

## NEW DIRECTIONS FOR OCULOMOTOR RESEARCH

ROBERT M. STEINMAN<sup>1</sup>, EILEEN KOWLER<sup>2</sup> and HAN COLLEWIJN<sup>3</sup>

<sup>1</sup>Department of Psychology, University of Maryland at College Park, MD 20742, <sup>2</sup>Department of Psychology, Rutgers University, New Brunswick, NJ 08903, U.S.A. and <sup>3</sup>Department of Physiology I, Erasmus University, P.O. Box 1738, 3000DR, Rotterdam, The Netherlands

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**Abstract**—This paper reviews major trends in the study of the oculomotor system since Westheimer published his doctoral research on this topic 35 years ago. Westheimer introduced the use of linear system analysis for the study of eye movements, an approach used a great deal by others ever since. Westheimer himself abandoned this approach within a decade, in part, because this kind of analysis becomes ambiguous when predictive properties of oculomotor system performance become prominent.

We discuss the implications of ignoring the prominence of predictive eye movements and describe recent evidence for their prevalence and power. This leads us to propose that a new approach to the study of oculomotor performance is required. We also discuss the recent trend to apply the "connectionist" (or "neural network") approach in studies of the oculomotor system, and point out that the "symbolic", rather than the "adaptive", nature of predictive eye movements makes successful extension of these models to oculomotor performance unlikely.

Our new approach emphasizes the use of natural stimulation in subjects free from bodily restraints. Accurate measurement of eye, head and torso movements under such conditions has become possible recently and data obtained in this manner has led to the discovery of a number of unexpected characteristics of oculomotor system performance. These developments have encouraged us to abandon the modular view of the oculomotor system, popular since Dodge launched the modern era of oculomotor research in 1903, which postulates five, or more, largely independent "subsystems". We suggest that only two subsystems (a fast saccadic and a somewhat slower smooth) are used to fixate and track a central representation of objects located in three-dimensional space. We show that this two-subsystem approach is consistent with current knowledge of oculomotor system neuroanatomy and neurophysiology.

Connectionist	Expectation	Linear systems	Neural network	Oculomotor subsystem	OKN
Saccade	Smooth pursuit	VOR			

### PROLOGUE

Professor Westheimer's distinguished career began with two publications, both based on his doctoral research on the oculomotor system. The first paper described saccadic eye movements (Westheimer, 1954a), the second described smooth pursuits (Westheimer, 1954b). Both papers have been, and continue to be, cited frequently since their publication 35 years ago. His other early publications with Conover (Westheimer & Conover, 1954) and Mitchell (Westheimer & Mitchell, 1956) were also on eye movements. The former described one of the rare subjects who could make voluntary smooth eye movements without a visible moving stimulus; the latter described convergence. A year later he published an important theoretical paper on the kinematics of the eye (Westheimer, 1957).

From the beginning, Westheimer's contributions to the oculomotor literature have been both empirical and theoretical. To illustrate, he began his doctoral research by improving the American Optical Ophthalmograph eye movement camera, getting its time-resolution down to 1 msec and its position-resolution down to 5 or 10 min arc. He made a wise, if not faddish decision, when he rejected the new, high-tech recording method of the 1950s, the contact lens-optical lever, because it "cannot be used for accurate recordings of larger eye movements" (Westheimer, 1954a). We confirmed this many years later (Collewijn, Martins & Steinman, 1981, 1983) when we compared the stability of a contact lens to the stability of a silicone annulus sensor coil (Collewijn, Van der Mark & Jansen, 1975) as we got ready to study large eye movements in human subjects, whose heads were free to move (Steinman & Collewijn, 1980).

Westheimer used his modified ophthalmographic camera to make careful measurements of oculomotor performance. He modeled selected aspects of these observations within the framework provided by "linear system control theory", in 1954 a novel theoretical framework for describing the behavior of a biological system. In doing this, Westheimer became the pioneer for much subsequent oculomotor research. This new theoretical approach was probably brought to his attention by one of his teachers at Ohio State, namely, the psychologist, Paul Fitts, who described its potential in his chapter on motor control published in the Stevens's *Handbook of Experimental Psychology* (Fitts, 1951). Fitts, in turn, was probably influenced by Kenneth Craik, the psychologist, who went to Cambridge after getting his degree with Margaret Vernon in Edinburgh. At Cambridge Craik (1947) developed these ideas sufficiently to influence many of his colleagues in the Departments of Physiology and Psychology, who acknowledged his contributions by naming an interdisciplinary sensory laboratory after him.

The 35 years since Westheimer's initial eye movement publications have seen many attempts to use the systems approach on various problems of oculomotor control, the approach pioneered by Westheimer in his doctoral work. Among the most important contributions in this vein were made by Westheimer when he visited Cambridge and collaborated with Cyril Rashbass. They used systems analysis to describe characteristics of ocular vergence (Rashbass & Westheimer, 1961a, b). At just about this time Fender and Nye (1961) published a linear systems analysis of eye tracking that was followed shortly by publications by Stark, Vossius and Young (1962) and Robinson (1964, 1965). By that time Westheimer himself had gone off in other directions, in part because he realized that linear systems analysis was probably inappropriate for the study of various aspects of the human oculomotor performance because of the prevalence of high-level predictive properties—a view he restated recently with respect to the potential futility of applying systems analysis to the initiation and control of saccades. In his words:

"To determine the systems equation one compares input with output. The output, of course, is eye position, but how would one characterize the input? Because the

majority of saccades are "voluntary", there isn't a readily determinable change in state, this is the crux of the question of whether systems theory is an appropriate mode of analysis . . . with any reasonable hope of success" (Westheimer, 1989, p. 6).

Westheimer did not discontinue his studies of the oculomotor system. He did, however, shift his research from human oculomotor performance to its anatomical and physiological substrate in infra-human primates, and published a number of papers on this topic in collaboration with Blair (1972a, b, 1973a, b, 1974). Fender came to appreciate the limitations of linear systems analysis for oculomotor research in the same decade within which he began to use it (St Cyr & Fender, 1969a, b), but others have continued along the path charted, but long since abandoned, by Westheimer.

Westheimer has been the harbinger of many other new directions for research in visual science throughout his career, e.g. the application of Fourier Optics to modulation thresholds in the living human eye (Westheimer, 1960). More recently, he renewed interest in what he called "hyperacuity", i.e. the psychophysical resolution of differences in the position of visual targets, whose offsets are smaller than the elements constituting the receptor mosaic (see Westheimer, 1981, for an overview). Work in each of these problem areas has kept a great many investigators gainfully employed for a great many years. To sum up, Westheimer has been a major innovator and leader throughout his career. He has contributed a great deal to many areas of visual science. Many of these contributions derived from his ability to recognize when something must be abandoned and when something new must be tried. Westheimer's ability to do this derived in large measure from his respect for the messages contained in carefully-made observations.

We intend to try to follow his example in this paper. 35 years ago Westheimer suggested a possible new direction for oculomotor research. We believe that a new direction is needed now. Our field has become very cluttered with *ad hoc* theoretical constructs and *ad hoc* assumptions. Available models cannot describe, much less predict, some of the most fundamental characteristics of human oculomotor performance. Progress, in our opinion, will not be made without major revisions in the way we think about human oculomotor control. We were

encouraged to assemble our reasons for proposing change, and for proposing what we see as a possibly fruitful new direction, by the career of the man whose numerous contributions we are acknowledging today. Many new directions and much progress in visual science can be traced to Westheimer's innovative work. We realize that it is unlikely that our efforts will be either as valuable, or as influential, as Professor Westheimer's early eye movement research, but our hope, in this and in our future collaborative work, is to try to follow the example he set so well.

## REASONS FOR CHANGE

### *New observations*

Our work during the past decade has made it clear that oculomotor system capacity, studied carefully under relatively unconstrained conditions, cannot be predicted in a number of important respects from the vast literature that has accumulated since Dodge's (1903) pioneering study of oculomotor performance. The rapidly increasing gap between classical observations and our data has encouraged us to question a number of firmly-held beliefs. For example, recently we reported that: (1) the "slow, smooth vergence subsystem" (Dodge's type 5) is actually very fast. Smooth vergence velocities can be as high as 200 deg/sec when testing conditions are appropriate to reveal this capacity; (2) "vergence" is mainly saccadic whenever targets are not located along the median plane, i.e. whenever target objects are in the locations they are most likely to occupy in any natural visual environment; and (3) conjugate and disjunctive gaze-shifts are not independent: the duration of the saccade in one eye (the eye required to traverse the smaller angle) is adjusted so that saccades in both eyes will finish at nearly the same time—a useful characteristic because it allows rapid scanning of nearby 3-D space without introducing large fixation disparities at saccade-offset that would then have to be reduced by smooth disjunctive eye movements (i.e. by the classical "vergence" response) (Erkelens, Van der Steen, Steinman & Collewijn, 1989a, b). All these findings go against the prevailing wisdom that "vergence" is an independent subsystem that is slow to start, slow to change and smooth (see Hallett, 1986; Carpenter, 1988), a view that has been in place for a very long time, ever since Dodge's classic paper of 1903.

