EYE MOVEMENT

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THE TASK

This paper provides an overview of a field more notable for variegated activity than for attempts to solve a limited number of fundamental problems. Many different areas have been explored during the past 25 years. The task of describing progress in all would be tantamount to describing progress in all branches of visual science in which psychophysical data were collected. Eye movement data have been used: (1) to understand the operation of various oculomotor subsystems, or (2) to make inferences about the role of eye movement in visual, perceptual and cognitive processing. Progress has been made in all areas. We are somewhat closer to understanding, or at least appreciating, what must be done if we hope to understand how visual, vestibular and cognitive information are used to control eye movements and how these behaviors are used to explore and abstract visual information as we sit and ponder or move about.

The task of summarizing progress can be made tractable only by excluding active areas which have been largely unproductive; for example, attempts to describe performance of the various primate oculomotor subsystems within the framework of time invariant linear servomechanical models. This approach goes counter to the way in which the oculomotor system is known to operate in primates (see Steinman, 1986, for elaboration of this point). The task can also be simplified by reference to publications summarizing major accomplishments; for example, studies of the oculomotor system of the rabbit. Rabbit studies have been more useful than primate studies because the rabbit's oculomotor system acts, perhaps not surprisingly, as if it is less under the influence of cognitive central processes so characteristic of ourselves and other primates. Progress made with the rabbit is not covered here because it can be read conveniently in Collewijn's (1981) fascinating monograph (Collewijn's first rabbit eye movement paper appeared in Vision Research, 1969). The rabbit's contribution to oculomotor science, in the hands of Collewijn, his collaborators and others, has been as fundamental as the contribution of the horseshoe crab and the fly to visual science.

The present paper is confined to only a few topics in human eye movement research—topics drawn from the areas listed above. The selection of specific topics was made on two grounds; namely, (1) topics representative of the diverse nature of the field and (2) topics well-represented in the pages of *Vision Research*. *Vision Research* has been an exceedingly valuable forum for the presentation of developments in all aspects of eye movement research. This journal has provided researchers with different interests and fields (bioengineering, physics, physiology, and psychology) the opportunity to report data and to exchange ideas in a single source.

PRIOR STATUS AND THE AUTHOR'S INITIAL INVOLVEMENT IN THE FIELD

Most eye movement investigators in the decade preceding publication of Vision Research were concerned with the role of eve movement in basic visual processing. This interest led to the development of techniques for stabilizing visual targets-a goal which required accurate registration of miniature fixational eye movements. Such developments led, quite naturally, to the first accurate descriptions of fixational eye movements as well as to speculation about their visual significance. Eye movement research in the fifties provided a training ground for many who would become our most distinguished visual scientists (e.g. Alpern, Barlow, Cornsweet, Ditchburn, Krauskopf, Nachmias, Ratliff, Riggs and Westheimer).

Raymond Dodge, whose eye movement publications began in 1898 and continued into the 1940's, prepared the way for modern eye move-

overly-simplified.

ment research by describing the basic kinds and significance of large eye movements. In 1954 Westheimer picked up Dodge's line of research and introduced concepts employed by linear

system modelers-the approach adopted formally in 1961 by Fender and Nye (see Steinman, 1986, for a review of Westheimer's contribution and an evaluation of its subsequent development by others). Westheimer's work on relatively large eye movements depended on his improvement of corneal reflection oculography. This technique can confound head translations with eye rotations if extraordinary efforts are not made to immobilize the head (Barlow, 1952), and, therefore, could not be used either to stabilize visual targets or to study details of the miniature fixational eye movement pattern—the problem of greatest interest to many other investigators. Riggs in the U.S.A., and Ditchburn and co-workers in Britain, solved this problem by developing the contact lens optical lever method while Yarbus (1967) developed this method independently in Russia. The fixational eye movement pattern was found to contain microsaccades (<15' vector magnitude) and intersaccadic drifts, encouraging Ditchburn to propose that microsaccades were essential for abstracting color and contour information from low contrast displays (completely stabilized images had already been shown to disappear). By 1956 Cornsweet had modeled the horizontal component of the fixational eye movement pattern, proposing that intersaccadic drifts were noisy in the sense that they allowed the fixation target image to drift away from some optimal retinal fixation locus. Microsaccades, which occurred once or twice each second, returned the target image to this optimal fixation locus assumed to be at the center of best vision. Microsaccades were re-

quired to keep the eye on target. Cornsweet also reported that fixation error elicited such position-correcting microsaccades and that microsaccades were not elicited by the tendency of a stabilized target to fade. Nachmias (1959, 1961) continued this line of research by using a contact lens optical lever to record the twodimensional fixational eye movement pattern. He found, in agreement with Cornsweet, that microsaccades tended to be in directions opposite to intersaccadic drifts, but he also found that there was an idiosyncratic drift direction from which errors introduced by drifts were

corrected by drifts rather than by micro-

saccades. Nachmias also found that the time

tor of when a microsaccade would occur than the size of the fixation error. Nachmias' results showed that microsaccades are emitted, rather than stimulus-elicited, behaviors. In short Cornsweet's model was inappropriate or, at best,

since the last microsaccade was a better predic-

This is where matters stood when Vision Research first appeared. My involvement in eve movement research and publication of Vision Research began together. At the time I was a doctoral candidate working in Nachmias' laboratory. I was examining the widely-held belief that a small red (>630 nm) fixation point guaranteed central foveal fixation, regardless of

the state of adaptation of the eye. Initially, this hypothesis was examined by means of an afterimage technique (Nachmias had left his twodimensional eye movement recording system at University of Rochester). Systematic differences in mean fixation position, as large as 30 min arc, were observed in the light- and dark-adapted eye. Nachmias and I thought that we had measured a potentially interesting oculomotor effect. Erich Heinemann, a member of my committee, suggested that it would be a nice addition to the thesis to have objective evidence

for this shift. Obediently, I built a two-

dimensional contact lens optical lever and redid

the experiment. Lo and behold, there was no

objective difference in mean fixation position.

