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THE NEED FOR AN ECLECTIC, RATHER THAN SYSTEMS, APPROACH TO THE STUDY OF THE PRIMATE OCULOMOTOR SYSTEM

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Abstract—The failure of the Systems Approach to add to our understanding of the primate oculomotor system is traced out from the introduction of this approach 30 years ago to recent developments which open up the possibility of studying, separately, stimulus and psychological inputs to the smooth pursuit subsystem. Prior failure to have a valid technique for separating complex central factors from underlying reflex mechanisms compromises current understanding of oculomotor performance and its putative neurological substrate.

Primate oculomotor system Smooth pursuit Vestibulo–ocular response Systems approach—failure of Saccades Prediction Learning Expectation

I was very pleased to be asked to participate in this workshop. I have many fond memories of when, in the 1960's, I first visited the Institute of Medical Physics, looked at flickering checkerboard patterns and assured Professors van der Tweel and Spekreijse that my visually-evoked cortical potentials had nothing to do with microsaccades. I did not make any while data were collected. I was flattered at the time to participate, albeit in a modest way, in experiments in the Netherlands. I was flattered because I have always admired Dutch science, going back to such pioneers as Hermann Boerhaave—the leader of the Leiden School which did so much to launch modern physiology. Many of the foreign students, who trained in the Netherlands, were also admirable. The Swiss, von Haller, for example, studied under Boerhaave and carried the physiology of the Leiden School to Germany. Also, Julian Offray de la Mettrie, another student of Boerhaave, is particularly relevant to our topic. Offray popularized the doctrine, introduced by Descartes while working in the Netherlands, that human beings are machines, somewhat more finely constructed than other animals. This workshop is devoted to consideration of recent progress of this doctrine. It is quite fitting that it takes place in the Netherlands where the doctrine was proposed more than 300 years ago.

I will begin the substantive portion of this paper by pointing out that the oculomotor system has only been studied in its own right since the beginning of this century. It is much newer than visual science and one cannot, therefore, expect it to be as well understood at this time. The major oculomotor pioneer was Raymond Dodge (1903), a psychologist, who provided us with descriptions of most of the oculomotor phenomena we study today. He distinguished saccades and various kinds of smooth eye movements. Dodge also demonstrated the importance of selective attention (1928) and prediction (1930) in oculomotor performance.

Dodge worked mainly with human subjects, the easiest preparation to use, once it is known that performance is influenced by cognitive factors. It is easy to instruct a human subject to attend to different features of displays. This makes it possible to separate a subject's oculomotor preferences from his oculomotor capacities. It was, in part, the failure of engineers to appreciate the importance of instructing subjects, human and monkey, that impeded progress when this approach began. It continues to be a problem.

There are three other problems frequently encountered in engineering research. First, there is the reluctance to deal with phenomena not readily incorporated into simple models. Second, there is the willingness to use techniques of doubtful validity. And, finally, there is the tendency to use measurements of questionable accuracy when testing models.

I will illustrate these points first by describing classical experiments from the pre-engineering period. These were good experiments. I will then turn to some of the original engineering papers and point out some problems. Next, I will describe my personal flirtation with systems and then conclude by describing some new techniques and recent findings which point the way to progress.

Let me make clear at the outset that my skepticism about the Systems Approach took years to develop. Let me also confess to some measure of antimechanistic bias. Namely, I agree with Julian Offray. We are machines. Our clockworks will ultimately be understood. I do not, however, believe that the Celestial Clockmaker designed us with techniques taught 35 years ago in circuit design courses. I am not even sure that His techniques are being taught currently.

I believe that the system models we now have, at best, deal only with the mechanics of eye rotation and patterns of neural activity that correlate somewhat with selected aspects of eye rotation. This is an advance, but only a very small step towards describing a control system whose performance is dominated by complex central processes used to select visual and vestibular information, relate this information to the prior history, needs and expectations of the organism and then command the eyes to move in functionally useful ways.

Westheimer (1954a) was the harbinger for the use of a servomechanical approach in the study of the oculomotor system. Thirty years ago most other eye movement researchers were studying the way in which miniature fixational eye movements contributed to visual processing. Westheimer recorded saccades made to target steps. He analyzed saccadic velocity and acceleration in terms of a linear servomechanical model, noticed departures from linearity and paved the way for Robinson's (1964, 1965) studies in which a strain-gauge measured the muscular forces used to move the eye.

Westheimer's (1954b) second paper is more germane for the present discussion because, here, he examined smooth tracking eye movements, explicitly hoping to study the smooth pursuit servomechanism, operating free from complex psychological factors. Westheimer began by listing factors at three levels which operate during eye movement. His analysis is as useful today as when proposed 30 years ago and reference will be made to his analysis throughout the remainder of this paper.

He called his levels: A, B and C. Where A refers to mechanical aspects of the orbit and all factors intervening between the initiation of nerve impulses designed to move the eye and the actual eye movements. B-factors are reflexive mechanisms which make the eye move so as to place and keep the stimulus accurately on the fovea. C-factors operate at higher levels of complexity. They can obscure processes at level-B. Westheimer knew from the prior work of Dodge that C-level complex processes operate when humans track. You cannot elicit reflexive responses simply by "injecting" a moving visual stimulus—a term and idea brought from engineering to studies of the oculomotor system (e.g. Stark, 1971).