Some of our recent observations on vergence are illustrated in Figs 1–4. Figure 1 shows Han Collewijn making vergence eye movements to track an object that was moved back and forth along his median plane, either by the experimenter (left column) or by the subject himself (middle column). In the right-hand column, the target remained in place and the subject changed the vergence angle of the target by moving his torso back and forth. (Target vergence was defined as the angle formed by the lines of sight as they intersect on a fixated target, whose distance from the subject is measured from the mid-point of the line that connects the centers of rotation of each eye.) Four ranges of target vergence velocities were employed, viz. "slow" in the top row to "very fast" in the bottom row. The average target vergence velocities ranged from about 13 to 135 deg/sec in these four conditions. The target was a painted nailhead mounted at the end of a rod that was viewed in a lighted, highly structured visual environment. Representative eye movement records (eye position against time) of an inexperienced eye movement subject, performing these same tasks, are reproduced in Fig. 2. Horizontal eye movements of each eye are shown in the left-hand records and vergence (left eye minus right eye) is shown in the right-hand records (here, the dotted line signifies the position of the target object). The rows show different movement conditions with the experimenter moving the nailhead on top, the subject moving it in the middle, and the nailhead stationary while the subject moves his torso back and forth on bottom. Tracking, carried out by smooth changes of vergence responding to a target moving back and forth as fast as 75 deg/sec (Erkelens et al., 1989a, b), was excellent under all but the least predictable conditions (illustrated in the lower left corner of Fig. 1).

There were two major differences between our and all prior work that could have accounted our subjects's excellent tracking performance. First, we used a natural target object and provided the subject with many salient cues to its distance relative to his eyes and to the position of other objects and frames in the visual scene. Second, these measurements were all made with the nailhead within arm's reach, the region within the subject's "lifespace" (Lewin, 1935) in which the "vergence subsystem" evolved to operate, i.e. the region in which varying vergence favors both nutrition and reproductive

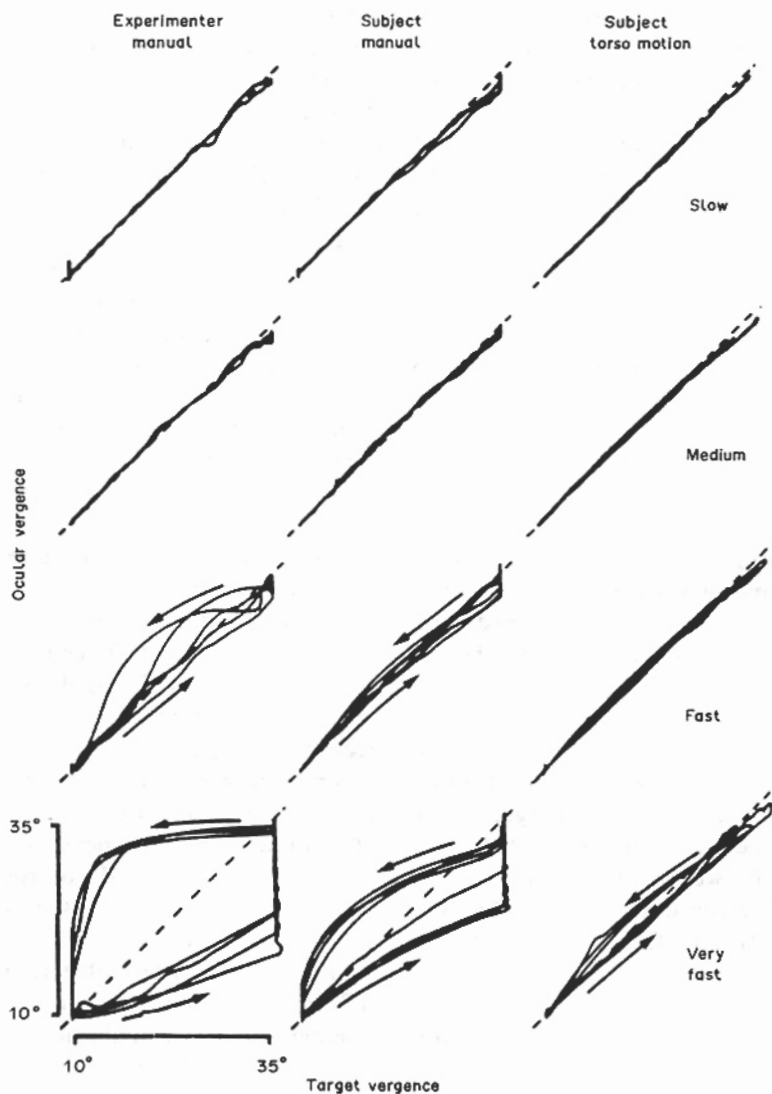


Fig. 1. Typical relationships between ocular vergence angle and target vergence angle of subject HC responding to slow (first row), medium (second row), fast (third row) and very fast (bottom row) changes in target distance. The three columns represent the three ways in which the distance of the target was varied. Diagonal, dashed lines represent completely accurate tracking.

success. Objects placed within reach of an adult's arm have target vergences ranging from about 6 deg (an extended adult man's arm can hold an object at about 65 cm, and if his interpupillary distance is 68 mm, the object's target vergence will be 6 deg). Target vergence will increase to about 30 deg when the object is brought in to 10 cm (the near-point of youthful adult eyes). Prior work on vergence, in general, did not explore targets nearer than the outer edge of this important nearby region. Enright (1984, 1986) is an important exception. He studied near targets and anticipated some of our most important recent findings under a relatively restricted range of target vergence changes with an eye movement recording technique with

rather limited bandwidth. In other prior work, the nearest targets subtended only 6 or 7 deg of target vergence. More often, "near" targets were located well-beyond arm's reach, at only 3 or 4 deg of target vergence, more than 95 cm from the eyes. Furthermore, in almost all prior work on vergence, highly restricted, unnatural targets were used in which only binocular disparity, only blur or only size were provided as cues for maintaining or changing ocular vergence. These cues would never be encountered in isolation in any visual environment outside of the laboratory (see Collewijn, Steinman, Erkelens & Regan, 1990a, for a review). Normally, all three covary and work together in guiding vergence.

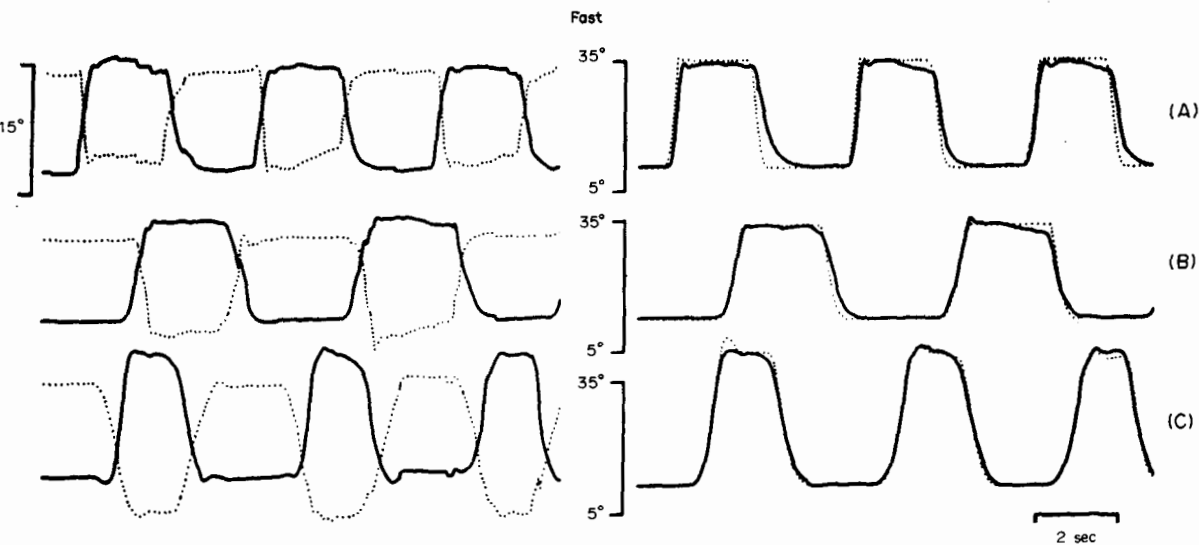


Fig. 2. Eye movements of subject R.D. made in response to "fast" changes in target distance. The left panels show movements of the left (continuous lines) and right (dotted lines) eye. The right panels show the corresponding changes of ocular vergence (continuous lines) and target vergence (dotted lines). Upward deflections: rightward monocular movement (left panels); convergence (right panels). (A) Target moved by the experimenter; (B) target moved by the subject; (C) changes in target distance induced by movements of the upper torso.

We believe that analytic experiments, which provide cues one at a time, are useful, necessary and interpretable *only after* performance has been observed under relatively natural conditions that permit the oculomotor system to perform at the limits of the capacity it developed under evolutionary pressures. Analytic experiments with impoverished cues do not substitute for determinations of system capacity with normal input. They are not only likely to underestimate oculomotor system capacity, they are also likely to give grossly misleading indications about how the normal system actually works (another illustration of this problem, viz. studying the VOR in darkness, will be discussed later). At present, our understanding of oculomotor system performance has been compromised by the reluctance, and rather limited ability, to observe its operation under relatively natural conditions.