This result came as a surprise to all concerned. If you cannot trust the perceived position of an afterimage, what can you trust? Two years of doctoral research had been wasted. I had no thesis, but I did have a nifty new eye movement recording system and proceeded to use it in a way that seemed, at the time, appropriate for finding out how the oculomotor system used visual information to maintain fixation. The approach was taken from studies of vision. A great deal of visual system performance has come to be understood by using stimulus properties as independent variables. I took a similar

tack, studying the effect of stimulus variables (size, luminance and color of the fixation target) on maintained fixation (Steinman, 1965). In retrospect this approach was absurd. Teleologically speaking, the last thing we would want for successful mate-selection, courtship and reproduction, or even for simply looking around, is to have oculomotor system performance controlled by such stimulus variables

(see Walls, 1962, for his last paper in which he

emphasizes the heuristic value of teleology in

view.

visual stimulus—properties which determine the appearance and thereby informational significance of the stimulus (see Steinman, 1976, for elaboration of this point). Mother Nature knew what she was doing, and only by using efficient experimental designs and powerful statistical techniques (balanced latin squares and analyses of variance) was it possible to show statistically reliable effects of stimulus variables on fixation performance. But, these effects were trivial smaller than 3 or 4 min of arc. Stimulus variables were not of oculomotor significance. There was, however, one striking result which we now know has nothing to do with properties of the fixation stimulus. Namely, subjects fixating at the imagined center of a large, homogeneously-lighted disk (about 1.5° diameter) made very few microsaccades. Furthermore, the precision of eye position at the imagined center of the large disk was as good as precision with a 2' fixation point despite the fact that microsaccades were much more frequent with the tiny target. Microsaccades were not needed for precise fixation. It would be a number of years and many experiments (most published in Vision Research) before it became obvious that fixational microsaccades are laboratory esoterica limited to human adults, whose heads are supported artificially, while they try very hard to be very sure that they are

THE ROLE OF EYE MOVEMENT IN THE PERCEPTION OF DIRECTION

fixating perfectly. The microsaccades they make

under these conditions either have no effect, or

a detrimental effect, on what they can see. The

low velocity fixational oculomotor subsystem

(now called "slow control") is adequate to

maintain the line of sight on a stationary target

when the fixator is less compulsive (see Ditch-

burn, 1980 and Kowler and Steinman, 1980 for

discussion of this point, and Martins et al.,

1985, for a recent experiment relating slow

control to smooth pursuit).

Another much studied eye movement problem asks how an individual knows where, in the frontal-parallel plane, objects are located in visual space. It has been appreciated, at least since Helmholtz and Hering, that the only way we can know where something is located relative to ourselves is by knowing the orientation of

guiding eye movement research). Our ability to our eye with respect to our head and the orienlook at or to track an object should be as tation of the head with respect to the torso. If we wish to do anything in addition to looking independent as possible from properties of the at the located object, we must know the orientation of our limbs with respect to our torso as well. Only retinal coordinates are required to look from one to another detail if the location of the details in space is not of interest. This is done simply by rotating the eye through the angle that brings the attended, nonfixated, detail to the foveal center. Accurate scanning of this kind is accomplished without difficulty, regardless of the optical arrangements intervening between the eye and objects in the outside world. For example, no difficulty is encountered during inspection of different stationary or moving details in a slide viewed through a microscope. However, once motor responses (other than the eye movements) must be made with respect to the position of objects in the visual world, novel optical arrangements present considerable difficulty. Practice is required to move, manually, the inverted image of a microscope slide so as to position different

parts of the slide at the center of the field of

Even with natural optical arrangements, once

the head is not restrained, it is necessary to know the orientation of the eye with respect to the head and the orientation of the head with respect to the torso in order to locate objects in space. The retinal coordinate system alone cannot tell you where an object is located in space relative to your arm or to your midsaggital plane. Matin and Pearce (1965) and Matin et al. (1969) began the current line of research on a portion of this problem by examining the nature and fidelity of what they called the "extraretinal signal"—the nonretinal oculomotor signal used to perceive the direction of an object in space. This extraretinal signal could be "inflow" (proprioception) or "outflow" (knowledge of commands sent to the extraocular muscles) or a combination of the two—what Matin (1972) called a "hybrid" signal. In their initial experiments, subjects with heads held on biteboards, were required to locate the position of targets in the frontal-parallel plane when the targets were presented in close temporal proximity to saccadic eye movements. Appreciable disturbances of perceived localization were observed preceeding, during and for a period of many milliseconds following these saccades. This result means that the extraretinal signal provides very poor information about the orientation of the

and points of light in darkness, is difficult to reconcile with our ability to do things well in the real world. Matin et al. (1970) analyzed the eye movement data collected during their perception ex-

