothness of the motion. They found that depth judgments became increasingly less accurate as the interval between the successive flashes of adjacent points increased, with the judgments falling to chance levels for interflash intervals of 150 ms or longer (Fig. 13a). Coincidentally, the effectiveness of smooth pursuit, assessed by the standard deviation of eye position around a trajectory representing perfect tracking, deteriorated markedly when the interflash interval exceeded 150 ms (Fig. 13b). Their results argue that the same motion analysers serve perception and pursuit.

A different sort of demonstration linking pursuit eye movements to apparent motion is the finding that intermittently illuminated (10–100 Hz) arrays of stationary points can be pursued, provided that both the smooth eye movements and the percepts of smooth motion are initiated by a continuously moving target; e.g., Heywood (1973); also Behrens and Grusser (1979), who called this phenomenon 'sigma OKN'. The perceived motion with the 'sigma OKN' stimulus depends on taking eye velocity signals into account, and it is in this sense comparable to the perceived motion of afterimages. The perceived motion of 'sigma OKN' is, to stay within the terminology used in this chapter, apparent motion in orbital coordinates.

Another argument for perception and pursuit sharing motion analysers comes from a study by Kowler and McKee (1987). They compared the ability of smooth eye movements and perception to discriminate differences in target velocity. (This is different from most of the measures encountered so far in this chapter, where the emphasis was placed on how fast the eye traveled relative to the speed of the target.) Kowler and McKee measured

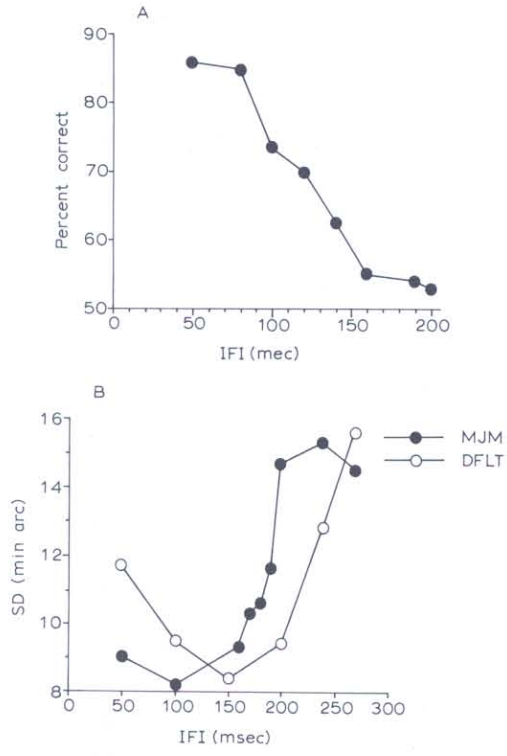

Fig. 13. (A) Percent correct judgments of depth as a function of the time between successive flashes of a target (IFI), which was perceived as moving in depth because each flash was presented to one eye slightly before the other. Data are the means over three observers. (B) The smoothness of the tracking of the same target motion. The graph shows the standard deviations of eye position around the best-fit regression of eye position over time. Data are from two observers. (Based on Morgan and Turnbull, 1978)

'oculomotor velocity discrimination' by having subjects pursue a different constant-velocity motion on each trial, with velocity selected at random from a set of five closely spaced values. Examples of velocity time-course functions, obtained from four different sets of target velocity, are shown in Fig. 14. Distributions of eye velocities in each velocity set were analysed to determine the proportion of each falling above a criterion value (the criterion was set to the mean eye velocity for the mean target velocity of the set). These proportions, plotted as a function of target velocity, constituted what they called the 'oculometric function', analogous to the conventional psychometric function. These functions, which were determined separately for each velocity set, were then used to find the 'oculomotor difference threshold', the smallest difference in target velocity that was needed to produce statistically distinguishable eye velocities. Kowler and McKee found that the oculomotor discrimination of velocity was very poor during the first few hundred milliseconds following the onset of target motion. The oculomotor difference threshold decreased steadily over time after the onset of target motion, reaching the lowest (hence, best) levels by about 600–700 ms after the target had begun to move (Fig. 15a). This shows that the initial velocity signal is imprecise, despite the fact that the eye could quickly achieve a velocity near the mean of the set of stimuli. (One reason that the pursuit response can be fast, yet imprecise, for several hundred milliseconds involves the consideration of predictive aspects of pursuit and will be taken up in section 3.7.3.) Kowler and McKee also found that oculomotor velocity discrimination depended on the velocity of the target. Once oculomotor velocity discrimination had reached its best levels (about 600–700 ms after the onset of target motion), both oculomotor and perceptual velocity discrimination varied in the same way with the velocity of the target (Fig. 15b), suggesting that both perception and smooth eye movement might be served by common motion analysers. The similarity between perception and smooth eye movements has limits, however. Principally, the similarity does not apply to the initial portion of pursuit. Oculomotor velocity discrimination is poor during the first few hundred milliseconds following the onset of target motion, as it is for very brief (200 ms) target motions. On the other hand, perceptual velocity discrimination with only 200 ms of exposure to the target motion is quite good and does not benefit much from increasing the stimulus duration. Perceptual velocity discrimination with only 200 ms exposures is as good as oculomotor velocity discrimination becomes much later in pursuit (Fig. 15b). This discrepancy between characteristics of motion perception and characteristics of the initial

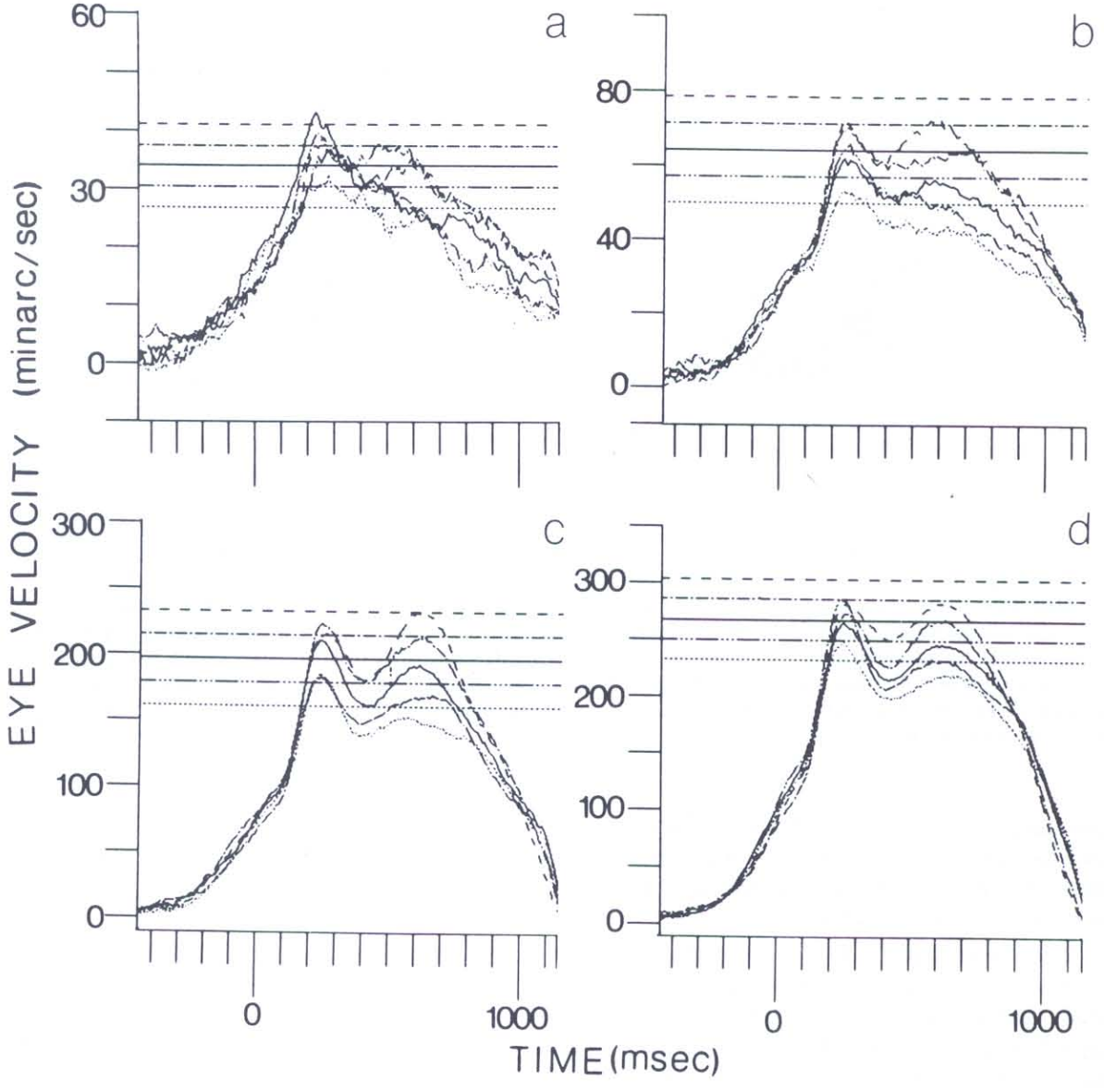

Fig. 14. Mean 100-ms eye velocity for subject EK pursuing leftward target motions in four different sets of constant-velocity target motions. Eye velocity is shown as a function of the midpoint of successive 100-ms intervals whose onsets are separated by 10 ms. Target motion began at 0 ms on the abscissa and ended at 1000 ms. Velocities less than 0′/s indicate rightward eye motion. The horizontal lines indicate the velocities of the targets. (From Kowler and McKee, 1987)

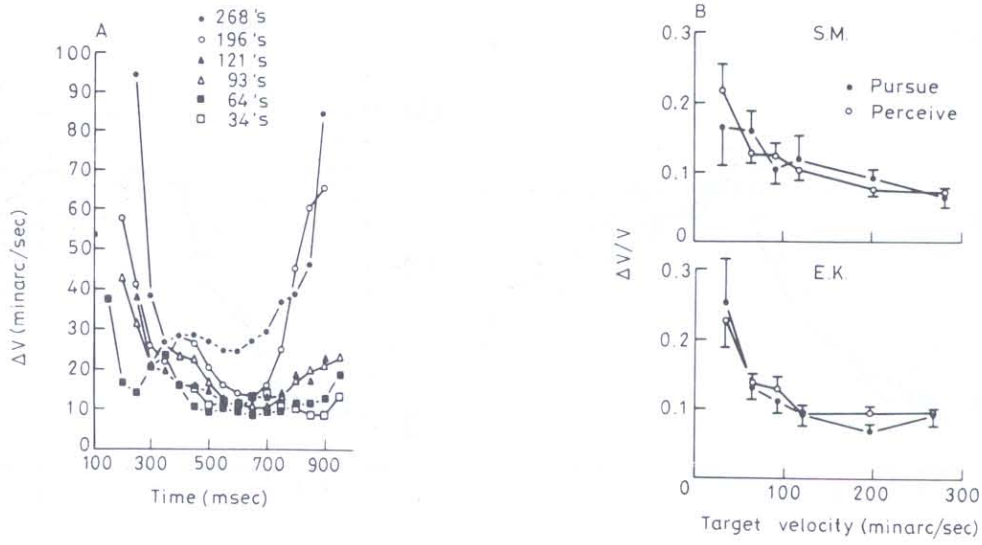

Fig. 15. (A) Oculomotor difference threshold (ΔV) as a function of time relative to the onset of target motion. Data are for subject EK. Difference thresholds were computed based on distributions of 100-ms eye velocities and are plotted as a function of the midpoint of the velocity sample. Each function shows the difference threshold for a different velocity set; the mean velocity of each set is listed on the figure. Difference thresholds decreased over time, reaching lowest values about 600–700 ms after the onset of target motion. The subsequent increases in the difference thresholds occurred when the eye began to slow down in anticipation that the target was going to stop moving. (B) Weber fractions ($\Delta V/V$) (the ratio of the difference threshold to the mean velocity of the set) as a function of the mean velocity of the set for subjects SM and EK. Filled symbols are Weber fractions based on the lowest difference threshold obtained for each velocity set. Open symbols are Weber fractions representing perceived differences of the same target velocities. (From Kowler and McKee, 1987)

portion of pursuit provides yet another reason to be cautious about concluding that initial pursuit reflects the information in neural motion-processing centers (see also section 3.4.3).

Links between pursuit and perception have also been demonstrated by reports of pursuit of centrally generated moving stimuli, which, clearly, require higher levels of motion processing than would be needed for velocity discrimination. For example, moving stereoscopic contours (Fox et al., 1978) and segments of dynamic visual noise (Ward and Morgan, 1978) can be pursued. Some individuals can pursue the movements of their own hand or finger in darkness (e.g., Steinbach, 1969; Gauthier and Hofferer, 1976). This response is weak and intermittent, however, and may be improved by allowing periodic, brief glimpses of the moving hand (Steinbach, 1969, 1976; Jordan, 1970) (see Fig. 16).

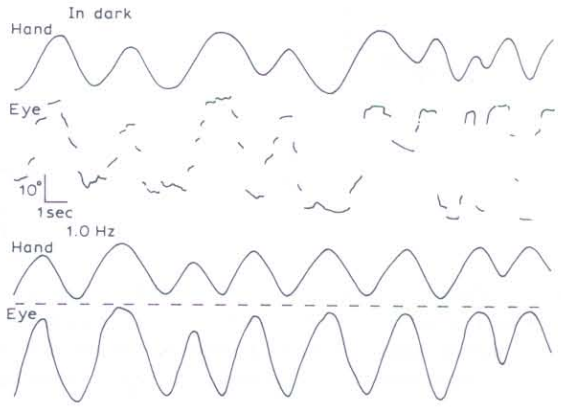

Fig. 16. The top pair of traces shows subject's attempt to track her own hand in complete darkness. There are some short episodes of pursuit, but tracking is mostly saccadic. The bottom pair of traces shows the marked improvement in pursuit that occurs when the hand is strobe-illuminated (microsecond pulses) at 1 Hz. (From Steinbach, 1976)

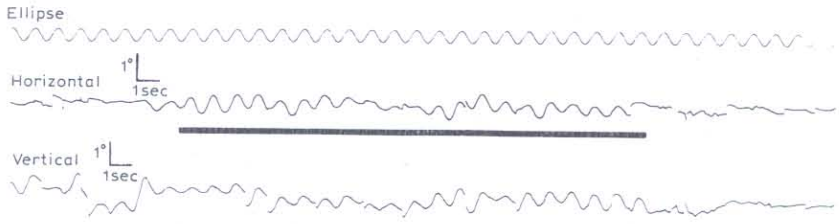

Fig. 17. Horizontal and vertical component of eye movements made while the subject tracked an ellipse (tilted at 45°) moving horizontally behind a narrow slit. Driving function for the ellipse is on the top trace. The heavy black line shows when the subject perceived the stimulus as an ellipse moving behind a slit, rather than two spots of light moving vertically in counterphase. The occurrence of horizontal pursuit is correlated with the percept of an 'object' seen moving behind the narrow slit. (From Steinbach, 1976)

Illusions of motion can be pursued. Steinbach (1976) reported that subjects were able to pursue the perceived, horizontal motion of a moving ellipse seen through a narrow vertical slit (Fig. 17). In this well-known illusion, often called 'anorthoscopic perception' (cf. Anstis and Atkinson, 1967), the only retinal motion was the vertical oscillation of the edges of the ellipse as it passed behind the slit. Steinbach's result confirmed an earlier suggestion of Anstis and Atkinson (1967), who used a subjective measure of eye motion (the perceived location of afterimages) to infer the pursuit of the anorthoscopic stimuli. Pursuit of anorthoscopic motion was also observed by Morgan (1981) and by Mack et al. (1982).

