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MODELING THE SMOOTH-PURSUIT EYE-MOVEMENT SYSTEM

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There is a 150 ms time delay in the smooth-pursuit eye-movement system, but humans can learn to overcome this time-delay and track smoothly moving targets with no latency. Open-loop experiments performed on the human smooth-pursuit system aided the development of a model that could do the same. The model had to be able to predict target velocity and compensate for system dynamics. Therefore, humans must also have the ability to predict target movement, and they must use internal models of their own system dynamics. These internal models must be adaptive, for they must change when temperature, fatigue, age, *etc.*, changes the system.

Keywords: Control systems; smooth pursuit; eye movements; open-loop experiments; predictors; time-delay systems; adaptive systems; modeling; ethyl alcohol

Most neuro-muscular systems have a time-delay of 150 to 200 milliseconds (ms). To show the effects of such a time-delay, hold a crisp dollar bill with George Washington's portrait between someone's outstretched finger and thumb. Tell them they can have the bill if they catch it. Then drop the bill and let them try to pinch it. Unless they make a real lucky guess, they will miss the bill, and it will drop to the floor. The time delay in the smooth-pursuit eye-movement system is 150 ms, but humans can learn to overcome this time-delay and track smoothly moving targets with no latency. To explain this phenomenal behavior we must develop a model.

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STEPS IN THE MODELING PROCESS

Describe the physical system to be modeled.
Gather experimental data that describe the system's behavior.
Make the model.
Investigate alternative models.
Validate the model.
  Show that the model behaves like the physical system.
  Use the model to simulate something not used in its design.
  Perform a sensitivity analysis.
Integrate with models for other systems.
Assess performance of the model.
Re-evaluate and improve the model.
Suggest new experiments for the physical system.

However, modeling is not a serial process; some of the above steps can be done in parallel and it is very iterative. This prescription for describing processes was developed by Bahill and Gissing [2].

DESCRIBE THE PHYSICAL SYSTEM TO BE MODELED

The purpose of the eye-movement system is to keep the fovea, the region of the retina with the greatest visual acuity, on the object of interest. To accomplish this task, the following four types of eye movements work in harmony: *saccadic eye movements* that are used in reading text or scanning a roomful of people; *smooth-pursuit eye movements* that are used when tracking a moving object; *vergence eye movements* that are used when looking between near and far objects; *and vestibulo-ocular eye movements* that are used to maintain fixation during head movements. These four types of eye movements have four independent control systems, involving different areas of the brain. Their dynamic properties, such as latency, speed and bandwidth are different, and they are affected differently by fatigue, drugs and disease. For simplicity, none of the other neural systems associated with vision or movement will be discussed in this paper.

The specific actions of these four systems can be illustrated by the example of a duck hunter sitting in a rowboat on a lake. He scans the sky using saccadic eye movements, jerking his eyes quickly from one fixation point to the next. When he sees a duck, he tracks it using smooth-pursuit eye movements. If the duck lands near his boat, he moves his eyes toward each other with vergence eye movements. Throughout all this, he uses vestibulo-ocular eye movements to compensate for the movement of his head caused by the rocking of the boat. Thus, all four systems are continually used to move the eyes.

This paper is primarily about developing and validating a model for the human smooth-pursuit eye-movement system. Others systems are only included when they interact with the smooth-pursuit system.

GATHER EXPERIMENTAL DATA THAT DESCRIBE THE SYSTEM'S BEHAVIOR

Experiments with nonpredictable target waveforms reveal a 150 millisecond (ms) time delay in the human smooth-pursuit eye-movement system [5, 7, 31]. The effects of this time delay are apparent during starting and stopping transients, as shown in Figure 1.

However, when a human (or a monkey) tracks a target that is moving sinusoidally, the subject quickly locks onto the target and tracks with neither latency nor phase lag. It is as if the subject creates an internal model of the target movement and uses this model to help track the target. This internal model has been called a predictor [23, 35, 39], a long term learning process [12], a percept tracker [25, 37, 45, 46], a neural motor pattern generator [15], and a target-selective adaptive controller [7, 8, 19, 27]. We conducted a series of experiments to find the characteristics of the target waveform that are necessary to allow such zero-latency tracking.

Predictable sinusoidal motion is the most common stimulus for the smooth-pursuit system [17, 18, 32, 42]. However, although a sinusoid is easy to track, it may not be the best waveform for studying the tracking of predictable targets, because the derivative of a sinusoid is a sinusoid. Therefore, single cell recordings that show a sinusoidal frequency modulation, could represent velocity cells, position cells with a time delay, or control signals. Linear ramps have been used as

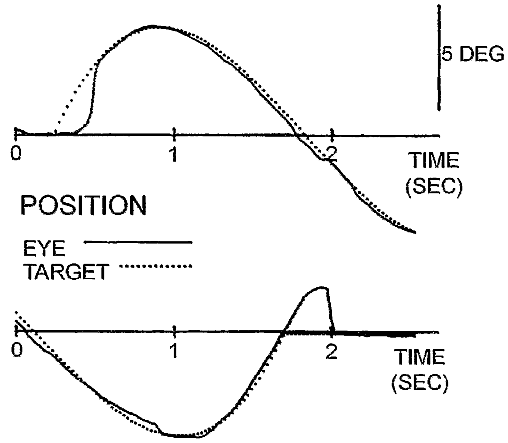

FIGURE 1 Typical beginning (top) and ending (bottom) of human tracking of a sinusoidal target. Smooth pursuit began 150 ms after the target started to move. It was followed by a corrective saccade at 200 ms and then by zero-latency, unity-gain tracking. The bottom trace shows a termination of sinusoidal smooth-pursuit tracking. The smooth-pursuit velocity started declining 125 ms after the target velocity dropped. It reached zero velocity at 250 ms, when a corrective saccade occurred to end the subject's tracking. Thus, the beginning and ending transients show the effects of the time delay. In contrast, steady-state tracking does not. Target movements were ± 5 degrees from primary position. The time axis is labeled in seconds, and upward deflections represent rightward movements [7].

smooth-pursuit target waveforms [9, 21, 33]. Often these ramps were repetitive with the same constant velocity (triangular waveforms). Such ramps are not suitable for studying a velocity tracking system such as the smooth-pursuit eye-movement system; many different velocities should be used. Furthermore, triangular waveforms induce numerous saccades at each target turn-around. Typical good tracking of triangular targets has three or four position correcting saccades per cycle. These saccades interfere with the study of the smooth-pursuit system. To prevent saccades at the turn-around [29] used a triangular waveform with sinusoidal turn-arounds. Other novel waveforms have also been devised. A "pure velocity" target was derived by using a long line of horizontally moving dots [41]. This target seems ideal for testing optokinetic nystagmus, but not the foveal smooth-pursuit system, because most of the target is peripheral not foveal. We have developed several target waveforms, with unique velocity profiles, to challenge the foveal smooth-pursuit system without inducing numerous saccades. They are shown in Figure 2.