eye in the head (orbit) as we look about. This

experimental result, obtained with the head held

periment and concluded that the eye executed a nearly random walk during the first few seconds spent in darkness—a result consistent with the lack of fidelity of the extraretinal signal they had demonstrated perceptually. These conclusions were at odds with a publication by Skavenski and Steinman (1970). We had demonstrated a relatively faithful extraretinal signal (accuracy 2 deg arc) by asking subjects to maintain an assigned fixation direction in total darkness for periods as long as 2 min. Similar results were obtained when subjects restored an assigned fixation direction in darkness after the eye had been driven to different positions in the orbit with a randomly-chosen pattern of large saccades, and also when the orientation of the torso was changed with respect to orientation of the head (the head was fixed in space in all of these early experiments which means that only knowledge of the orientation of the eye in the head was under study). Skavenski (1971) next showed that an assigned fixation direction could

model developed by Matin et al. (1970). Skavenski (1972) went on to show that an extraretinal signal can be used to compensate passive displacements of the eye introduced in total darkness, and also that the subject can sense the position of his eye. More recently Skavenski and Hansen re-

be maintained within about 3.5° for periods in

darkness as long as 7.5 min and even restored

with the same accuracy after walking around the laboratory for 15 minutes. He also used a

correlational analysis to reject the random-walk

corded eye movements with a free head during a manual visuomotor task (hammering at a briefly-flashed small target) (Hansen and Skavenski 1977; Skavenski and Hansen, 1978; Hansen, 1979; Hansen and Skavenski, 1985). These experiments allowed them to show that signals arising from or sent to the neck, torso and arm, as well as extraretinal signals arising from or sent to the eye in the head, have considerable

fidelity. Mean hammering position errors were

as small as 20' when the target was flashed

during smooth pursuit, vestibulo-ocular and

saccadic eye movements. They have also shown

that the knowledge of eye, torso and arm posi-

signals, providing coordinates of objects in space, were only delayed by about 10 msec. N.B.

tion is timely—the extraretinal ocular and body

the target was always located in front of the subject at random positions along the radius traced out by his hammering hand. So far we have a striking, unresolved prob-

lem. The perceived direction of a target viewed in darkness is not located in an accurate or timely fashion if eye movements are made even when the head is held in place. If a motor response, rather than a perceptual discrimination is required, however, the motor response is almost dead on target even when the head, torso and arm, as well as the eye, move in space.

Does this mean that the motor and perceptual systems use qualitatively different extraretinal signals? Alternatively, does this difference reflect short term memory deficiencies in the perceptual experiments not present in the motor experiments, or perhaps differences in the frames of reference used for discriminating the perceived direction of a target rather than hitting it? Hansen and Skavenski (1978, 1985) have discussed these alternatives and prefer the frame of reference explanation. Definitive experiments

must still be done. In recent years, we have also learned more about the likely nature of the orbital extraretinal signal used for the perception of direction. Skavenski et al. (1972) showed that the perceived direction of an object in space depends in an orderly way on the efferent command sent to the oculomotor muscles (Helmholtz's claim). They also reported that perceived direction was not influenced by conflicting inflow information (proprioception) produced by passive displacement of a nonviewing eye. A similar source (the

extraretinal signal for the perception of direction is apparent in the data obtained in perceptual experiments on perceived direction done with human subjects under curare (Stevens et al., 1976; Matin et al., 1982). The latter authors, however, emphasize the importance of visible frames, rather than monitored efferent oculomotor commands, for providing the basis for the veridical perception of direction in a lighted environment (see O'Regan, 1984, for recent

experiments on the significance of visual factors

on localization during saccades in a lighted

environment). As matters stand, the monitored

efferent command seems a good bet to be the

orbital extraretinal signal underlying perceived

direction, at least in subjects whose heads are

monitored efferent command) of the orbital

immobilized. The same command that seems to be sufficient to guide saccades in monkeys whose inflow signals have been disrupted surgically (Guthrie *et al.*, 1983).

To conclude this section, the problem of the relationship of the perceptual to the visuomotor response remains. There is also continuing confusion in understanding the possible roles of extraretinal orbital signals, perceptual signals and retinal signals that might be used for saccadic scanning and smooth pursuit eye movements. Matters have not been helped by the

equation of orbital with perceptual contri-

butions or by the equation of spatial with orbital coordinate systems (Robinson, 1975). The latter oversimplification has spilled over into the physiological literature where demonstration of a possible extraretinal orbital oculomotor signal is discussed as though it offers support for a spatial coordinate model (Mays and Sparks, 1980; Sparks and Mays, 1983) this oculomotor model is based on idiosyncratic perceptual as well as idiosyncratic eye movement observations (Cushman et al., 1984). Mack et al. (1982, 1985) have discussed problems inherent in confusion of perceptual, retinal and motor contributions to saccadic and smooth eye movements. When these confusions are put aside and the relationship of the perceptual to the visuomotor experiments are worked out, we can begin to find out what we actually need to know in order to bring this work closer to perceptual and motor demands made in everyday life. Namely, we need to know how localization fares in perceptual and visuomotor space as a target or the subject moves in planes other than the frontal-parallel or on a radius

traced out by his arm.* Movement in three-

dimensions is ubiquitous in everyday life and, at

present, we know very little about how the oculomotor and other motor systems integrate

visual, extraretinal and bodily signals under

*Skavenski (private communication) found appreciable

such complex conditions.