The importance of observing eye movements under natural conditions is also illustrated in Fig. 3, which reproduces results from an experiment in which subjects were required to shift gaze between two stationary targets located at different distances (varying from 10 to 91 cm) along the median plane (Erkelens et al., 1989b). Average performance of three subjects, whose ages ranged from 35 to 60 years, is shown. These gaze-shifts were accomplished primarily with smooth eye movements, whose velocities in both

con- and divergent directions could be quite high, as high as the fastest observed smooth pursuit, a "type" of eye movement that had been thought to be produced by an entirely different oculomotor subsystem. Pursuit and vergence were believed to be independent primarily because pursuit had shorter latencies and much higher maximal velocities than vergence. The high speed of the smooth "vergence" gaze-shifts vitiate this argument. These high-speed, smooth gaze-shifts were also quite accurate, as is shown in Fig. 4, where average binocular fixation errors remaining at the end of these "vergence" eye movements are plotted for each subject. So, given relatively natural input and the ability to measure ocular vergence accurately in both time and space, we found that oculomotor system capacity was far better than could have been predicted from prior analytic experiments that: (1) deprived the oculomotor system of most of the cues it normally has to initiate and guide disjunctive eye movements; and (2) studied disjunctive eye movements only at, and beyond, the outer edge of its teleologically important, functional range.

#### *Effects of expectations on large and fast smooth pursuits*

Our claim that a new approach to the study of oculomotor system performance is needed is

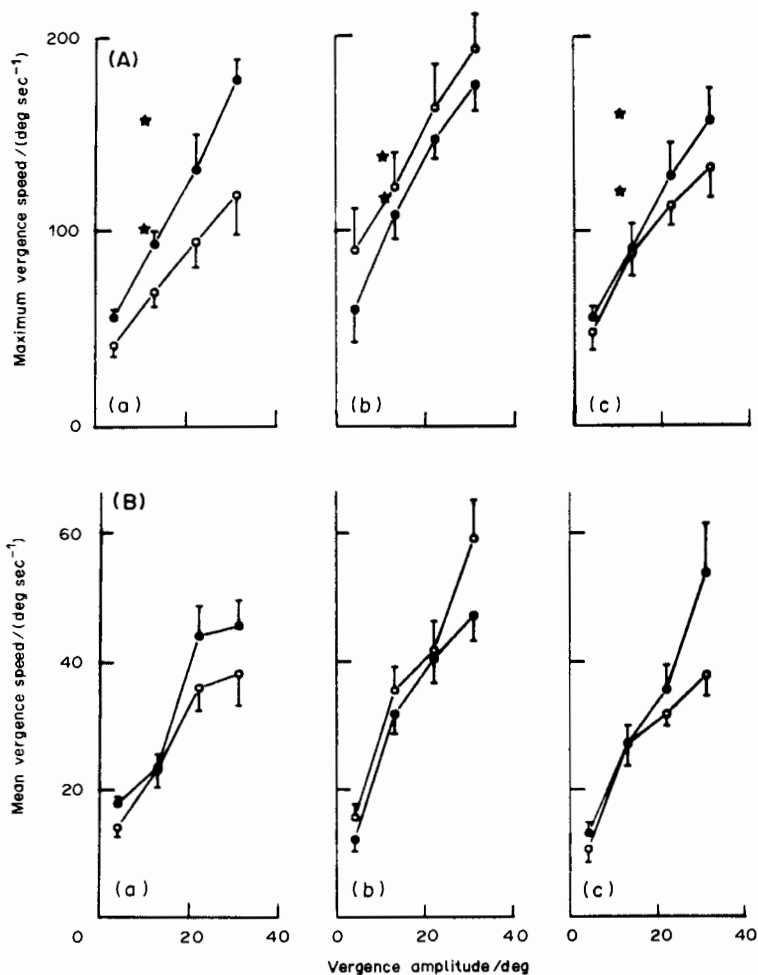


Fig. 3. (A) Mean maximum smooth vergence speed of each of the three subjects plotted as a function of the amplitude of the vergence change required. (a) RS, (b) HC (c) CE. The target pairs were located along the subject's median plane (connected symbols) or asymmetrically (asterisks). Means are based on 6 trials, each containing 4–5 convergent responses and an equal number of divergent responses. Error bars indicate 1SD. (○), convergence, (●) divergence. (B) As (A), showing mean average vergence speeds for gaze shifts between targets in the median plane. (a) RS, (b) HC, (c) CE.

motivated to a large degree by relatively novel observations such as those described above. They encourage us to believe that our present knowledge of oculomotor system capacity has been distorted by constraints imposed by older recording methods, which had a very limited dynamic range, and required that the head be stabilized on a biteboard or chin-rest. Present knowledge, in our view, has also been distorted by the unflagging commitment of some oculomotor researchers to time-invariant, linear system models. This class of models cannot describe oculomotor system performance without ignoring, or using protocols specifically developed to obscure, the effects of prediction, long known to be a fundamental characteristic of oculomotor system performance (see Kowler, Martins & Pavel, 1984a, for a review of the role

of prediction since Dodge's convincing demonstration of 1903, and Kowler, 1990, and Pavel, 1990, for reviews of predictive performance that trace out its history in greater detail). Even elaborations of linear system models that attempt to allow for prediction by adding learning or "adaptive" properties (e.g. Dallos & Jones, 1963) are inadequate because these models use "learning operators" that predict future errors and initiate actions to prevent them solely on the basis of target motion or tracking performance in the immediate past. See Kowler and Steinman (1979a), Steinman (1986) and Pavel (1990) for discussion of limitations inherent in such "adaptive" control system models. These papers point out that even Dallos and Jones' data show that prediction was present during the first tracking cycle, i.e. before an

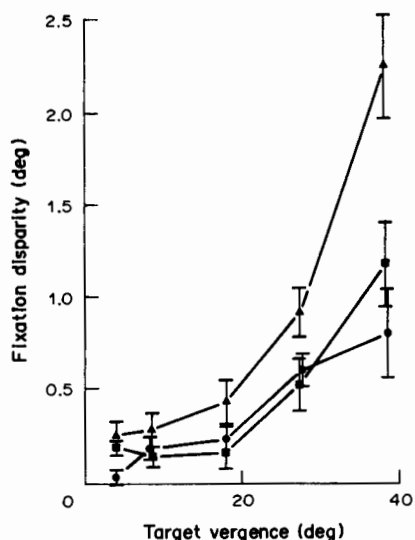


Fig. 4. Residual fixation disparities (target vergence minus ocular vergence) at the completion of gaze-shifts. The left panel shows the results for the five targets (A–E) in the median plane (symmetrical condition). Viewing was binocular. Subjects: RS (▲), HC (■) and CE (●). Bars represent the variability (1 SD) between successive fixations.

appreciable opportunity for “learning” had been provided.

Particularly vivid examples of the effects of a subject’s expectations about future target motion on smooth pursuit performance are illustrated in Fig. 5. Han Collewijn (top) is waiting for the experimenter to move a target (an LED, shown by the dashed line) to the left (downward) through an angle of about 75 deg (Collewijn, Steinman & Van der Steen, 1985; Van der Steen, 1990). His eye (the solid line) started to move about 300 msec before the target and achieved a velocity of 50 deg/sec in the direction of the expected target motion just prior to making a saccade back towards the still stationary target. The target began to move at just about the time this re-fixation saccade had ended. The anticipatory smooth eye movement and the smooth pursuit of the objectively moving target had about the same maximal velocities. The re-fixation and “catch-up” saccade velocities, and the anticipatory smooth eye and smooth pursuit velocities, are best seen in the velocity profiles plotted below the position profiles. Lenard Ferman is participating in a similar set of measurements in the bottom half of Fig. 5, except that in this experiment, he is to track the LED with coordinated head and eye movements (Van der Steen, 1990). Note, in his case, his eye velocity also got up to about 50 deg/sec before the target started to move. His

head started moving after his eye, but it also reached about 50 deg/sec just as the target began to move.

In both cases illustrated in Fig. 5, the subjects knew the direction in which the target would move at some future time. They also knew about how fast and how far it would go. They did not know when it would start moving, however. In both cases, their anticipatory smooth eye movements attained about 20% of the future target velocity (about 250 deg/sec) before the target started to move. These were among the higher values observed. Anticipatory smooth eye movements were observed on 95% of the trials, but most anticipatory smooth eye velocities were lower, most frequently about 5–10 deg/sec (Van der Steen, 1990). These values for anticipatory smooth eye movement velocities are about what would be expected from the prior research on anticipatory smooth eye movements in which much slower target velocities were tracked (under 10 deg/sec) (Kowler & Steinman, 1979b, 1981; Kowler & McKee, 1984, 1987; Kowler, 1989). In these prior experiments, anticipatory smooth eye movement velocities were also found to attain 10–25% of the velocity of the expected velocity of the target. The results reproduced in Fig. 5 show that anticipatory smooth eye movements are not restricted to situations in which the subject expects the target to move relatively slowly.