Westheimer gave an example of C-level processes in action. Namely, if you present a square-wave pattern of target steps, after only five or six steps, the subject will make saccades when the target steps. The subject may also saccade before the target steps. Westheimer called this C-level factor "learning". Here we have a hint of what will become a problem in later work. Westheimer's example served his purpose—it illustrated that there is a level of operation above level-B—the visuomotor reflexes. However, his use of the term, "learning", for this example is unfortunate because it can be misinterpreted to mean that the oculomotor system, itself, is learning. Nothing of the kind is going on.

The example simply shows that an uninstructed subject needs to see a few steps before he chooses, perhaps for cultural reasons, to adopt the rhythm of the pattern. Adult subjects tend to do this after a second or two if step frequency is kept low—under 1 Hz. They always do this, or quit tracking, if frequency is high because it becomes impossible to wait for the step and also keep up with the target.

The same kind of information can be communicated by saying, "the target will jump once each second—saccade at the same time as the target." If Westheimer, or another skilled musician, were the subject saying, "allegretto, steps at Maëlzel metronome marking 60", would allow him to start in time with the first step, providing, of course, that the metronome was running and you gave him a downbeat. What I am trying to get across here is that the saccadic eye movement subsystem, which is used to scan visual space, always reflects the operation of C-level factors—the subject's decisions to look at one or another region. This means that the saccadic subsystem is not a good candidate for servomechanical modeling beyond level A—

orbital mechanics. At least not unless the modeler is prepared to model decision processes.

Westheimer knew this and turned instead to the smooth pursuit subsystem, assumed to be less susceptible to C-level factors because smooth eye movements cannot normally be made in the absence of what is perceived to be a smoothly moving target. The three features Westheimer described of most interest to this discussion are that the eye matches velocity with the target, providing target velocity is modest. When target motion is periodic, pursuit gets better both in gain and phase as the subject continues to pursue. Westheimer also confirmed Dodge's observation that (in Dodge's terminology) "anticipatory reversals" occur. The eye leads the target. In current jargon, this would be called "predictive tracking."

Westheimer believed that C-level factors only operated with periodic stimuli. He thought that his random movements of the target revealed only level-B factors—properties of the smooth pursuit servomechanism which he described as a "closed loop or feedback circuit in which errors are used to modify performance." Westheimer would ultimately prove to be wrong. C-level factors always operate as will be shown 25 years later (Kowler and Steinman, 1979a, b; 1981; Kowler *et al.*, 1984).

Westheimer's planting blossomed in 1961. This year saw the publication of two influential eye movement papers. The first was by Fender and Nye (1961) who studied tracking of simple harmonic target motions and described their results within the Systems' metaphor as is shown in Fig. 1.

There are a number of features of significance in this graph. The feature to notice is the failure of the eye to match velocity with the target at all frequencies, including those as low as 0.2 and 0.3 Hz. The amplitudes of the target motion were only 1.1 and 3.4°. Peak target velocities were well under the saturation level reported by Westheimer. So we have, here, a demonstration that the eye does not match velocity with the target even when target motion was relatively slow as well as completely predictable. Only a few months later Rashbass (1961) published a study of the pursuit of unpredictable target ramps with modest velocities ($<10°/\text{sec}$). He reported that the eye matched velocity with the target, a result consistent with Westheimer's earlier report, but clearly at odds with Fender and Nye who used a stimulus much more likely to be matched.

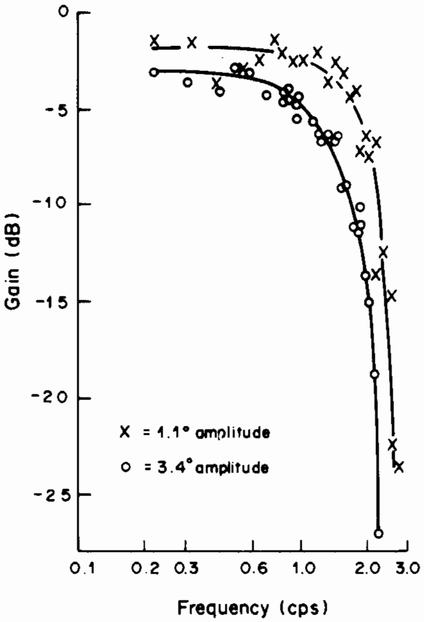

Fig. 1. Gain vs frequency characteristics during smooth pursuit of sinusoidal target motion. (Reproduced from Fender and Nye, 1961.)

Fender and Nye (1961) also varied the gain of the retinal error feedback loop and produced an involuntary pendular nystagmus as control theory would predict. They included a proprioceptive feedback loop in their control model—perhaps an untimely feature, once it is noted that Brindley and Merton (1960) had just published a paper claiming, incorrectly as Skavenski (1972) would subsequently prove, to have demonstrated the absence of proprioceptive input to the oculomotor system.

So engineering and confusion begin together. By the end of 1961, it was clear that Systems Analysis was well underway. It was also clear that a few problems remained.