THE ROLE OF EYE MOVEMENT-PRODUCED RETINAL IMAGE MOTION IN BASIC VISUAL FUNCTION

Another ongoing area of oculomotor research, whose publication began in Vision Research, examines retinal image motion resulting from failures of oculomotor compensation. We are all under the impression that we can see rather well during those brief periods when we remove our heads from our bite-boards or chin-rests and go about our less important daily business. This rather commonplace experience had encouraged a kind of oculomotor chauvinism. It was claimed that we see well because of the virtual perfection of oculomotor compensation (e.g. Melvill Jones, 1979, p. 287; Barr et al., 1976). It was claimed that virtual perfection was provided by the vestibulo-ocular response assisted by smooth pursuit eye movements. Evidence for this assumption was based primarily on informal perceptual observations. But, do these oculomotor compensatory subsystems actually perform this well? If they do not, what are the consequences for visual processing?

Work in this area represents a return to problems that were under study in the fifties, using new instrumentation which permits accurate and precise registration of eye and head movements in unrestrained and even freelymoving subjects. A brief description of these developments is useful here to set the stage for current research. Contemporary work was made possible by an important contribution of Robinson (1963) who introduced the magnetic field-search (sensor) coil technique for measuring eye movement. The subject's eye, fitted with a coil mounted on a suction scleral contact lens, is placed inside a cube made of two pairs of Helmholtz coils (one oriented horizontally, the other vertically). Until recently these coils were rather small, typically about 0.6 m diameter. Magnetic fields, orthogonal in space and time, are produced by driving these coils with suitable a.c. currents. A phase-lock amplifier detects the amplitude of the signal induced in the sensor coil with respect to both the horizontal and vertical meridians. The amplitude of this signal varies with the sine of the orientation of the sensor coil. If the recording field is limited to only a few degrees, noise levels below 1 min arc are possible with this original technique. Bandwidths of d.c. to about 200 Hz can be measured with such instruments (e.g. Collewijn and Tamminga, 1984; Hansen and

localization errors in his initial pilot work with Hansen when the flashed target was positioned in the frontal-parallel plane rather than on the radius traced out by the subject's arm. Such adverse effects on the visuo-motor response probably occurred because the subject had to allow for changes in the distance of the target from his torso as well as its lateral position in space. This result is not surprising inasmuch as the experiments were done monocularly and the monocular cues to target depth were very sparse, as well as brief, in the environment in which the target was flashed.

fully.

made by a subject attempting to sit or stand motionless. A clear interpretation of our records was impossible. The solution to the problem is illustrated in Fig. 1 where Skavenski is standing, as still as possible, with his right eye and head carrying sensor coils located in the measured homogeneous region (a cube 2 cm on a side) in large Helmholtz coils (1.8 m on a side) while fixating a target at optical infinity. Skavenski et al. (1979) found that, when translational artifacts were kept to <1', retinal image motion during slow control was 2-4 times faster than retinal image motion measured when the head was supported by a biteboard. The unsupported

Skavenski, 1985)* We now appreciate that it is

critical that sensor coils are located in the

minuscule region of homogeneous magnetic flux and also that they are not allowed to translate

in and out of this region. We discovered the

importance of these limitations somewhat pain-

Hansen, Robinson, Skavenski and Winterson

tried to use the original Robinson method to

measure natural head and eye movements

Steinman (1975, 1976) in collaboration with

What happens if the subject is actually allowed to move? Collewijn's (1977) ingenuity with instrumentation made research on this problem possible. He provided a convenient technique for making magnetic fields with a large homogeneous region, and introduced the revolving magnetic field-sensor coil technique. This method uses the phase of the signal induced into the sensor coil, rather than its amplitude, to indicate the orientation of the sensor

head, both sitting and standing, provided an

unsteady platform. It oscillated with frequencies

ranging from d.c. to 7 Hz. These natural head

movements were only partially compensated by

eye movements, guaranteeing appreciable retinal image motion under even these most re-

strictive natural postural constraints.

coil with respect to an earth-fixed framework. Collewijn's technique gives linear indications of the orientation of the sensor coil throughout 360°, is capable of absolute calibration, and can be used with subjects who are free to translate over appreciable distances (many centimeters with the 2 m or larger multiple cube-surface coils usually employed). Collewijn et al. (1975) also developed the suction silicone annulus sen-

*Claims of bandwidths an order of magnitude higher

relatively modest noise-levels claimed.

appear frequently in the literature. It seems unlikely

that such bandwidths were actually measured with the

man eye.

on the human eye. The silicone annulus, which has been shown to stay put even in the presence of the most violent eye and head movements (Collewijn et al., 1981), can even by used under closed eyelids without being displaced or inter-

fering with normal movements of the eye (Collewijn et al., 1985). Most recently, its stability during maintained fixation with the head supported has been shown to be 1' or better in a vernier afterimage experiment (de Bie, 1985). Figure 2 shows Collewijn preparing one of these remarkable inventions for attachment to a hu-

component of binocular eye and head movements when subjects oscillated their heads while viewing distant targets (40,000 m). They found appreciable failures of compensation in each of the eyes as well as differences in the amount of compensation achieved by each eye. The failure to observe virtually perfect compensation should have been expected because it is unreasonable to expect any biological compensatory system to work with much less than 5% error. For example, if the head oscillates, approximately sinusoidally, about a vertical axis