Attempts to discourage effects of expectations in the laboratory by randomizing stimulus variables in the hope of studying pure “reflexive” responses to target motion, do not work. Randomization of stimulus variables, such as the speed, direction or duration of target motion, does not abolish expectations. When motions are random, effects of expectations are based on the past history of target motions as well as on the immediate target motion. The effect of past history is seen both in the purely anticipatory portion of pursuit, before the target begins to move, and also during the initial few hundred milliseconds of pursuit, when the target is actually in motion (Kowler & McKee, 1987; Kowler, He & Pizlo, 1985). Distinguishing the contribution of expectations from the contribution of immediate stimulus motion on pursuit might be accomplished by analytical techniques, developed by mathematical psychologists interested in modelling reaction time data (cf. Luce, 1986), but these techniques have so far received only scant attention from oculomotorists (Kowler et al., 1984a; Pavel, 1990).

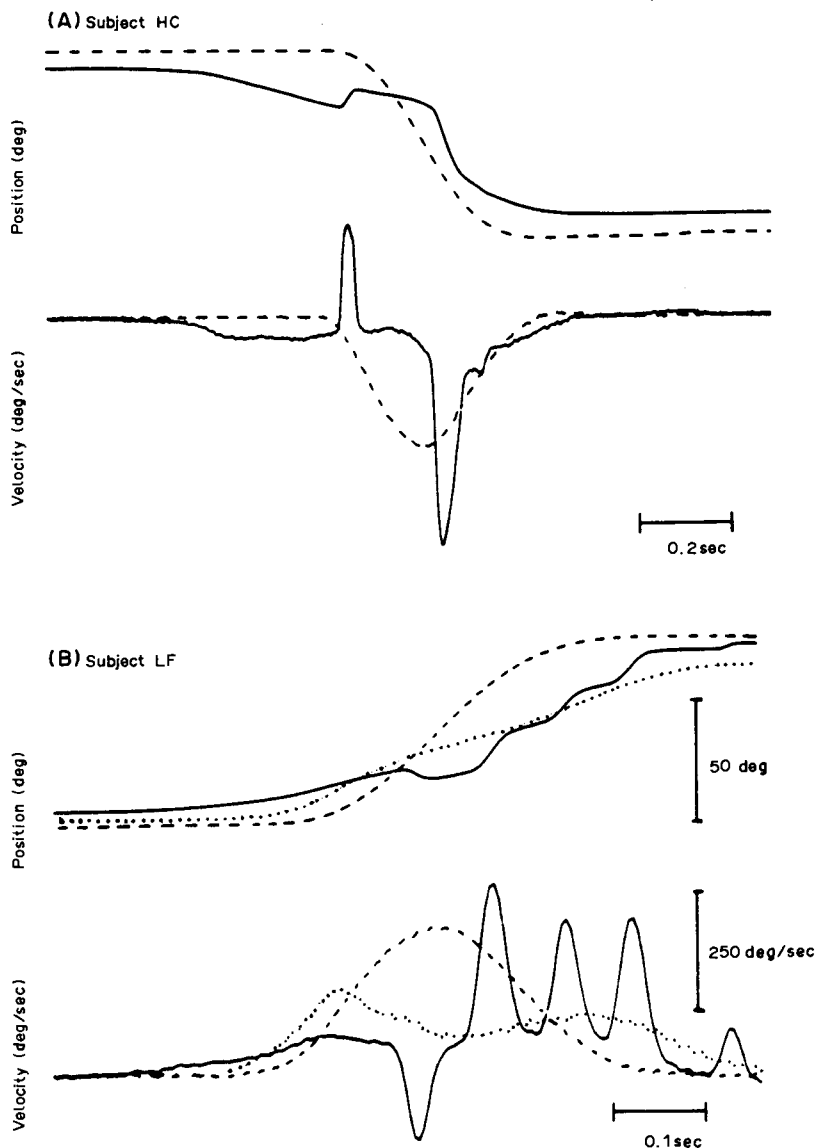


Fig. 5. Velocity and position profiles of horizontal eye and target movements of subject HC and LF. The solid lines represent eye position, the dashed lines target position. The dotted lines in the bottom pair of profiles represent the position and velocity of the head. See the text for an explanation of this figure (from Van der Steen, 1990).

### Origin of anticipatory smooth eye movements

Anticipatory smooth eye movements could be based solely on the tracking history experienced by the subject in a given experiment. There is, however, a plausible alternative source of anticipation.

Human oculomotor performance, like most other human behavior, operates on the basis of a great deal of *a priori* knowledge that is used to make guesses and predictions about likely future events. These events and outcomes are coded in signs and symbols, i.e. internal representations that have abstract meanings and

contain information far more complex and qualitatively different from stored, periodically updated, parameter values (the internal representations produced when an adaptive servo "learns"). For example, an adult human observer watching an animal, knows that if the animal moves, it is likely to go in a forward direction, that is, in the direction symbolized by the animal's head, unless, of course, the animal looks like a crab, in which case, it will probably move sideways. Even if the animal being watched does not look like a crab, a human observer is likely to anticipate that it will move to the side or even move backwards if a



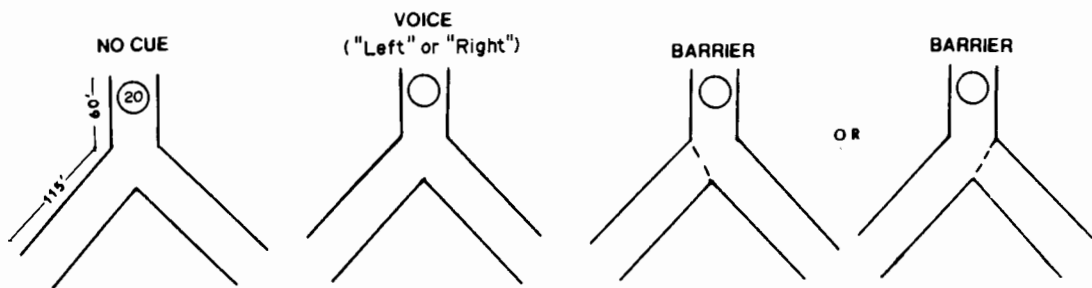


Fig. 6. The stimulus display, consisting of a stationary inverted Y-shaped tube and an annulus that served as the moving target. The velocity of the target was 130 min/sec. The target moved down the tube and continued at the same velocity down either the righthand or lefthand oblique branch of the Y (horizontal component of velocity when the target was in either branch of the Y was 92 min/sec). The target was equally-likely to travel down either branch. The four drawings show the different experimental conditions in which the branch to be traveled by the target was either: undisclosed before each trial (*no cue*); disclosed by a *voice cue*; or disclosed by a *visible barrier cue* blocking access to either the left-hand or right-hand branch.

potential threat is seen approaching from the front; unless, of course, the threatened animal happens to be a rabbit, in which case, it will probably "freeze" if the threat is near and run if it is far.

In essence, human oculomotor performance can be based on knowledge brought to the situation and on information conveyed by signs and symbols in the situation, as well by the presence of potential oculomotor stimuli or by residual influences of prior oculomotor performance. Both kinds of information could be important. Their relative contribution to smooth pursuit has been examined recently (Kowler, 1989). This was done in an experiment that compared the relative importance of recent tracking history with the importance of symbolic information that could facilitate the use of higher-order cognitive knowledge.

Figure 6 shows the stimulus configuration and conditions. The disk-target moved downwards and entered one of the arms of the inverted Y-shaped tube. The arm was either not disclosed to the subject in advance or disclosed to the subject either by an auditory or a visual cue. Figure 7 summarizes the average performance of the experienced subject (EK) in the upper row of three graphs and of a naive, relatively inexperienced subject (JW) in the lower row of graphs. Time 0 on the abscissae shows when the disk entered either arm and the horizontal component of motion began (at 92 min/sec, the velocity indicated by arrows on the ordinates). When auditory or visual symbolic cues were not provided to indicate which arm the target would take, the horizontal anticipatory smooth eye movements depended on the

direction of target motion in the preceding trial (Fig. 7A). These anticipatory effects were not restricted to the early portion of the trial when target motion was exclusively in the downwards direction. Even after the disk target entered the arm of the inverted Y, the horizontal velocity of the eye was higher when the direction of target motion was in the same direction as it had been in the preceding trial than when direction changed between trials. This shows that past history produced anticipatory smooth eye movements, but it proved to be much less effective than the influence of symbolic cues, telling the subject the target's path in advance. Symbolic cues dominated, causing the effects of motion on the prior trial to be virtually eliminated (Fig. 7B, C). Visual and auditory symbolic cues had rather similar effects, with a modest advantage for the visual barrier, but both were very much more effective than the prior tracking history.