There have also been attempts to demonstrate that the same cortical regions serve both motion perception and smooth eye movements. These studies consisted of demonstrations that lesions to extrastriate areas implicated in motion perception (e.g., the middle temporal area; Newsome and Paré, 1988) decrease the velocity of smooth pursuit (Newsome et al., 1985, 1988; Dursteler et al., 1987; Dursteler and Wurtz, 1988). Electrical stimulation can produce a small, brief increase in pursuit velocity, or a relatively larger and longer-lasting decrease, depending upon which location is stimulated (Komatsu and Wurtz, 1989). Decreases in eye velocity are hard to interpret because, as noted earlier, subjects can voluntarily decrease pursuit velocity (Steinman et al., 1969) and may do so if distracted from the task or stimulus. So it is possible that some or all of the effects of lesions and stimulation on pursuit might represent the animal's behavioral reaction to an alteration in the appearance of the moving target, rather than distortion of the motion signals necessary to generate smooth pursuit. More elaborate behavioral testing will be needed to sort out the various alternative interpretations of the animal's performance.

The studies reviewed in this section illustrate various ways in which smooth pursuit and motion perception appear to share common motion analysers. Despite these demonstrations, it has nevertheless become clear that oculomotorists will go astray if they choose to simply borrow ideas about the central processing of pursuit stimuli from researchers in motion perception. This is because stimuli producing vivid percepts of motion are not often able to stimulate pursuit. For example, Mack et al. (1979, 1982) found that neither motion aftereffects nor induced motion (perceived motion of a stationary target inside a moving surround) were pursued. These results were also obtained with retinally stabilized targets so that, in principle, the position and velocity errors which would have discouraged the continued pursuit of illusions would be absent. Collewijn and Tamminga (1986) also found that the induced motion of a stationary target was not pursued when the target was either unstabilized or retinally stabilized and was superimposed on a large moving background. (The story for stabilized images became a bit more complicated, as might be expected from the research described in

section 3.4, when Van den Berg and Collewijn, 1987, demonstrated that subjects could choose to pursue a superimposed, stabilized target either in or opposite to the direction of the moving background.)

Mack et al. (1982) attempted to reconcile the various instances in which perceived motion did and did not influence pursuit by suggesting that percepts are influential only when the stimulus perceived as moving has no competing 'retinal counterpart'. Stimuli with no retinal counterpart can be pursued, they argued, because "there is no retinal feedback which can constrain or inhibit pursuit" (p. 86). The anorthoscopic stimulus does not have a retinal counterpart because the entire ellipse is never present on the retina, but is instead generated centrally. Although it is not completely clear why the portion of the ellipse seen through the slit, or the portion of the ellipse painted on the retina as the eye pursues the percept, should not qualify as 'retinal counterparts', the hypothesis of Mack et al. (1982) is interesting because it reminds us that there are different ways of coding motion. Some kinds of codes, such as the motion of a target with respect to the observer (including even centrally generated targets, such as the stereoscopic contours or the moving ellipse), may influence both pursuit and perception. Other codes, such as the relative motion of two regions of the retinal image, may influence only the percepts. Why should one type of motion – motion relative to the observer – be able to influence smooth eye movement, while another, which is so important for perception – motion relative to other objects in the field – apparently does not? Perhaps the decision rules about which types of motion will and will not be influential are hardwired into the perceptual or the oculomotor machinery. Alternatively, the smooth oculomotor system may contribute to the formation or selection of its own moving stimulus by evaluating the effectiveness of the tracking eye movements. For example, pursuit of a target undergoing induced motion will not bring the line of sight closer to the target, and so may not be maintained. The capacity of smooth eye movements to make internal adjustments depending on the effectiveness of prior responses is discussed in more detail in the section on predictive eye movements (3.7.4) and is also discussed in Pavel's chapter. See also Collewijn and Erkelens' chapter for a related discussion of the relationship between binocular eye movements and the perception of depth.

This section has shown that central representations of motion serve as stimuli for smooth pursuit. This is *not* the same as saying that perceived motion drives pursuit because the stimuli for perception and pursuit are different: pursuit depends on motion relative to the observer, while percepts often depend on the relative motion of different objects in the visual field. The emphasis on central representations of motion as stimuli for pursuit moves us away from the view that the pursuit stimulus is simply an internal replica of retinal velocity, with perhaps a signal representing the motion of the eye added in at some stage. The description of the central representation of stimulus motion will be extended in the next section, which deals with the role of selective attention in determining the target for smooth eye movement.

3.6. Selective attention determines which one of many possible retinal signals serves as the input to the smooth oculomotor system

3.6.1. Visual fields containing more than one pattern of motion

At the beginning of the section on smooth eye movement we saw that there are profound limits to the voluntary control over smooth eye movement. For example, we cannot voluntarily initiate smooth eye movements without a smoothly moving target, or voluntarily suppress them without a stationary target. This section describes what happens when a variety of targets, both stationary and moving, are present at the same time.

A straightforward way for smooth eye movements to respond to more than one target at the same time is to respond to the pooled contribution of all of the targets. Adding more targets would simply change the available input, and would not

invoke any new oculomotor processes. The main problem that would face researchers who want to understand the response to multiple targets would be the need to discover how the various retinal velocity signals combine mathematically, and how stimulus attributes, such as intensity or retinal location, affect the relative contribution of each velocity signal to the pool.

This straightforward scheme is wrong. When the visual field contains a variety of targets, moving at different velocities, the observer selects which target is to be tracked. The ability to select the target for smooth eye movements was suggested as early as 1906 by Ernst Mach, who realized that selective capacity is essential to explain how we are able to keep looking at the goal ahead of us as we walk about, without the eye being dragged off by the retinal motion of the world streaming by. The ability to select the target for smooth eye movements means that velocity signals must be sorted out so that only the selected signals will reach the smooth oculomotor subsystem. The hard problem is to understand how this sorting and selectivity is achieved. I will review a few suggested solutions. These range from those proposed in some early studies, which stressed the importance of retinal location, to later work, which showed that voluntary selective attention is more important. I will then argue that the way in which selectivity is achieved has general implications for characterizing the stimulus for smooth eye movements.

3.6.2. Retinal position vs. voluntary selection

Much of the early work on selection of the target for smooth eye movements emphasized not so much the voluntary selective capacities, but rather the apparent advantage accorded to stimuli that fall on the fovea relative to stimuli falling on more eccentric retinal locations. Investigators were surprised to find that the smooth pursuit of a large, moving striped pattern (the classic 'OKN' stimulus; see section 3.1) could be inhibited easily by fixation of a mere stationary point superimposed on the stripes (Dodge and Fox, 1928; Fisher and Kornmuller, 1930; Stark, 1971).

Later studies described the effects of retinal location more systematically and precisely. For example, Murphy et al. (1975) found that fixation of a superimposed stationary point or a small (30′ diameter) annulus was able to eliminate almost all traces of pursuit of a moving background grating. Extrafoveal annuli (147′ diameter) were much less effective. Similarly, Collewijn and Tamminga (1984) found that a moving point could be smoothly tracked across a stationary grating about as well as it could be tracked across a dark background, provided that the subjects looked directly at the moving point. [Note: There were small effects of the background on pursuit, just as there were small effects of a moving background on fixation of a superimposed stationary point (Collewijn and Tamminga, 1986). These effects were found in only some of the subjects, who may have allowed themselves to be distracted a bit by the background.] In contrast with the accurate tracking of a foveal point across a patterned background, Collewijn and Tamminga (1986) found that it was hard to pursue a point which was kept at an eccentricity of 5 deg as it moved across the stationary background, a situation in which the fovea was filled with the image of the moving visual pattern. In interpreting this result keep in mind that retinal eccentricities of a few degrees have little or no effect on smooth pursuit of targets moving across dark or homogeneous backgrounds (Winterson and Steinman, 1978; Collewijn and Tamminga, 1986). Eccentricities of a few degrees become important only when a competing pattern of motion is in the fovea. In such instances, the stimulus in the fovea has an advantage.

There is more to smooth oculomotor selectivity, however, than the advantageous placement of the chosen image on the fovea. For example, investigators who studied selectivity by superimposing a stabilized scotoma on a large moving pattern (Cheng and Outerbridge, 1975; Dubois and Collewijn, 1979b) noticed that the scotoma tended to inhibit the pursuit of the background, with the pursuit becoming slower as the scotoma became larger. Nevertheless, retinal location was not the whole story because special effort – what we would refer to

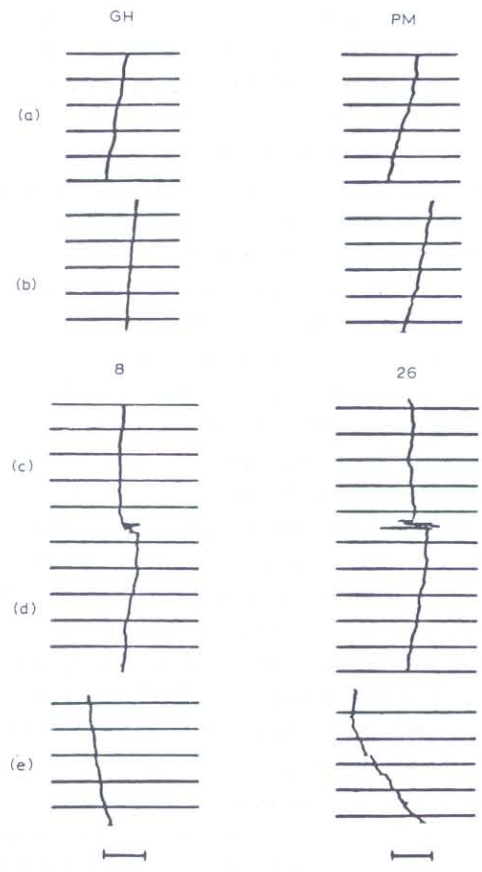

Fig. 18. (a) Representative records of horizontal eye movements of two subjects (GH and PM) who drift to the right when they use slow control to maintain the line of sight on a stationary point superimposed on a 4° diameter stationary grating. (b) Same as (a) except that the point was removed, leaving only the stationary grating. (c) The point was removed and the grating moved to the left at 8′/s for GH and at 26′/s for PM. Note that the grating's motion, in the absence of the superimposed point, nullified the rightward drifts. (d) The superimposed stationary point was restored to the display and subjects tried to fixate the point. Their usual rightward drift returned, despite the leftward motion of the grating. (e) Subjects successfully tried to track the leftward motion of the grating. Records are read from bottom to top. Horizontal lines are 1-s time-markers. The bar below each subject's records represents 1° arc rotation. (From Murphy et al., 1975)

colloquially as paying 'attention' to the background – could increase the velocity of pursuit (Dubois and Collewijn, 1979b). The contribution of 'effort' or 'attention' shows that the selection process is not simply a matter of positioning the desired target on the fovea. Selectivity is a matter of decisions made by the subject about which target to attend to. (I will discuss evidence linking oculomotor and perceptual attention in section 3.6.4.)

An unusual illustration of the power of selectivity to determine the target for smooth eye movements is shown in Fig. 18, taken from Murphy et al. (1975). Murphy et al. studied two subjects who had natural tendencies to drift horizontally when fixating a stationary target (Fig. 18a,b). The unusual aspect of the performance was that these subjects showed the same drifts when they tried to fixate a point superimposed on a grating which moved opposite to the direction of their natural drift (Fig. 18d). This meant that the smooth eye movements continued to be determined by the selected target (the stationary point) even as the line of sight was drifting away from the stationary point, across the moving grating.

3.6.3. Selection with stimuli occupying the same retinal location: implications for the central organization of the pursuit stimulus

The demonstrations summarized in the previous section, showing that the advantage for foveal over extrafoveal stimuli is not absolute, but instead depends on attention, suggest that an unambiguous estimate of the capacity to select the target for smooth eye movements requires targets whose retinal locations overlap completely. This situation was studied originally by Ter Braak (1957) and Ter Braak and Buis (1970). They used what they called 'ambivalent optokinetic stimulation'. This consisted of a drum painted with interleaved sets of stripes on its outer surface. The stripes were painted so that one set appeared to be moving to the right and the other to the left when the drum was rotated. Subjects were able to smoothly track either set of stripes, and they were able to switch from one set to the other at will. This shows that foveal placement of a stimulus does not ensure that it will serve as the target for smooth pursuit, because, with the 'ambivalent' stimuli, the images of both sets of stripes

fell on the fovea, but it was up to the subject to decide which set to track.

Ter Braak (1957) and Ter Braak and Buis (1970) did not report eye velocities and, therefore, did not know whether the set of stripes moving in the background interfered with pursuit of the selected set of stripes. Kowler et al. (1984b) measured eye velocities with overlapping stimuli similar to those used by Ter Braak. Kowler et al.'s stimuli consisted of two, identical, superimposed, full-field patterns of randomly positioned dots, one stationary and the other moving to the left. The velocity of the moving pattern was deliberately set to a low value (1 deg/s) so that either field would be seen clearly regardless of which field the subject was tracking (Westheimer and McKee, 1975; Murphy, 1978). They found that subjects could keep the line of sight on either the stationary or the moving pattern with virtually no influence (<4%) of the background (Fig. 19). This result demonstrated that selectivity can be almost perfect when there were no differences in the retinal locations, indeed no differences of any sort, between the target and the background. Kowler et al. (1984b) also emphasized that subjects had tried their best to pay full attention to the target field. This kind of effort is important when drawing conclusions about selective capacity, because effects of backgrounds on smooth eye movements could easily result from instances of the subject not fully attending to the target, but allowing attention to wander to the background as well.