Steinman and Collewijn (1980) used Colle-

wijn's method to study the horizontal or vertical

slip velocities as high as 6°/sec should be expected even when the frequency of head oscillation is only about 1 Hz. We found compensation to be better than 5% on average, but certainly not sufficiently good to encourage one to believe that successful visual processing, off the bite-board, could arise entirely from the virtual perfection of compensatory eye movements. We already knew from the work of Murphy (1978) and Westheimer and McKee (1975) that contrast discrimination and vernier

through angles only as large as 40° (less than

half of its rotational range), peak retinal image

acuity were essentially insensitive to image motork.

tion below 2°/sec. We often found, however, much faster natural retinal image motion without out adverse effects on our ability to see a clear fused world. These casual observations encouraged us to measure contrast sensitivity functions in our subjects, whose natural retinal image motion during head oscillation was known. We also made psychophysical determinations of stereo acuity and the fusion of random-dot stereograms (see Julesz, this issue) concurrent

with eye movement recording during head

movement (Steinman et al., 1985). Our results

suggest that monocular and binocular vision in

sor soil—a new device for mounting sensor coils

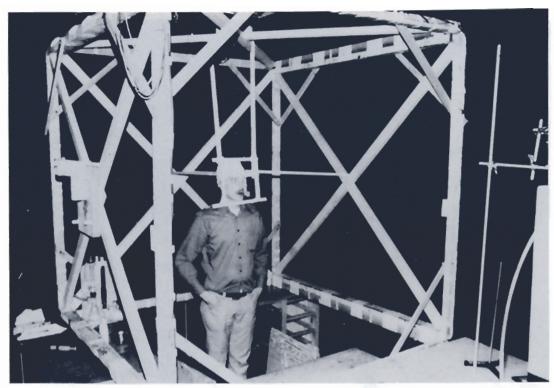


Fig. 1. Skavenski standing, as still as possible, and fixating a target at optical infinity while 2-dimensional movements of his right eye and head were recorded. The sensor coil was mounted on a scleral contact lens. The lens was held on the eye by means of the suction apparatus shown at the lower left side of the large field coils (1.6 m on a side). His head coil was supported by an arm extending upwards from a biteboard so as to be located near his eye (the white disk seen at the bridge of his nose). Both sensor coils were located within the small measured homogeneous region in the magnetic field. The wooden frame seen around his head defines this region within which the head and eye must stay while measurements are made. Skavenski is wearing a surgical stocking cap to prevent his relatively long curly hair (stylish in the seventies) from touching the localizing framework which only permitted movements through ± 2 cm on horizontal and vertical meridians.



Fig. 2. Collewijn preparing a silicone annulus sensor coil (held with the thumb and forefinger of his left hand) prior to attachment to a human eye. His right hand holds a metal suction ring, which is used to hold the annulus as it is carried to the eye, where it is firmly pressed in place and adheres by the suction produced by its shape. The annulus weighs about 0.1 g and its twisted leads are very thin (\sim 47AVG).

the presence of natural retinal image motion, image motion resulting from naturally occurring failures of oculomotor compensation, are better than would be expected from work done with the head held artificially and retinal image motion imposed on stabilized contrast displays

(Kelly, 1979) or when stereo displays are sta-

bilized and disparity varied (Hyson et al., 1983). This line of research has just begun. It needs to be extended to near targets and, like the work on the perception of direction, to targets moving in other than the frontal-parallel plane. Such work requires development of sensitive techniques to measure translations of the subject, given that rotations of his parts can now be measured with sufficient accuracy and precision. Research on the role of eye movements on basic visual processing in the eighties is different from research in the fifties. We have come about 180°. We now know that eye movements did not evolve to guarantee sufficient retinal image motion to prevent visual fading—the point emphasized by Barlow, Cornsweet, Ditchburn, Krauskopf, Ratliff, Riggs and Yarbus. Once artificial supports are removed, images are always moving. We must now find out how we see a fused, clear and stable world in the presence of such monocular and binocular image

EYE MOVEMENT AND COGNITIVE PROCESSES The role of cognitive processes in eye move-

ment and the role of eye movement in cognitive

perturbations.

processing have both been under study. This last section sketches highlights in both areas. It has been shown, with instruments capable of resolving the smallest eye movements, that subjects can attend selectively either to a stationary feature (a small centered dot) or to moving features (a 5° diameter moving striped field) presented simultaneously in a visual display. The unattended feature had only a very modest effect (<5%) on oculomotor performance (Murphy et al., 1975). Such independence, proposed by Mach (1906/1959, p. 143), has also been shown when the entire visual field was filled with densely-packed dots, half of which were stationary while the other half were moving (Kowler et al., 1984). Kowler and Zingale (1985) have taken this problem further by raising the question of whether useful perceptual information can be acquired from the unattended background—a stimulus to which smooth eye movements are effectively blind.