The next major Systems' paper was published in 1963 by Dallos and Jones (1963). This paper was a landmark because these authors used the Systems Approach to model learning factors. The paper is important for two reasons. First, the recognition by engineers of the importance of C-level factors. Second, the use of a technique believed to prevent the operation of C-level factors. Namely, make target motion unpredictable. This, of course, is the same assumption and technique Westheimer had used in 1954.

Figure 2 shows the smooth pursuit transfer functions Dallos and Jones obtained with predictable and unpredictable target motions.

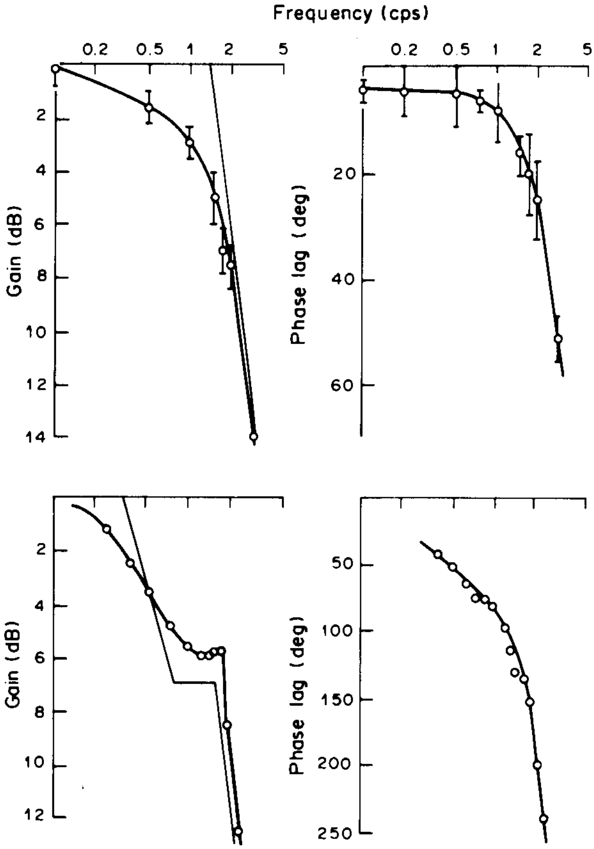

Fig. 2. Top graphs—average gain and phase frequency plots based on sinusoidal inputs. Bottom graphs—average gain and phase frequency plots based on Gaussian random noise inputs. (Reproduced from Dallos and Jones, 1963.)

In the top figures, the subject tracked sinusoidal target motion; in the bottom figures, filtered Gaussian noise. Differences can be seen both in gain and in phase. Phase lags were very short for the predictable stimulus as compared with the unpredictable stimulus. Gain at all frequencies was also higher when the stimulus could be predicted. If Westheimer's technique of obtaining B-level observations by providing unpredictable target motion works, the bottom graphs describe the operating characteristics of the smooth pursuit reflex. A reflex which Dallos and Jones proceeded to model.

Dallos and Jones went even further. They modeled what they called the "predictor mechanism" by looking at the differences between the predictable and unpredictable tracking functions. They describe the task for this "Predictor Mechanism" (also called a "learning operator") quite appropriately. They say it "knows when it is necessary to initiate eye motions, . . . also what direction and how fast those movements should be. In addition to this knowledge it is necessary that active control should be maintained over the functioning of the mechanism during the actual smooth tracking motion."

Kowler and Steinman (1979a) in their series of papers examining what they call "expectation" in the smooth oculomotor subsystem, called attention to a feature of their data that has not been given sufficient attention, either by Dallos and Jones or subsequent authors. This is illustrated in Fig. 3.

The function standing alone at the top (near the symbol key) shows the latency of the smooth pursuit response to the onset of motion of what will *become* a predictable target at each of 6 target frequencies. The clump of functions near the abscissa shows steady state and cycle by cycle latencies. All of the learning occurred *before* the first cycle. This was true at all target frequencies. "Learning" does not seem to be an appropriate concept to use for data such as these. "Expectation" seems more to the point.

The next engineering landmarks were published by Robinson (1964, 1965), who, based on

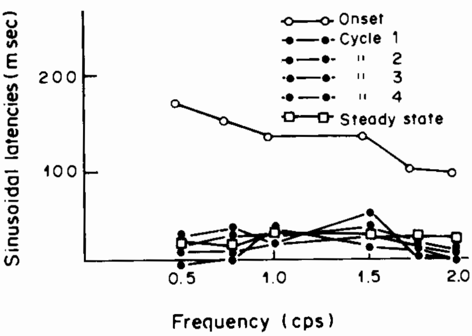

Fig. 3. Average latencies of the first few cycles of sinusoidal tracking. Steady-state latencies are also shown. (Reproduced from Dallos and Jones, 1963.)

Dallos and Jones, believed that unpredictable target motions permitted study of reflexes uncontaminated by C-level factors. Both of Robinson's papers were concerned largely with muscle dynamics, A-level factors. The first paper dealt with the saccadic subsystem, the second with the smooth pursuit subsystem. The paper on smooth pursuit, however, went beyond muscle dynamics. Robinson reported, in agreement with Rashbass (1961) and Westheimer (1954b), that smooth pursuit velocity matched target velocity when target velocity was below saturation. Robinson also used open loop measurements to model the smooth response. Here he reported encountering some difficulty in obtaining stable results, allowing that the "efforts were obscured by both variability and plasticity in the response system." Robinson ascribed these difficulties, in part, to the subject's going in and out of Dallos and Jones' "predictor mode." We have here our first printed hint that the open loop technique, potentially so valuable for Systems Analysis, may be difficult to use in the human oculomotor system. Actually, it is useless. More will be said about this later.