This dominance of symbolic cues might, of course, be modified by a high degree of over-learning of a particular pattern of responses. Smart, thoughtful responses can be overwhelmed by habits, providing the habits are firmly established, as we all know from the errors we make when we are suddenly forced to change our habitual route home or to our place of work; it can take quite a while before "wrong turns" disappear from our motor repertoire. In fact, over-learning and punishment have been the techniques used in attempts to minimize or obscure the effects of expectations in monkey and some human oculomotor research on smooth pursuit. For example, smooth pursuit in monkeys is studied after hundreds

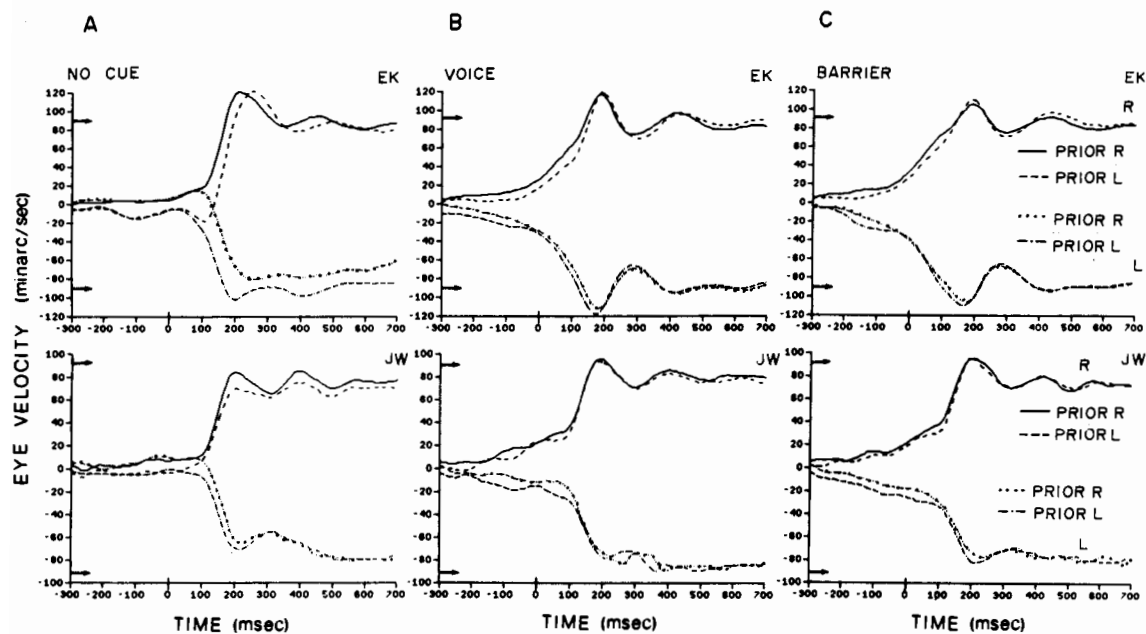


Fig. 7. Mean horizontal eye velocity during successive 100 msec intervals (onsets 10 msec apart) as a function of the midpoint of the interval when either: (A) *no cue*; (B) *voice cue*; or (C) *barrier cue* about the direction of future horizontal target motion was given. Top graphs, EK; bottom, JW. Time 0 is the start of horizontal target motion (the first entry of the moving target into the oblique branch of the Y-shaped tube). Arrows on the ordinate show horizontal target velocity; negative values denote leftward motion. The top pair of functions in each graph show eye velocity when the target moved down the right-hand branch; the bottom pair when it moved down the lefthand branch. One function in each pair shows eye velocity when the target motion in the prior trial was to the right; the other when the target motion in the prior trial was to the left. Each mean is based on 80–100 observations. Standard errors were 1–2 min/sec and as high as 3 min/sec (5 min arc/sec with *no cue*) only during the interval (0–200 msec) of most rapid eye acceleration.

and even thousands of training trials in which anticipatory smooth eye movements are punished by delaying reinforcement. After such long, very unnatural, periods of “pre-training” it may become possible to observe the onset of smooth pursuit without obvious anticipatory smooth eye movements. How data obtained in this manner can be considered to reflect the operation of a built-in, pre-wired, visuo-motor reflex, rather than some kind of esoteric, over-learned inhibitory oculomotor pattern, is a matter of some wonder to the authors of this paper. Similarly, the “express” saccade (step-tracking saccades with latencies below about 100 msec) is another putative “reflex” that is also only manifested, in monkeys and in some human beings, after extensive practice with sets of target steps, whose sizes, timing and directions are limited in number (see Becker, 1989). These are precisely the kinds of procedures and constraints that would encourage the development of over-learned motor patterns that are *not* representative of the fundamental responses of the system under study before

unnatural patterns are established by extensive practice.

#### *Potential new mechanistic models*

New models are required now that the limitations of existing approaches for handling phenomena like prediction are apparent. Plausible models of oculomotor performance, placing emphasis on the high level cognitive processes demanded by the experiments and considerations just described, are not likely to be based on a “mechanistic” approach. Not even if the mechanistic approach is new and “high-tech”. “Connectionism” is, perhaps, the best example of a contemporary, high-tech mechanistic approach that has begun to attract the attention of oculomotor theorists. Connectionistic models emphasize “massively distributed parallel processing”—a kind of processing scheme compatible with the architecture and activities present in the brain. Relatively inexpensive devices with properties like this can now be approximated (on very small scale) by wiring-up many thousands of microprocessors in

parallel (currently, 16–64 k microprocessors are practical). New models, based on properties of circuits such as these, called “networks”, place primary emphasis on “learning”, which, like the “adaptive” servo control models, require practice or repetition to produce behavior that can simulate the prediction of future states. The repetition or practice that produces “learning” in these networks is called “recursive optimization”.

In the authors’s view, shifting from an old to a new style of mechanistic switching model will probably delay, and almost certainly not solve, the problem of developing valid models of oculomotor system performance. Potential limitations of models of this type are well and long known (see the Prologue and Epilogue to Minsky & Papert’s, 1988, republication of their 1969 book on “perceptrons”).

The most significant feature of oculomotor system performance is the fact that its activities are initiated from high-level neural centers. Signals from the semicircular canals, otoliths or the position or motion of images on the retina

do not initiate oculomotor responses. What the “system” does depends on what the subject selects as his “goal” (i.e. the selection of one or another object on which to rest the line of sight even as he, or it, moves). The chosen goal in turn determines the relevance of one, or several, low-level inputs. The low-level inputs become operative only after the goal is selected (e.g. Kowler, Van der Steen, Tamminga & Collewijn, 1984b; Erkelens et al., 1989a). A human being has a very wide variety of options in any natural situation. The performance observed when these options are severely restricted by presenting isolated sensory cues, as is often done in traditional analytical experiments (e.g. studying VOR in the dark) is not equivalent to side-stepping a selection stage, and succeeds only in providing a distorted view of the operation of the oculomotor system. Such distortions are not likely to provide the basis for valid oculomotor models (see Collewijn, 1989a, b, for elaboration of this point)\*. It is important to keep in mind that input selection is based on high level symbolic representations.

There is no reason to assume that a neural “network” in the 1990s is inherently more likely to handle such high level cognitive processes than the neural “analogues” of the 50s and 60s. It seems more likely that models having “artificial intelligence” (AI) will fill this role. N.B. this belief is based on the requirements to be met and not on the current state of work in AI or the progress made in this direction during the past two decades. In other words, we recognize that saying “symbolic input is important” is a statement of a problem and not the solution to a problem. The nature of these symbols and their representation in a biologically meaningful mechanism is not at hand. Realization of this, however, does not minimize the importance of symbols nor does it free the modeler from ignoring their importance.

In short, we are not inclined to climb on the connectionistic, neural network bandwagon because historical precedent going back at least to Descartes and Locke, as well as common sense, makes it clear that the problem of internal symbolic representation is unlikely to be solved simply by plugging in a few thousand switching devices and allowing them to form associations (or SR bonds), empirically, by Aristotelian or Pavlovian principles of contiguity, by Thorndikean trial and error learning, by

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\*The selection stage might be circumvented, but only, it seems to us, in unusual and special circumstances. A good example of such a circumstance would be a startle response in which the eye, as well as the head and body, might quickly turn in the direction of a sudden loud noise or a flash of light. Another good example would be the oculomotor and postural reflexes that would come into play should you trip while descending a staircase or even while walking across a level floor. Ongoing coordinated visuomotor activities will be suspended, momentarily, when such “unpredictable” events occur. Success of the organism requires that its lifestyle and selected environment is such as to make such “unpredictable” events unlikely. Responses made when the selection stage is circumvented should, therefore, be viewed as very special activities that do not represent the normal operational goal of the oculomotor, or other visuomotor, systems. Normal oculomotor responses depend heavily on successful predictions because prediction can facilitate highly coordinated activities. The emergency reflexive responses, which come into play when the environment or the condition of the organism changes in unexpected ways, are designed to take over operational control only very briefly in unexpected or crisis situations. Such brief reflexive responses are not likely to be representative of the building blocks for coordinated complex motor activity. They are “default” patterns of action, clearly important for survival, but not likely to serve as the basis of successful goal-directed acts. Similar points have been made recently by individuals studying postural control, long thought to be maintained automatically by low-level, isolated sensory cues, but more recently discovered to rely on more abstract central control of body position with respect to the environment.

simulated annealing in a Boltzmann machine or by using the Widrow-Hoff or Delta rule for error-back propagation.

