Vision Res. Vol. 23, No. 12, pp. 1573–1583, 1983
Printed in Great Britain.
0042-6989/83 $3.00 + 0.00

SMOOTH PURSUIT EYE MOVEMENTS IN RESPONSE TO PREDICTABLE TARGET MOTIONS

A. TERRY BAHILL* and JACK D. MCDONALD†

Biomedical Engineering Program, Department of Electrical Engineering, Carnegie-Mellon University, Pittsburgh, PA 15213, U.S.A.

(*Received* 4 *October* 1982; *in revised form* 4 *April* 1983)

Abstract—The human smooth pursuit eye movement system has a latency of about 150 msec. However, this study shows that humans can learn to perform zero-latency tracking of targets that move with continuous velocity and amplitude-limited acceleration. Superposition of eye velocity and target velocity records, for our unique target waveforms, demonstrated that the subject was using the correct waveform and not just approximating it with a sinusoid or some other simple waveform. Calculation of the mean square error between target and eye position gave a quantitative measure of how well the human can track. The mean square error between target and eye position was 0.32 deg^2 for one thousand seconds of steady-state tracking by seven subjects. For several cycles at a time all subjects were able to reduce this error to less than 0.1 deg^2.

Human Smooth pursuit Eye movements Prediction Error Correlation Latency Learning

INTRODUCTION

Experiments with transient target waveforms reveal a 150 msec time delay in the human smooth pursuit eye movement system (Rashbass, 1961). The effects of this time delay are apparent during starting and stopping transients, as shown in Fig. 1, and during tracking of unpredictable targets, as shown in Fig. 2. However, when a human (or a monkey) tracks a target that is moving sinusoidally, the subject quickly locks on to 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 (Westheimer, 1954; Stark *et al.*, 1962), a long term learning process (Dallos and Jones, 1963), a percept tracker (Yasui and Young, 1975; Young, 1977; Steinbach, 1976; Mack *et al.*, 1982), a neural motor pattern generator (Eckmiller, 1981), and a target-selective adaptive controller (Bahill and McDonald, 1981). We conducted a series of experi-

*Also with the Neurology Department, University of Pittsburgh Medical School.
†Present address: The Mitre Corporation, Boston, MA 01730, U.S.A.

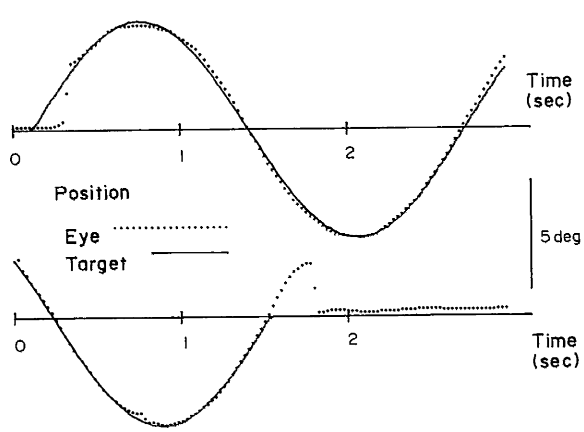

Fig. 1. Typical beginning (top) and ending (bottom) of sinusoidal tracking. The eye position (dotted line) is superimposed on the target position (solid line). When the target started, there was a 150 msec delay before the eye velocity increased; when the target stopped, there was a 120 msec delay before the eye velocity began to decrease. The position mean squared errors (pmse) were 0.12 and 0.36 deg^2 respectively, for the top and bottom records. Target movements were ±5 deg from primary position. For all of our figures, the time axis is labeled in seconds, and upward deflections represent rightward movements.

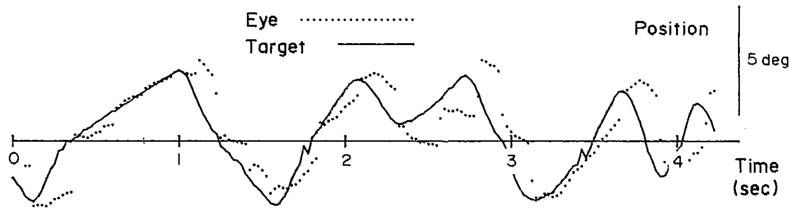

Fig. 2. Effects of the time delay were apparent when the subject tracked a nonpredictable target waveform. The display format is the same as in Fig. 1. This target waveform is the pseudorandom binary sequence based waveform of Bahill *et al.* (1980) low-pass filtered at 1.5 Hz. This figure is from unpublished data of Jon Lieberman. The pmse was 1.59 deg^2. Subject: J.L.

ments to find the characteristics of the target waveform that are necessary to allow such zero-latency tracking.