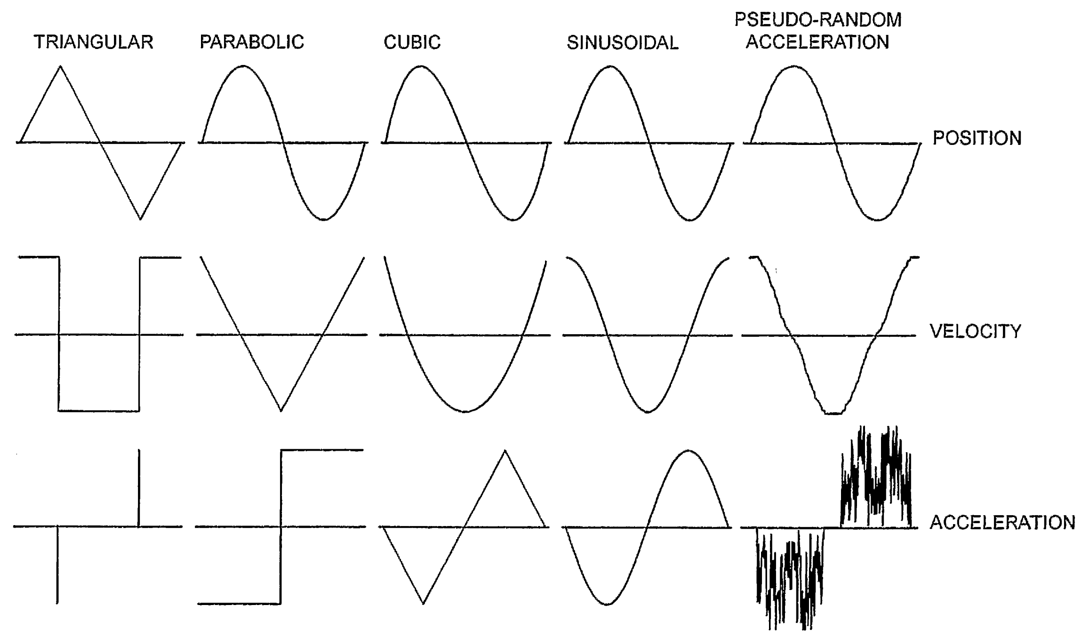

FIGURE 2 The predictable target waveforms [8].

This section summarizes McDonald's [8] studies of smooth-pursuit tracking of predictable target waveforms. Our subjects overcame the time delay inherent in the smooth-pursuit system and produced zero-latency tracking of all target waveforms, as long as the velocity was continuous and the acceleration was limited. All of these target waveforms had continuous velocities and amplitude-limited accelerations. We believe these two properties are necessary for zero-latency tracking. We limited acceleration to 300 deg/sec^2, and we kept the maximum velocity between 5 and 40 deg/sec. The target amplitude was ± 5 degrees. This was a convenient amplitude: it was comfortable to track, it did not fatigue the subject rapidly, and it was large enough to provide a large signal to noise ratio. Each three-minute session was composed of several cycles of each waveform presented in random order. Frequencies varied between 0.1 and 1 Hz. Best tracking occurred for frequencies between 0.2 and 0.6 Hz.

Mean Square Errors

A quantitative measure was needed to show how well the subject tracked the target. Previous investigators have used position gain, velocity gain, phase, coherence, or the number and size of saccades. Because the purpose of the eye movement control system is to keep the fovea on the target, we felt that the error between the fovea of the eye and the target was the most appropriate measure of the quality of tracking. Our primary metric was the mean square error between eye position and target position (pmse). The human fovea (specifically the inner foveal pit) has a radius of 0.5 deg [13, 15]. Therefore, a target consistently on the outer edge of the fovea produces a pmse of 0.25 deg^2. If the pmse is greater than 0.25 deg^2, then the target is off the fovea at times. If the pmse is less than 0.25 deg^2, then the target is usually on the fovea.

The Sinusoidal Target Waveform

The sinusoid is the most common smooth-pursuit target waveform, because it is easy to generate and easy to track. Our subjects said sinusoids were 'comfortable,' 'non-confusing,' and 'natural'. Our sinusoidal target waveform is given by

$$r(t) = A \sin \omega t$$

The normal amplitude, A, was 5 degrees (± 5 degrees from primary position).

Figure 1 shows the beginning (top) and ending (bottom) of human tracking of a target moving sinusoidally. Steady-state smooth-pursuit tracking of a sinusoidal target is shown in Figure 3, where the position mean square error (pmse) was $0.02\,deg^2$. This is exceptionally good tracking; most subjects did not typically track with such accuracy.

As shown in Figure 1, our subjects overcame the 150 ms time delay very quickly, in less than one-quarter cycle of the target waveform. To track a sinusoid with zero-latency, the subjects must estimate the amplitude, period, and the initial phase of the target. We were surprised that these parameters were estimated before the first complete half-cycle of the target waveform. We suspected the subjects were guessing that the amplitude, phase and waveform were the same as those used in the calibration procedure.

To determine if the subjects were guessing the target parameters, we changed the initial phase and offset so that the beginning of target motion provided poor clues about the frequency, phase and amplitude of the target. Figure 4 shows a subject attempting to track a target waveform that begins with a 90-degree phase shift and a negative offset. Our subjects could not track this targzet waveform until after a

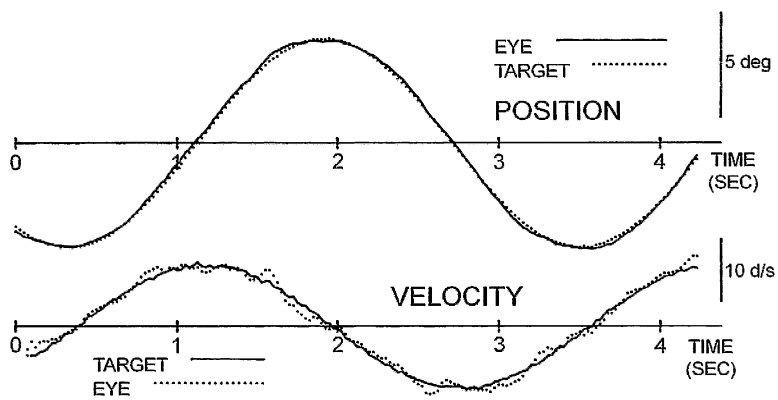

FIGURE 3 Zero-latency steady-state tracking of a sinusoidal target waveform. The top trace shows target (dotted) and eye (solid) position, and the bottom trace shows target (solid) and eye (dotted) velocity. Target movements were ± 5 degrees from primary position. The time axis is labeled in seconds, and upward deflections represent rightward movements. The pmse was $0.02\,deg^2$ [8].

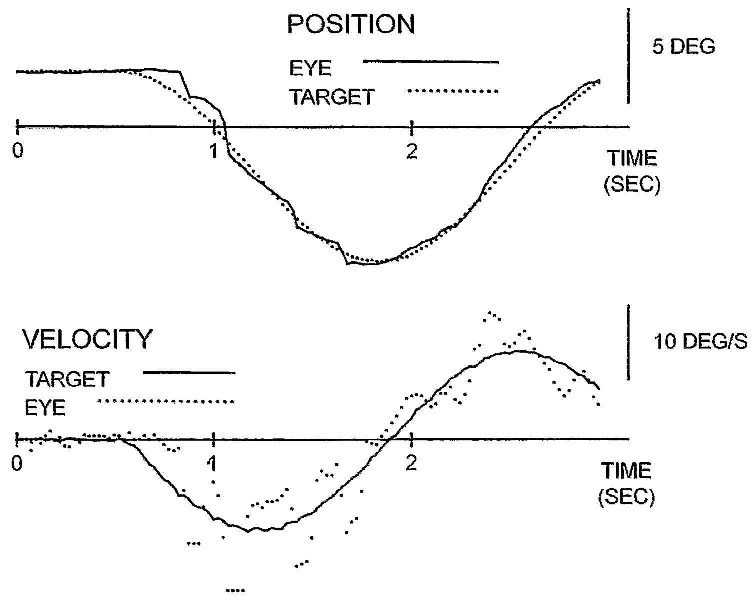

FIGURE 4 Start-up transient for a sinusoid with unexpected initial phase and offset. Same display format as Figure 3. The errors are large, particularly during the first half cycle. The pmse was 0.19 deg^2 [8].

full half-cycle of the waveform had been presented. Similar performance was observed throughout the experiment with the size of the initial target change affecting the ability to track quickly. For simple target waveforms, such as a sinusoid with no initial phase or offset, our subjects guessed the waveform and tracked with zero-latency after one-fourth of a cycle. For more complicated waveforms, such as a sinusoid with non-zero initial phase or offset, guessing was unsuccessful; our subjects tracked with zero-latency only after one-half of a cycle. The initial offset or phase did not change steady-state tracking.