Kowler et al.'s (1984b) results had implications for the way in which the selectivity was achieved. A plausible view, consistent with the observations that had been made before their study, would be that selectivity is a matter of choosing velocity signals from one or another location in the display. This view is attractive because it is easy to envision neural motion detectors 'tagged' according to the location of their receptive fields. But selection of location could not explain how the subjects were able to pursue one dot pattern and eliminate influence of the other, superimposed pattern, because the stimulus fields were so dense that dots from one pattern were continually passing across dots of the

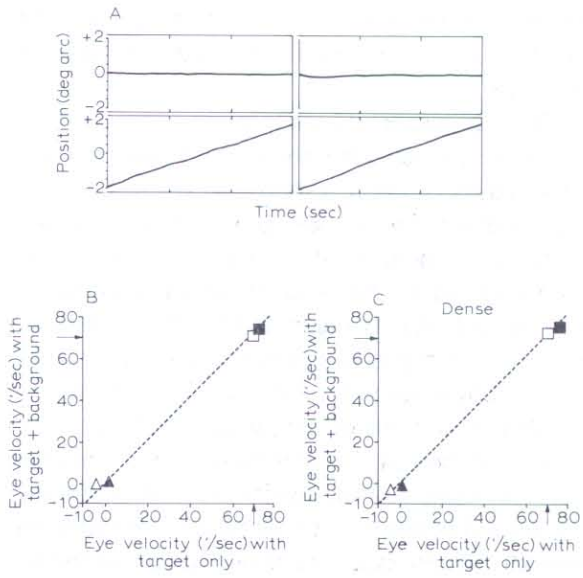

Fig. 19. (A) Representative records of horizontal eye movements for subject RS under instructions to maintain the line of sight on the stationary (top two graphs) or moving (bottom two graphs) field of random dots. In the lefthand graphs, only one field was present; in the right both were presented superimposed. Tick marks on the *x*-axis separate 1-s intervals. Upward deflections of the eye trace indicate movements to the left. (B) Mean 21-ms 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)

other. So, selection based on location would not distinguish the target field from the background field. Selection of one or the other stimulus velocity (or, simply, direction of motion) could be ruled out as well because the vivid, compelling percept of induced motion of the stationary field was never

reflected in the smooth eye movements (another example of not pursuing what we perceive; see section 3.5).

The elimination of both location and velocity as the basis for selection shows that selection was achieved by choosing a particular distinct perceptual configuration – a group of dots in the target field that was perceptually isolated from the dots in the background. This outcome means that the superimposed velocity signals must first be organized into distinct, segregated patterns before they reach the smooth oculomotor circuitry. This result, like the demonstrations of the pursuit of illusory motion, described in the previous section, provides another example of the significant central processing needed before motion signals are available for smooth eye movement control. Explaining the selectivity in Kowler et al.'s experiment requires the motion of the two superimposed fields to be segregated and the signals representing the velocity of each to remain 'tagged' according to the appropriate pattern of origin so that only the selected signals will be sent to the smooth oculomotor subsystem. How central motion analysers accomplish this is not known.

Kowler et al.'s (1984b) results also show that voluntary selective attention determines the target for smooth eye movement, but it does not determine smooth eye velocity directly. Had voluntary selection determined the eye velocity, the eye would have pursued the perceived induced motion. Instead, the eye velocity was determined by the retinal (or by the orbital) velocity of the selected field. This means that the voluntary selective processes are limited to telling the smooth oculomotor subsystem *what* to track. Information about the velocity of the chosen target, which is then used to compute the oculomotor commands, is carried separately by mechanisms that are not amenable to voluntary control and, unlike our percepts, blind to relative motion. (This 2-stage process, selection of input followed by computation of the motor command, will prove to be useful in accounting for some properties of saccadic eye movements, to be described in section 4.7.)

3.6.4. Perceptual and oculomotor selective attention

Is selecting the target for smooth eye movements equivalent to paying perceptual attention to the target? Or, do we have access to distinct selective processes, one serving the needs of perceptual judgments and the other of motor performance?

To answer this question Khurana and Kowler (1987) studied perceptual and oculomotor selection concurrently. Their experiment required subjects to pursue a target (a pair of rows of moving characters), while at the same time searching for a numeral located in the target rows and a numeral located in nearby, untracked background rows (Fig. 20). Subjects were better able to identify and locate the numeral in the tracked, target rows than in the untracked, background rows. Moreover, the superior performance for the target was due to attention – effects of retinal speed or retinal position were carefully ruled out. The results show that a single selective attentional decision determines the target for pursuit and for perception.

It is an ideal arrangement: we can control smooth eye movements by doing nothing other than paying attention to what we find of interest, regardless of the visual backgrounds streaming by. (And even this might not be too demanding. Khurana and Kowler (1987) found that shifting a bit of attention to the background improved its perceptibility slightly, while barely perturbing the ongoing pursuit.) Once we pay sufficient attention to our chosen target, the relevant velocity signals (whatever they may be) will determine the smooth eye movement command with no extra effort on our part.

This section on selective attention showed that central representations of the motion of selected (attended) targets provide the effective stimulus for pursuit. The next extends the description of the central representation of motion by showing that the effective stimulus consists of what we know about a target's future motion, as well as what we sense about its present motion.

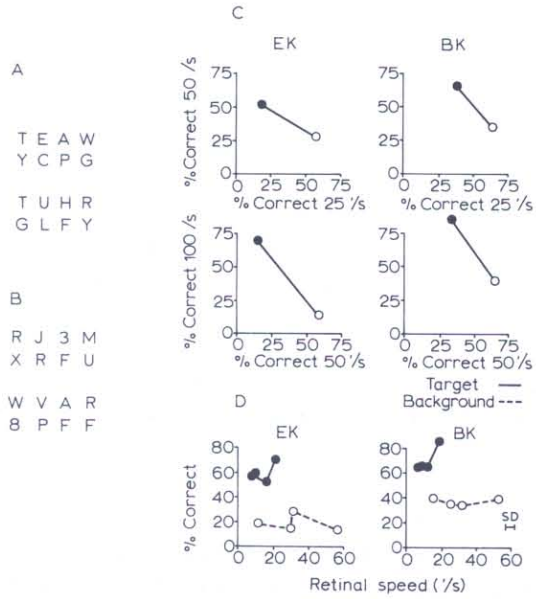

Fig. 20. (A) The stimulus used in an experiment which measured smooth eye movements and selective perceptual attention at the same time. An array of 16 characters began moving horizontally at the beginning of a trial. The velocity of characters in row 1 (top row) was the same as the velocity of row 3. Similarly, the velocity of row 2 matched that of row 4. (Velocities were as follows: when one pair of rows moved at 25′/s, the other moved at 50′/s; when one pair moved at 50′/s, the other moved at 100′/s.) The subject kept the 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 ms) by an array such as that shown in (B). Note that one numeral is present in each pair of rows. In this example, a '3' is in row 1 and an '8' is in row 4. Subjects had to identify both numerals and report the row in which they were located. (C) 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 filled symbol shows performance when the slower pair was the target, the open symbol when the faster pair was the target. Performance was always better for the target rows. (D) The same data points as in (C) plotted as a function of measured retinal speed. Performance was always better for the target rows and retinal speed was largely irrelevant. (From Khurana and Kowler, 1987.)

3.7. Smooth eye movements depend on expectations about the future path of target motion

The discussion of smooth eye movements up to this point has described sensory, perceptual and attentional contributions to pursuit. This section will show that smooth eye movements can be initiated and maintained by internal signals, representing expectations of future target motion, which are not derived from any immediate sensory or perceptual cues. One of the major themes of this section is that the processes which operate to produce anticipatory pursuit will contribute regardless of whether the target motion is 'predictable' or 'random'.

3.7.1. Anticipatory reversals

The effect of expectations on smooth eye movement was observed in some of the earliest studies of smooth pursuit. Dodge (1931) and Dodge et al. (1930) discovered that the eye would often turn around before the target during pursuit of periodic target motion – a phenomenon they named 'anticipatory reversal'. They also noticed 'preliminary drifts' (Dodge et al., 1930, p. 29) (drifts before the start of target motion) and said that the origin of this sort of eye movement was 'not yet clearly understood'. (There will be more discussion of the 'preliminary drift' in section 3.7.2.)

Westheimer (1954) also encountered the 'anticipatory reversals' in the first study to suggest the application of control theory to the study of eye movement. Westheimer, like Dodge before him and several others to follow, believed that anticipatory reversals were due to learning. The idea was that a stereotypical smooth oculomotor response would be learned after repeated cycles of tracking the same periodic, oscillating motion. Pursuit of random target motions, unlike the pursuit of periodic motions, was assumed to be immune to learning and anticipation, and dependent only on the underlying sensorimotor relationships (what Westheimer called 'psycho-optic reflexes').

Interest in anticipatory reversals reappeared in the 1960s when several investigators, in attempts to apply linear systems analysis to smooth pursuit, tried to predict the pursuit of a complex pattern of motion from the pursuit of its sinusoidal components. This proved to be impossible, as might be expected from the earlier work of Dodge and West-

heimer, because of the influence of anticipation on the pursuit of sinusoidal motions. Pursuit of sinusoidal motion showed higher gain and shorter phase lags than did pursuit of aperiodic, random motions (i.e., sums of sinusoids or bandwidth-limited Gaussian noise) (Stark et al., 1962; Dallos and Jones, 1963; Michael and Melvill Jones, 1966; St. Cyr and Fender, 1969b; Collewijn and Tamminga, 1984). Phase leads were often observed. The difference between the pursuit of the two types of motion can be seen in Fig. 10, which shows the average gain and phase of pursuit of sinusoidal motions (Fig. 10a) and random motions (Fig. 10b). Pursuit of random motions also depends on the bandwidth of the stimulus; the higher the bandwidth, the poorer the pursuit (Michael and Melvill Jones, 1966; Collewijn and Tamminga, 1984). In general, pursuit of random motions is quite poor and may not reduce retinal velocity sufficiently to support clear vision.

Modelers have tried to deal with the differences between the pursuit of sinusoidal and random target motions by assuming that a special, predictive element contributes only when the target motion is sinusoidal. For example, Dallos and Jones (1963) began their model with this assumption: "Probably the most straightforward way to think about these differences [between pursuit of sinusoidal and random stimulus motions] is to assume that all elements that are operating during the tracking of a randomly moving target will also be in the control loop during the following of a predictable input. The difference in system behavior for those two cases then must be sought in the presence of some compensating element during the tracking of periodic stimuli. This compensating element will be referred to as a predictor or learning operator" (p. 225).

Dallos and Jones provided a mathematical description of their 'predictor' by assuming that it was responsible for the observed differences between the response to sinusoidal and to random stimuli. The 'predictor' would have to 'know' when to participate, and Dallos and Jones suggested that it would be activated after the periodicity of the sinusoidal target motion had been detected. They assumed that the predictor was able to learn the repetitive pattern of motion and use what had been learned to pre-program the appropriate smooth oculomotor commands. But they found that phase lags dropped to asymptotic levels during the first cycle of pursuit (see Fig. 21), raising a major problem for the model because it seems unlikely that the 'predictor' would be able to learn the pattern of motion so quickly. Perhaps learning was not involved after all.

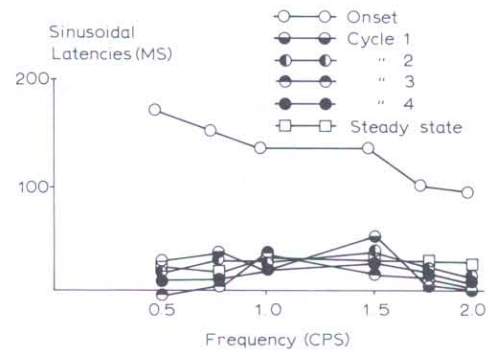

Fig. 21. Average latencies of one subject for the first few cycles of sinusoidal tracking. Steady-state latency is also shown. Note that latency reaches steady-state levels during the first cycle of tracking. (From Dallos and Jones, 1963)

There were also problems with the assumption that anticipation was restricted to the tracking of sinusoidal motion. Studies showed that the gain of pursuit of random motions was low (as expected) but, surprisingly, tended to *increase* with increasing target frequency, at least for target frequencies below 1 Hz. This was noticed by St. Cyr and Fender (1969b) and later by Collewijn and Tamminga (1984), whose analysis eliminated saccades from the measurements and left the pure smooth response (Fig. 10b). Collewijn and Tamminga (1984) also found pronounced phase leads for the smooth pursuit of the lower-frequency components of the random motions (Fig. 10b) – hardly what would be expected of pure sensorimotor processes.

If anticipatory influences were not due to the learning of a response to a stereotyped pattern of target motion, then what was going on? Considera-

tion of this question continues in the next section, which discusses modern studies of Dodge's 'preliminary drift'.

3.7.2. Anticipatory smooth eye movements before the onset of expected target motion

Recall that the 'preliminary drift' described by Dodge was a smooth eye movement that began before the start of target motion. This type of movement, which I will call 'anticipatory pursuit', does not conform to what investigators have come to expect of smooth eye movement, that is, anticipatory pursuits are not provoked by an immediately available sensory or perceptual signal because they occur while the target is still stationary. Also, anticipatory pursuits create, rather than correct, position and velocity errors because they take the eye away from the stationary target. Examples of anticipatory pursuit are shown in Fig. 22. An example of a particularly fast anticipatory pursuit (about 50 deg/s), is shown in Fig. 23.

Anticipatory pursuit has been observed often and has been studied in detail (e.g., Kowler and Steinman, 1979b,c, 1981; Kowler et al., 1984a; Becker and Fuchs, 1985; Boman and Hotson, 1988). These movements are about 10–25% of the velocity of the expected constant velocity motion. They are fastest when the direction of future target motion is known in advance, but they occur before motion in unpredictable directions as well (Kowler and Steinman, 1981). When the direction of target motion is unpredictable, the eye drifts in the direction the subject guesses the target will move (see Fig. 24). Anticipatory pursuits also occur before target motions at unpredictable times (Kowler and Steinman, 1979c) and at unpredictable velocities (Kowler and McKee, 1987). When the velocity of the target is unpredictable, the velocity of the anticipatory pursuit increases as the average velocity of the stimulus set increases (Kowler and McKee, 1987). These results show that randomization of stimulus parameters, by itself, does not prevent anticipatory pursuit. Instead, randomization affects the speed, direction or time of onset of the anticipatory pursuit so that these characteristics are best suited to the stimulus that is most likely to be presented.

