Using Open-Loop Experiments to Study Physiological Systems, With Examples From the Human Eye-Movement Systems

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To analyze the contribution of each element in a sensory feedback control system, it is necessary to study the system with the feedback loop opened. Some physiological systems have multiple or even unknown sources of feedback, which makes it exceedingly difficult to open the loop. Conversely, it is relatively easy to open the loop on the human eye-movement system. Study of this system should help us understand how physiological control is maintained by sensory feedback.

Most physiological systems are closed-loop negative-feedback control systems. For example, consider someone trying to touch his nose with his finger. He would command a new reference position and let the arm start to move. But before long he would use sensory information from his visual and kinesthetic systems to signal the actual finger position. This sensory feedback signal would be compared with the reference or command signal to create the error signal that drives his arm to the commanded output position.

In the analysis of such systems, it is difficult to see which effects in the output are due to elements in the forward path and which are due to sensory feedback. To understand the contribution of each element it is necessary to open the loop on the system, i.e., to remove the effects of feedback. For some systems it is easy to open the feedback loop, whereas for others it is exceedingly difficult, since they have multiple or even unknown feedback loops. It is easy to open the loop on the human eye-movement system.

Many investigators have studied the human smooth pursuit eye-movement system under open-loop conditions; these studies have helped us understand this system. However, some investigators reported varied and inconsistent responses; they found open-loop responses to be idiosyncratic. It is suggested that the reason for these difficulties is that physiological systems, unlike man-made feedback control systems, are capable of changing their control strategy when the control loop is opened. Several specific changes in eye-movement control strategy are shown in this paper. Although the specific system studied was the eye-movement system, the technique presented should generalize to other physiological systems.

Previous open-loop studies

Systems engineering theory has provided physiologists with a powerful set of techniques for investigating physiological systems. Nowhere is this more apparent than in the study of the oculomotor systems, where systems analysis techniques have been applied widely and frequently (15). An important tool in systems analysis is the technique of "opening the loop" in a closed-loop feedback control system, allowing the investigator to examine the performance of the system without feedback and to identify its characteristics more completely. Many recent papers have discussed opening the loop on the smooth pursuit eye-movement system (2, 5–7, 9, 11, 13, 19, 20). However, the results of these studies are confusing and seem to be contradictory. The responses of subjects in some open-loop studies have been varied enough to lead the investigators to state that the use of this systems analysis technique is "useless" (18) and "unsuitable as a tool for analyzing the response characteristics of the smooth pursuit system" (5). Thus some investigators have expressed dissatisfaction with a technique that has potential value not only for the oculomotor systems but also for the analysis of other physiological control systems. This dissatisfaction demands a reexamination of these studies.

Opening the loop on a system

Before discussing these studies, we think some detailed comments are in order about opening a feed-

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back loop. A linear system can be schematically represented as a closed-loop system, as shown in Fig. 1*A*. In this figure *R* represents the reference input, *Y* is the output. The output is measured with a transducer, *H*, and the resulting signal(s) is subtracted from the input to yield the error signal, *E*. In many systems (such as the oculomotor systems) the element in the feedback loop, *H*, is unity; therefore, the output is compared directly with the input, which explains the reason for calling the resultant the error. This error signal is the input for the main part of the system, represented by *G*. This is called a closed-loop system because of the closed loop formed by *G*, *H*, and the summer. This system can be redrawn as shown in Fig. 1*B*. Although the transfer function of this equivalent system describes the input-output relationship of the system, it is not very useful for modeling physiological systems, because it hides specific behavior by lumping everything into one box. On the other hand, important information about the system's performance can be gained by techniques that examine components within the loop. One such technique for studying a system is to "open the loop," as shown in Fig. 1C, and then study the response of this open-loop system. The open-loop transfer function is defined as the total effect encountered by a signal as it travels once around the loop. That is, the open-loop transfer function is

$$G_{ol} = GH$$

Note that this is not the input-output transfer function of the system with its loop opened (which would be *G*), nor is this the transfer function of the equivalent redrawn closed-loop system shown in Fig. 1*B*. When we open the loop on a closed-loop system, bizarre behavior often results. In response to a step disturbance, a closed-loop system with its loop opened will usually vary its output until it is driven out of its normal operating range. For instance, if *R* in Fig. 1C is a step and *G* is a pure integrator, the error will be constant and the output will increase until the system reaches its limit of linearity.