The influence of cognitive processes on

smooth pursuit eye movements has also been studied. It has been shown that a subject's expectations about future target motions, as well as properties of the target motion such as its onset-time and direction, determine the time and direction in which smooth eye movements are made even when target motions are random (Kowler and Steinman, 1979b, c; Kowler and Steinman, 1981; Kowler et al., 1984; Collewijn and Tamminga, 1984). Recently, Collewijn et al. (1985) have observed anticipatory smooth eye movements as fast as 50°/sec when very large target motions ($>70^{\circ}$) were about to be tracked. The implications of such anticipatory smooth eye movements for smooth pursuit models in which control depends exclusively on properties of the stimulus have been discussed by Kowler et al. (1984). There has also been research on the role of

saccadic eye movements in a number of different cognitive tasks. Saccades have been shown to

play a role in counting, but only when the items to be counted were arranged haphazardly within a relatively large display (2° diameter) (Kowler and Steinman, 1977). Saccades had no beneficial effect when the items were kept in a small region (30' diameter) circumscribed around the foveal center (Kowler and Steinman, 1979). Here, shifting the "mind's eye" proved to be as good as shifting the line of sight. Saccades were also not needed to solve problems requiring visual imagery, as had been suggested by Hebb (1968), or to execute finely-guided visuomotor tasks (Winterson and Collewijn, 1976). We also know that saccades cannot provide a simple way to look at thought processes during visual search. Noton and Stark (1971) thought that they might, and attempted to relate what they called a subject's "scan-path" to his success in recognizing a picture. They found that a given subject tends repeatedly to use an idiosyncratic scan-path to examine a particular display, but subsequent investigators could not relate the use of this scan-path to the likelihood

of recognizing a particular visual form (Locher

and Nodine, 1974). Hochberg (1981) has at-

tempted to relate eye movements to the percep-

tion of form itself, claiming that sequential

patterns of saccades are required to construct

the form from a series of foveal glimpses. His

ideas are yet to be tested in experiments that

combine eye movement recording with concur-

perception.

many papers.

general questions about the relationship of perceptual schema to eye movement control (Hochberg, 1968; Neisser, 1978) have been discussed critically by Mack et al. (1985). There has also been research on the role of saccades in reading. Little agreement exists about the specific cognitive processes that can be inferred from analysis of saccade size or timing during reading (e.g. Bouma and de Voogd, 1974; Hochberg, 1975; Rayner and McConkie, 1976; O'Regan and Lévy-Schöen, 1983). The role of eye movement in cognitive processing has a long history, going back at least to

rent determinations of form perception. More

Lotze (1852) who proposed that we construct the concept of extension in visual space (local signs) by making eye movements from one to another detail. Eye movement has also figured prominently in theories of form perception and in illusions of visual extent for almost as long (e.g. Wundt, 1910; Hebb, 1949; Festinger, 1971; Murphy et al., 1974). It seems certain that interest will continue but the form that future progress will take is less clear at this time.

FINAL COMMENT This paper tried to give the reader, unfamiliar

Progress probably must await development of

predictive quantitative models of form and size

with the area, some feeling for the variety, nature and vitality of research on eye movement. This goal required selection of a limited number of topics, each one of which could fill a chapter or, in some cases, an entire book if a traditional review were to be attempted. The selections and their treatment were idio-

syncratic. I apologize to fellow specialists for

omitting their favorite topic and failing to cite

The interdisciplinary nature of eye movement research, from its inception in the last century, guaranteed a variety of theoretical approaches, the development of novel methods. and potential controversies—precisely the ingredients required for a lively exchange of ideas as

well as scientific progress. The last quarter-

century of eye movement research has been fun. It shows every sign of continuing to be fun in the foreseeable future.

Acknowledgements—Supported by NIH-EY Grant 04647. I

thank T. Park and I. Nicholson for technical assistance.

REFERENCES*

Barlow H. B. (1952) Eye movements during fixation. J. Physiol., Lond. 116, 290-306. Barr C. C., Schultheis L. W. and Robinson D. A. (1976) Voluntary, non-visual control of the human vestibulo-

ocular reflex. Acta otolar. 81, 365-375. de Bie (1985) An afterimage vernier method for assessing the precision of eye movement monitors: results for the scleral

search coil technique. Vision Res. 25, 1341-1343. Bouma H. and de Voog A. H. (1974) On the control of eye

saccades in reading. Vision Res. 14, 273-284. Collewijn H. (1969) Optokinetic eye movements in the rabbit: Input-output relations. Vision Res. 9, 117-132. Collewijn H., van der Mark F. and Jansen T. C. (1975)

Collewijn H. (1977) Eye and head movements in freely moving rabbits. J. Physiol., Lond. 266, 471-498. Collewijn H. (1981) The Oculomotor System of the Rabbit and its Plasticity. Springer, Berlin.

Collewijn H., Martins A. J. and Steinman R. M. (1981)

Natural retinal image motion: origin and change. Ann.

15, 447–450.

Precise recording of human eye movements. Vision Res.

N.Y. Acad. Sci. 374, 312-329. Collewijn H., Steinman R. M. and van der Steen (1985) The performance of the smooth pursuit eye movement system during passive and self-generated sitmulus motion. J. Physiol., Lond. 366, 19P.

Collewijn H. and Tamminga E. P. (1984) Human smooth and saccadic eye movements during voluntary pursuit of different target motions on different backgrounds. J. Physiol., Lond. 351, 217-250. Collewijn H., van der Steen and Steinman R. M. (1985) Human eye movements associated with blinks and pro-

longed eyelid closure. J. Neurophysiol. 54, 11-27. Cornsweet T. N. (1956) Determination of the stimuli for

involuntary drifts and saccadic eye movements. J. opt. Soc. Am. 46, 987-993. Cushman W. B., Tangney J. F., Steinman R. M. and Ferguson J. L. (1984) Characteristics of smooth eye

movements with stabilized targets. Vision Res. 24, 1003-1009. Ditchburn R. W. (1980) The function of small saccades. Vision Res. 20, 271-272.

Fender D. H. and Nye P. W. (1961) An investigation of the mechanisms of eye movement control. Kybernetik 1, 81-88.