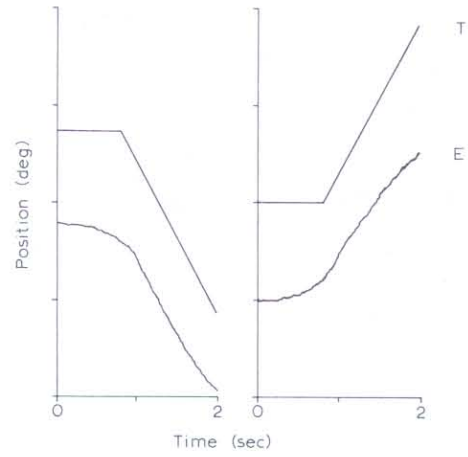

Fig. 22. Horizontal eye position (bottom traces) as a function of time during smooth pursuit of constant-velocity target motion (top traces) to the left (left-hand graph) and to the right (right-hand graph) for a naive subject. Note the start of pursuit about 300 ms before the target started to move. (From Kowler, 1989)

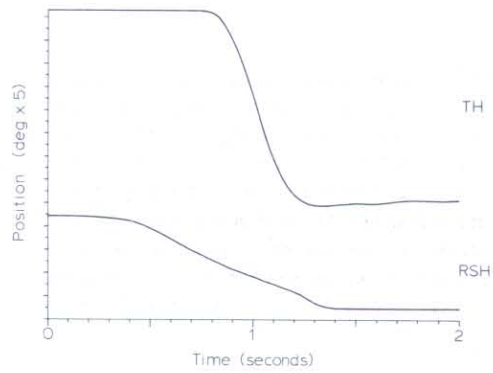

Fig. 23. Movements of the right eye (RSH) of a subject tracking a single point target (TH) moved by an experimenter across the subject's visual field. The subject knew the direction of target motion but did not know when the target was to begin moving relative to the onset of the trial. (Based on Collewijn et al., 1985)

The significance of finding anticipatory smooth eye movements before the onset of random target motions was stated clearly by Dodge (1931, p. 87):

"Some of our records show an important variant of the general picture of the first phase of pursuit. Possibly due to some more or less clear anticipation

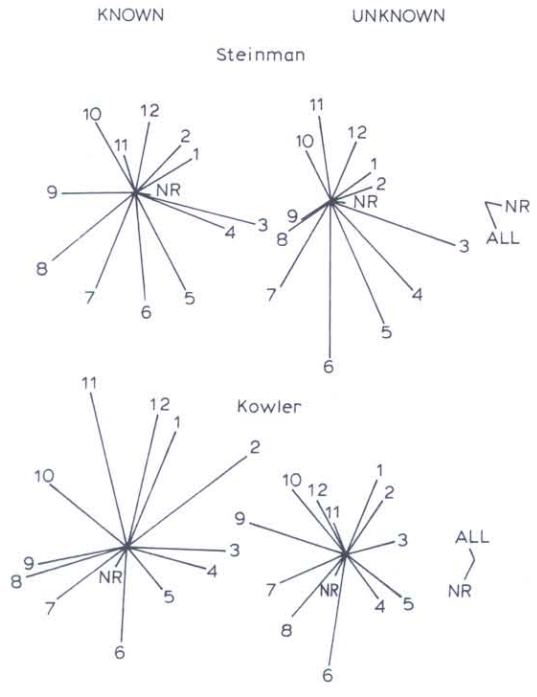

Fig. 24. The mean velocity of an anticipatory smooth pursuit eye movement before the onset of expected ramp motion away from center in the direction of the hours of the clockface. The numbers on the vectors denote the direction of ramp motion when ramp direction was *known* to the subject; the numbers when ramp direction was *unknown* denote the expected direction, which was reported before each trial. Mean eye velocity averaged over all directions (All) and in trials when no ramp motion was expected (NR) are also shown. (From Kowler and Steinman, 1981)

or set of which the record is the only indicator, the eye record may show a preliminary slow glide before the first saccadic refixation. In one record the preliminary glide is almost simultaneous with the beginning of objective motion in the other direction. It is obviously an anticipatory false reaction . . . *The unique feature of this record is the false anticipatory glide. If the start has been made in the right direction, this initial glide might have been read by the uninitiated as a true reaction with an extraordinarily short latency.* Such records should make us very conservative in measuring latencies from initial glides." (Italics mine.)

Dodge realized that anticipatory phenomena may easily escape notice, with significant consequences for the interpretation of the results. This is illustrated in the next section, which describes how expectations about future target motions continue to influence the pursuit response even after the target starts to move.

3.7.3. Effects of expectations on ongoing pursuit

As Dodge (1931) realized, anticipation is easy to detect when it produces something bizarre, such as a drift opposite to the direction of ongoing target motion (e.g., Kowler and Steinman, 1979c; Lisberger et al., 1981b). Anticipation is hard to detect when it produces something that, in principal, could have been accomplished by a reflexive sensorimotor process, such as an increase or a decrease in the speed of the eye relative to the speed of the target. Nevertheless, a role for anticipation during ongoing pursuit can be inferred because the pursuit response, even with randomly chosen stimuli, is modified according to the set of stimuli presented during an experimental session.

The effect of stimulus context is shown in Fig. 25. Each graph in the figure compares the response to the same constant-velocity target motion when it was tracked as part of a set of faster targets or a set of slower targets. The graphs show that the pursuit was faster when the target was tracked as part of the faster set.

The influence of the velocity-context is particularly clear during the first few hundred milliseconds of pursuit. Velocity-context acts to fashion a response that is suitable for the entire set of stimuli, rather than a response based exclusively on the current stimulus. As a result distinctions between responses to different stimuli are diminished. This is shown in Fig. 14, which contains eye velocity time-course functions taken from Kowler and McKee's (1987) study of oculomotor velocity discrimination (section 3.5). Each graph shows the response to the five target velocities tested during an experimental session. The particular target velocity was unknown to the subject and was selected at random before each trial. Each graph shows that the eye quickly accelerated to about the same value (near the mid-

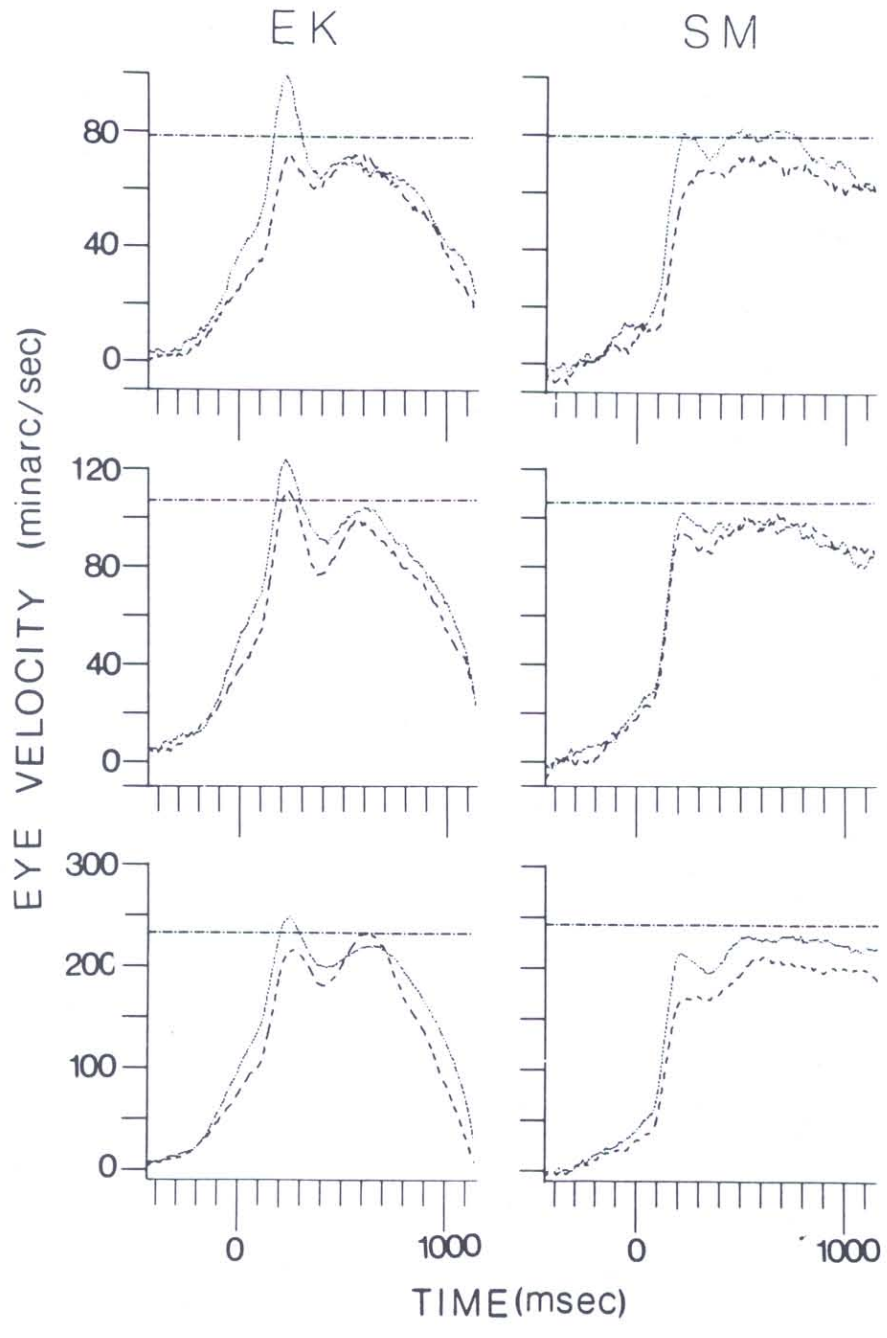

Fig. 25. Mean 100-ms eye velocity for subject EK (left) and SM (right) pursuing leftward target motion (target velocities given by the horizontal line in each graph). The dashed line shows eye velocity when the target was the fastest in a set of lower velocities, the dotted line when it was the slowest in a set of higher velocities. Eye velocity is shown as a function of the midpoint of successive 100-ms intervals whose onsets are separated by 10 ms. Target motion began at the interval labelled 0 on the absicissa and ended at 1000 ms for EK and at 1800 ms for SM. Velocities less than 0°/s indicate rightward motion. (From Kowler and McKee, 1987)

dle velocity of the set) for each of the five target velocities tested during an experimental session. The eye velocity functions did not fully sort themselves out until more than 0.5 s after the target had started to move – despite the fact that independent measurements of perceptual velocity discrimination showed that precise information about target velocity was available with 100–200-ms exposures. Evidently, smooth eye movements do not use such precise signals early in pursuit.

A similar tendency of context to obscure differences between responses to different targets was observed by Carl and Gellman (1987), whose data are shown in Fig. 26. One subject (Fig. 26c) tracked all the targets poorly. The other two (Fig. 26a,b) showed effects of context in that the slower targets in the set (5 and 10 deg/s) were tracked too fast and the faster targets (20 and 40 deg/s) too slowly. These effects of velocity-context are similar to the 'acceleration saturation' reported for smooth pursuit (e.g., Robinson et al., 1986) in that eye acceleration early in pursuit is slower than expected for the faster targets of a set, and faster than expected for the slower targets. It is tempting to attribute the 'acceleration saturation' to low-level sensory or sensorimotor phenomena, but the dependence of the initial acceleration on context suggests that higher-order processes are involved. These processes act before a target is presented to help generate a smooth response that is suitable for the likely, upcoming stimulus motion.

The dependence of the initial portion of pursuit on velocity-context shows that pursuit is launched based as much or more on the target motions of the immediate past, and the target motions expected in the near future, as on the current retinal signal. In this sense initial pursuit becomes an extension of the earlier, purely anticipatory portion. Becker and Fuchs (1985) also concluded that initial pursuit is an extension of the earlier anticipatory response based on their study of the pursuit of periodic, trapezoidal target motions. They found brisk initial pursuit during randomly selected episodes in which the visual target was removed from view just as the smooth target motion was expected to begin.

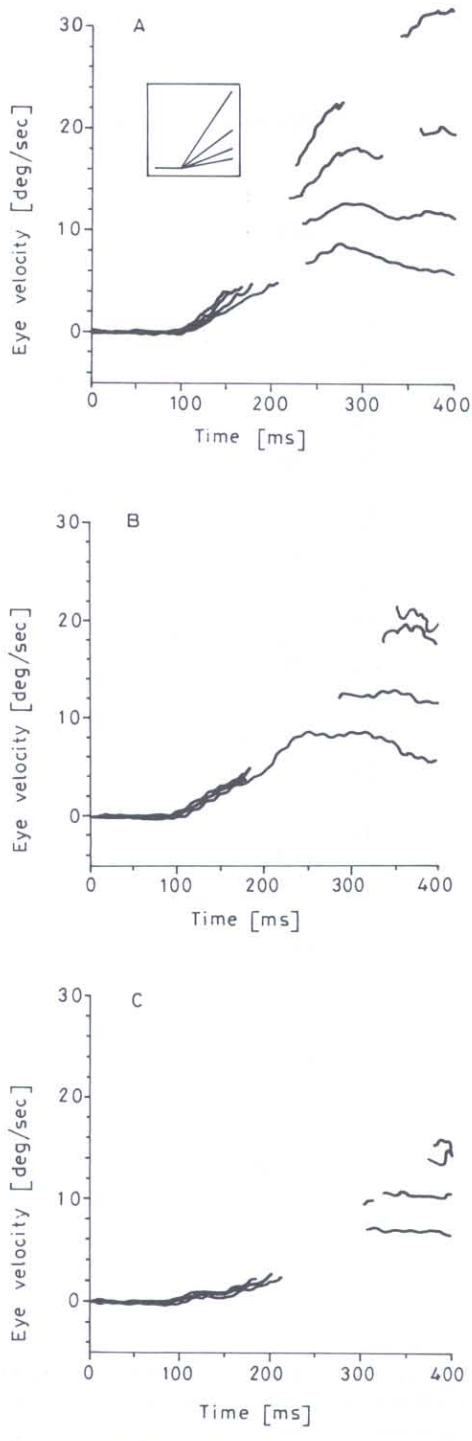

Fig. 26. Mean responses of three subjects to ramps of 5, 10, 20 and 40°/s. Each panel shows the responses of a different subject. (From Carl and Gellman, 1987)

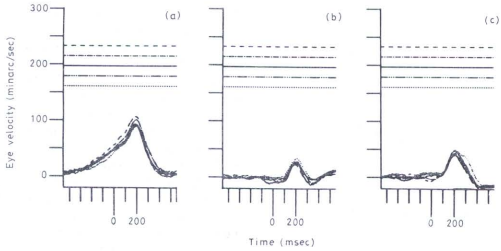

Fig. 27. Mean 100-ms eye velocity for subject EK pursuing briefly presented, constant-velocity target motion. (a) Leftward target motion when direction was known before the trial; (b) leftward and (c) rightward target motion when direction was selected at random. Eye velocity is shown as a function of the midpoint of 100-ms intervals whose onsets were separated by 10 ms. Target motion began at the interval labelled 0 on the abscissa and ended at the interval labelled 200. Velocities less than 0°/s indicate rightward eye motion in (a) and (b), and leftward motion in (c). The horizontal lines indicate the velocities of the targets. (From Kowler and McKee, 1987)

The dependence of the initial portion of pursuit on past history and expectations is shown vividly by the effects of expected duration. If the initial acceleration of the eye were to be evoked exclusively by the initial sweep of the target across the retina, then removing the target from view after the eye has had time to reach target velocity (usually within 200 ms of the onset of the target motion) should make no difference. But removing the target turns out to drastically inhibit the pursuit. When the duration of target motion is reduced to 200 ms, the eye hardly gets off the ground (see Fig. 27). Apparently, there is no brisk initial pursuit unless the target motion is expected to continue. Of course, it is possible to produce a faster response to the short-duration motions by mixing in some long trials. But this outcome does not mean that randomization lets the sensorimotor processes be revealed. It is another example of expectations intervening. When the duration of the target motion is randomized, the resulting pursuit response is a compromise: brief targets are tracked faster, and the longer-duration motions more slowly than when the duration of target motion is the same from trial to trial (see Fig. 28).

The evidence described in this section shows that the initial pursuit response is quite sensitive to the past history of stimulus motions and to expectations about future motion. In particular, past history and expectations reduce the sensitivity to stimulus differences in favor of the preparation of a response suited to the entire stimulus set. The contributions of past history and expectations make the initial response a poor indicator of the contents of the immediate sensory signals because these signals act on a system that is already predisposed to respond in a particular way. Indeed, the initial response may be the last place to look for fine-grain properties of the afferent signals, and one of the best to study past history and expectations.