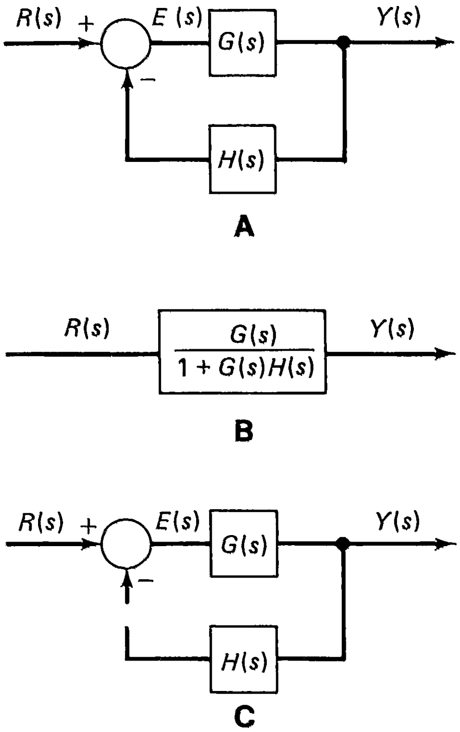

FIGURE 1. *A*: closed-loop control system; *B*: equivalent representation; and *C*: closed-loop system with its loop opened. Many analysis techniques require studying open-loop system of *C*. See text for definitions of abbreviations. (From Bahill (1). Reprinted by permission of Prentice-Hall, Inc.)

Often the success of a systems analysis depends on being able to open the loop on a system. If it is an electrical circuit, one might merely cut a wire. However, if it is a human physiological system, such an approach is not feasible, and other techniques must be developed. Such techniques usually involve manipulating the variable normally controlled by the system so that the feedback is ineffective in changing the error signal. For example, in the physiological sciences, some of the earliest examples of opening the loop are the voltage-clamp technique developed by Marmount (12) and Cole (4) and the light modulation technique used by Stark (16) to study the human pupil. In the voltage-clamp technique, the experimenters fixed the voltage across the membrane, the parameter that is normally controlled by the neuron: struggle as it may to open and close ionic channels, the neuron could not regulate the membrane voltage, and therefore the loop was opened. In the case of the pupil of the eye, the experimenters controlled the amount of light falling on the retina: struggle as it may to open and close the pupil, the pupillary system could not control the light falling on the retina, and thus the loop was opened. Similarly, the use of force and length servos in research on motor systems provides a means of examining components within feedback loops, although setting up these studies is complicated by the multiplicity of feedback loops in these systems (for example, see Ref. 17).

We think these open-loop techniques can be used in a broad range of physiological systems. Of course nothing is easy, and some problems must be overcome. In many systems the difficulties lie in trying to isolate one system so that others do not interfere, as in the previously mentioned pupillary and motor control systems. In other cases the difficulty lies in opening the loop on the system. For example, if the output of the respiratory system is defined to be the ventilation rate, then one could study the open-loop behavior of the system by controlling the concentration of the gasses being breathed while monitoring the ventilation rate. However, when modeling a different aspect of this system, such that a different quantity is defined as the output, opening the loop would become difficult, for example, as in controlling the venous concentration of CO_2.

Physiological systems often have several parallel feedback loops (e.g., hormonal and neural) acting simultaneously. One of the greatest challenges in studying a physiological control system is that one may not even be aware of all the feedback pathways.

Opening the loop on the eye-movement control system

An easy way to open the loop on the eye-movement system is to stabilize an object on the retina. This can be done, for example, by looking a few degrees to the side of a camera when someone triggers a flash. There will be an afterimage a few degrees off your fovea. Try to look at the afterimage: you will make a saccade (a fast eye movement) of a few degrees, but the image (being fixed on the retina) will also move a few degrees. You will then make another saccade, and the image will move again. Thus, no matter how you move your eye, you cannot eliminate the error and put the image on your fovea. This is the same effect as if someone opened the loop on an electronic system by cutting a wire (as in Fig. 1C). Therefore this is a way of opening the loop on the eye-movement system. There is also another simple way to study open-loop saccadic behavior. Gaze at the blue sky on a sunny day and try to track your floaters (sloughed collagen fibers in the vitreous humor). These hairlike images move when the eye moves; therefore your initial saccades will not succeed in getting them on the fovea. However, with a little practice, one can learn to manipulate these images, because they are not fixed on the retina and a human can rapidly learn to manipulate the system. This latter point often confounds attempts to open the loop on a physiological system. When the experimenter attempts to open the loop, the human quickly changes control strategy, thus altering the system under study.