Preference for mechanistic models have a long, and sometimes successful, tradition in biological and behavioral science—they make the problems to be solved seem more tractable (e.g. the impedance matching accomplished by the ossicles of the ear or the correlation between the varying location of the peak of the traveling wave on the basilar membrane and variations of perceived pitch as the frequency of an auditory stimulus is varied). This preference can, however, lead researchers very far astray when attempts are made to carry this preference over to models of different classes of problems (e.g. Hull's "mechanistic" treatment of animal learning and Skinner's "mechanistic" treatment of the development and nature of human language). This danger cannot be avoided by assuming that a new mechanistic approach with new terminology and new operators can, simply by virtue of its newness, avoid fundamental problems encountered before. Specifically, traditional mechanistic approaches assume that low-level reflexive processes can be worked out while techniques to study and model the more complex, high level and often voluntary, cognitive processes are being developed. We, following the lead of Lashley (1951), reject this assumption completely. The higher central processes cannot be turned-off in an intact, conscious human being. You can provide such a subject with stimulation that: (1) confuses him; (2) makes him guess rather than plan his response; and (3) encourages him to lose interest in the task at hand, which will, for example, cause him to let his line of sight fall behind a moving target. You can even provide stimulation that has never been encountered before by him, or, possibly even by anyone else in the entire evolutionary history of our species outside of the oculomotor laboratory. You can do all of these things but you cannot instruct or fool a human being in such a way that he will not have expectations, make plans or guess. In short, a confused human being is not a bundle of revealed reflexes. He is a confused human being. Activities seen when the oculomotor system is studied under highly restricted or deliberately obscure or otherwise physiologically unnatural conditions are distortions of the systems's operation, not instances of its underlying reflex action.

## BASIS OF OUR NEW APPROACH

### *Paradigm*

Our new approach to the study of the oculomotor system uses novel instrumentation to make accurate and precise observations of oculomotor system performance throughout the entire range within which the oculomotor system has evolved to operate. The eyes can scan the entire visual field quite rapidly and accurately once the head and body are permitted to move. Our instrumentation is faster and more accurate than the biological motor systems we are trying to study. Its sensitivity is better than 1 min arc, its linearity is better than 0.01%, its effective bandwidth is 244 Hz. It has all of these properties within a dynamic range that covers 360 deg on the horizontal, North-South and East-West vertical meridians. (See Collewijn, Erkelens & Steinman, 1989a, b; for characteristics of the novel revolving magnetic field-sensor coil phase-detecting instrument we use to measure binocular eye and head rotations and Collewijn, Steinman, Erkelens, Pizlo & Van der Steen, 1990b; or Kowler, Pizlo, Zhu, Erkelens, Steinman & Collewijn, 1990; for a description of its use along with a sound-ranging device that measures translations of the head to about 1 mm.) We believe, largely on the basis of our recent work done with these instruments, that we are only now beginning to study the oculomotor system as it is actually used. Performance observed with the relatively modest constraints imposed by our new methods is different in important ways from what could have been expected on the basis of work we, and others, had done previously when only bits and pieces of performance could be studied under very stringent constraints.

### *Underlying principles*

Our new approach also starts with a simplification. It drops the common assumption of one fast and three or more independent slow subsystems (a scheme based on properties of potential sensory inputs) and replaces it with only two independent subsystems; a single fast (saccadic) subsystem and a single slow (smooth) subsystem, each responding to a variety of stimulus features (more about this approach, including the beginnings of its justification, can be found in Erkelens et al., 1989b; Collewijn et al., 1990).

This simplification is organized around goal-directed saccadic and smooth eye movement responses that are used, synergistically, to look

at real objects in 3-dimensional space. It may also add a sorely needed degree of coherence to our field, which has become exceedingly fragmented recently with "subsystems" proliferating with each minor variation in experimental protocols. To illustrate, there have been recent proposals to add an independent, involuntary subsystem that is responsible for "express" saccades, and another independent subsystem responsible for "averaging" saccades, to the traditional, relatively long latency, voluntary saccadic subsystem. This voluntary saccadic subsystem only incorporated a putative independent, involuntary fixational microsaccadic subsystem and a putative independent, "fast phase OKN" subsystem during the last two decades. A voluntary human "smooth pursuit" subsystem is often assumed to be distinct from a reflexive "OKN slow phase" subsystem (Dodge knew better). There has even been a recent proposal to add an independent smooth subsystem that maintains the line of sight during intersaccadic intervals when a stationary target is fixated (Nachmias, 1959, proposed that this kind of "slow control", so-named by Steinman, Haddad, Skavenski & Wyman, 1973, was "smooth pursuit" of a zero-velocity target—an idea, not requiring the addition of a new smooth "subsystem" that serves to maintain fixation during intersaccadic intervals).

Compelling evidence for so many independent subsystems is lacking; simpler alternative explanations are available for results leading to these claims (e.g. recently, He & Kowler, 1989, eliminated the need to assume an independent subsystem for "averaging saccades"). If such a cornucopia, overflowing with five or more independent subsystems, were actually represented in the organization of the oculomotor system, the hope of untangling the nature of its operation would become exceedingly remote. We doubt that the oculomotor system is organized in this way. Some of our most recent work is directed explicitly towards reducing what we see as an excessive, and ever-growing, number of superfluous theoretical constructs.

The theoretical utility of even such time-halved subsystems as the vestibulo-ocular reflex (VOR) can be questioned. Collewyn (1989a, b) has pointed out that the VOR,

"traditionally described as a distinct, phylogenetically old oculomotor subsystem, which serves to stabilize gaze direction . . . is supposed to act as a stereotyped

reflex with definite input-output relations, which can be measured by rotating a subject passively in darkness, and which is kept at an ideal level by adaptive, parametric adjustments . . . is not realistic [because]: (1) the VOR in darkness does not have an ideal, or even well-defined, gain; (2) a fixed, automatic VOR is not appropriate in most behavioral situations, and would require continuous conditioning by other subsystems. As there is no compelling phylogenetic, physiological or anatomical evidence for an independent VOR subsystem, a more fruitful hypothesis may be that vestibular signals are just one of many inputs to a spatial localization process, which computes the relative position (and motion) between the subject and a target of his choice" (Collewyn, 1989a, b).

Our hypothesis of only two oculomotor subsystems, one smooth, the other saccadic, receives support from neurophysiological and neuroanatomical data, despite the fact that most oculomotorists take for granted that such data provide important underpinnings for their traditional belief in five (or more) independent subsystems. While this issue is much too broad for a thorough discussion in this paper, our point can be illustrated by a few examples, which emerge from the reading of a recent highly competent review of present concepts of oculomotor neural organization by Büttner and Büttner-Ennever (1988). The reader should consult this source for the references that document our statements in the following, very brief summary.

Büttner and Büttner-Ennever organize their review, traditionally, by stating that there are five different types of eye movements, each controlled relatively independently by separate neural pathways, which only converge at the level of the eye muscle motoneuron. But on reading their very balanced review of the anatomical structures involved in these five postulated subsystems, it becomes clear that the parcelling into five separate clusters is actually very tenuous. Many structures are involved in more than one of the five types of eye movements, and if the latter exist as subsystems they are certainly not separated at the immediate premotor level. In fact, only two major inputs to the ocular motoneurons are described: (1) the paramedian pontine reticular formation (PPRF)

in combination with the rostral interstitial nucleus of MLF (riMLF), which are involved exclusively in the generation of horizontal and vertical saccades; and (2) the vestibular nuclei, which appear to be involved in every type of smooth eye movement.

This architecture suggests a division of the immediately premotor oculomotor system into a smooth and a saccadic subsystem, but no further subdivision is clear at that level. To identify structures related exclusively to one of the five traditional subsystems, one has to move very close to the sensory level, i.e. to a level at which a "subsystem" would be defined on the basis of some isolated attribute of the stimulus. For the VOR one has to revert to the primary vestibular afferents. For OKN the nucleus of the optic tract (NOT) and the nuclei of the accessory optic tract carry information on large field visual motion. Disparity-tuned visual cortical neurons may be involved in the control of vergence, although this remains to be proven, because very little is really known about premotor structures and pathways for vergence movements (Büttner & Büttner-Ennever, 1988, p. 23). For smooth pursuit, neurons in the middle temporal area (MT) in the superior temporal cortical sulcus may encode the retinal slip of the visual target. However, the best that neuro-anatomical or neurophysiological studies at the sensory level have been able to do to date is to identify possible sensory contributions to eye movements. They have not demonstrated separate subsystems. Pursuit, for example, is not uniquely controlled by retinal slip, just as saccades are not uniquely controlled by the positional eccentricity of targets. Processes such as voluntary choice, spatially-selective attention and expectations play decisive roles in these activities. The posterior parietal lobe (area 7) has been implicated in some aspects of the higher-level control of saccades, smooth pursuit and fixation, but the way in which such higher-level factors combine with low-level sensory cues to determine oculomotor programs is not known. Behavioral experiments, such as those described in this paper, are just beginning to be able to characterize the information contained in the representations of target position or motion that guide smooth or saccadic eye movements.

At levels that are intermediate between predominantly sensory and immediately premotor levels, eye movement-related structures are almost never linked exclusively to one of the five

traditional subsystems. For instance, the region in and around the prepositus hypoglossi nuclei, possibly involving also part of the vestibular nuclei, appears to serve the function of "neural integration", which is common to the integration of velocity to position in the VOR and OKN, to the integration of pulses into steps in saccades, and to the holding of gaze in any eccentric position.