The target motion predominantly used to test the smooth pursuit system is predictable sinusoidal motion (Robinson, 1964; Fuchs, 1967; Winterson and Steinman, 1978; Greene and Ward, 1979). Although a sinusoid is easy to track, it may not be 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, or position cells with a time delay, or control signals. Linear ramps have been used as smooth pursuit target waveforms (Jurgens and Becker, 1975; Baloh *et al.*, 1976; Schalen, 1980). Often these ramps were repetitive with the same constant velocity (triangular waveforms). This is 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 Miller *et al.* (1980) 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 (Williams and Fender, 1979). 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.

This report summarizes our 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. To measure the quality of tracking we used the mean square error between the target and the eye, and we also studied the similarity of the eye velocity and target velocity waveforms.

METHODS

Eye movement measurements

The movements of each eye were measured with a standard photo-electric system (Bahill, 1981) that had light emitting diodes (National Semiconductor Xciton XC88PA) and photo-transistors (Fairchild FPT-120) mounted on spectacle frames worn by the subject. The LEDs were connected in series and they were supplied with 25 mA. Target and eye movements were amplified (0–100 Hz bandwidth), passed through a 12 bit analog to digital converter sampling at one msec intervals, digitally low-pass filtered at 80 Hz, and then stored on a disk in the computer. The linear range for measuring horizontal eye movements extended ± 10 deg from primary position. Linearity was assessed while the subject tracked a target moving sinusoidally. Calibration factors were derived from data collected while the subject tracked a target that jumped between points ± 5 deg from primary position. Calibration factors for each eye were computed by averaging 1–2 sec of data from 4 to 10 manually selected periods when the eye was stationary and looking at the target. Instrumentation noise was less than 10 mV, corresponding to eye movements of less than 1 min of arc. Saccades as small as 10 min of arc have been analyzed from the data of this report.

We also have a horizontal and vertical eye movement monitor that is linear for 15 deg (Bach *et al.*, 1983). We call it the DDA Oculometer after the engineer who designed it. This instrument produced the data of Fig. 2. Data for the other figures were collected with the standard photo-electric system.

It took 1–10 min to adjust the equipment and ensure linear recordings. After this the subject rested for a few minutes and then tracked the target for 3 min. A 3 min rest period was allowed; and then the 3 min test was repeated. A calibration routine was incorporated into the beginning and ending of each 3 min test.

The target

The target was a small (3 mm dia.) red laser dot projected on a white, curved screen 57.3 cm in front of the subject. The target voltage drove a galvanometer

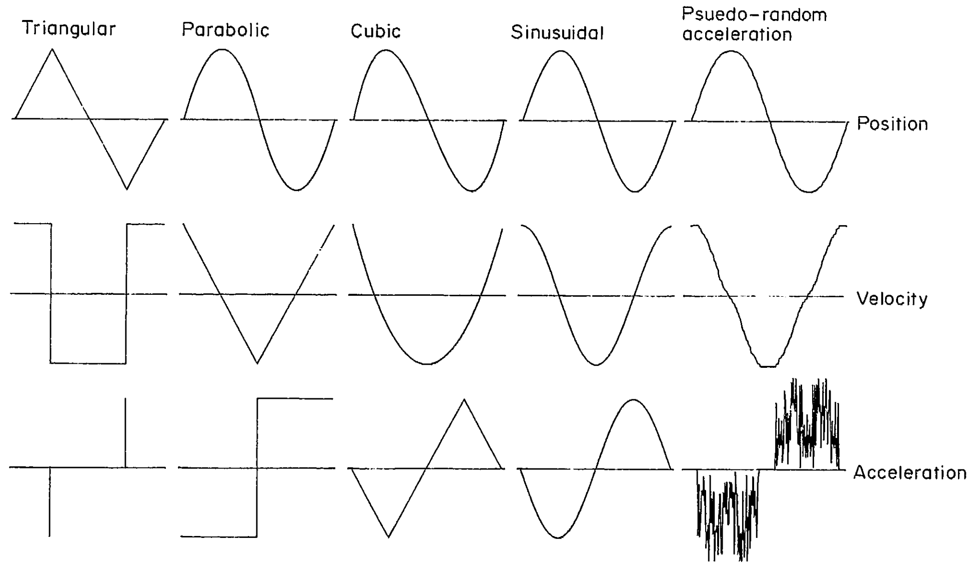

Fig. 3. The predictable target waveforms.

that had a small mirror attached. The movement of the mirror deflected the laser beam to produce a horizontally moving dot on the screen. The bandwidths for the galvanometer and the d.c. amplifier exceeded 200 Hz. Subjects viewed the target binocularly in a dimly illuminated room (vision was photopic). The target was kept at a fixed distance to eliminate vergence eye movements. The subjects' heads were restrained with a head rest and bite bar to eliminate effects of the vestibulo-ocular system.