3.7.4. Cognitive expectations vs. habits

The anticipatory phenomena described so far could have come from two sorts of process. One is the genuine cognitive expectation about the nature of the impending target motion. The second is more automatic and involuntary, for example, a trial-by-

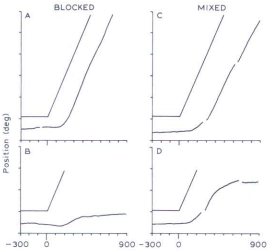

Fig. 28. Representative eye movement records showing smooth pursuit of 9.5°/s target motion, On the left (Blocked) the duration was set to a constant value of either 1 s (top graph) or 200 ms (bottom graph). On the right (Mixed), duration was selected randomly to be either 1 s or 200 ms on each trial. Note the brisk initial pursuit of the longer duration and the poor initial pursuit of the shorter duration motion in the Blocked condition. The initial response took on a value roughly in between these two extremes when durations were randomly mixed. The gaps in the eye traces indicate when saccades occurred. The eye traces were shifted by amounts roughly equal to the size of these saccades.

trial adaptive modification of some as yet unspecified aspect of pursuit whose goal is to promote the repetition of successful responses and discourage repetition of unsuccessful ones. Either of these processes could account for the findings summarized so far in this section, because in all cases the expectations about the future target motion were based on the past history of target motions.

Cognitive expectations and past history were separated in the following experiment (Kowler, 1989). Subjects pursued a target that moved downward inside an outline drawing of an inverted Y-shaped tube (see Fig. 29). At the junction of the right- and left-hand branches of the Y, the target would take either path with equal probability. The novel feature of this experiment was that in some sessions the path was disclosed before the trial by either an auditory cue (a synthesized voice saying 'right' or 'left') or by a visual cue (a barrier blocking access to the untravelled path).

In the sessions that did not contain cues, the velocity of anticipatory pursuit, measured before the target entered either oblique branch of the tube, was determined by the past history of target motions (Fig. 30a). The eye drifted rightward when prior stimulus motions were to the right and leftward when prior motions were to the left. The dependence on prior stimulus motions needs a bit more elaboration, because these 'sequential dependencies' illustrate the contribution of anticipatory processes when the subject does not know which motion will be presented. Kowler et al. (1984a) found the same pattern of sequential dependencies for anticipatory smooth eye movements before target steps in randomly chosen directions. Falmagne et al. (1975) had found an analogous pattern for two-choice manual reaction time in a button-pressing task. The sequential dependencies in both studies could be predicted by Falmagne et al.'s finite-state Markov model, in which the subject was assumed to prepare for one of the two possible stimuli before each trial. The model represents an adaptive process in that the preparatory state tends to be preserved following effective (accurate) responses and to change following ineffective (or inaccurate) responses (see Pavel's chapter for further discussion of adaptive models).

Adaptive processes, based solely on the effectiveness of prior responses, cannot, however, be the whole story. In the presence of the cues, which told the subject which stimulus would be presented, the anticipatory pursuits were determined by the direction in which the subject expected the target to move (Fig. 30b,c). Effects of the past were small, and clearly overridden by the cognitive expectations about future events.

This experiment shows that internal signals, representing expected target motion, and based on the processing of symbolic cues in the environment, can serve as stimuli for pursuit, just as if they were signals representing actual target motion. High-level, symbolic information, contained in the visual array, is being represented in a form that provides

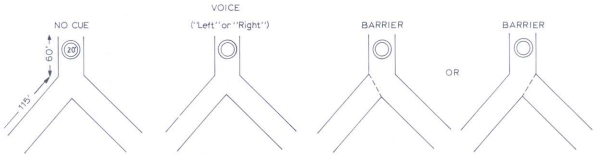

Fig. 29. The stimulus display in the experiment comparing habits to cognitive expectations. It consisted of a stationary inverted-Y-shaped tube and an annulus which served as the moving target. The velocity of the target was 130°/s. The target moved down the tube and continued at the same velocity down 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°/s). 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 right-hand branch. (From Kowler, 1989)

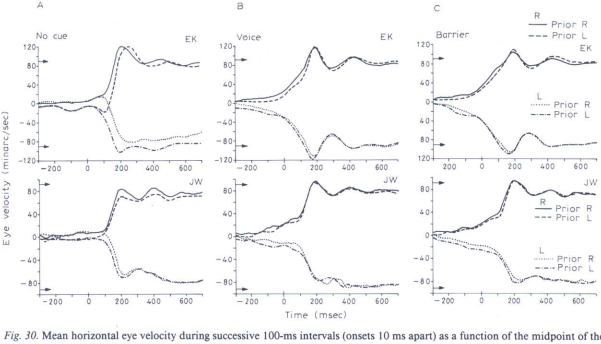

Fig. 30. Mean horizontal eye velocity during successive 100-ms intervals (onsets 10 ms apart) as a function of the midpoint of the interval when either (A) *No Cue*, (B) a *Voice* cue or (C) a *Barrier* cue about the direction of future horizontal target motion was given. Top graphs, EK; bottom, naive 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 preceding trial was to the right; the other when the target motion in the preceding trial was to the left. Each mean is based on 80–100 observations. Standard errors were 1–2°/s and as high as 3°/s (5°/s with *No Cue*) only during the interval (0–200 ms) of most rapid eye acceleration. (From Kowler, 1989)

an effective, compelling signal to drive what is historically taken to be a low-level reflexive response.

3.7.5. Implications for the study of random target motions

The studies of anticipatory pursuit have implications for the interpretation of pursuit in the typical laboratory situation, in which stimuli are selected at random, often from large and diverse stimulus sets. This procedure has been defended on the grounds that randomization will eliminate or minimize the contribution of expectations, leaving the response solely in the hands of low-level sensorimotor processes. We have already seen that randomization, with no cues provided about the direction of future motion, does not eliminate the effects of stimulus set on pursuit (section 3.7.3) and does not eliminate anticipatory pursuit (Fig. 30a). Randomization is not eliminating expectations – it will not prevent guessing (Kowler and Steinman, 1979c, 1981) or sequential dependencies (Kowler et al., 1984a). Randomization is determining a particular preparatory state adopted before each experimental trial. An important consequence of this fact for models is that the stimulus-response relationships observed in one particular experimental context might not hold up in others. This limitation could be addressed by extensive investigation of various experimental contexts, or, preferably, by developing models which explictly incorporate *both* expectations and sensorimotor constraints, rather than models which assume that expectations can be ignored. It seems that incorporating expectations would be particularly useful because in most studies the random stimuli tested actually share many features (such as the duration or the meridian of the target motion), which would allow expectations to improve pursuit in ways that would not be readily noticeable in the data.

A different, and potentially more serious, problem with drawing conclusions based exclusively on studies with random motions is that such studies might not reveal the fundamental principles determining how smooth eye movements work. Realize that smooth pursuit is not particularly effective when randomization is sufficient to preclude accurate anticipatory movements. For example, pursuit of complex, random patterns is poor (3.7.1) and pursuit of randomly selected constant-velocity motions takes several hundred milliseconds to settle down (3.7.3). This suggests that, left to themselves, the low-level sensorimotor reflexes might not be able to guarantee pursuit which is accurate enough to support clear vision. And perhaps it is just as well. Random stimuli are unnatural. In natural environments, cues about the future direction and speed of target motion are plentiful. We have already seen that such cues can be used by observers for the programming of accurate anticipatory pursuits. Perhaps the best way to understand smooth eye movements, in the long run, will require studies of pursuit of cued patterns of motion, so that the stimulus to the lower-level sensorimotor circuits, consisting of the present target motion along with the expectations, will always be known.

3.8. Overview of smooth eye movement

This section on smooth eye movement has challenged the conventional assumptions, described in sections 3.1 and 3.2, that sensory signals operate in some automatic fashion to determine smooth oculomotor commands. This assumption may work very well for animals such as the rabbit (3.3), but for human beings the assumption was called into question because of the prominent role of central and subjective factors. We have seen, for example, that centrally organized motion signals can drive pursuit (3.5). We have also seen that velocity signals are organized into patterns before the selected signals reach the smooth oculomotor circuitry (3.6). And we have seen that the effective stimulus for pursuit includes a signal representing the stimulus motion hundreds of milliseconds into the future (3.7).

Cognitive and subjective factors are not, of course, the whole story. In the absence of normal visual feedback, idiosyncrasies are rampant (3.4). Moreover, the sequential dependencies show that the results of pursuit are closely monitored to keep the response within acceptable limits (3.7). At this

point, we are very much in the dark because basic questions have not been addressed. What, for example, defines an acceptable pursuit response? Achievement of some optimal retinal velocity, or, perhaps, some indication that the target is seen clearly?

The theme of this section has been that answers to such questions, and a more complete understanding of pursuit, may be better obtained if we acknowledge the role of central and subjective factors from the outset and try to formulate as complete a description as possible of the complex input signals which are sent to the lower-level oculomotor circuitry. In the meantime, we might enjoy the cleverness of nature in linking the involuntary oculomotor pursuit to an active and busy consciousness. Why, after all, should one go to the trouble of designing a visual algorithm for selecting a target or computing its velocity purely from momentary sensory cues when the human being has already decided which target is of interest and already knows something about when and where it will begin to move?

The following section considers saccades. These are voluntary motor responses, in the sense that they can be initiated in whichever direction one wishes, regardless of the presence or the nature of the visual array. As a result no special demonstrations will be needed to show that central and subjective factors must be included in order to correctly interpret the performance.

4. Saccades

4.1. Saccades, unlike smooth eye movements, may be, and probably always are, initiated voluntarily

Voluntary control of saccades may be demonstrated simply by noticing that it is possible to look around all sorts of visual environment whenever or wherever you choose.

The wide appreciation of volitional control has encouraged the use of saccades as overt indicators of otherwise hidden cognitive processes. (For comprehensive reviews and evaluations, see the chapters by Suppes, Viviani and O'Regan.) Reading thoughts from saccades is a dangerous business if it is assumed that where one looks, or how long one looks in a given place, is completely a function of choice or interest, independent of the constraints imposed by the saccadic programming apparatus itself. On the other hand, equally troublesome would be a search for invariant relationships between the visual stimulus and saccades under the assumption that performance is completely a function of the stimulus configuration, ignoring the contributions of voluntary choice, selective attention and expectations. The following sections will summarize research on saccadic capacities with the goal of elucidating the constraints imposed by sensorimotor processes and by central and subjective factors.

4.2. The endpoint of saccades relative to a target stimulus may be controlled by the subject

A conventional way of studying saccades has been to ask a subject to move the eye to a small target that appears suddenly in eccentric vision. The reaction time, the size and the direction of the saccade are measured. The target usually disappears from its central location just as the new eccentric target appears; thus, the target is actually moving from one location to another and is appropriately called a 'target step'.

Observers often make saccades that are inaccurate ('undershooting' or 'overshooting') (e.g., Becker and Fuchs, 1969; Frost and Poppel, 1976; Wyman and Steinman, 1973a), sometimes with reliable errors of offset position of up to 30–50% of the size of the step (Timberlake et al., 1972). Such errors are not compulsory. Saccades to continuously visible targets can be far more accurate (Collewijn et al., 1988a,b; Lemij and Collewijn, 1989). Also, subjects can control the endpoint of the saccades. They can decide to make a saccade that either falls short of, or exceeds, the position of the target (Steinman et al., 1973), or is in a direction opposite to the direction of the target step (e.g., Hallett's (1978) 'anti-saccades'), or lands in a selected location with-

in a simple outline drawing of a form (He et al., 1988). Some of the deliberate mislocalizations, such as the 'anti-saccades', occur at the cost of increased latency or decreased spatial precision. Nevertheless, the capacity to adjust saccade size shows that the endpoint can be chosen by the individual using visual information as a guide.

How precisely the chosen saccadic endpoint can be reached will depend on limitations imposed by sensorimotor processes. Examples of such limitations will be described in the next section.

4.3. The eccentricity of the visual target affects the spatial precision and the latency of saccades

The effect of the retinal eccentricity of the target on the spatial precision of saccades is shown by the increase in the variability of the size of the saccade as the size of the target step increases (Timberlake et al., 1972). Fig. 31, based on Timberlake et al.'s data, shows the effect of target eccentricity on the *relative* precision of saccades. Relative precision is described by the ratio of the standard deviation of saccade size to the size of the target step. (This measure is analogous to Fitts' (1954) 'index of difficulty' for manual responses and to the Weber fraction for perceptual reports.) Fig. 31 shows that the ratio of the standard deviation of saccade size to the size of the target step decreases as the size of the step increases, reaching an asymptotic value of about 0.1 at a step size of 2 deg. An interesting property of this curve is the discontinuity at 40′, near the edge of the foveal floor (Polyak, 1941), which represents a transition to a less precise localization mechanism. A discontinuity occurs at the same place in standard tests of visual acuity (e.g., Millodot, 1966), suggesting that the precision of visual mechanisms which code the spatial location of the target sets a limit on the spatial precision of saccades.

Limitations other than those imposed by visual mechanisms are probably needed to explain the reduction in the relative precision of saccades for target steps smaller than 30 minutes of arc, shown in Fig. 31. Nonvisual sources are involved because the relative precision of perceptual judgments of

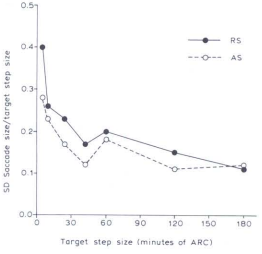

Fig. 31. The ratio of the standard deviation of saccade size to the size of the target step as a function of the size of the target step for subjects RS and AS. (Based on Timberlake et al., 1972)

spatial distance is quite good for distances smaller than 30 minutes of arc. For example, observers can reliably discriminate differences of about 8% in the size of small target steps; perceptual discrimination improves to about 2% when the task is to discriminate the distance between two stationary references (Westheimer, 1979). Clearly, we can estimate small distances more precisely than we can track small displacements of a target.

The spatial imprecision of small saccades is not limited to the tracking of target steps. Haddad and Steinman (1973) asked subjects to make the smallest saccade they could away from a stationary point target. They found that the average size of the saccade was about 5.5′, with a standard deviation of 2.5′. The ratio of the standard deviation to the size of the saccade is about 0.45, about the same ratio observed for the saccades made to track 5′ target steps (see Fig. 31).

The large SD/step-size ratios for small target steps, described above, show that precise control of small saccades is difficult to achieve. The difficulty is further demonstrated by the long latency of the saccades made to track small target steps. Average saccadic latency in target step-tracking tasks in-

creases only slightly (about 20 ms) as step size increases from 30′ to 40 deg (Bartz, 1962; White et al., 1962; Heywood and Churcher, 1980; Frost and Poppel, 1976), but latency increases sharply (by more than 100 ms) as step size decreases from 30′ to 3.5′ (see Fig. 32) (Wyman and Steinman, 1973b; Kowler and Anton, 1987). The long latency of the saccades made to track small target steps shows that the increase in the SD/step-size ratio for small saccades (Fig. 31) was not due to a decision to sacrifice the spatial precision of saccades in order to shorten the latency, and suggests that small saccades are relatively difficult to program.