The Parabolic Target Waveform

Because sinusoidal oscillations are so common in nature, we thought zero-latency tracking might be a unique feature of sinusoids. To test this hypothesis we created non-sinusoidal target waveforms. We thought that humans might fit an internally generated sinusoid through these predictable target movements. For our first non-sinusoidal waveform, we connected two parabolas to form a target waveform that differed from a sinusoid by only 0.03 deg^2 pmse. This parabolic target waveform is given by

$$r(t) = A\left(1 - \left[\frac{t-(T/4)}{(T/4)}\right]^2\right) \quad \text{for } 0 < t \leq T/2$$

and

$$r(t) = A\left(-1 + \left[\frac{t-(T/4)}{(T/4)}\right]^2\right) \quad \text{for } T/2 < t \leq T.$$

The terms A and T are amplitude and period, respectively. The amplitude was fixed at five degrees, but the period was varied from run to run.

Figure 5 shows excellent tracking of this parabolic target. Close comparison of the velocity records indicates that this subject tracked

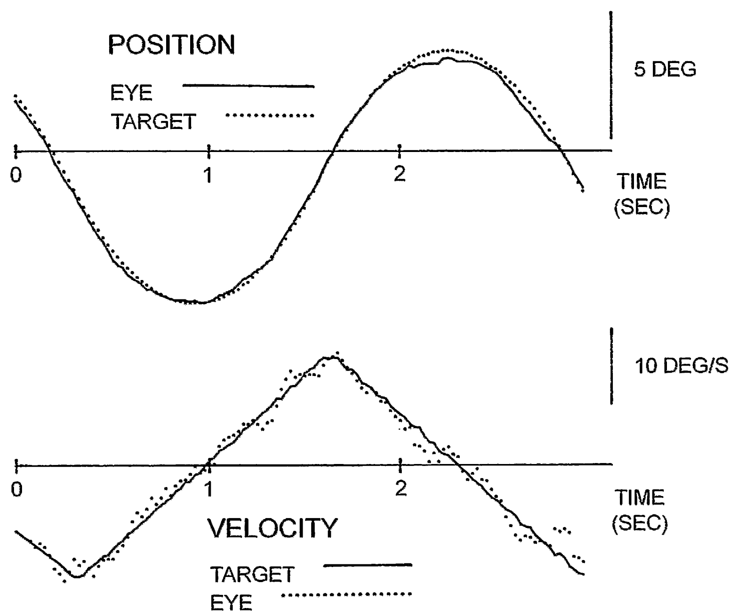

FIGURE 5 Steady-state tracking of a parabolic target waveform. The clustering of the eye velocity dots about the target velocity line shows that the subject was using the correct waveform. Same display format as Figure 3. The pmse was 0.05 deg^2 [8].

the correct target waveform and not some internally generated sinusoid. The shape of the eye velocity trace, which is the important record, shows the linear shape characteristic of a parabolic trajectory. Most of our subjects were able to track this parabolic waveform after observing only a few cycles. The transient performance when the target started to move was the same as for sinusoidal targets.

Zero-latency tracking suggests that the subject uses a compensation signal from an internal model to augment the visually derived target velocity signal. When the target stops abruptly, the output of the internal model differs from the visual image, causing the model to be turned off abruptly. To study this turn off under different conditions we moved the laser target behind an opaque barrier at the end of target presentation as shown in Figure 6. Without a fixation target, this subject merely brought the smooth pursuit to a halt; there was no saccade at the end of tracking. The time delay between the disappearance of the target and the decrease of the smooth-pursuit velocity was 150 ms. The smooth-pursuit velocity reached zero, 420 ms after the disappearance of the target. Wyatt and Pola [30] have reported similar results. Deflecting the laser behind the barrier meant that there was no error between the visual image and the output of the

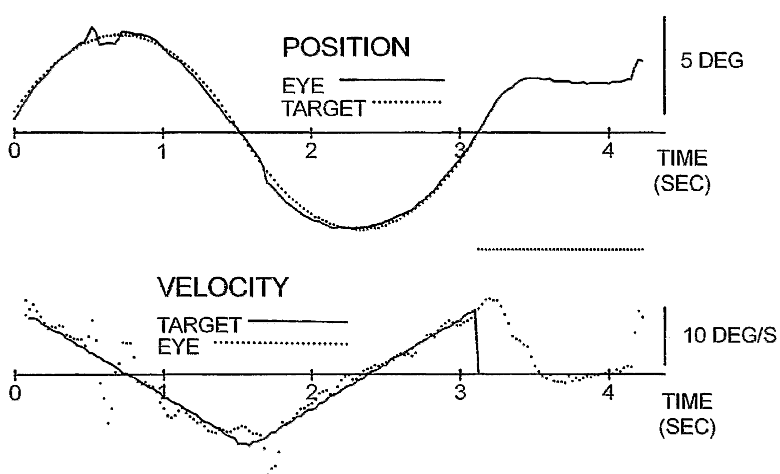

FIGURE 6 End of tracking transient for a parabolic waveform. At 3.1 seconds, the target disappeared. The eye velocity then took 420 ms to decay to zero [8].

internal model. Consequently, it took longer to turn off the model and stop smooth-pursuit tracking. When the target disappeared, the subject's training and volition also became factors. One subject made saccades to primary position, another made large blinks, and one subject (who knew that the barrier was on the left side of the mirror galvanometer) made a saccade to the leftward location of the invisible target. Others have also studied tracking after the target disappeared. Humans [40] and monkeys [16] have been trained to continue smooth-pursuit tracking of a one Hz sinusoidal target for more than a second after it disappeared. So, in summary, when the target disappears, smooth pursuit stops, but not as fast as when a visible target stops.

The Cubic Target Waveform

Humans can overcome a large internal time delay and track sinusoidal and parabolic target waveforms with unity-gain and no time delay. Moreover, they learn to do this very quickly. To help determine if humans can easily track every predictable waveform we created a cubic waveform. The cubic waveform is simple; it is the next order polynomial above a parabola. But we could not imagine a naturally occurring cubic visual target. Our cubic target waveform, which satisfies the requirements $r(0) = 0$, $r(T/2) = 0$, and $r(T) = 0$, is

$$r(t) = 10.39A\left[2\left(\frac{t^3}{T}\right) - 3\left(\frac{t^2}{T}\right) + \left(\frac{t}{T}\right)\right] \quad \text{for } 0 < t \leq T$$

The quantity T represents target period and A is the amplitude.

Figure 7 shows excellent tracking of the cubical target waveform. Using only smooth-pursuit eye movements, the subject was able to keep the fovea on the target for over 8 seconds. Saccades were not removed or filtered out of the eye position traces; indeed small conjugate saccades can be seen at the 8.5 sec mark.

The Pseudo-random Acceleration Target Waveform

To discover whether a subject could learn *any* predictable waveform, we constructed the most difficult predictable target waveform we could imagine. It was derived using a table of random numbers. These random

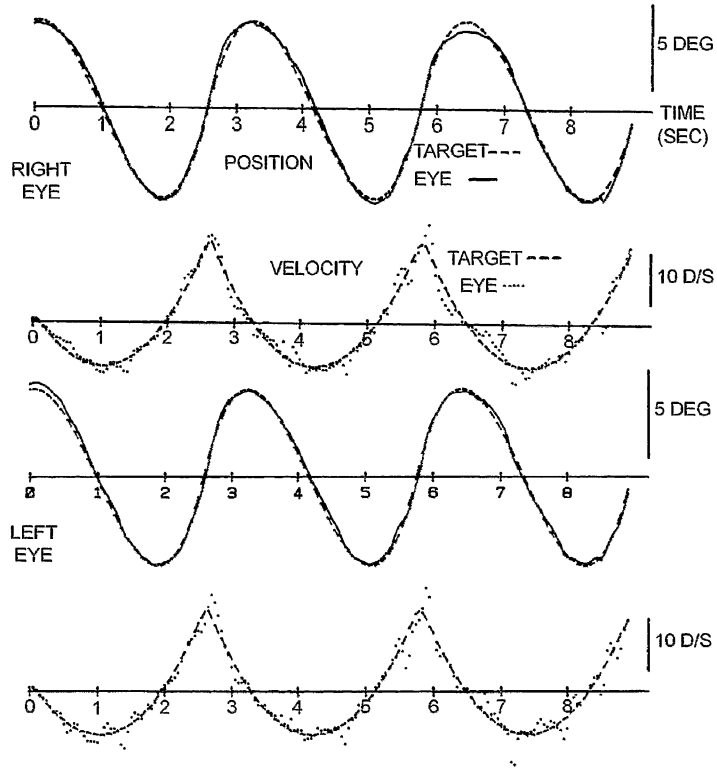

FIGURE 7 Binocular eye movements for a subject tracking the cubical target waveform. The pmse was 0.07 deg^2 for the right (dominant) eye and 0.06 deg^2 for the left eye [28].