A particularly illustrative example is the flocculus, which is part of the "vestibulo-cerebellum". In lower mammals, such as the rabbit, this structure is involved in vestibulo-ocular reflexes, particularly adaptive processes, which recalibrate the VOR (see e.g. Ito, 1984). Recent experiments with temporary suppression of floccular function by GABA agonists (Van Neerven, Pompeiano & Collewijn, 1989) have shown that normal performance of OKN, as well as the VOR, depends on the integrity of floccular function in the rabbit. However, the flocculus cannot be simply relegated to such lowly functions as the control of primitive reflexes. In primates (man and monkey) the flocculus is an essential link (intercalated between the pontine nuclei and the vestibular nuclei) in the circuit serving the very advanced function of smooth pursuit, which is strongly impaired after floccular lesions. Even vergence may be affected by such lesions. These assembled findings strongly suggest that the flocculus is involved in the control of all smooth eye movements, i.e. all eye movements except saccades, which are controlled, at the cerebellar level, by the posterior vermis.

An equally pregnant example is found in the "vestibular" nuclei, which actually receive multiple types of sensory information and contain a large variety of neuron types, the activities of which have been correlated with each of the five types of eye movements, except vergence, until now. Actually the vestibular nuclei may be instrumental in the generation of all types of smooth eye movements, while its activity related to saccades is likely to reflect feedback from the PPRF. Given the strong coordination between smooth and saccadic eye movements, one would expect strong reciprocal connections between the PPRF and the vestibular nuclei, the main premotor stations serving these two types of eye movement. These connections have indeed been demonstrated (for references see the excellent review on brainstem regions related to saccade generation by Hepp, Henn, Vilis & Cohen, 1989).

On the basis of this, admittedly very fragmentary, examination of some recognized neurophysiological facts, we strongly suggest that a more complete review of neurophysiological and neuroanatomical correlates will not support a distinct neuronal substrate for the "five subsystems" theory. Rather, it seems likely to support a major division between the generation of smooth and saccadic eye movements, each with different hierarchical levels of control, but strongly intertwined from the cortical to the premotor (and obviously the motor) level.

### 3-D TRACKING OF REAL OBJECTS WITH THE HEAD FREE

Examples of recent experiments, inspired by the ideas outlined above, are our recent studies of eye and head movements made while tracking real objects moving at near distances. All of these experiments were done in the Maryland laboratory with the revolving magnetic field instrument, whose characteristics were described briefly above. During this past year we were able to add an acoustic ranging device to measure translations of the head in the three cardinal directions ( $XYZ$ ) with an accuracy of 1 mm. The addition of this device (a highly modified *SAC 3-D Grafpen*) allowed us to study the binocular control of gaze while an unrestrained subject viewed nearby objects. We recorded head movements and binocular gaze-shifts between nearby widely separated targets, binocular eye and head movements during reading of normal text and also during the tracking of a target that moved in three dimensions. All measurements were made in a highly structured, lighted visual environment and all were made with targets within arm's length. Here, we will only describe highlights of this research germane to our claim that a new approach to the study of oculomotor control is possible, as well as necessary (see Collewyn et al., 1990b; Kowler et al., 1990, for technical details and additional results).

A schematic diagram of the experimental situation for binocular gaze-shifts and 3-D tracking is shown in Fig. 8 (the target moved horizontally, vertically and in depth). The stimulus for the tracking records reproduced in Figs 9 and 10 moved in a square trajectory (15.3 cm on a side; velocity of 25.4 cm/sec; frequency 0.42 Hz) with the plane of the trajectory rotated 30 deg with respect to the subject's median plane. Under these conditions the

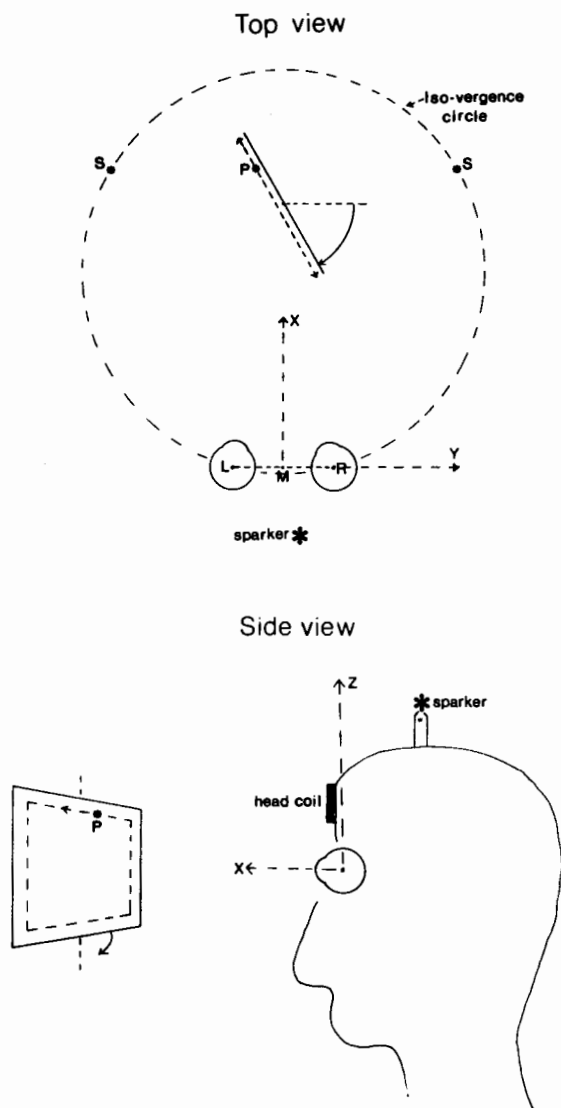


Fig. 8. Diagram showing the experimental conditions (not to scale). Upper panel: view from above, with the subject's eyes aligned on a biteboard in the standardized initial position. L, R: centers of rotation of the left and right eye. M: mid-point of the line connecting the centers of rotation of the eyes, which in the standard position, coincides with the origin of the  $X, Y, Z$  coordinate system. P: pursuit target, consisting of an LED moved by an  $X-Y$  plotter, that can be rotated around a vertical axis. The plotter is shown rotated 30 deg with regard to the subject's median plane. S: stationary targets, subtending equal target vergence. Lower panel: side view, showing the locations of the head coil and the sparker. The  $X-Y$  plotter, in front of the subject, shows the pursuit target (P), rotated 30 deg out of the median plane and thus moving sideways, vertically and in depth as it followed a square trajectory.

horizontal, vertical and vergence components of the target path subtended angles of about 10, 25 and 3 deg, respectively. Representative "version" components of 3-D tracking are shown in

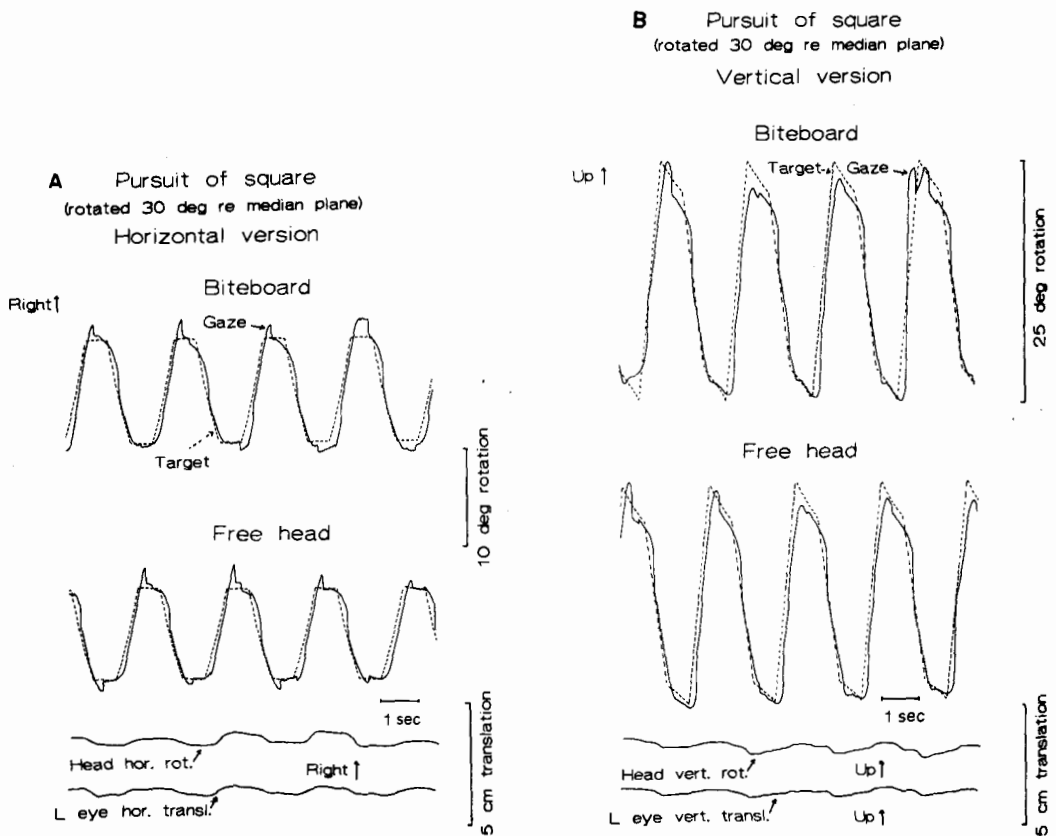


Fig. 9. Comparison of pursuit with the head immobilized on the biteboard (left panels) or with the head free (right panels). The target followed a square trajectory in a vertical plane, rotated 30 deg with regard to the median plane (see Fig. 8). This figure shows composite binocular version eye movements (continuous lines) of the eyes, i.e. (L eye gaze + R eye gaze)/2. In other words, the average direction of the combined lines of sight. Horizontal (A) and vertical (B) rotations and translations of the head are also shown when the head was free. The interrupted lines show target version, i.e. the angle subtended by the target at M, the midpoint between the eyes. Subject: RS.