This is where matters stood when I began working on eye movements. Initially, I was interested in the functional significance of smooth and saccadic eye movements during fixation. I found that microsaccades, frequently seen during fixation, can be eliminated by simple instructions (Steinman *et al.*, 1967). I then set out to show that microsaccades were part of the voluntary behavioral repetoire rather than B-level reflexes elicited by small fixation errors (see Steinman *et al.*, 1973; Kowler and Steinman, 1980 for reviews).

During the course of this work, Puckett and I (1969) looked at saccades made during smooth pursuit. Our initial experiment was modeled after Rashbass' except that our subjects pursued unpredictable ramps under two different instructions. They were asked either to make as many saccades as necessary to keep dead on target or to make as few as possible, paying attention only to target velocity. We found that the prevalence of saccades during pursuit depended on what the subject was trying to do and not on the presence of fixation errors. But, when we measured smooth pursuit velocity under both instructions, we found that eye and target velocity did not match. There was more than 10% retinal image slip with even the slowest ramps. I thought that it might be of some importance to know whether the eye matches target velocity. Intuitively, I rather liked the idea that the target image was slipping on the retina and that this slip was used to keep the eye following along. But, perhaps Rashbass (1961), who knew much more about machinery, was right in thinking that the machine used the initial acceleration of the target and told the smooth pursuit subsystem exactly how fast to go. It then did just this—matching target velocity, give or take "fixation noise" (5 or 6 min arc/sec). Of course our data argued against this, but the conflict got me thinking about machinery.

At just this time Collewijn (1969) published a study of the optokinetic response of the rabbit. Lo and behold the rabbit never matched velocity with the target either. Collewijn (1972) went on to provide a servomechanical model of the rabbit's optokinetic subsystem—a model using image slip during pursuit. I began to wonder whether the Collewijn model could be used to describe human, as well as rabbit, smooth pursuit?

There were some problems however. Rabbits are not humans for one. But, engineers like Robinson had brought Systems Analysis to primates. This seemed particularly promising at the time because Fuchs (1967), doing his thesis work with Robinson, had reported that the rhesus monkey did not do predictive tracking—pure B-level observations were possible. As a psychologist I found this result puzzling. I did not think an animal had to be very smart to do predictive tracking. But, perhaps, the rhesus monkey was dopier than I thought. He proved not to be as Barmack (1970) and Eckmiller and Mackeben (1978) would subsequently show.

In any case I was certainly not a skeptic at the time. I was ready to climb on the Systems

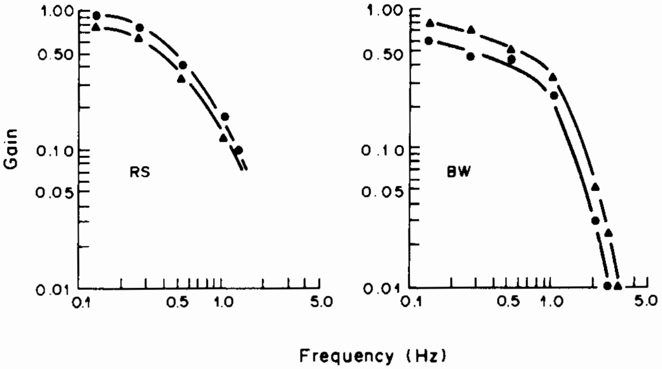

Fig. 4. Subject R.S.'s (left) and B.W.'s (right) smooth pursuit gain as a function of the frequency of sinusoidally moving targets. The photopic target (1.85 log units above absolute foveal threshold) is shown by triangles and the scotopic target (0.5 log units above absolute scotopic threshold) is shown by circles. (Reproduced from Winterson and Steinman, 1978.)

bandwagon. There was, however, the problem of consensus in prior human work. Remember Fender and Nye had reported smooth pursuit gains of less than 1. Westheimer, Rashbass and Robinson had unity gains. Puckett and I had reported less than unity gain. Some resolution of this conflict seemed desirable. The failure of consensus proved not to be a problem. I wrote to Robinson who replied, explaining that he and Rashbass had been interested primarily in other aspects of performance and that, actually, when they spoke of velocity matching in their publications "it was only in a loose manner of speaking or based on casual inspection of the data" (letter dated 14 March, 1973).

This was a useful, as well as reassuring, piece of information. It meant that there was no reason to believe that the slip signal was not present during pursuit. Collewijn's (1972) smooth pursuit model might be used to describe human performance as well as performance of the Dutch-belted rabbit. These were the best of times. I think of these years, fondly, as my Alice in Wonderland period.

A representative experiment from this period looked for evidence of rabbit-like relatively low gain smooth pursuit in the human scotopic visual system. Under these conditions pursuit would be controlled only by rods which are free from the requirements of fine detail vision, characteristic of the primate fovea. Results are summarized in the Figure 4.