numbers were used to form a uniformly distributed random acceleration sequence. To form the target position waveform this acceleration sequence was integrated twice, the acceleration was held at zero for a short period and then the negative of this acceleration sequence was integrated twice. The net result was a regular, predictable target waveform that had a pseudo-random acceleration, but a symmetrical and smooth position waveform. Two distinctive features of this waveform were recognizable in the target velocity record: a period of zero acceleration that occurred at peak velocity and a period of low acceleration that occurred near zero velocity. The right column of Figure 2 shows this waveform.

The data of Figure 8 show excellent tracking of this pseudo-random acceleration target waveform after the subject had observed this waveform for 135 seconds in a 20-minute interval. The subject used the appropriate velocity waveform, as is evidenced by the flattening of the velocity trace near zero velocity and at peak velocity for both the target and the eye.

It is understandable that, in a world full of wheels and pendulums, humans have learned to track sinusoids with zero-latency. After some consideration, the same can be said of parabolic trajectories that describe the path of a ball, or any other unrestrained object under constant force. There is, however, no naturally occurring analog to the cubic and pseudo-random acceleration waveforms. Yet, humans can track these waveforms with no time delay. This is truly a phenomenal feat.

Database Averages

The figures in this paper show very good target tracking. They were chosen to illustrate the capabilities of the human smooth-pursuit system. They are not meant to illustrate typical smooth-pursuit tracking. Typical tracking has saccades and occasional periods of off-foveal tracking. It is unusual to have more than a cycle without at least a microsaccade. To provide a metric indicating typical performance, we summarized all data from seven subjects tracking targets moving with frequencies between 0.2 and 0.6 Hz. For the 1059 seconds of steady-state tracking, without starting and stopping transients, the average pmse was $0.32\,\text{deg}^2$ with standard deviation $0.28\,\text{deg}^2$. Over the long term, humans track with pmse around $0.32\,\text{deg}^2$. In the short term, (much as a sprinter can perform optimally for short periods of time) a human can track accurately with pmse around $0.05\,\text{deg}^2$ as shown in Figures 3, 5, 7 and 8.

Learning to Track the Cubical Waveform

Figure 7 shows that a human can track the cubic target waveform very well. But this capability is not inherent. It must be learned as was shown in McHugh's experiments [28]. Our standard learning protocol began with a 6 second square wave calibration target waveform, followed by 9 seconds of the cubical target waveform, 3 seconds of the square wave

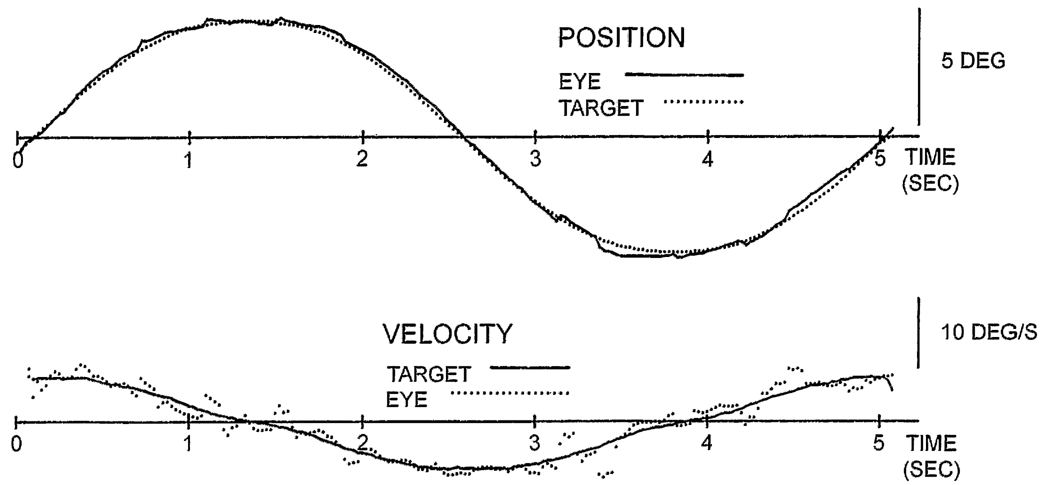

FIGURE 8 Zero-latency tracking of a pseudo-random acceleration target waveform. The target velocity line is slightly flattened at zero velocity and at maximum velocity. The eye velocity dots also reflect this flattening. The pmse was 0.04 deg^2 [8].

target waveform, another 9 seconds of the cubical waveform, and finally another 6 seconds of the square wave calibration target waveform. The subjects were allowed to rest for five minutes and then the sequence was repeated. This process continued for about two hours.

Because the purpose of the eye movement control system is to keep the fovea on the target, we felt that the error between the eye and the target was the most appropriate measure of the quality of tracking. Our primary metric was the mean square error between eye position and target position (pmse). Single and double exponential curves were fit to the pmse data. The best fit was usually an exponential of the form

$$\text{pmse} = Ae^{-Bt} + C$$

The solid lines of Figure 9 show the exponential curves fit to the data of our four best-tracking college students. We were trying to quantify the ultimate capabilities of the human smooth-pursuit system, so we

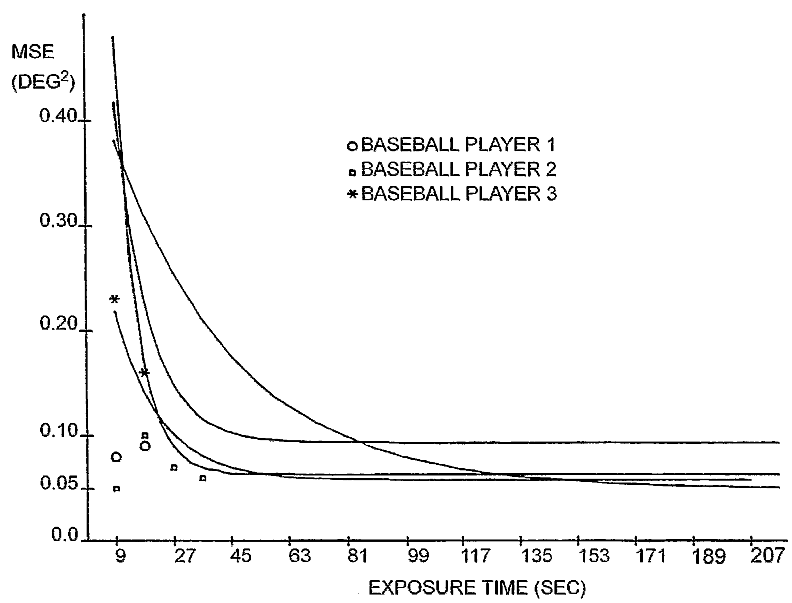

FIGURE 9 Time course of learning for seven subjects. Solid lines are the exponential curves fit to the data of our four best-tracking college students. Circles, asterisks, and squares are data points for three professional baseball players. A target consistently on the outer edge of the fovea produces a pmse of 0.25 deg^2 [28].

only report the performance of our best subjects. In this figure, we only show data of four of 20 college students. The other students did not demonstrate such low error tracking.