The most common experimental technique for opening the loop on the eye-movement system, pioneered by Young and Stark (21), employs electronic feedback as shown in Fig. 2. In operation, the target is given a small step displacement, say 2° to the right. After ~200 ms, the eyes saccade 2° to the right. During this movement, the target is moved 2° farther to the right so that at the end of the saccade the target is still 2° to the right. After another 200-ms delay, the eyes saccade another 2° to the right, and the target is moved another 2°, maintaining the 2° retinal error. The saccadic eye movements are not effective in changing the retinal error; therefore the loop has been opened. In this open-loop experiment the subject produces a staircase of 2° saccades ~200 ms apart, until the measuring system becomes nonlinear. (Such behavior is shown in the beginning of Fig. 4.)

Electronic feedback has also been used to open the loop on the smooth-pursuit system. In these experiments the target was moved sinusoidally. When the eye moved, attempting to track the target, the measured eye position signal was added to the sinusoidally moved target position (as shown in Fig. 2). Thus the eye movements became ineffective in correcting the retinal error, and the feedback loop was, in essence, opened. In contrast to open-loop saccadic experiments, open-loop smooth-pursuit experiments do not stabilize the image on the retina, but rather the target is moved across the retina in a controlled manner by the experimenter. This is done because the saccadic system is a position tracking system and retinal position must be controlled, whereas the smooth-pursuit system is a velocity tracking system and retinal velocity must be controlled.

Results of open-loop experiments on the smooth-pursuit system

Open-loop experiments should provide results that not only describe the characteristics of elements within the feedback loop but also provide a description of the system's performance under closed-loop conditions. Consequently, similarity of actual closed-loop behavior with that predicted from open-loop data is an indication of the success of the investigation. Such agreement has been found by Wyatt and Pola (19, 20) in experiments in which subjects tracked sinusoidal waveforms. Although idiosyncratic differences were found between their subjects, agreement was found between actual and predicted closed-loop behavior for individual subjects. However, subsequent investigators were not able to replicate their results (11). In other studies (2, 5), individualistic behavior was varied enough to obviate any meaningful description of the system using such data.

Several factors can be identified that possibly contribute to the differences between individual subjects and between different experiments. One such factor is the predictability of the target waveform used in testing. While Wyatt and Pola (20) used predictable sinusoidal waveforms and obtained consistent results, Collewijn and Tamminga (5) used a pseudorandom mixture of sinusoids and found great variability between subjects. However, sinusoids were also used by Bahill and Harvey (2) with inconsistent results between subjects. Another factor may be the influence of prior experience on subject performance. When the results from several studies (2, 15, 20) were examined, open-loop gains were found to be larger in subjects with more experience in laboratory tracking tasks.

The one common element shared by these studies is intersubject variability, although the magnitude of this variability changed considerably in different studies. It is noteworthy that not only is such variability found between subjects but also in the performance of individual subjects in single trials. Such variation has been observed by Bahill and Harvey (2) and also by Leigh et al. (9) in a subject in which open-loop behavior was observed by stimulating a patient's paralyzed eye while monitoring the motion of the normal, covered eye. These findings show that the variability inherent in open-loop studies is attributable not only to differences between subjects but also to changes in the performance of individual subjects.

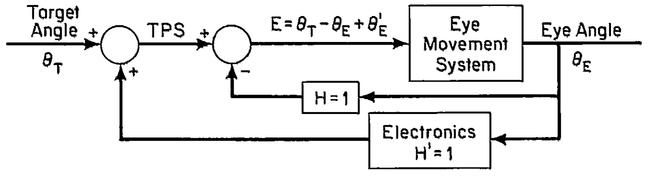

FIGURE 2. Electronic technique for opening loop on human eye-movement system. Eye position, θ_E, is continuously measured and is summated with the input target signal, θ_T. For eye-movement system, $H = 1$, because if the eye moves 10°, image on retina also moves 10°. If the eye movement monitor and associated amplifiers are carefully designed so that $H' = 1$, then any change in actual eye position, θ_E, is exactly canceled by the change in measured eye position, θ'_E. Thus the error signal, *E*, is equal to the target signal. This is the same effect as if the feedback loop had been cut, as in Fig. 1*C*. The target position in space, *TPS*, is the sum of the input signal and the measured eye position; care must be taken to keep this position within the linear range of the eye movement monitor (From Bahill and Harvey (2), ©1986 IEEE.)