Festinger L. (1971) Eye movement and perception. In The Control of Eye Movement (Edited by Bach-y-Rita P.,

Collins C. and Hyde J.). Academic Press, New York. Guthrie B. L., Porter J. D. and Sparks D. L. (1983) Corollary discharge provides accurate eye position infor-

mation to the oculomotor system. Science, N.Y. 221, 1193-1195.

Hansen R. M. (1979) Spatial localization during pursuit eye movements. Vision Res. 19, 1213-1221.

^{*}A list of eye movement papers appearing in Vision Research between 1961-1985 can be obtained by writing to the author. This list does not contain references to papers on "saccadic suppression," i.e. threshold elevations associated with saccadic eye movements. This topic is covered in the paper by Volkmann, to follow in this issue.

Hansen R. M. and Skavenski A. A. (1985) Accuracy of spatial localizations near the time of saccadic eye movements. Vision Res. 25, 1077-1082.

Hansen R. M. and Skavenski A. A. (1977) Accuracy of eye

919-926.

position information for motor control. Vision Res. 17,

- Hebb D. O. (1949) The Organization of Behavior. Wiley,
- New York. Hebb D. O. (1968) Concerning imagery. Psychol. Rev. 75,
- 466-477.
- Hochberg J. (1968) In the mind's eve. In Contemporary
- Theory and Research in Visual Perception (Edited by
- Haber R. N.). Holt, Rinehart & Winston, New York.
- Hochberg J. (1975) On the control of eye saccades in reading. Vision Res. 15, 620.
- Hochberg J. (1981) Levels of perceptual organization. In
- Perceptual Organization (Edited by Kubovy M. and Pomerantz J. R.). Erlbaum, Hillsdale, N. J.
- Hyson M. T., Julesz B. and Fender D. (1983) Eye movements and neural remapping during fusion of random-dot stereograms. J. opt. Soc. Am. 73, 1665-1673.
- Kelly D. H. (1979) Motion and vision. II. Stabilized spatiotemporal surface. J. opt. Soc. Am. 69, 1340-1349. Kowler E., Martins A. J. and Pavel M. (1984) The effect of
- expectations on slow oculomotor control-IV. Anticipatory smooth eye movements depend on prior target motions. Vision Res. 24, 197-210. Kowler E. and Steinman R. M. (1977) The role of small
- saccades in counting. Vision Res. 17, 141-146. Kowler E. and Steinman R. M. (1979a) Miniature saccades: Eye movements that do not count. Vision Res. 19, 105-108.
- Kowler E. and Steinman R. M. (1979b) The effect of expectations on slow oculomotor control-I. Periodic target steps. Vision Res. 19, 619-632. Kowler E. and Steinman R. M. (1979c) The effect of
- expectations on slow oculomotor control-II. Single target displacements. Vision Res. 19, 633-646. Kowler E. and Steinman R. M. (1980) Small saccades serve no useful purpose: Reply to a letter by R. W. Ditchburn.
- Vision Res. 20, 273-276. Kowler E. and Steinman R. M. (1981) The effect of expectations on slow oculomotor control—III. Guessing unpredictable target displacements. Vision Res. 21, 191-203.
- Kowler E., van der Steen J., Tamminga E. P. and Collewijn H. (1984) Voluntary selection of the target for smooth eye movement in the presence of superimposed, full-field stationary and moving stimuli. Vision Res. 24, 1789-1798.
- Kowler E. and Zingale C. (1985) Smooth eye movements as indicators of selective attention. In Attention and Performance XI (Edited by Posner M. I. and Marin O. S. M.). Erlbaum, Hillsdale, N.J. Locher P. and Nodine C. (1974) The role of scanpaths in the
- 308-314. Lotze R. H. (1852/1966) Medicinische Psychologie. Bonet, Amsterdam. Mach, E. (1906/1959) Analysis of Sensations. Dover, New

recognition of random shapes. Percept. Psychophys. 15,

- York. Mack A., Fendrich R., Chambers D. and Heuer, F. (1985) Perceived position and saccadic eye movements. Vision
- Res. 25, 501-505. Mack A., Fendrich R. and Wong E. (1982) Is perceived

77-88.

- - Martins A. J., Kowler E. and Palmer C. (1985) Smooth pursuit of small-amplitude sinusoidal motion. J. opt. Soc. Am. A 2, 234-242.

Matin L. (1972) Eye movements and perceived visual direc-

- tion. In Handbook of Sensory Physiology (Edited by Jameson D. and Hurvich L.), Vol. 7, pt 4. Springer-Verlag, Berlin. Matin L., Matin E. and Pearce D. G. (1970) Eye movements
- in the dark during the attempt to maintain a prior fixation position. Vision Res. 10, 837-857. Matin L. and Pearce D. (1965) Visual perception of direc-
- tion for stimuli flashed during voluntary saccadic eye movements. Science, N.Y. 148, 1485-1488. Matin L., Pearce D., Matin E. and Kibler G. (1966) Visual
 - perception of direction in the dark: Roles of local sign, eye
 - movements, and ocular proprioception. Vision Res. 6, 453-469.
- D. and MacArthur R. (1982) Oculoparalytic illusion: Visual-field dependent spatial mislocations by humans partially paralyzed with curare. Science, N.Y. 216, 198-201. Mays L. E. and Sparks D. L. (1980) Saccades are

Matin L. Picoult E., Stevens J. M., McIver Jr, W. E., Young

- spatially, not retinocentrically coded. Science, N.Y. 208, Melvill Jones G. (1979) In Mammalian Vestibular Physiology (Wilson V. J. and Melvill Jones G.). Plenum Press, New York.
- Murphy B. J. (1978) Pattern thresholds for moving and stationary gratings during smooth eye movement. Vision Res. 18, 521-530. Murphy B. J., Haddad G. M. and Steinman R. M. (1974) Simple forms and fluxuations of the line of sight: Impli-
- cations for motor theories of form processing. Percept. Psychophys. 16, 557-563. Murphy B. J., Kowler E. and Steinman R. M. (1975) Slow oculomotor control in the presence of moving backgrounds. Vision Res. 15, 1263-1268.