The difficulty subjects have in exercising precise control over the spatial and the temporal properties of small saccades may account for previous beliefs in a ¼to ½deg saccadic 'dead zone'. The saccadic 'dead zone' was proposed by Rashbass (1961), who found that target steps this small were not tracked. Yet subjects will track target steps as small as 3′ if they are explicitly asked to do so (Wyman and Steinman, 1973a), showing that the 'dead zone' is not a hard-wired limit, and may represent no more than the understandable reluctance to try to do a hard task.

Fortunately, the difficulty subjects have controlling small saccades, and any consequent reluctance to use them, should not cause any visual difficulties. Psychophysical studies have so far turned up no useful role for saccades smaller than about 15′. For example, subjects choose to avoid making any saccades when they perform finely guided visuomotor tasks (such as threading a needle) which force attention to be paid to small, circumscribed areas (Winterson and Collewijn, 1976; also, Bridgeman and Palca, 1980, for the same result using a video version of a needle-threading task, which did not involve any movements of the arm or fingers.) Also, using saccades to count the items haphazardly arranged in a 30′ diameter field does not improve counting accuracy beyond what can be achieved with a stationary eye, even though larger saccades (about 20–30′) are helpful when items are contained in a 2° diameter field (Kowler and Steinman, 1977, 1979a). The retinal transients accompanying

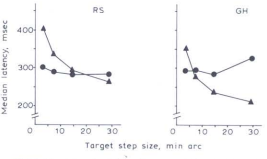

Fig. 32. Median latencies of the first saccade in the direction of the target step for target steps of different magnitudes when the subject was instructed to track the target step (triangles). The circles show latency when the target step served as a signal to go to a continuously visible second target located 14′ below the target that stepped (circles). Saccades to the continuously visible target were unaffected by step-size, showing that the long latency of the saccades used to track small steps (triangles) was due to factors connected with saccadic programming, rather than with stimulus detection. The left graph shows the data for subjects RS; the right graph for subject GH. (From Wyman and Steinman, 1973b)

saccades are not particularly helpful for vision (cf. Kowler and Steinman, 1980), or for visual information processing (Kowler and Sperling, 1980; 1983). Smooth movements of the eye are optimal for visibility (see Steinman and Levinson's chapter) and, if anything, saccades will produce retinal smears and rapid retinal image motion, which can impair various sorts of perceptual judgment (Volkmann, 1986; also, Sperling's chapter, this volume).

It is unlikely that any useful role for the small saccades will ever emerge. The studies of latency and spatial precision, described above, have shown that saccades are hardest to use just where we need them the least: in the central ½deg of the retina where visual discrimination is most acute. This makes previous ideas that small saccades control the position of the eye during maintained fixation (Cornsweet, 1956; Krauskopf et al., 1960), or constitute a controlled, miniature search pattern of small regions (Steinman et al., 1973), or reduce visual thresholds (Ditchburn, 1980), or contribute to the perception of forms (Gaarder, 1960), seem implausible. Small saccades are simply not up to any of these jobs, and they are not needed for them.

The precision of visual capacities in the central retina is much better than the precision of the saccades that can be made to inspect this region.

The spatial imprecision of small saccades, in contrast with the highly precise visual judgments in the central fovea, also implies that saccades do not have access to the same precise information about target position that is available for visual judgments, or else that saccades receive precise information about target position, which is then obscured by other sources of variability, such as limitations inherent in the oculomotor output machinery.

The material in this section summarizes some of the relationships between saccades and the spatial properties of the stimulus. The next section explores some of the relationships between saccades and the temporal properties of the stimulus. This discussion will bring back the issue of anticipation, which was considered in the section on smooth eye movements (see 3.7). For example, anticipation is needed to explain why saccades can be used to track 'predictable' target steps (square-wave target motion) with little or no latency (Stark et al., 1962; Dallos and Jones, 1963). Further discussion of the role of anticipation in saccadic performance begins in the next section.

4.4. Saccadic commands can be prepared, in whole or in part, before the appearance of the eccentric target

When a subject is asked to make some sort of manual response, a button press, for example, to indicate which of many possible stimuli were presented, the reaction time of the response is found to depend on the number of possible stimulus alternatives (see Luce, 1986, for a review and analysis of this phenomenon). The demonstration that the reaction time to a stimulus depends on the number of alternatives is a classic indication that the response is not evoked reflexively by a stimulus, but depends, in part, on preparations that occur before the stimulus appears.

Oculomotorists have not been able to agree about whether there is a comparable dependence of saccadic reaction time on the number of alternative stimuli, a disagreement which has led to some confusion about whether to treat saccades as voluntary motor responses, or as reflexes elicited by eccentric stimuli. Hackman (1940) found that saccadic latency decreased when subjects knew which one of 8 possible stimulus locations would contain the target. But Saslow (1967b), who criticized Hackman's experiment because an audible click accompanied each stimulus, found that reaction time remained the same (about 200 ms) as the number of possible target locations increased from 2 to 8, regardless of whether the locations were on the same or opposite sides of the fixation target. Saslow's (1967b) results were later confirmed by Heywood and Churcher (1980), who found no effect on saccadic latency of increasing the number of alternative target locations from 2 to 16, but not by Michard et al. (1974), who found that latency increased as the number of alternatives increased from 2 to 4. Interpretation of the relationship between reaction time and the number of possible stimulus alternatives is complicated because many unambiguously voluntary responses, such as speaking, do not show this dependence either (Luce, 1986).

The number of alternative stimuli did prove to be influential when the task was harder than the tracking of a single, stepping target. For example, Viviani and Swensson's (1982) subjects were told to look at a target form which was embedded in a field of many different background forms. They found that the latency of saccades was reduced by decreasing the number of alternative locations that might contain the target form.

There is less disagreement that saccades are affected by changing the relative probability of finding a target in a given location. Norcia et al. (1979) and Kowler et al. (1984a) found that the latency of saccades was shorter for targets in more probable locations. (Kowler et al. (1984a) also found sequential dependencies analogous to those observed for anticipatory pursuits (see section 3.7.4), i.e., shorter latency and improved accuracy for saccades to steps preceded by steps in the same direction.) He and Kowler (1989) found effects of location probability

on saccadic accuracy when the task was to look as quickly as possible at a target presented in the company of a nontarget stimulus. Saccades were accurate, and location probability was not influential, in an easier task in which the target was presented alone, without a nontarget. (See section 4.7.1 for further discussion of this experiment.)

The studies summarized above show that location probability is most influential when the task is fairly difficult, and when subjects are encouraged to respond quickly, even if responding quickly diminishes the accuracy of the saccade. This is not too surprising. There have been several reports that subjects can trade-off saccadic latency for accuracy (e.g., Steinman et al., 1973; Findlay, 1981; Viviani and Swensson, 1982; Ottes et al., 1985; Coëffé and O'Regan, 1987). The need to respond quickly in a difficult task would encourage the preparation of saccadic programs before target localization was completed. Such programs would be expected to incorporate information about the likely location of targets, rather than be based exclusively on information acquired from the immediate visual display.

The studies of the effects of probability on saccades show that saccadic performance results from the combined influence of newly acquired visual information, along with the past experience and expectations of the subject. The same point was made about smooth eye movements in section 3. The discussion of how past experience, expectations and lower-level sensorimotor factors determine saccadic programming continues in the next section, which considers what happens when various sorts of stimulus appear (or disappear) in the field of view at about the time that the visual target appears.

4.5. Saccadic latency is affected by the abrupt appearance or disappearance of stimuli

4.5.1. Signals that facilitate or delay saccadic programming

A classic characteristic of manual responses is that a warning about the impending appearance of the stimulus reduces the reaction time (cf. Luce, 1986). Saccades show the conventional effects of warnings in that the latency is reduced when the warning stimulus precedes the appearance of the target (Saslow, 1967a; Ross and Ross, 1980).

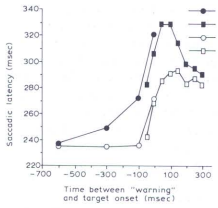

Fig. 33. Mean saccadic latency as a function of time between a warning signal and the appearance of an eccentric target. Filled symbols show latency when the warning was conveyed by the onset of a central stimulus, open symbols by the offset. Negative values on the abscissa indicate that the warning preceded the appearance of the target. Data are taken from experiments 1 (circles) and 2 (squares) of Ross and Ross (1980).

An example of the effects of warning signals on saccadic reaction time appears in Fig. 33, based on Ross and Ross (1980). They found that saccadic latency was shortened by warning signals which preceded the appearance of the target. Things were a bit more complicated, however, because warnings conveyed by the offset of a central stimulus (that is, the offset of a stimulus located near the initial fixation point) were more effective than warnings conveyed by the onset of a central stimulus. Moreover, central onsets that occurred while programming was in progress, i.e., during the 200 ms interval following the appearance of the visual target, were harmful, increasing saccadic latency by about 40 ms. Central offsets during this period had no effect. Mackeben and Nakayama (1988) demonstrated a comparable dissociation between the effects of central onsets and central offsets in a psychophysical task requiring a shift of attention to an eccentric target while the eye remained stationary.

These studies, describing what happens when central stimuli abruptly appear or disappear, have shown that saccades are clearly subject to conventional 'warning' effects. In addition, the abrupt appearance of a central stimulus can delay saccadic programming, and the abrupt disappearance of a central stimulus might facilitate programming, for reasons which appear to be unrelated to the preparatory processes usually invoked to explain the effects of warning signals.

4.5.2. 'Express' saccades

The effects of the onsets and offsets of central stimuli on saccades, described in the previous section, should not be confused with the so-called 'express' saccades (Fischer and Boch, 1983; Fischer et al., 1984; Boch et al., 1984; Boch and Fischer, 1986; Schiller et al., 1987, in monkey; Fischer and Ramsperger, 1984, 1986; Mayfrank et al., 1986; Fischer and Breitmeyer, 1987, in human beings). 'Express' saccades are said to have unusually short latencies (about 100 ms) and are observed when the sudden disappearance of a central fixation stimulus is followed after a temporal 'gap' of 200 ms by the onset of the eccentric target. ('Express' saccades are extremely rare when the fixation point remains visible; Mayfrank et al., 1986; Becker, 1989.) 'Express' saccades have been referred to at various times as 'reflex-like eye movements' governed by a distinct mechanism (Schiller et al., 1987; Fischer and Breitmeyer, 1987) or as a distinct 'population' of saccades attributed to a special 'internal state' of the visual or oculomotor system (Mayfrank et al., 1987).

Not all saccades are 'express', according to the references cited above. The latency distributions are said to be bimodal, with the second peak occurring at a latency of about 150 ms. Mayfrank et al. (1986) and Fischer and Breitmeyer (1987) have attributed the 'express' saccades to what they have called a 'disengagement of attention' from the central visual target. But the experiments are open to a simpler interpretation, namely, that the instances of extremely short latencies were due to conventional warning effects. In the experiments cited above, the offset was a completely reliable warning about the time of appearance of the target because the time between the offset and the appearance of the target (the 'gap') was always 200 ms. In one experiment in which 'gap' duration was randomized, the range of tested 'gaps' was small (200 vs. 220 ms) and the location of the eccentric target was always the same (Fischer and Ramsperger, 1984; Fig. 2c). Even in cases in which target position was randomly varied (4° right vs. 4° left) and the fixation point remained visible (a situation producing relatively few 'express' saccades) the target, nevertheless, appeared at a known time (2 s after the onset of the fixation point). So, the experimental arrangements that produce 'express' saccades offered considerable advance information about when or where the target would appear and, therefore, allowed the subjects to save time by preparing at least a portion of the saccadic program in advance.

The advanced preparation of saccadic programs would seem not to have played a role in Schiller et al.'s (1987) studies of 'express' saccades in monkey, because both the location of the target and the duration of the 'gap' were randomly chosen from among a few possibilities (fewer than 6 target locations and 7 gap durations). The distribution of saccadic latencies was bimodal, with the earlier saccades (latency 100 ms) representing the 'express' variety, and the rest representing ordinary saccades (latency about 150 ms). Distributions of saccadic endpoints were not provided, but for the purposes of the present discussion possible latency-accuracy relationships (see section 4.4) will be ignored and the distributions of the endpoints of the short- and long-latency saccades will be assumed to be the same. Could the advance preparation of saccades have accounted for Schiller et al.'s results?

An 'all-or-none' advanced preparation of saccades would not. By 'all-or-none' I mean that the subject prepares an unmodifiable saccadic program before the stimulus appears. This kind of advance preparation would be expected to lead to many errors, or to saccades occurring before the appearance of the target. It was the absence of either of

these phenomena in Schiller et al.'s (1987) experiment (monkeys were not rewarded either for early or for erroneous saccades) that led the authors to discount advanced preparation. Nevertheless, there are other ways for advanced preparation to influence saccades which would not necessarily produce either errors or early saccades. These include: (1) the advanced preparation of a selected aspect of a future saccade, such as the preparation of the saccade size without specification of its direction until the stimulus appears (see Rosenbaum et al., 1984, who demonstrated the advanced preparation of selected aspects of finger movements); (2) the storage of prepared motor programs in a memory buffer, which is scanned for the appropriate program after the reaction signal is given to begin responding (Sternberg et al., 1978a,b; Zingale and Kowler, 1987); or (3) the establishment of overlearned, habitual motor sequences, which can be executed at unusually high speeds (Craik, 1947; Lashley, 1951; Levy-Schoen, 1981; Steinman et al., 1973). The kinds of preparatory process described above could have played a role in Schiller et al.'s (1987) experiments without producing either erroneous or early saccades. For example, consider the experiment which tested four gap durations (0, 50, 100, 200 ms) and four possible target locations. Suppose that the monkey begins to prepare motor programs for the four saccadic commands in sequence as soon as the warning stimulus occurs and stores the programs in short-term memory. (Properties of this memory, such as its capacity and the length of time its contents can be maintained without decay, would have to be determined experimentally.) The preparation continues until the eccentric target appears, when the monkey begins to search the set of prepared, stored programs for the one he needs. If the appropriate program had already been prepared, and was still present in the memory buffer, then saccadic latency would be quite short because all the monkey would need to do is retrieve the program from memory and begin execution. If, however, the appropriate program had not been prepared, then preparation would have to begin from scratch and, as a result, saccadic latency would be increased. This model predicts that the proportion of accurate 'express' saccades would increase with increasing 'gap' duration because the probability that the appropriate saccade was pre-programmed would increase the more time the monkey had to complete the preparation. In fact, the proportion of 'express' saccades did increase (from 32% to 94%, in the example given in Fig. 2 of Schiller et al.) as the 'gap' duration increased from 0 to 200 ms. Attributing the short-latency saccades made by Schiller et al.'s monkeys to a preparatory process, such as the simple one I have described, rather than to a special 'express' saccade generator, seems reasonable in the light of the fact that the animals were highly trained (Schiller et al. report that the animals performed 1000 to 2000 trials per day). Training would be expected to facilitate saccadic programming processes based on learning and memory, and would not be expected to influence low-level reflexes.