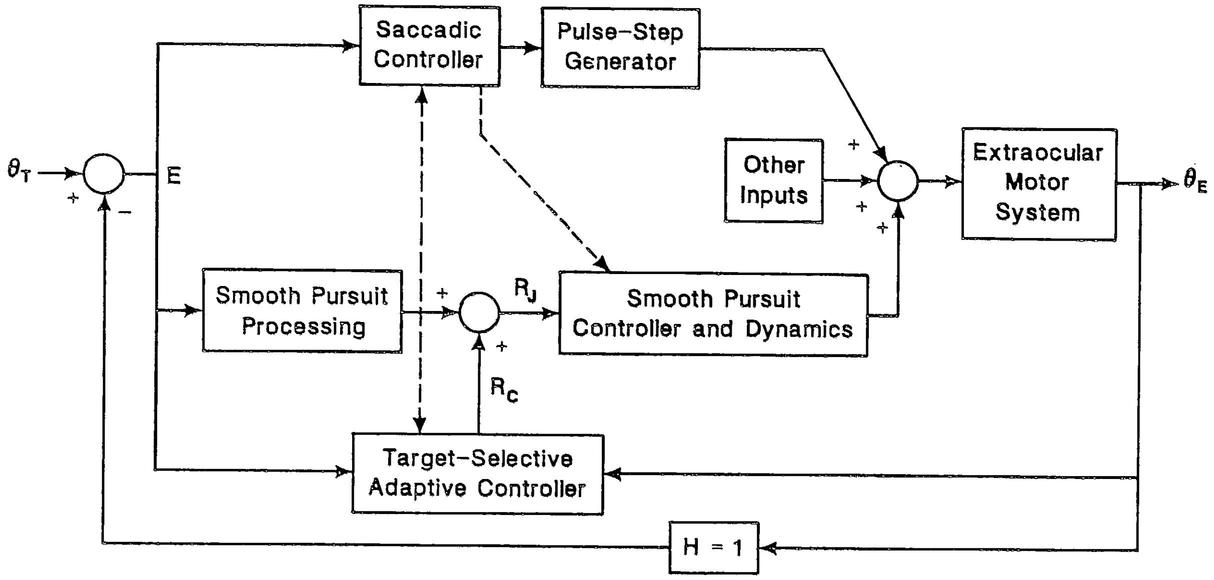

FIGURE 3. Target-selective adaptive control model. See text for definitions of abbreviations.

Comparing open-loop experiments with simulations

Insight into the behavior of the smooth pursuit system under open-loop conditions was sought by Bahill and Harvey (2) through a comparison of experimental results with those from simulations. The simulations were performed using the target-selective adaptive control model (3) shown in Fig. 3. This model has three branches. The first branch, the saccadic branch, generates a saccade, after a short delay, whenever the disparity between target and eye position is too great. The second branch, the smooth pursuit branch, produces smooth tracking of moving targets. The input to the smooth pursuit branch is velocity, so the first box (labeled smooth pursuit processing) contains a differentiator and a limiter. The box labeled smooth pursuit controller and dynamics contains a first-order lag (called a leaky integrator), a gain element, a time delay, a saturation element, and an integrator to change the velocity signals into the position signals used by the extraocular motor system. The last branch contains the target-selective adaptive controller that identifies and evaluates target motion and synthesizes an adaptive signal that is fed to the smooth pursuit branch. This signal permits zero-latency tracking of predictable visual targets, which the human subject can do, despite the time delays present in the oculomotor system. The adaptive controller must be able to predict future target velocity, and it must know and compensate for the dynamics of the rest of the system. All of these branches send their signals to the extraocular motor system, consisting of motoneurons, muscles, the globe, ligaments, and orbital tissues. Of course the final component of the model is a unity-gain feedback loop that subtracts eye position from target position to provide the error signals that drive the system. The solid lines in this figure are signal pathways, whereas the dashed lines are control pathways. For instance, the dashed line between the saccadic controller and the smooth pursuit controller carries the command to turn off integration of retinal error velocity during a saccade.

In the experiments many different target waveforms were used. The step target was presented to the subject to verify that the technique of opening the loop using electronic feedback was working. Because the step target introduced a position error rather than a velocity error, this experiment opened the loop on the saccadic system rather than the pursuit system. A position error with the feedback loop opened should have elicited a staircase of saccades. If this expected open-loop response to the step target was seen, then the electronic feedback was opening the loop correctly, as in the beginning of Fig. 4.