These gain vs frequency graphs are taken from Winterson and Steinman (1978). The subjects pursued sinusoidal target motions while the target moved horizontally in the perifovea. The subjects kept the target 6° above the foveal center. This placement was used because rods and cones are about equally numerous in this area.

Triangles show smooth pursuit with target luminance about 2 log units above light-adapted photopic threshold. Circles show pursuit with targets 1/2 log unit above dark-adapted scotopic threshold. These functions, which differ only slightly, were obtained with about a 1000-fold difference in luminance. We expected to find large effects of luminance on gain. We expected scotopic functions somewhat like the rabbit's OKN. Rabbit OKN gain is about 0.95 until peak drum velocity is about 1°/sec (Collewijn, 1969). Gain falls off fairly steeply thereafter. When peak drum velocity is only about 6°/sec, rabbit OKN gain is down to 0.1. We found nothing like this. We needed peak target velocities of about 27°/sec to push gain down to 0.1. Note, also, that one subject (R.S.) had higher gains with the scoptic targets.

We expected to find large luminance effects on smooth pursuit gain because of an engineering report by Wheeless *et al.* (1967). We had to do our own experiment, however, because these authors had overlooked the fact that the fovea has a relative central scotoma. No attempt had been made to keep the low luminance targets in parts of the retina where they would be visible. This is, of course, another example of "injecting stimuli" without due care to instructions.

I was beginning to think that it was time to step back through the looking glass and leave Wonderland. Some other observations made during this period also contributed to my skepticism about the value of the Systems Approach.

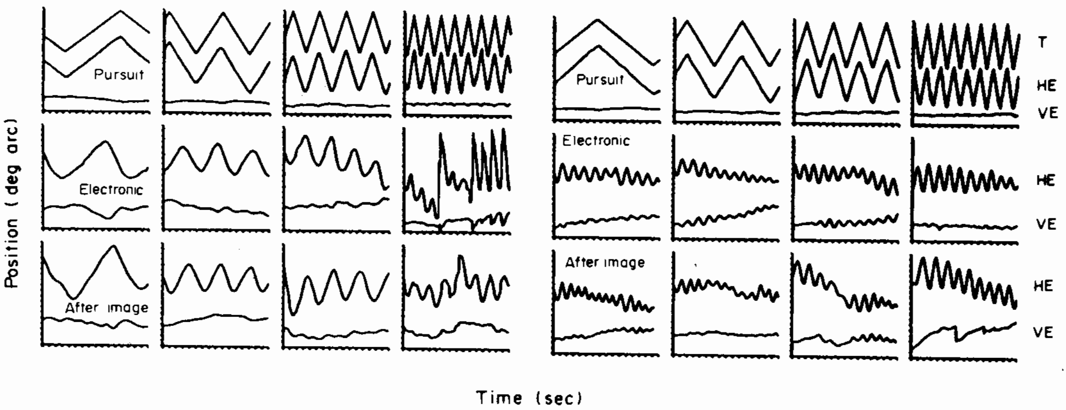

Fig. 5. Best-case analog records of subject J.T. (left) and W.C. (right) pursuing a triangular target motion (top graphs), attempting to make the same eye movement pattern with an electronically stabilized target (middle graphs) and with an afterimage (bottom graphs). Target velocities were: 1, 2, 4 and 8°/sec. Traces are reproduced for the target (T), the horizontal position of the eye (HE) and the vertical position of the eye (VE.) The time scale shows 1 sec intervals. The position scale shows 1° distances. Upward displacements of the traces signify eye movements to the right or upward. (Reproduced from Cushman *et al.*, 1984.)

Open-loop experiments have been prominent in papers using control systems analysis ever since Fender and Nye (1961) There is frequent mention of Tantalus-like effects of eccentric afterimages (e.g. Robinson, 1965), oscillations under negative feedback (e.g. Fender and Nye, 1961), and efference copies inferred from afterimage movements during head rotations (e.g. Yasui and Young, 1976). It had even been reported that smooth eye movements, indistinguishable from smooth pursuit, can be made with a stabilized target (Heywood, 1972).

Cushman, Tangney, Ferguson and I (1984) became suspicious about many of these claims sitting around one day and describing our eye movement patterns while we fired a flashgun at one another. There was sufficient disagreement in what we claimed to be able to do to encourage the experiment summarized in Fig. 5.

Figure 5 shows results from the two subjects who were best able to make smooth eye movements with a stabilized target. The top row of 2-dimensional eye movement records show them smoothly pursuing a moving target. Their performance was virtually identical at each of the 4 frequencies.

In the experiment, they pursued one of these triangular waveforms for a number of trials. The target was then stabilized, first, electronically with a Double Purkinje Image Tracker. They then tried to imitate the smooth pursuit pattern they had just made (the middle records). An afterimage was made next and, once again, they tried to imitate their smooth pursuit on a number of trials (the bottom records). The bottom 2 rows of records only show horizontal and vertical eye movements. The stimulus was stabilized and moved with the eye. In all conditions, recording started when the subjects felt that they were either smoothly pursuing or imitating as well as they could. When all recording was done and the afterimage had faded, the subjects were required to set the signal generator to the target velocity they had seen at the beginning of the session.