To narrow in on this exquisite tracking performance, we decided to study optimal humans performing optimally. Who is an optimal human? For eye tracking capability, we thought professional athletes would fit the bill. So, we invited some professional baseball players to participate in our experiments. The pmse's for three members of the Pittsburgh Pirates Baseball Club are represented by circles, asterisks and squares in Figure 9. In viewing the target for the first time, professional baseball players 1 and 2 had much smaller pmse's, 0.05 and 0.08, than our other subjects. They had never seen a cubical waveform before, yet they started out with low pmse's. Baseball players 1 and 2 each played in the major leagues for over ten years. Player number 3 never got out of the class A Farm System. These data seem to indicate that the ability to track the cubical waveform is correlated with baseball performance.

MAKE THE MODEL

There is a model that can perform like the human and overcome its time delay and track smoothly moving targets with no latency. It is McDonald's Target-Selective Adaptive Control (TSAC) Model [7, 27], shown in Figure 10.

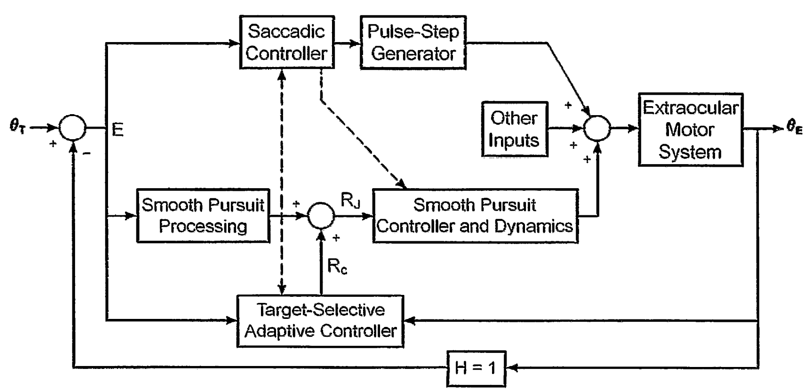

FIGURE 10 The general form of the Target-Selective Adaptive Control Model [27, 3].

The TSAC Model

The TSAC model has three branches. The top branch, the saccadic branch, generates a saccade, after a short delay, whenever the disparity between target and eye position exceeds a threshold (which might be variable). The middle 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 bottom branch contains the target-selective adaptive controller that identifies and evaluates target motion and synthesizes an adaptive signal R_C 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. The adaptive controller is separate from the smooth-pursuit system in the model and also in the brain [23]. The adaptive controller sends signals to the smooth-pursuit system and other movement systems [38]. All of these branches send their signals to the extraocular motor system, consisting of motoneurons, muscles, the globe, ligaments and orbital tissues. And 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, while 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.

Now we would like to derive numerical values for the parameters in this model. But this is difficult because it is a closed-loop feedback control system.

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

By merely studying the output of a physiological system, it is difficult to see which effects are due to elements in the forward path and which are due to sensory feedback. In order 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; while for others it is exceedingly difficult, since some systems have multiple or even unknown feedback loops. Fortunately, it is easy to open the loop on the human eye-movement system.

There are many studies of 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 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.

Opening the Loop on a System

There are many ways to model a system. A system can be schematically represented as a closed-loop system, as shown in Figure 11(a). In this figure, R represents the Reference input and Y is the output. The output is measured with a transducer, H, and the resulting signal 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 Figure 11(b). Although the transfer function of this equivalent system describes the input-output relationship of the system, it is not very useful for

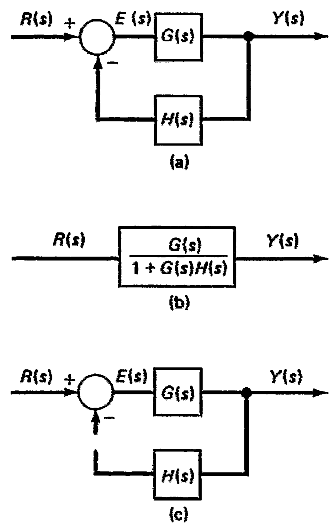

FIGURE 11 (a) A closed-loop control system, (b) an equivalent representation, and (c) the closed-loop system with its loop opened. Many analysis techniques require the study of the open-looped system of (c) [1].

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 Figure 11(c), and then study the response of this open-looped 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 $G_{\text{ol}} = GH$. 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 Figure 11(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 Figure 11(c) is a step, and G is a pure integrator, the error will be constant and the output will increase linearly until the system is driven into its nonlinear range.

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 [26] and Cole [10] and the light modulation technique used by Stark to study the human pupil [34]. In the voltage clamp technique, the experimenters fixed the voltage across a neuronal membrane, the parameter that is normally controlled by the neuron: struggle as it may opening and closing ionic channels, the neuron could not regulate the membrane voltage, 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 opening and closing the pupil, the pupillary system could not control the light falling on the retina, 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 [36].

Most physiological systems have several parallel feedback loops (*e.g.*, hormonal and neural) acting simultaneously. One of the greatest challenges in studying a physiological control system is being aware of all the feedback pathways.

Opening the Loop on the Eye-movement Control Systems

An easy way to open the loop on the saccadic 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 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. 11(c)). Therefore, this is a way of opening the loop on the saccadic 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 hair-like 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 [47], employs electronic feedback as shown in Figure 12. The position of the eye, θ_E, is continuously measured and is summated with the input target signal, θ_T. For the eye-movement system $H = 1$, because if the eye moves ten degrees, the image on the retina also moves ten degrees. If the eye movement monitor and associated electronics 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 Figure 11(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.

To open the loop on the saccadic eye movement system, the target is given a small step displacement, say two degrees to the right. After about 200 ms, the eyes saccade two degrees to the right. During this movement,

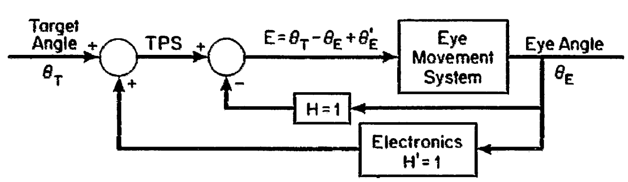

FIGURE 12 Electronic technique for opening the loop on the human eye movement system [4].

the target is moved two degrees farther to the right, so that at the end of the saccade the target is still two degrees to the right. After another 200 ms delay, the eyes saccade another two degrees to the right, and the target is moved another two degrees, maintaining the two-degree retinal error. The saccadic eye movements are not effective in changing the retinal error; therefore, the loop has been opened. In such an open-loop experiment, the subject produces a staircase of two-degree saccades about 200 ms apart, until the measuring system becomes nonlinear. Such a staircase of saccades is shown in the beginning of Figure 13.

To open the loop on the smooth-pursuit system the target is moved sinusoidally. When the eye moves, attempting to track the target, the measured eye position signal is added to the sinusoidally moved target position (as in Fig. 12). Thus the eye movements become ineffective in correcting the retinal error and the feedback loop is, 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.

Parameter Determination for the TSAC Model

Armed with these data from open-loop experiments, we are now ready to determine parameters for the TSAC model shown in Figure 14. The

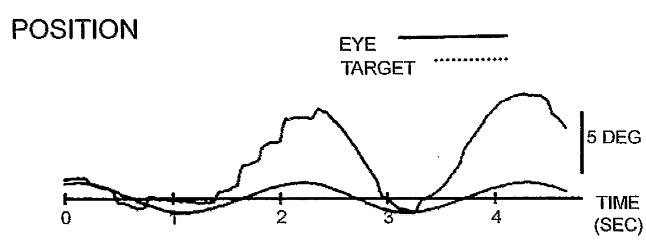

FIGURE 13 Position of the target and eye as functions of time for typical human open-loop tracking. After the feedback loop was opened, at the 1-second mark, the subject made a series of saccades trying to catch the target. When this strategy did not work, he seemed to turn off the saccadic system, and produce only smooth-pursuit eye movements. This subject was experienced in oculomotor experiments. The large open-loop gain appears to be a characteristic of such experienced subjects [4].