The research summarized in this section shows that, while the offset of a central stimulus can be a more effective 'warning' signal than the onset (Ross and Ross, 1980), central offsets (or 'disengagements of attention') do not evoke the so-called 'express' saccades. Evidence does not warrant attributing a subset of saccades with very short latencies to a special class of eye movements. Short-latency saccades can result from conventional 'warning' effects, or from a variety of potentially interesting phenomena involving the advanced preparation of saccades. The suggestion of bimodality in a response latency distribution is insufficient reason to posit separate classes of saccades.

To make this point more clearly, it is instructive to consider that the suggestion of bimodality in a distribution of latencies of finger movements is insufficient reason to posit a separate class of finger movements. There are other approaches to the analysis of latency distributions which do not propose different classes of responses. Studies of manual reaction time have long focused on the analysis of latency distributions and the development of analytic techniques to predict the parameters of the distributions based on the probabilities of the subject's being in one or another preparatory state. For

example, in a model proposed by Falmagne et al. (1975) (mentioned briefly in section 3.7.4) to account for sequential dependencies in a two-choice manual reaction time task, subjects are assumed to be preparing for either one of the two possible stimuli before each trial. If the stimulus presented in a trial is the one the subject had anticipated, then reaction time is drawn from one distribution; if the other stimulus appeared, reaction time is drawn from a different distribution with a higher mean value. The resulting distribution of reaction times to the presentation of each stimulus is thus a weighted mixture of the two underlying distributions, one for the trials in which the subject had been prepared for the stimulus, and the other for trials in which he had not been prepared*. In other words, short latency responses aren't special reflexes; they are responses to those stimuli which happen to have been correctly anticipated by the subject. The important point is that the same preparatory process needed to explain distributions of manual reaction times may explain distributions of saccadic reaction times as well without proposing separate short and long-latency saccadic mechanisms. Development of saccadic models based on ideas about preparatory processes, and investigation of the different internal operations that constitute 'preparation', may in the long run lead to more satisfactory models of saccades than speculations about special saccadic mechanisms.

* Falmagne et al. (1975) described the preparatory process in terms of memory search. They proposed that the subject identifies the stimulus (consisting of one of two simple forms) presented on each trial by comparing it, in sequence, with memory representations of each of the two possible stimuli. So, preparation for stimulus 'A' meant that the actual stimulus presented on the trial was compared first to the memory representation of stimulus 'A' and then to the memory representation of stimulus 'B'. Although Falmagne et al. chose to describe preparation in terms of memory search, a variety of other internal preparatory processes would also be consistent with the formal properties of their model.

I will next consider inferences drawn about saccadic programming from what would appear to be simple variants on the typical single target-step experiment described so far. These are: (1) saccades to two consecutive target steps, which led to inferences about the integration of target-location information over time, and (2) saccades to a target among visual backgrounds, which led to inferences about the integration of target-location information across space.

4.6. Saccades to two consecutive target steps suggest an ability to adjust saccadic programs quickly on the basis of newly acquired stimulus information

Interest in studying the saccades made to track two consecutive target steps began with Westheimer (1954), who presented a target step away from center followed 40–240 ms later by a step back. He found that the subjects always tracked both target steps in sequence, even for the shortest interstep interval, when the target had already returned to the center before the first saccade was made. Westheimer's (1954) subjects obviously took the instruction to track the motion quite literally.

Subjects adopted a more lenient interpretation of the two-step tracking task in the 1960s and 1970s. Wheeless et al. (1967) found that 93% of saccades neglected the first target step and headed directly for the target's final position when the inter-step interval was as short as 50 ms; 77% went to the final position when the interval was 100 ms and 32% when it was 200 ms. What intrigued Wheeless et al. about their result was that so many of the saccades with the longest (200 ms) inter-step interval headed directly for the final target position. This seemed odd because the latency of saccades to the presentation of a single target step was only about 280 ms. This meant that as early as 80 ms before a saccade to the first step would have occurred, the saccade was cancelled and replaced by a new saccade to the final target position. One strong assumption contained in this interpretation is that the neglect of the first step was due exclusively to cancellation and re-

programming, rather than to the programming of a single saccade to the final target position based on the expectation that a second step might occur. Wheeless et al., aware of this problem, tried to dissuade subjects from expecting double steps by testing mostly single-step trials. Nevertheless, the expectation of a double step probably played some role, because they noted that the latency to single steps was 25 ms longer in experimental sessions containing both single- and double-step trials than in sessions containing single-step trials exclusively.

Subsequent studies of the tracking of two consecutive target steps explored effects of the spatial properties of the stimulus. For example, saccades were more often directed to the final target position when the second step brought the target closer to, rather than further from, the starting fixation point (Levy-Schoen and Blanc-Garin, 1974). Also, the average latency of saccades made to the final target position was shorter if both targets were on the same side (rather than opposite sides) of the starting fixation point (Komoda et al., 1973). The effects of the spatial properties of the stimulus suggested to these authors that the 'cancellation' of a saccade, described by Wheeless et al. (1967), was not complete, but was more a matter of revising certain programmed saccadic parameters based on newly acquired visual information.

A case for the revision of parameters was also made by Becker and Jurgens (1979), who found that subjects often tracked a sequence of two consecutive target steps (both on the same side of the fixation point) with a single saccade that landed between the endpoints of the two steps. The 'averaging' of the two target endpoints suggested to Becker and Jurgens (1979) that saccadic amplitude is computed after saccadic direction, and that the amplitude computation pools all the positional information that is available within a certain temporal window. The generality of this pooling process would have to be limited, however, because Becker and Jurgens (1979) found that 'averaging' occurred more often, and required less time, when the second step brought the target closer to, rather than further from, the fixation point. This implied that it is

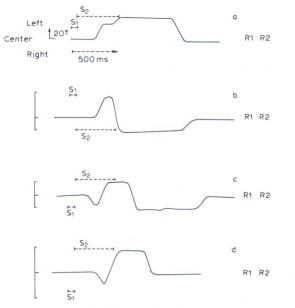

Fig. 34. Records c and d show examples of exceptionally brief pauses between saccades. (From Levy-Schoen and Blanc-Garin, 1974)

easier to decrease the size of saccades than increase it. Ottes et al. (1984) found that the proportion of 'averaging' saccades depended on the distance between the first and second locations of the target, with 'averaging' occurring only rarely when the distance between the endpoints of the two consecutive target steps exceeded 15 deg.

There were also suggestions that the programming of two saccades could occur at the same time, provided that the programming of each saccade was at a different stage. This conclusion was based on the timing pattern of the two consecutive saccades made to track two consecutive target steps. The latency of the second saccade was found to be independent of both the interval between the two target steps and the interval between the two saccades (Becker and Jurgens, 1979). The programming of one saccade was not completely independent of the programming of the other, however, because there was usually a minimum pause of about 100–150 ms between the saccades. One of the rare exceptions to this minimum pause is shown in Fig. 34, taken from Levy-Schoen and Blanc-Garin (1974), which shows

instances of unusually brief pauses between successive saccades.

The studies of saccades made to track two consecutive target steps suggest that we have the capacity to modify saccadic programs shortly before their execution, based on newly acquired visual information. Alternatively, instead of modifying programs, we might instead delay specification of saccadic parameters as long as possible (see Rosenbaum et al., 1984, who advocate such a model for the control of finger movements). Either of these two schemes might prove to be valuable in natural situations, where the retinal image is always moving about due to incomplete compensation for head movements (section 2.3). Delaying the final, irrevocable specification of the saccadic program as long as possible is one way of making it more likely that perturbations of the retinal location of the target will be taken into account in the final saccadic program. (See Collewijn et al., 1990, for discussion of the current status of saccadic control with the head unrestrained.)

There is, however, one caveat before we leap from the laboratory to natural scanning, or before we claim to understand how the saccadic parameters are specified. As was pointed out earlier in the discussion of Wheeless' et al.'s (1967) experiment, it was always clear to the subject that on some portion of the trials the target would be taking a second step. The expectation that modification of an initial saccadic program might be required could make it easier to carry out the modification. This could occur in a variety of different ways. For example, the expectation that modification might be required could encourage preparation of more than one saccadic program, or could affect the way in which new visual information is sampled while programming is in progress. Of course, any such processes which make it easier to modify saccadic programs would be expected to operate in natural situations, as well as the laboratory, because in natural situations we expect the retinal location of the target to be perturbed by our own eye or head movements. The important point for the present discussion is that until we understand the role of the subject's expectations, it may not be correct to assume that the specification of saccadic parameters necessarily operates in a purely automatic fashion. The relative contribution of expectations and lower-level processes to the rapid modification of saccadic parameters has yet to be determined.

The relative contribution of expectations and lower-level, sensorimotor processes to saccadic programming is also considered in the next section, which deals with the spatial analog of the 2-step experiments. Here, the target appears in the company of other, nontarget stimuli.

4.7. Is the endpoint of a saccade influenced by the presence of a visual background?

4.7.1. 'Center-of-gravity' tendencies

When we scan natural visual scenes, we try to look at chosen targets, which appear not in isolation, as they do in the laboratory, but in the midst of patterned visual backgrounds. The problem facing us is to bring the line of sight to the chosen location without it being drawn to features in the background. In section 3.6 we saw that we can smoothly track targets moving across visual backgrounds with little or no influence of the background on the eye movements. Does the same selective capacity hold for saccades, that is, how well can we bring the line of sight to a stationary visual target which is presented along with visual background stimuli?

Surprisingly, and in apparent contrast to the successful elimination of background influence on smooth eye tracking, there have been several reports that background stimuli do influence the endpoint of saccades (e.g. Findlay, 1982; Ottes et al., 1984, 1985; Coëffé and O'Regan, 1987). These studies reported that saccades often land in the center of the entire stimulus configuration, consisting of the target stimulus, along with neighboring visual background stimuli. For example, Ottes et al. (1985) asked subjects to look at a green target spot which was presented along with a red, nontarget spot. One spot was above and to the right, and the other below and to the right, of the central fixation target. The subject did not know which of the two locations would contain the target until the stimuli

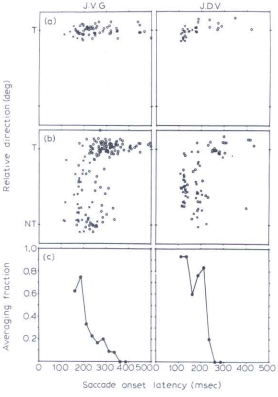

Fig. 35. Direction of first saccade to a single spot (row a) and a double-spot stimulus (row b) (directional separation = 30 deg) plotted as a function of saccadic latency. The vertical axis scaling is relative to the first saccade directions of responses to single spots at each of the double-spot positions. The data from the stimuli with a target direction of +15 deg have been pooled with those with a target direction of −15 deg after direction reversal of the latter responses. Two instructions were used: saccade as fast as possible (crosses) or as accurately as possible (circles). In row (c) the fraction of 'averaging' responses to the double spots, within each 25-ms latency bin containing at least 5 saccades, is plotted against mean latency of the same saccades. Data in (c) are pooled across instruction. A saccade is defined as 'averaging' if its direction is in between the two 95% ranges of the single-spot response. Left-hand column of panels contains the data of subject JVG, right-hand of subject JDV. (From Ottes et al., 1985)

appeared. Ottes et al. found that saccades with shorter latencies (less than about 300 ms) landed in between the two spots, provided that the directional separation of the spots was 30 deg or less. This is shown in Fig. 35, which shows the endpoints of the saccades as a function of their latency. More widely separated stimuli led to errors of a different sort in which the saccades were often directed either to the target or to the nontarget, and less frequently in between the two. Saccades with latencies longer than 300 ms were accurate, regardless of the directional separation. Ottes et al. (1985) attributed the centering tendency of the short-latency saccades to poor spatial resolution of the sensory stimulus, and proposed two hypotheses to explain why spatial resolution was poor. One was that centering saccades are produced by a separate, fast, saccadic subsystem with poor spatial resolution. This subsystem was said to program saccades 'automatically' based on stimulus 'energy content and relative timing'. The second hypothesis was that there was a single saccadic subsystem whose input became more precise over time. Short-latency saccades were assumed to be drawn toward the center of this poorly resolved spatial input, rather than to a selected location within it.

Coëffé and O'Regan (1987) later showed that short-latency saccades did not necessarily have to be drawn to the center of the stimulus array. They found that if the target location was known in advance, centering tendencies would be reduced and saccadic accuracy improved. They proposed that the improvement in saccadic accuracy came from the contribution of an independent 'target extraction' process. This process was assumed to operate concurrently with a tendency of saccades to land in what they called a 'gaze attraction position', which was said to depend on the 'summed influence of all the elements in the whole stimulus configuration'.

He and Kowler (1989) obtained results leading them to question whether two subsystems, or two independent processes, one directing saccades to the center and the other directing saccades to the true target location, were needed to explain performance. They presented a target stimulus ('+') and a nontarget stimulus ('x') at the same time, with one of the stimuli above and to the right and the other above and to the left of the central fixation point. The new feature of the study was that the probability that the target would appear in the right-hand location was varied (see section 4.4 for discussions

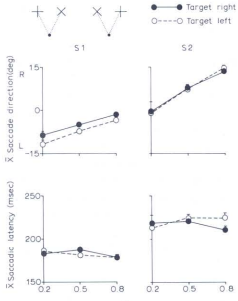

Fig. 36. Mean saccadic direction (top) and latency (bottom) as a function of the probability (P_R) of the target's appearing on the right for two naive subjects (S1 and S2). The target was either on the right (solid lines) or on the left (dotted lines). The directional separation of the target and nontarget was 30 deg. Standard errors were smaller than the plotting symbols except where noted by vertical bars. (From He and Kowler, 1989)

of effects of probability on saccades). They found that the saccadic endpoints were biased toward the more probable location, as is shown in Fig. 36, which plots the mean saccadic endpoint as a function of location probability. (Note that the mean latency, in contrast to the mean endpoint, was unaffected by probability.) Fig. 36 also shows that the actual location of the target did not matter too much – saccadic endpoints were about the same regardless of whether the target had appeared on the right or on the left. This suggests that the bias to direct saccades toward the more probable location did not require a special saccadic mechanism with information about the actual location of the target. The bias was due to the influence of the memory for the past history of target locations. Given that biases can draw the line of sight away from the center of the array, it is reasonable to suppose that biases could have been responsible for drawing saccades toward the center of the array in the first place. If this is true, then 'centering' tendencies need not be automatic, or require special saccadic subsystems, or imply poorly resolved spatial inputs. 'Centering' saccades might be no more than an efficient visual search strategy employed when one is asked to make a saccade before the target has been located. Genuine 'centering' tendencies, if they exist at all, would be best described as tendencies to look to the center of *selected* regions of the display, with the selection process under high-level control (He and Kowler, 1989; He et al., 1988).