Both subjects performed very differently in the open-loop conditions both from each other and from their actual smooth pursuit. The subject on the left had some control of smooth eye velocity during imitation. The subject on the right could be described as oscillating. Their difficulties had nothing to do with their failure to remember characteristics of the pursuit targets. We looked at two other subjects under these conditions. One oscillated like the one on the right, the other could only make smooth eye movements in a rightward direction with a stabilized target.

The subject seen oscillating in this figure was not actually unstable. He only oscillated when he tried to imitiate triangular pursuit. He had no difficulty with directional control. He could, on command, stop oscillating and he could also imitate a right- or left-going ramp. He could not, however, vary the speed of his smooth movements with a stabilized target.

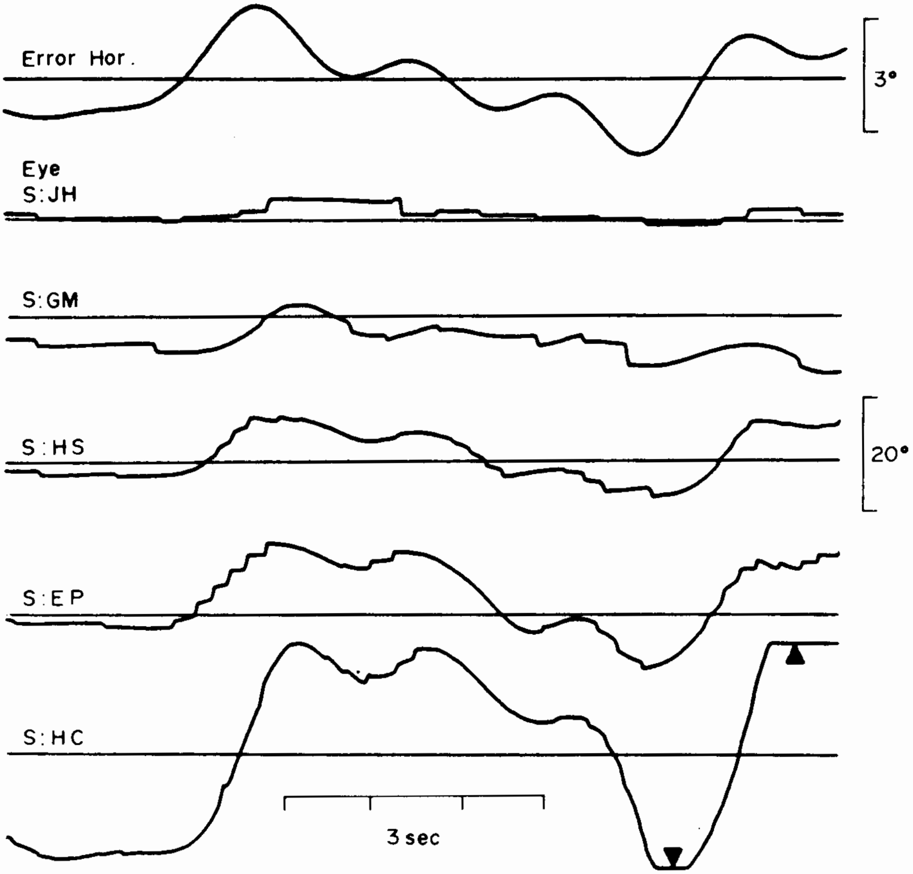

Fig. 6. Recordings of the horizontal eye movements of 5 subjects in response to the stimulus (top trace) presented in an open-loop condition. The stimulus and eye trace calibrations differ. The arrows in the trace of the lowest subject (H.C.) indicate that his eye movements exceeded the 20° range of the recording equipment. (Reproduced from Tamminga, 1983.)

We also found that the position of the afterimage did not predict the direction of smooth movements. Nor did we find a Tantalus-like effect with effect with eccentric targets. In fact the subject on the right could only make voluntary smooth eye movements when the stabilized target was at his central fixation position. We also attempted some smooth pursuit with variable gains in the feedback loop and obtained confusing results.

Figure 6 shows recent results from Collewijn's lab where Tamminga (1983), surely with some optimism coming from his engineering background, tried to use the open-loop technique to study smooth pursuit. He abandoned this effort for reasons apparent in these records. This plate shows the performance of 5 subjects asked to track, under open-loop conditions, the imposed unpredictable target motion shown in the top trace. All subjects performed very differently leading Tamminga to conclude that "in an open-loop condition pursuit eye movements primarily reflect idiosyncracies of the particular subject used in the experiment." I completely agree and will add that the enthusiasm with which engineers, with the commendable exception of Tamminga, have used this technique to model the oculomotor system is a tribute to the way in which a theoretical commitment will inspire one to plow on despite all obstacles.

Is there an easy way to get around this? Can open-loop performance be estimated from measurements made during the first 100 msec or so after a target moves and before the eye starts pursuing? This brings me to research on the effects of expectation on smooth eye movements (Kowler and Steinman, 1979a,b; 1981; Kowler *et al.*, 1984). The initial observation is shown in Fig. 7.