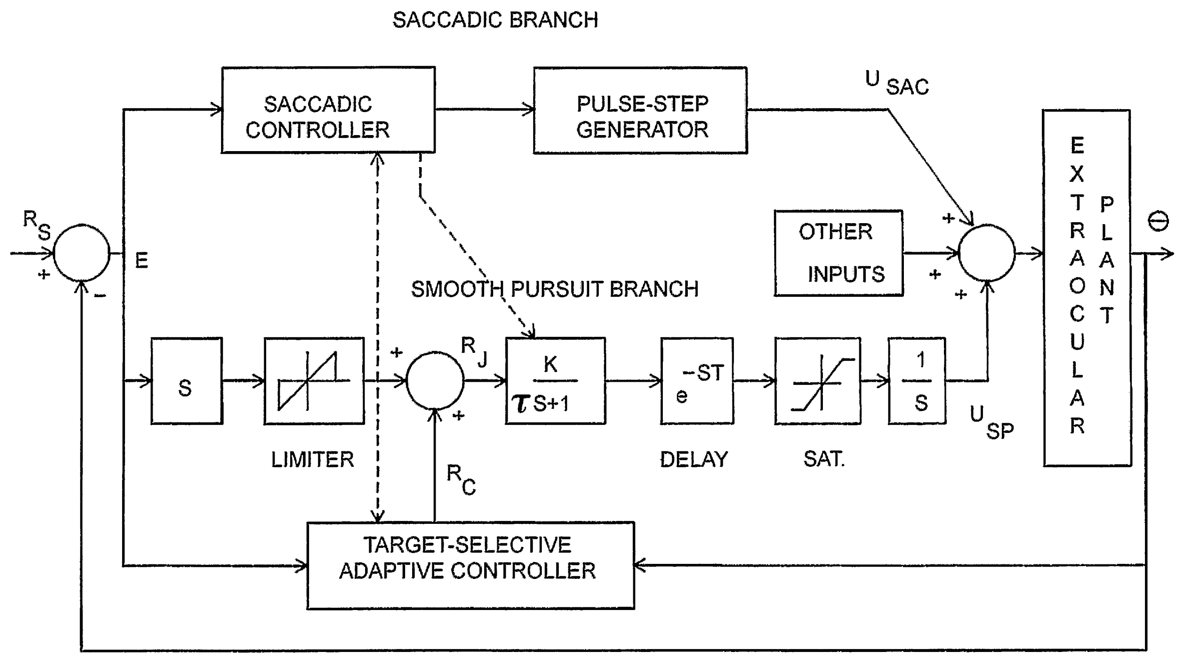

FIGURE 14 The detailed form of McDonald's [27] Target-Selective Adaptive Control Model [19].

input to the smooth pursuit branch is retinal error, which is converted to velocity by the differentiator. The limiter prevents any velocities greater than 70 degrees per second from going through this branch. (The numbers given in this section are only typical values, the standard deviations are large, *e.g.*, LaRitz [48] showed smooth pursuit velocities of 130 deg/sec for a baseball player.) The leaky integrator $K/(\tau s + 1)$ is suggested from experimental results showing that humans can track ramps with zero steady-state error [31], and open-loop experiments that showed a slope of -20 decibels per decade for the pursuit branch's frequency response [4]. The gain, K, for the pursuit branch must be greater than unity, since the closed-loop gain is almost unity. Currently used values for the gain are between two and four [4, 46]. The e^{-sT} term represents the time delay, or latency, between the start of the target movement and the beginning of pursuit movement by the subject. A time delay of 150 msec is currently accepted [4, 30]. The saturation element prevents the output of any velocities greater than 60 degrees per second; the maximum velocity produced by most human smooth pursuit systems. Considering the literature and her own extensive open-loop experiments, Harvey [4] derived the following values: $K = 2.0$, $T = 150$ ms and $\tau = 130$ ms, which produces the TSAC model of Figure 14.

Governing Equations for the Adaptive Compensation Signal

The model must be able to overcome the 150 ms time delay and track with zero latency. Because the smooth-pursuit system is a closed-loop system, the model's time delay appears in the numerator and the denominator of the closed-loop transfer function,

$$\frac{\dot{\theta}_E}{\dot{\theta}_T} = \frac{Ke^{-sT}}{\tau s + 1 + Ke^{-sT}} \tag{1}$$

The predicted target velocity from the adaptive predictor compensates for the effects of the time delay in the numerator of the transfer function of Eq. (1). To overcome the effects of the time delay in the denominator, compensation for the model's dynamics must be done. This means that the brain must have a model for itself and the rest of the physiological system, and that it uses this model to generate the required compensation signal.

When linear state-variable feedback notation is used for a system, its closed-loop transfer function is

$$\frac{Y(s)}{R_i(s)} = \frac{\mathbf{h}'(s\mathbf{I} - \mathbf{A})^{-1}\mathbf{b}Ke^{-sT}}{1 + \mathbf{k}'(s\mathbf{I} - \mathbf{A})^{-1}\mathbf{b}Ke^{-sT}} \tag{2}$$

where

$Y(s)$ = system output, θ in Figure 14
$R_i(s)$ = system input, R_S in Figure 14
T = time delay
$\mathbf{A}$ = system matrix
$\mathbf{b}$ = input coefficient vector
$'$ = vector transpose operation
$\mathbf{k}'$ = transposed control vector
$\mathbf{h}'$ = transposed output coefficient vector
K = the gain.

Boldface is used for vectors and matrices. Capital letters are used for Laplace transforms, *i.e.*, functions of frequency, *e.g.*, $R_i(s)$, and, in a little bit, lower case letters will be used for functions of time, *e.g.*, $r_i(t)$. The general method of compensating for model dynamics involves computing an adaptive signal R_A, which, when added to the target position R_S, produces a system input R_J that will facilitate zero-latency tracking. This method was developed by McDonald [27]. We will now briefly show how we used it.

For the human eye movement system the order of the system, the control vector and the output vector are one, so that the following values are appropriate.

$$A = -\frac{1}{\tau}$$
$$b = \frac{1}{\tau}$$
$$h = 1$$
$$k = 1.$$

The system's input, $r_j(t)$, is the sum of the target reference signal, $r_s(t)$, and the adaptive signal, $r_a(t)$ that must be computed. To obtain zero latency tracking $y(t)$ must equal $r_s(t)$. Putting all of this information into Eq. (2) gives

$$r_s = \frac{(s+1/\tau)^{-1}(1/\tau)K\mathrm{e}^{-sT}}{1+(s+1/\tau)^{-1}(1/\tau)K\mathrm{e}^{-sT}}(r_s + r_a)$$

Solving for r_a gives

$$r_a = \frac{\mathrm{e}^{+sT}}{K}(\tau s + 1)r_s \tag{3}$$

The e^{+sT} term shows that predictions must be made. However, the smooth-pursuit system is a velocity tracking system, not a position tracking system, so the controller must be able to predict future values of target velocity. For example, if $\dot{r}_s(t)$ is the present target velocity, it must be able to produce $\dot{r}_s(t+T)$, where T is the time delay of the smooth-pursuit system. And the controller must modify this prediction to compensate for the dynamics of the system in accordance with Eq. (3). Therefore, the compensation signal, R_C of Figure 14 becomes

$$r_c(t) = \frac{1}{K}\left[\frac{d}{dt}\tau\dot{r}_s(t+T) + \dot{r}_s(t+T)\right] \tag{4}$$

In the general case, we called this the adaptive signal, R_A. Now that we are discussing a particular instantiation, the smooth-pursuit velocity tracking system, we call this signal a compensation signal, R_C. This compensation signal allows the smooth-pursuit system to overcome the time delay. To synthesize this signal the adaptive controller must be able to both predict future values of the target velocity, and compute first derivatives. These are reasonable computations for the human brain. Therefore, Eq. (4) is the algorithm that is in the box of Figure 14 labeled Target Selective Adaptive Controller.