Fig. 9 and representative "vergence" components of 3-D tracking are shown in Fig. 10. It is clear in Fig. 9 that there was generally good agreement between the trajectories of the target and the trajectories of binocular gaze (N.B. no arbitrary offsets were introduced to improve the match between the target and the eyes in these records). Note that both saccades and smooth eye movements contributed to performance and tracking accuracy was frequently virtually perfect. Also note that tracking with the head free was, at least to a first approximation, as good as when the head was restrained by a biteboard. This result requires excellent coordination of rotations of the head with rotations of the eyes. It also requires that our measurements of head and eye rotations and translations are accurate and that our trigonometry is appropriate. Figure 10 shows vergence under the same conditions. Once again, eye movements are both saccadic and smooth, highly coordinated and

synergistic with respect to rotational and translational movements of the free head.

Binocular tracking of a target moving simultaneously horizontally, vertically and in depth was accomplished by a combination of smooth and saccadic eye movements (see Figs 9 and 10). Both, very different types of eye movements, produced "version" and "vergence" eye movement responses. No obvious partitioning of these effective 3-D tracking eye movements between the operation of a conjugate smooth pursuit (version) "subsystem" and a disjunctive smooth vergence "subsystem" is apparent in these records; version and vergence seem indistinguishable, at least at this initial stage of analysis. By this we mean that if you did not know the plane of the target's trajectory relative to the subject's fronto-parallel plane, it would be impossible to distinguish "version" from "vergence" by virtue of the movement dynamics present in these eye movement records. It is also



Pursuit of square  
(rotated 30 deg re median plane)

Vergence components

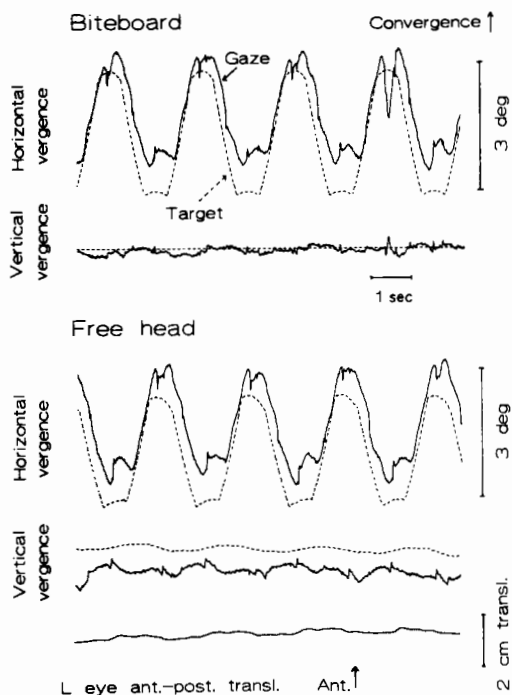


Fig. 10. Same pursuit episode shown in Fig. 9, but plotting vergence of the eyes (L eye gaze - R eye gaze) and of the target (difference between the angles subtended by the target at each eye). For the free head, anterior-posterior translation is also shown.

worth noting that the addition of a smooth contribution from the so-called "slow-phase VOR subsystem", which came into play when the head was free, also made no obvious difference in the 3-D eye movement tracking pattern when tracking with the head free is compared to tracking when the head was restrained by a biteboard and sensory signals from the semi-circular canals were not present.

We also examined saccade characteristics during gaze shifts with the head free as compared to performance with the head restrained by a biteboard (Collewijn et al., 1989a, b). Prior work on saccade dynamics with the head free had been done primarily with EOG recording, a technique with very low bandwidth and behavioral, rather than absolute, calibration of rotational angles. In all of this prior work, a subsystem-oriented approach served to guide the research. The main issue considered was whether the VOR "subsystem" was turned off when saccades were made as the head rotated. It had been claimed that coordinated head-eye

saccades might be faster than saccades of the same size made when the head was restrained. This raised the issue of whether the higher velocities of head-free saccades reflected the summation of the velocities of the head and the eye as they moved in space, a very low-level process requiring only that the VOR subsystem is switched off. We found, with much better recording methodology than EOG, that the dynamic properties of head-free saccades were indeed very different from the dynamic properties of saccades made when the head was restrained (free-head saccades were faster), but *these differences were observed before any appreciable head movement had occurred*. Even when the head moved appreciably, the eye reached its peak velocity well before the head reached its peak velocity (see Fig. 11 for a quantitative summary of these results and see Collewijn et al., 1990b, for the waveforms of the two kinds of saccades). Our findings show that prior discussions about the interaction of the so-called VOR "subsystem" and the saccadic subsystem are essentially irrelevant to the

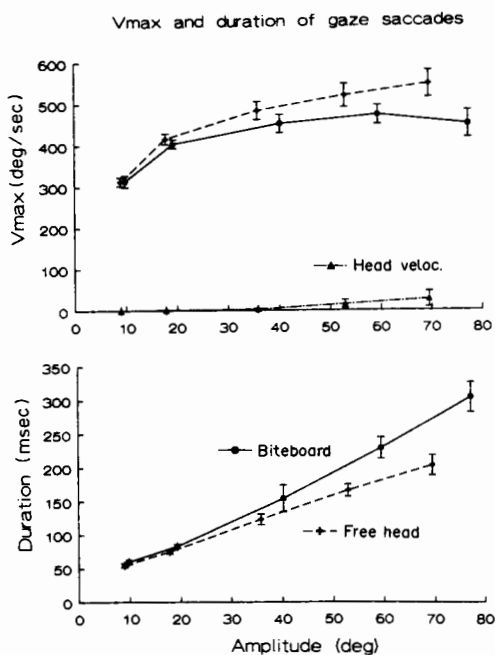


Fig. 11. Comparison of peak velocity ( $V_{max}$ ) and duration as a function of the amplitude of horizontal saccades used to shift gaze between stationary targets separated by different amounts (10-80 deg) when the head was immobilized on a biteboard (continuous lines) or when it was free (interrupted lines). Each datum point represents the mean of 10-20 saccades of subject RS. Vertical bars represent  $\pm 1$  SD. Equal numbers of temporally and nasally-directed saccades were pooled. In the upper panel, head velocity at the moment of peak gaze velocity is also shown (triangles).

important effects of freeing the head on saccades. They probably have little, if anything, to do with oculomotor system capacity or function. The advantages of freeing the head on the dynamics of saccades most likely reflect the operation of central, rather than low-level mechanical, processes. The better dynamics of saccades made with the head free seems likely to arise from allowing the subject to issue natural, uninhibited commands to shift gaze. Shifting gaze is a coordinated activity of both the head and the eye and restraining the head on a biteboard leads to sub-normal performance (see Zingale & Kowler, 1987 and Berthoz & Grantyn, 1986, for other reasons to propose an automatic linkage of concurrent head and eye programming and Kowler et al., 1990, for a preliminary exploration of "natural vs unnatural" head-eye coordination).

These results, as well as our observations of 3-D tracking described above, emphasize the importance of the unity of function of the various parts of the oculomotor and the head-motor system. Findings such as these encourage us to continue work along these lines, and to claim, admittedly with more enthusiasm and optimism than proof, that working with unrestrained subjects, presented with highly predictable, nearby stimuli in a lighted environment that contains objects and events likely to be encountered in everyday life, can provide the new insights into the nature of the operation of the oculomotor system that will be required to develop appropriate models for study of its operation. The specific form these models will take cannot—and should not—be spelled out at this early stage, but it is clear from these first measurements of 3-D tracking and free-headed gaze-shifts that appropriate models will emphasize the importance of the integrated, rather than the modular, nature of the oculomotor system. The performance of the oculomotor system, acting synergistically with the head and the trunk, seems to be much better coordinated and much more efficient than would be expected from the compartmentalized concept of the oculomotor system as an assembly of many separate, independent "subsystems". These "subsystems" have been defined largely on the basis of *a priori* assumptions about the teleological significance of different types of stimulation and on a very limited range of observations of oculomotor system performance. We need many new types of observations, as well as a new approach to selecting conditions for

making them. We also must develop new models, more fitting to the biological control system under study than the models presently on hand. Tools are becoming available that will make it possible to observe aspects of oculomotor system performance as it works naturally at the limits of the system. At present, our knowledge of what the oculomotor system can do and how it does it lags far behind oculomotor system capacity. The tools to make these observations are in hand now, and, in our view, there is reason for optimism, providing only that we follow Westheimer's example and are prepared to recognize when it becomes time to abandon our current new approach and try something new.

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