These studies of saccadic 'centering' illustrate how complicated it is to correctly interpret the performance of subjects who are asked to make saccades before they have distinguished a target from its background. Such situations may encourage the reliance on memory for prior target locations and expectations about future locations. Interestingly, this is *not* the experimental strategy that was successful in demonstrating that smooth eye movements can be made to track selected targets, independently of visual stimuli in the background (section 3.6). In such experiments subjects were not confused about which stimulus was target and which was background. Indeed, to have encouraged such confusion would be an inappropriate test of selective capacity because the failure to eliminate the influence of the background on the eye movement would have represented a failure to pay full attention to the target, and not an automatic integration of the visual information in the target and the background. The same point can be made about saccades: if we want to describe the capacity to look at a selected target in the presence of backgrounds, it is necessary to be certain that the saccade is being programmed when the visual target can be clearly distinguished from the background. Otherwise, we risk confusing perceptual or attentional limitations with lower-level oculomotor events.

We still do not understand the extent to which saccadic programs are influenced by background stimuli when subjects have fully distinguished the target from its background. It is possible that backgrounds will make no difference, provided that the

subject is paying sufficient attention to the target. This would imply that saccadic programs are determined by a two-stage process, similar to that proposed for smooth eye movement (section 3.6), in which a target is selected by paying attention to it and a saccadic program is then computed based on the position signals contained in the selected target.

There is some suggestive evidence in support of a two-stage model (target selection followed by computation of the saccadic response) (He and Kowler, 1989; He et al., 1988), but this support is only tentative, because a firm link between selective attention and saccades has yet to be established. This issue is discussed in the next section.

4.7.2. Saccades and selective attention

Despite the plausibility of a link between selective attention and saccades, it is still not clear that such a link exists. Selective attention can be moved about without saccades (Reeves and Sperling, 1986), but this shows that shifts of attention do not require saccades, and leaves open the question of whether saccades require corresponding attentional shifts. Klein (1980) did conclude that saccades could be made without shifts in attention based on experiments in which saccades were programmed while, in the same block of trials, subjects were also preparing to press a button in response to the appearance of a light. The light and the target for the saccade were either on the same, or on the opposite, side of the fixation point. Klein found that the reaction time of the button press was the same regardless of the location of the light, and he concluded that the programming of saccades did not compel a shift of attention to the saccadic target. Klein's interpretation can be questioned, however, because the saccadic and the button-pressing tasks were not performed concurrently. Instead, subjects were told which task to do before each trial. So, it is possible that the reaction time of the button press was not affected by saccadic programming because subjects did not program saccades in the button-press trials.

At this point the question of whether saccades require corresponding shifts of attention, or whether saccades and attention shifts can be carried out independently (e.g., in different directions), has not been resolved.

4.8. Saccades are planned as patterned sequences

Much of the research on saccades up to this point has dealt with the performance of subjects who were uncertain about the location of the target or the time of its appearance. This section will describe characteristics of saccades when uncertainty about the spatial or temporal properties of the stimulus was reduced, and subjects had to look from one stationary target to the next. These studies show that high-level plans for the entire sequences of saccades place constraints on their spatio-temporal pattern.

The rationale for studying sequences of movements is given quite clearly in Lashley's famous (1951) paper, 'The Problem of Serial Order in Behavior'. Lashley's eloquent description and insightful analysis of voluntary motor action is as timely today for the study of saccades as it was several decades ago for the study of voluntary movements.

Lashley argued that motor responses are organized into structured sequences whose main feature was the spatial and temporal integration of distinct elements into an effective, purposeful pattern of activity:

"Certainly language presents in a most striking form the integrative functions that are characteristic of the cerebral cortex and that reach their highest development in human thought processes. Temporal integration is not found exclusively in language; the coordination of leg movements in insects, the song of birds, the control of trotting and pacing in a gaited horse, the rat running the maze, the architect designing a house, and the carpenter sawing a board present a problem of sequences of action which cannot be explained in terms of successions of external stimuli" (p. 113).

Lashley looked for what he called "a syntax of movement", or, "an habitual order or mode of relating the expressive elements... which may be imposed upon a wide range and a wide variety of specific acts" (p. 122). For example, different mo-

tor activities were not triggered by independent sensory inputs, but were made with reference to a central "system of space coordinates", which defined the location of an object in external space and also with reference to the position of the organism as a whole. This, argued Lashley, would not only account for the spatial integration of distinct movements, but would also explain the remarkable capacities of animals to adjust quickly to gross distortions or deprivations of sensory information: the system of space coordinates was a product of all sorts of signals, including memories, and so could survive the loss of some of the signals without disruption of its essential character.

Movements were temporally organized as well. This is shown most clearly by the pervasiveness of rhythmic patterns of movements, found in speech, in walking, and even in breathing. The rhythmic action not only provides for temporal coordination of a single motor activity, but also suggests the existence of an internal clock, which ensures the temporal coordination of different movements carried out at the same time.

Lashley's arguments have been very influential in modern research on voluntary motor control. Studies have sought to discover the nature of the spatial and temporal coordination of specific motor activities and, in so doing, lead to a better understanding of the neural processes underlying the control of coordinated movements. For example: (1) Viviani and Terzuolo (1980) studied the consistent spatial and temporal patterns of handwriting, which survived changes in the overall speed of writing or the size of the written characters; (2) Sternberg et al. (1978a,b) studied the temporal pattern of sequences of typed keystrokes or spoken syllables. They found that both the latency for the initiation of a sequence and the time between successive movements depended on the length of the sequence as a whole. This led them to propose that all the motor programs for a sequence of responses are stored in a special memory buffer, which is scanned for the appropriate program before the execution of each response; (3) Rosenbaum at al. (1983) concluded that motor programs are stored in

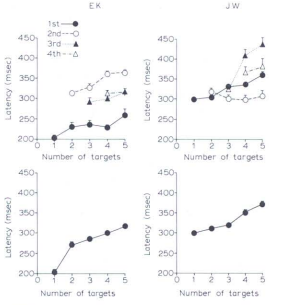

Fig. 37. The mean latency of the 1st–4th saccades of a sequence (top) and averaged overall saccades (bottom). as a function of the number of targets in the sequence for subject EK and naive subject JW. Vertical bars represent 1 SE. (From Zingale and Kowler, 1987)

a hierarchically structured memory, and that programs may be elaborated to specify particular parameters of the movement right before the execution of a sequence begins (Rosenbaum et al., 1984).

It is not obvious that the spatial or temporal patterning of movements, described above for voluntary motor responses, must also apply to saccades. Unlike movements of the fingers, or spoken syllables, which can be initiated without a specific sensory cue, saccades are usually directed toward eccentric, selected, visual targets. In principle, the visual target can provide all the information needed to program the size or direction of the movement, so that remembered motor commands, or patterned sequences of motor responses, would not appear to be needed.

Zingale and Kowler (1987) demonstrated that both remembered motor commands and patterned sequences of responses do apply to saccades, much as they apply to finger movements or to speech. Their experiment was modeled after Sternberg et al.'s (1978a,b) experiment, in that the subjects ex-

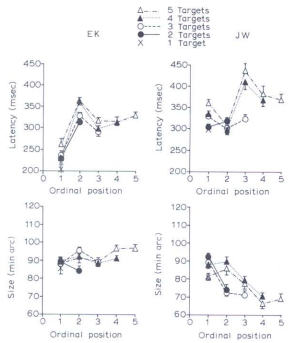

Fig. 38. Mean latency (top graphs) and mean saccade vector size (bottom graphs) as a function of the ordinal position of the saccade in the sequence for each of five sequence lengths. (From Zingale and Kowler, 1987)

ecuted saccadic sequences of different lengths. Specifically, subjects scanned a sequence of from 1 to 5 points, arranged in a simple 2-dimensional pattern. Zingale and Kowler (1987) (also Kowler, 1982; Inhoff, 1986) found that the latency of the first saccade, and the time between successive saccades, increased with the number of points that had to be scanned (Fig. 37). This suggests that the kind of memory-scanning process that Sternberg et al. (1978a) proposed for typing and speech may apply to saccades as well.

The dependence of the properties of a single saccade on the properties of the sequence in which it occurs, shown by the increase in latency with increasing sequence length, is also illustrated by the variation of intersaccadic interval as a function of the serial position of the saccade in the sequence (Fig. 38). The variation in intersaccadic interval as a function of serial position was quite similar to the pattern of inter-response times that characterizes sequences of spoken syllables (Sternberg et al., 1978b). The temporal pattern of the saccades made to look at the visual targets was also remarkably similar to the pattern of saccades observed when the targets were removed right before the execution of the sequence was to begin, and subjects had to direct saccades to remembered target locations. The visual targets were not completely irrelevant, however: saccades to remembered locations were about 20% too large, showing that the retrieved programs could be modified 'on-line' by the visual information.

What is the benefit of programming sequences of saccades? The answer to this may lie in remembering Lashley's insights about the importance of successfully integrating distinct motor response elements into coordinated patterns of activity. Saccades are only one kind of response element, and are rarely made in isolation. In natural situations, saccades are part of general searching or scanning patterns, which include movements of the head, limbs and fingers, as well as movements of the eyes. Perhaps the programming of saccadic sequences reflects not a process unique to saccades, but the operation of a single central motor controller, which uses the rhythm of the sequence to link the disparate motor elements into an effective pattern of activity.

4.9. Overview

The section on saccades described ways in which performance is limited by both low-level, sensorimotor constraints, and higher-level, central and subjective, factors. For example, the spatial precision of saccades is limited by mechanisms that code the location of the image (section 4.3). The precision of saccades smaller than 30′ is limited by other factors, however, because we can estimate the distance between two points far more precisely than we can make saccades from one to the next. In general, small saccades are hard to use and visually useless. The goal of saccades may not be to bring the target of interest to a central 'king' cone, but rather to a larger region, perhaps as large as 30′ – a region only slightly larger than the foveal bouquet which

might contain the 'chamber of deputies' most concerned with the limits of visual resolution (Le Grand, 1967).

There is ample evidence that saccadic programs can be prepared, at least in part, before the location of targets is fully discerned. For example, 'warning' signals reduce latency (4.5), and advanced information about the probable locations of targets influences both saccadic latency and accuracy (4.4 and 4.7.1). Any programs prepared in advance are by no means immune to the influence of new, visual signals. For example the abrupt disappearance of a central stimulus can facilitate programming and the abrupt appearance of a central stimulus can delay the initiation of a saccade (4.5.1). There is, however, no convincing evidence that the facilitation acts by invoking a special class of reflexive 'express' saccades (4.5.2). The effects of the abrupt appearance or disappearance of central stimuli may be one of the many threads linking saccades to spatially selective attention, a link which is still not well understood (4.7.2).

Abrupt changes in target location that occur while saccadic programming is in progress can also influence the endpoint of the saccade (4.6). This suggests a remarkable ability to incorporate new visual information into programs on rather short notice. On the other hand, the abrupt changes produced experimentally were never a complete surprise to the subjects, so that some of the groundwork for the expected modifications might have been incorporated into the preparation of the initial response.

The problem of how saccades are programmed in patterned visual environments is still unsolved (4.7). Automatic 'center-of-gravity' tendencies have been described, but these seem to work in opposition to voluntary process, which would presumably take the line of sight to a chosen location in the visual array. The conflict between these two is discomfiting. The resolution may lie in a 'centering' mechanism that receives only the spatial information selected (attended to) by the subject. This general description, however, succeeds only in better defining, rather than resolving, the issue, namely, that separate constraints may be imposed from two different sources, (1) our ability to focus attention on one stimulus to the exclusion of others, and (2) the way in which a lower-level mechanism goes about computing a single saccadic endpoint from a spatially extended input. Solving the problem of saccadic programming in patterned environments requires more studies of saccades made to inspect stationary environments in which subjects are more certain about where they are trying to look, rather than more studies in which randomly chosen stimuli are used to try to elicit automatic responses. Randomization makes it more difficult to distinguish the operation of the always-present high-level selection processes from the lower-level computations of the oculomotor command.

Studies of other voluntary motor responses – finger movements or speech, for example – have made a great deal of progress of late by rejecting randomization and seeing how well subjects can execute specified sequences of movements. The temporal patterns of these responses are remarkably similar to those found when subjects use saccades to scan sequences of visible points (4.8). This suggests that saccades, like other voluntary movements, are planned as patterned sequences, not one at a time. Planning of saccadic sequences may be essential for the proper temporal coordination of saccades with the movements of the head, limbs and fingers, which usually accompany eye movements in natural viewing.

5. Future directions

This chapter has summarized some of the evidence showing that human eye movement is a product of both visual and cognitive influences, both of which need to be taken into account if theories are to truly represent the way in which eye movements operate in the natural world. We saw that eye movements depend on attentional decisions, expectations, memories and plans and, at the same time, are constrained by the structure of the visual array. Cognitive processes (in particular, expectations and memory for the past history of stimuli and re-

sponses) were shown to play a role even when the experimental stimuli were chosen at random. The role of selective attention and the capacity to plan patterned sequences of movements were discovered by testing more complicated stimuli than the conventional point of light moving in darkness; for example, studies of eye movements in the presence of background stimuli, and studies of saccades made to track sequences of target points.

We are still a long way from understanding how visual and cognitive influences combine to determine the effective eye movement patterns we rely on to see the world clearly. I suspect that if we are to succeed in developing new models and approaches, two things will have to happen.

The first is to ask anew the most basic question about eye movements: what are they good for? 'Producing the retinal conditions that are adequate for vision' was an acceptable answer for Raymond Dodge's time, when we knew what adequate conditions meant. But we can no longer be confident that achieving stationary images, every millisecond, is the goal. A little (or a lot) of motion may be harmful, helpful, or ignored. It may depend on what you are trying to see or do while the eye is moving. Concurrent study of visual, cognitive and oculomotor performance is needed. The directions for this research are suggested in many of the remaining chapters in this book, which deal explicitly with the role of eye movements in the performance of visual and cognitive tasks.

The second task for the future is to begin to seriously consider 'natural' oculomotor demands. We oculomotorists play fast and loose with the term 'natural'. Uncover an eye to do binocular recording, include a visual background stimulus, leave the room lights on, or unbolt the head and all of a sudden, we're 'natural'. Let me not discourage this development, but instead argue that there is a long way to go. The most important of the natural demands may be the coordination of different concurrent activities (again, Lashley was right). Small retinal errors are harmless. But sending an arm in one direction and eyes and head in another might be a disaster. Equally disastrous would be to make the task of coordinating the separate activities an active, deliberate process rather than something that the motor systems are naturally and automatically predisposed to do. This I believe to be the central message of the last few years of the research: that oculomotor performance, voluntary or involuntary, smooth or saccadic, is automatically and effortlessly coordinated because the motor commands are derived from one set of decisions, plans and ideas that we have about perceived objects in the world. Verification of this idea and the development of new oculomotor models which emphasize the central coordination of eye movements with the other sensorimotor and cognitive activities seems to be an appropriate goal for future oculomotor research. Achieving this goal will require new research techniques which let us simultaneously explore eye movements along with the many other activities that naturally occur at the same time.

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