Figure 7 shows subjects tracking square-wave target motions. The events of interest are found in the intersaccadic intervals. Note how the eye

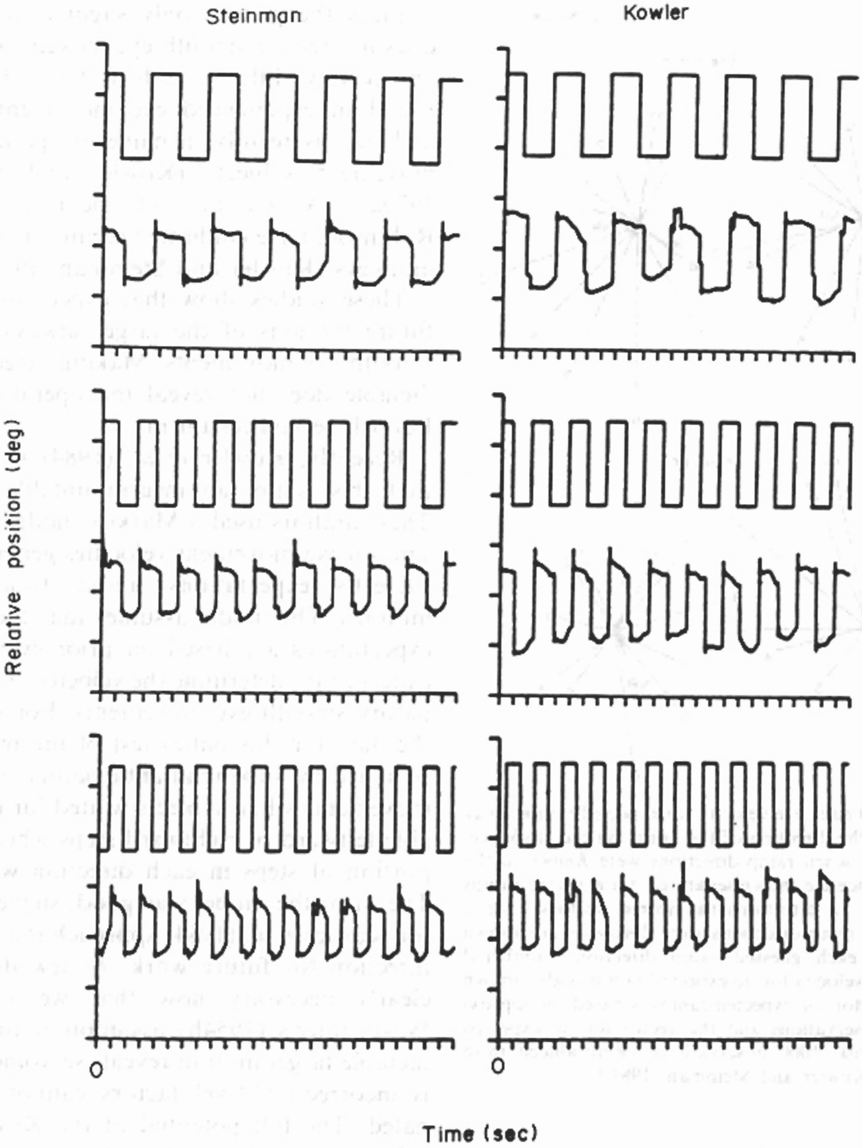

Fig. 7. Horizontal anticipatory smooth eye movements (bottom traces in each graph) with periodic target steps (top traces in each graph) at 0.25 Hz (top graphs), 0.375 Hz (middle graphs), and 0.50 Hz (bottom graphs). The time scale shows 1 sec intervals. The position scale shows 1° distances. The records begin at $T = 0$. Upward displacements of the traces signify movements to the right. (Reproduced from Kowler and Steinman, 1979a.)

drifts in the direction of the expected step before the target steps. Space does not permit a detailed description of the many results reported in this series of papers, but the message is clear. Once a subject expects a target to move, the smooth subsystem begins to work in the direction of the expected motion, several hundred milliseconds before the target moves.

These anticipatory smooth movements cannot be eliminated by asking the subject to suppress them or by distracting the subject with mental arithmatic while he waits for the target to move. They are also found before target motions occurring at randomly chosen times.

Perhaps the most striking result is the fact that they occur before target motion in as many as 12 randomly-chosen directions. In this case the smooth eye movements go in the direction of the subject's guess about the direction of future target motion. This result is shown in Fig. 8.

Figure 8 shows 2-dimensional eye movement velocity vectors while expecting a target ramp to move in one of the 12 clockface directions.