There was difficulty in getting consistent results of sinusoids with the loop opened. The most consistent results obtained for such presentations came from the first few seconds after the loop had been opened. This finding suggests that the difficulties with open-loop sinusoids were probably due to the in-

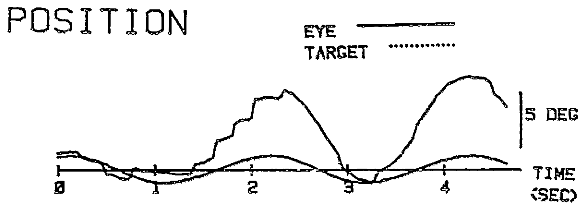

FIGURE 4. Typical human open-loop tracking. After feedback loop was opened, at 1-s mark, subject made a series of saccades trying to catch target. When this strategy did not work, he seemed to turn off saccadic system and produce only smooth pursuit movements. This subject was experienced in oculomotor experiments. Large open-loop gain appears to be a characteristic of such experienced subjects. (From Bahill and Harvey (2), ©1986 IEEE.)

volvement of high-level processes, such as prediction. Once the loop was opened, the behavior of the target changed. Often the subjects would appear to respond to this change in target behavior by changing their tracking strategies. Figure 4 shows an example of such a change in human tracking strategy. For the first half of this record the subject behaved as one would expect for a subject tracking an open-loop target; there is a saccade every 200 ms (approximately the time delay before the saccadic system responds to a position error). However, in the middle of the record the saccades cease; it seems that the subject turned off the saccadic system. Such saccade free tracking was common in these experiments and in other open-loop experiments (7, 9, 11, 19, 20). The records are strikingly devoid of saccades in spite of the large position errors, a finding that, oddly, received little comment by previous investigators, although it is often seen in their data.

By way of comparison, the model is shown tracking a sinusoid under open-loop conditions in Fig. 5. To simulate the changes in strategy that are apparent in the human data of Fig. 4, the model characteristics were changed at intervals. From 2 to 4.25 s there is normal closed-loop tracking. At 4.25 s the loop was opened, the adaptive controller was turned off, and the smooth pursuit gain was reduced to 0.7, thus producing a staircase of saccades similar to those shown in Fig. 4. At 7.25 s the saccadic system was turned off, the adaptive controller was turned back on, and the gain of the smooth pursuit system was returned to its normal value; the model tracked with an offset similar to that of Fig. 4. This type of position offset was often noticed in human subjects during open-loop tracking. Finally at 10.5 s the adaptive controller was turned off and the model tracked without an offset, as was seen in some subjects.

These simulations help explain some confusing data in the literature by allowing us to suggest that when the loop on the human smooth pursuit system is opened, subjects alter their tracking strategy to cope with altered target behavior. Some subjects continue to track with all systems (producing a staircase of saccades), some turn off the saccadic system (producing smooth tracking with an offset), some also turn off the adaptive controller (producing smooth tracking without an offset), and some change the gain on the smooth pursuit system. Thus each subject appears to adapt to the novel tracking task created by opening the loop by selecting subcomponents of the smooth pursuit system and/or changing parameters within those subsystems. All these strategy changes are within the possibilities provided by the model.

Multifaceted control is also common in other physiological systems (for example, see Refs. 8, 10). Thus the potential exists in other physiological control systems for changes in strategy, i.e., a change in the balance of control subsystems in different physiological states, whether these states occur "naturally" or are imposed by an investigator. Such changes may occur in different behavioral states, as observed, for example, for respiratory control in the newborn (14). Consequently, it should not be surprising that when an investigator attempts to open the loop on a control system, control strategy changes. This paper demonstrates this principle for the eye-movement system.

The technique of opening the loop on a physiological system to better understand its behavior seemed to hold great promise when it was first used 20–40 years ago. However, in the past decade it seemed that the technique was no longer working. With the results of this study we can once again see promise for the technique of opening the loop, as long as care is taken to acknowledge that the human is a complex organism and is likely to change its behavior when the input changes its behavior.

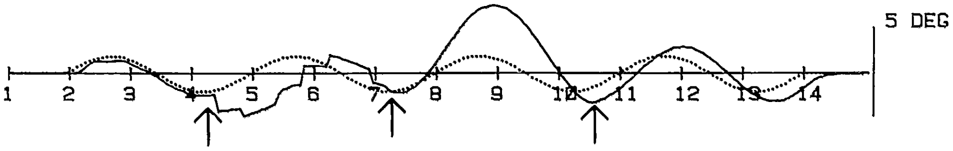

FIGURE 5. Model (solid line) tracking a sinusoidal target (dotted line) under a variety of conditions. At first arrow loop was opened, at second arrow saccadic system was turned off, and at third arrow adaptive controller was turned off. Tracking patterns similar to each of these are common in human records. (From Bahill and Harvey (2), ©1986 IEEE.)

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