Variability of Human Smooth-pursuit

Open-loop Experiments

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 indication of the success of the investigation. Such agreement has been found in experiments where subjects tracked sinusoidal waveforms [43, 44]. Although idiosyncratic differences existed among 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 [25]. And in other studies [4, 11], individualistic behavior was varied enough to obviate any meaningful description of the system using such data.

Several factors could contribute to the differences between individual subjects and between different experiments. One such factor is the predictability of the target waveform used in testing. Predictable sinusoidal waveforms sometimes produced consistent results [44] whereas a pseudorandom mixture of sinusoids produced great variability between subjects [11]. However, sinusoids were also used by Harvey [4] with inconsistent results between subjects. Another factor may be the influence of prior experience on subject performance. Examining the results from several studies [4, 11, 44] reveals that open-loop gains are 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 varied 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 Harvey [4], and by Leigh *et al.* [24] in a subject in which open-loop behavior was observed by presenting a visual target to the patient's paralyzed eye while monitoring the motion of the normal, but covered eye. Each subject's performance also depends on the instructions given to the subject [30]. These findings show that the variability inherent in open-loop studies is attributable not only to differences between subjects but also to time-varying performance of individual subjects.

Comparing Human and Model Open-loop Tracking

To gain insight into the behavior of the smooth-pursuit system under open-loop conditions Harvey compared experimental human results with those from simulations [4]. At the beginning of an open-loop experiment, a 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 Figure 13, and the experiment could be continued. It was hard to get consistent open-loop tracking with sinusoids. 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 involvement of high-level processes such as adaptation. 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 13 shows a presumed 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 [14, 24, 25, 30, 43, 44]. The records are strikingly devoid of saccades in spite of the large position errors, a finding that, oddly, received little comment by previous investigators (except for [30]) although it is often seen in their data.

To help explain this human tracking, the model is shown tracking a sinusoid under open-loop conditions in Figure 15. To simulate the changes in strategy that are apparent in the human data of Figure 13, the

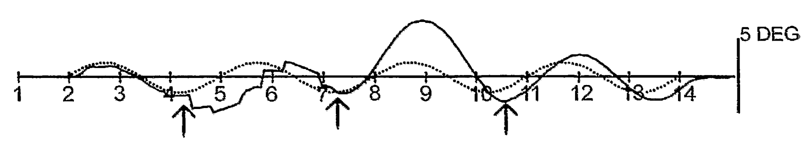

FIGURE 15 Position of the target (dotted) and model (solid) as functions of time under a variety of conditions. At the first arrow, the loop was opened, at the second arrow the saccadic system was turned off, at the third arrow the adaptive controller was turned off. Tracking patterns similar to each of these are common in human records [4].

model characteristics were changed at intervals. From 2 to 4.25 seconds there is normal closed-loop tracking. At 4.25 seconds 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 Figure 13. At 7.25 seconds 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 Figure 13. This type of position offset was often noticed in human subjects during open-loop tracking. Finally, at 10.5 seconds 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.

The technique of opening the loop on a physiological system in order to better understand its behavior is very powerful, 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.

INVESTIGATE ALTERNATIVE MODELS

We used many techniques for predicting target velocity including the following predictors: (1) Difference Equations, *e.g.*, $r(n+1) = A\, r(n) + B\, r(n-1)$ *etc.*, (2) Menu Selection, (3) a Recursive Least Square Filter in conjunction with Menu Selection, (4) Recursive Least Square (RLS) Filters, (5) Kalman Filters, (6) Adaptive Lattice Filters, and (7) Least Mean Square (LMS) Adaptive Filters. All seven techniques produced tracking at least as good as the human.

Difference equations were the simplest and least accurate. In the Menu Selection technique, the system has a limited menu of waveforms to choose from. In our models, we allowed sinusoidal, parabolic, cubic and pseudorandom waveforms. The model tracked the target and tried to identify the target waveform as one of these. It then used an equation for that waveform to help predict target motion. The system also had to identify the frequency and amplitude of the waveform. The third technique used a Recursive Least Square Filter to identify the waveform and then used equations off the menu to track the target. The other four techniques are typical filters described in digital signal processing literature.

When we first searched for literature on prediction we found very little. Then we realized that any digital filter could also be used for prediction. In fact, if you can either model a system, or identify a system, or filter a signal, or predict a signal, then you can do the other three operations with no additional effort. All of these predictors allowed zero-latency tracking, just like the human. But, as will be discussed later, some matched other aspects of human behavior better than others did.

The principle of Ockham's Razor [20] states that if two models are equal in all respects except complexity, then the simpler model is the better one (see also http://pespmc1.vub.ac.be/OccamRaz.html). This is one reason why we like the menu selection predictors. They are simpler than the digital filters, which require complex matrix manipulations. Such calculations are fine for serial processing digital computers, but are not likely to be used by parallel processing analog computers such as the brain.

VALIDATE THE MODEL

Validation means proving that the system does what it is supposed to do. For an eye-movement model, this means the model must track targets just like the human.

Show that the Model Behaves Like the Physical System

The model tracks targets just as humans do. The bottom trace of Figure 16 shows the model tracking with smooth pursuit, saccades and

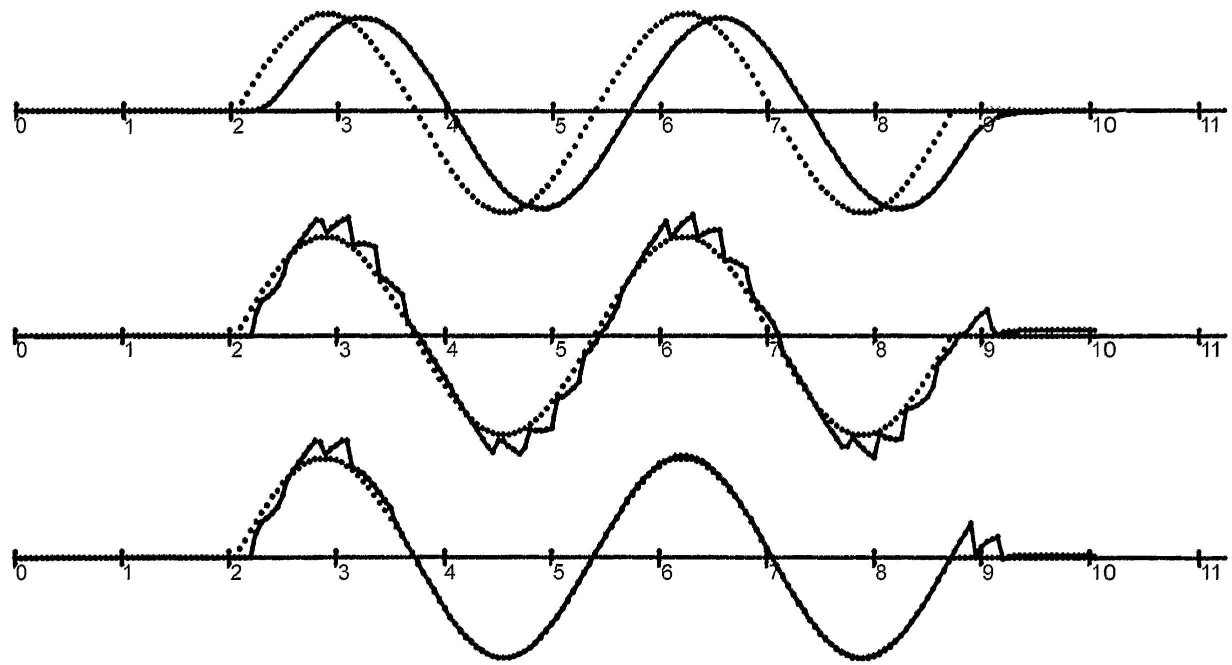

FIGURE 16 Position as a function of time for the TSAC model tracking a target with only the smooth-pursuit branch (top), smooth-pursuit and saccadic branches (middle) and all three branches turned on (bottom). Only the bottom trace resembles tracking of a normal human. Target movement was ± 5 degrees: time is in seconds [7].

the adaptive predictor. This tracking behavior is very similar to the human tracking shown in Figures 1 and 3.