Nachmias J. (1959) Two-dimensional motion of the retinal

- image during monocular fixation. J. opt. Soc. Am. 49, 901-908. Nachmias J. (1961) Determiners of the drift of the eye during monocular fixation. J. opt. Soc. Am. 51, 761-766. Neisser U. (1978) Perceiving, anticipating and imagining. In
 - Perception and Cognition; Issues in the Foundations of Psychology (Edited by Wade Savage C.), Vol. IX. Minnesota Studies in Phil. Sci. Noton D. and Stark L. (1971) Scanpaths in saccadic eye
 - movements while viewing and recognizing patterns. Vision Res. 11, 929-942. O'Regan J. K. (1984) Retinal versus extraretinal influences in flash localization during saccadic eye movements in the
 - presence of a visible background. Percept. Psychophys. O'Regan J. K. and Lévy-Schöen A. (1983) Integrating visual information from successive fixations: Does trans-
 - Rayner K. and McConkie G. W. (1976) What guides a reader's eye movements? Vision Res. 16, 829-837. Robinson D. A. (1963) A method of measuring eye movement using a scleral search coil in a magnetic field.

saccadic fusion exist? Vision Res. 23, 765-768.

- I.E.E.E. Trans. Biomed. Electron. BME 10, 137-145. Robinson D. A. (1975) Oculomotor control signals. In Basic Mechanisms of Ocular Motility and their Clinical Impli-
- cations (Edited by Lennerstrand G. and Bach-y-Rita P.). motion a stimulus for smooth pursuit? Vision Res. 22, Pergamon Press, Oxford.

Skavenski A. A. (1971) Extraretinal correction and memory

for target position. Vision Res. 11, 743-746. Skavenski A. A. (1972) Inflow as a source of extraretinal eye position information. Vision Res. 12, 221-229.

Skavenski A. A., Haddad G. M. and Steinman R. M. (1972)

The extraretinal signal for the visual perception of direction. Percept. Psychophys. 11, 287-290.

Skavenski A. A. and Hansen R. M. (1978) Role of eye position information in visual space perception. In Eye Movements and the Higher Psychological Processes (Edi-

ted by Senders J. W., Fisher J. F. and Monty R. A.). Erlbaum, Hillsdale, N.J. Skavenski A. A., Hansen R. M., Steinman R. M. and Winterson B. J. (1979) Quality of retinal image sta-

bilization during small natural and artificial body rotations in man. Vision Res. 19, 675-683. Skavenski A. A. and Steinman R. M. (1970) Control of eve position in the dark. Vision Res. 10, 193-203. Sparks D. L. and Mays L. E. (1983) Spatial localization of saccade targets. I. Compensation for stimulation-induced

perturbations in eye position. J. Neurophysiol. 49, 45-63. Steinman R. M. (1965) The effect of target size, luminance and color on monocular fixation. J. opt. Soc. Am. 55. 1158-1165. Steinman, R. M. (1975) Oculomotor effects on vision. In

Basic Mechanisms of Ocular Motility and their Clinical

Implications (Edited by Lennerstrand G. and Bach-y-Rita P.). Pergamon Press, Oxford. Steinman R. M. (1976) The role of eye movements in maintaining a phenomenally clear and stable world. In Fig. Movements and Psychological Processes (Edited by Monty

R. A. and Senders J. W.). Erlbaum, Hillsdale, N. J. Steinman R. M. (1986) The need for an eclectic, rather than

systems, approach to the study of the primate oculomotor system. Vision Res. 26, 101-112.

Steinman R. M. and Collewijn H. (1980) Binocular retinal image motion during active head rotation. Vision res. 20. 415-429.

Steinman R. M., Levinson J. Z., Collewijn H. and van der Steen J. (1985) Vision in the presence of known natural retinal image motion. J. opt. Soc. Am. A 2, 226-233. Stevens J. K., Emerson R. C., Gerstein G. L., Kallos T., Neufeld G. R., Nicols C. W. and Rosenquist A. C. (1976)

Paralysis of the awake human: visual perceptions. Vision Res. 16, 93-98. Walls G. L. (1962) The evolutionary history of eye movements. Vision Res. 2, 69-80.

Westheimer G. (1954) Eye movement responses to a hori-

932-941.

zontally moving visual stimulus. Archs Ophthal. 52, Westheimer G. and McKee S. P. (1975) Visual acuity in the presence of retinal image motion. J. opt. Soc. Am. 65, 847-850.

Winterson B. J. and Collewijn H. (1976) Microsaccades during finely-guided visuomotor tasks. Vision Res. 16, 1387-1390. Wundt W. (1910) Grundzuge der Physiologischen Psycho-

logie, Vol. 2. Engelmann, Leipzig. Yarbus A. L. (1967) Eve Movements and Vision. Plenum Press New York