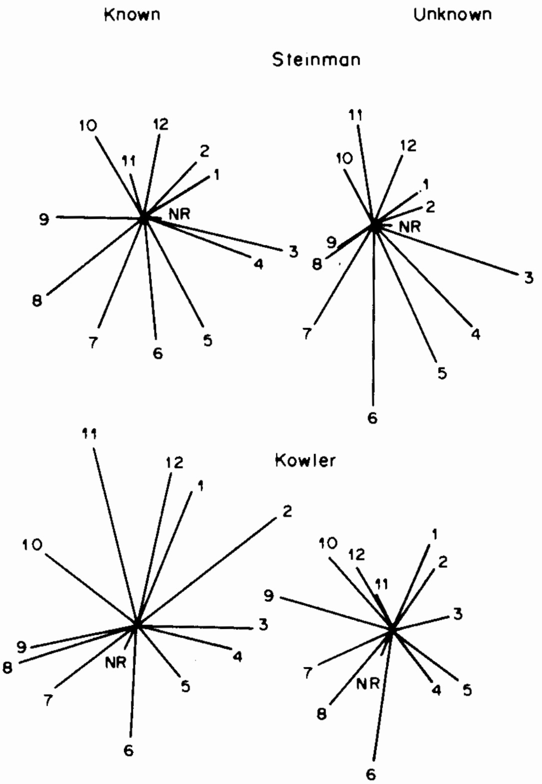

Fig. 8. Mean 50 msec eye velocity for expected ramps away from center in the direction of the hours on the clockface. Mean velocities when ramp directions were *Known* to the subject in advance are shown separately for expected ramps in each of the 12 directions (numbered vectors). Mean velocities when ramp directions were *Unknown* are shown separately for each guessed ramp direction (numbered vectors). Mean velocity for no expected ramps is also shown (NR). Each vector for expected ramps is based on approximately 150 observations and the vector for no expected ramps on approx. 1000 observations. (Reproduced from Kowler and Steinman, 1981.)

Vectors on the left show the smooth eye movements made while waiting for the target to move when the direction of the future ramp had been announced before the trial. Drifts when the subject had been told the target would not move are labeled *NR* (no ramp). These NR vectors average about 2′/sec.

The clock-face vectors on the right show what happened when the subject was *not* told the direction of the upcoming ramp. He was required to report his guess about direction (the clockface number) just before each trial. The plots on the right are eye velocity as a function of guessed direction. These are little mental maps, drawn with smooth eye movements, of a subject's expectations about future target motion. Clearly, there are appreciable directed smooth eye movements while anticipating ramps. Making ramp direction unpredictable changes the picture only slightly. It certainly does not reduce smooth eye movement velocity appreciably. Effects, such as these, have been found in experienced eye movement subjects and just as readily in naive inexperienced eye movement subjects (Kowler and Steinman, 1979a). A number of people, including Robinson, have confirmed seeing such effects in monkeys (Kowler and Steinman, 1979a).

These studies show that expectations about future motions of the target always influence smooth eye movements. Making targets unpredictable does not reveal the operation of the Level-B servomechanism.

Recently, Kowler *et al.* (1984) have shown that this is not an insurmountable problem. These authors used a Markov model to predict smooth eye movement velocities generated by a subject's expectations about future target motions. The model assumes that the subject's expectations are based on prior events. These expectations determine the velocity of the anticipatory smooth eye movements. For simplicity, the data for this initial test of the model were obtained by looking at anticipatory smooth eye movements while subjects waited for unpredictable leftward or rightward steps when the proportion of steps in each direction was varied. The fit of the model was good, suggesting that the Kowler *et al.* (1984) approach is a promising direction for future work. A new direction is clearly necessary now that we know that Westheimer's (1954b) assumption that unpredictable target motion reveals servomechanisms is incorrect; C-level factors cannot be eliminated. The full potential of the Kowler *et al.* (1984) approach is still to be tested in experiments in which a subject is smoothly pursuing and expecting target velocity to change.

Regardless of the future success of the Kowler *et al.* (1984) model in allowing separation of the C-level factor, expectation, from the B-level factor, stimulus motion, in observed smooth pursuit, an approach like theirs is preferable to the approach taken by Dallos and Jones (1963), not only because it predicts the data better, but also, as Kowler *et al.* (1984) have pointed out, because the approach is simpler. Only a single smooth pursuit mechanism, which always processes both C-level and B-level factors, need be postulated. Dallos and Jones (1963) required 2 separate mechanisms—one for predictable motions, the other for unpredictable motions.

There are many more examples I could give which have contributed to my loss of enthusiasm for the engineering approach to the study of the primate oculomotor systems. Work on the vestibulo–oculomotor subsystem is even more fun than the visuo–oculomotor subsystem. Barr *et al.* (1976) made this clear when they showed that good VOR in the dark requires a mental image of a target attached to an imaginary wall. An afterimage proved no better than pure imagery. This fact makes it very difficult to study the operation of the VOR in infrahuman primates. A technique for instructing the monkey to imagine a distant stationary target is required. Also, the VOR has long been known to be plastic (Rönne, 1923). A fact which forces relatively complex adaptive servomechanical models. Plasticity, as well as sensitivity to instructions, is a fundamental feature of the VOR. Its characteristics can change very rapidly. Recently, Collewijn, Martins and I (1981, 1983) have shown that the VOR, measured in darkness, completely adapts to 35% changes in optical magnification factors in less than an hour. Smaller optical demands require only a very few minutes.

So, looking back over these past 30 years, I am struck by the fact that, despite the power of the analytic tools, the Systems Approach has added little to our understanding of how the primate oculomotor system works.

At this point it is not possible to know whether the fault lies with the models or the modelers. Are there limitations inherent in systems theory, which make it incapable of explaining primate eye movements? Or, have all previous attempts to apply the approach failed because investigators tried to make their observations fit into constraints of simple linear models rather than try to develop models which fit their observations? I am inclined, personally, to favor the second interpretation, but will conclude, judiciously, by leaving both alternatives open.

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