In addition to replicating normal human tracking, we can run the model in abnormal situations. The top trace of Figure 16 shows the model tracking with only the smooth-pursuit branch turned on, that is the saccadic branch and the adaptive predictor were turned off. This tracking looks like the human tracking at the end of Figure 13.

The middle trace of Figure 16 shows the model tracking with smooth pursuit and saccades only, *i.e.*, the adaptive predictor was turned off. If there were a patient with a lesion in a part of the brain that produced or conducted signals from the adaptive predictor, then that patient's eye tracking would look like the middle trace. If one were to try to find such cells or pathways in a monkey's brain, cubical target waveforms should be used, so that there would be a clear distinction between position, velocity and predictor signals.

Use the Model to Simulate Something not Used in its Design

A powerful technique for validating a model is to use it to simulate something that was unknown when the model was developed. Figure 17 shows some human tracking was that was noted to be unusual when the data were collected. The target velocity had a sinusoidal waveform, but the eye velocity waveform did not. This behavior had not been seen before and no explanation was apparent. But then we ran the menu selection model forcing it to choose the wrong waveform. Figure 18 shows the model tracking a sinusoidal waveform using a wrong guess of the parabolic waveform. These waveforms look very much like the human tracking of Figure 17. This is evidence that the human might use menu selection predictors.

Perform a Sensitivity Analysis

In a sensitivity analysis each parameter of the model is varied by a small amount and the model is studied to see what effects that variation had. The results of a sensitivity analysis can be used to (1) validate a model, (2) warn of strange or unrealistic model behavior, (3) suggest new experiments or guide future data collection efforts, (4) point out

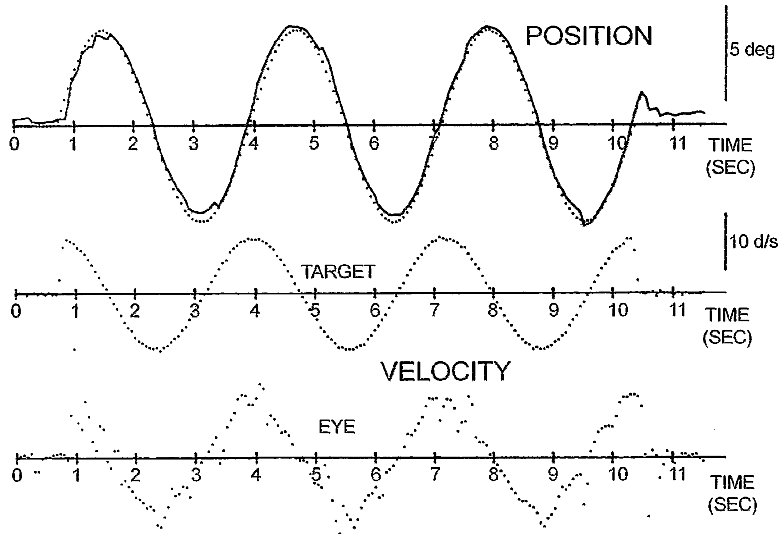

FIGURE 17 Human tracking of a sinusoidal target waveform. The top trace shows target position (dotted) and eye position (solid), the middle trace shows target velocity and the bottom trace shows eye velocity. The eye velocity waveform does not match the target velocity waveform [7].

important assumptions of the model, (5) suggest the accuracy to which the parameters must be calculated, (6) guide the formulation of the structure of the model, (7) adjust numerical values for the parameters, and (8) allocate resources. The sensitivity analysis tells which parameters are the most important and most likely to affect predictions of the model. Following a sensitivity analysis, values of critical parameters can be refined while parameters that have little effect can be simplified or ignored. If the sensitivity coefficients are calculated as functions of time, it can be seen when each parameter has the greatest effect on the output function of interest. This can be used to adjust numerical values for the parameters. The values of the parameters should be chosen to match the physical data at the times when they have the most effect on the output.

Space limitations prevent presentation of sensitivity studies of this model. Sensitivity of the model with respect to the gain K is discussed by McDonald [7]. Sensitivity of the model to parameters in the adaptive predictor is discussed by Harvey [19]. A sensitivity analysis of the extraocular motor system of Figure 13 was performed by

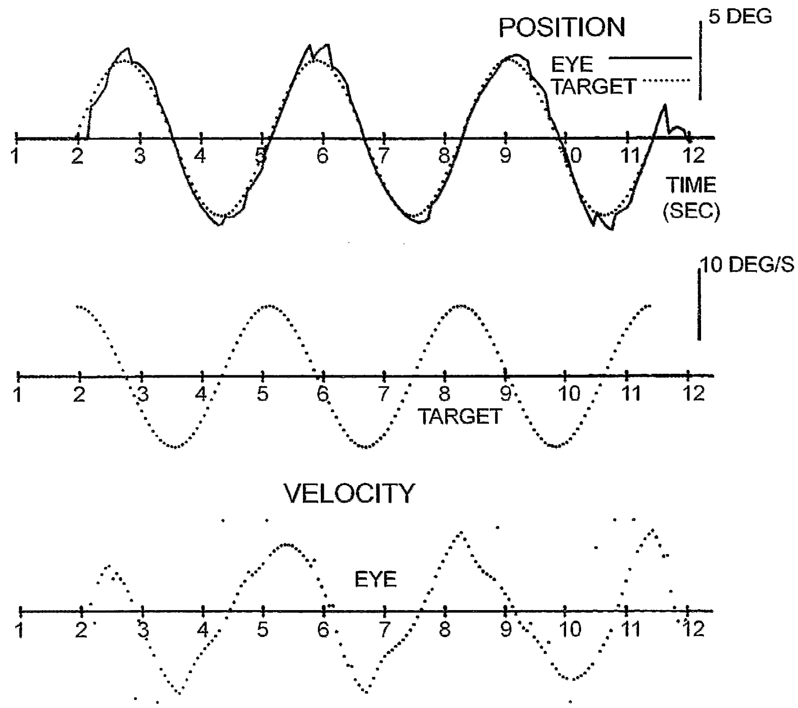

FIGURE 18 TSAC model with menu selection predictor tracking a sinusoidal target with an incorrect (parabolic) adaptive signal. The top trace shows target position (dotted) and model eye position (solid), the middle trace shows target velocity and the bottom trace shows model eye velocity [7].

Latimer [6]. And a general discussion of sensitivity analysis is given by Karnavas [22].

INTEGRATE WITH OTHER EYE-MOVEMENT SYSTEMS

The eye-movement systems are affected differently by fatigue, drugs and disease. With regards to ethyl alcohol consumption, the adaptive predictor of the smooth-pursuit system is affected first. Then with higher blood concentrations of alcohol, the basic smooth-pursuit system degrades. With even higher concentrations, saccades become slow and fragmented. With yet higher concentrations, the vergence system deteriorates and subjects get diplopia, double vision. Finally with very high concentrations, the vestibulo-ocular system degrades; the subjects get vertigo and think the room is swirling around them.

ASSESS PERFORMANCE AND RE-EVALUATE

The smooth-pursuit eye-movement system models shown in this paper were developed over a decade with a dozen major contributors. Performance of the models was continuously evaluated and the models were continually upgraded. In addition, the results of the modeling were used to suggest experiments that were then performed on the human smooth-pursuit eye-movement system.

CONCLUSION

What does this modeling teach us about the physiological system? We know that humans can overcome the 150 ms time delay of the smooth-pursuit eye-movement system, and track smoothly moving targets with no time-delay. To do the same, the model had to be able to predict target velocity and compensate for system dynamics. Therefore, we think that humans have the ability to predict target velocity, and they have internal models of their own physiological systems. These internal models must be adaptive, because they must be updated when the system is changed by exercise, fatigue, drugs or temperature variations.

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