An LSI-11/2 microcomputer generated the following predictable target waveforms: triangular, parabolic, sinusoidal, cubic, and pseudo-random acceleration. Figure 3 shows position (top), velocity (middle), and acceleration (bottom) as functions of time for these waveforms. Each of these waveforms will be discussed later when human tracking is shown.

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 deg. 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 3 min 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.

Digital computation of velocity

We used a two-point central difference algorithm to compute velocities (Bahill *et al.*, 1982; Bahill and McDonald, 1983). Our analysis program allowed the operator to interactively choose the step-size: the most common choices were 25 and 50 msec. These choices yielded bandwidths of 8.9 and 4.4 Hz respectively. We used the 8.9 Hz bandwidth to plot the figures of this report. This 8.9 Hz algorithm produced clean smooth pursuit velocity records. It deliberately distorted the velocity and duration of the fast saccadic eye movements.

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 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 (Davson, 1976; Eckmiller, 1981). 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 average pmse for monkeys tracking sinusoidal targets with frequencies between 0.1 and 1.0 Hz was 1.4 deg^2 (Lanman *et al.*, 1978). The behavior of monkeys is similar to humans in most other oculomotor tasks, so the human mean square errors should be similar in magnitude. The velocity mean square error (vmse) is also of interest, because the smooth pursuit system is a velocity tracking system. The velocity mean square error indicates the fidelity of smooth pursuit tracking and reflects the reduction of saccades during good performance. With their "pure velocity target", Williams and Fender (1979) found that on the average the human is about 20% faster or slower than the target. For their slow target velocities, this represented an approximate vmse of 0.2 (deg/sec)^2. For higher frequencies, the vmse would be larger. Therefore, we expected humans to track our predictable target waveforms with a position mse between 0.1 and 1.4 deg^2 and a velocity mse between 0.2 and 20 (deg/sec)^2.

Human subjects

The subjects were volunteers from Carnegie-Mellon University and the Pittsburgh Baseball Club. Informed consent was obtained after the investigator explained the purpose of each test and the functioning of the laboratory equipment. We studied more than 20 subjects during two years of experimentation. The results from eight of these subjects are included in this paper. Six subjects had normal near vision: two subjects usually wore spectacles; they had acuities of 20/400 and 20/100. The subjects were healthy and between 21- and 37-yr old.

RESULTS

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 deg ($\pm$5 deg from primary position).

Figure 1 (top) shows tracking of the beginning of sinusoidal movement. Smooth pursuit began 150 msec after the target started to move. It was followed by a corrective saccade at 200 msec and then by zero-latency, unity-gain tracking. Figure 1 also shows a termination of sinusoidal smooth pursuit tracking. The smooth pursuit velocity started declining 120 msec after the target velocity dropped. It reached zero velocity at 220 msec, 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. Steady-state smooth pursuit tracking is shown in Fig. 4. 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 Fig. 1 our subjects overcame the 150 m sec 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 5 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 target until after a full half cycle of the target 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. Variation of the phase angle at target cessation sometimes caused the eye to continue moving for as much as 500 msec after the target stopped. The initial offset or phase did not change steady-state tracking.

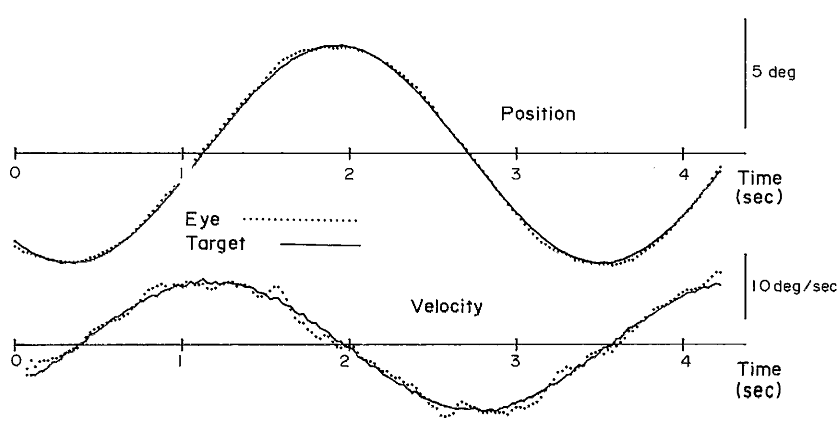

Fig. 4. Zero-latency steady-state tracking of a sinusoidal target waveform. The top trace shows target (solid) and eye (dotted) position, and the bottom trace shows target (solid) and eye (dotted) velocity. The pmse was 0.02 deg^2 and the vmse was 0.7 deg^2/sec^2. Subject: J.K.

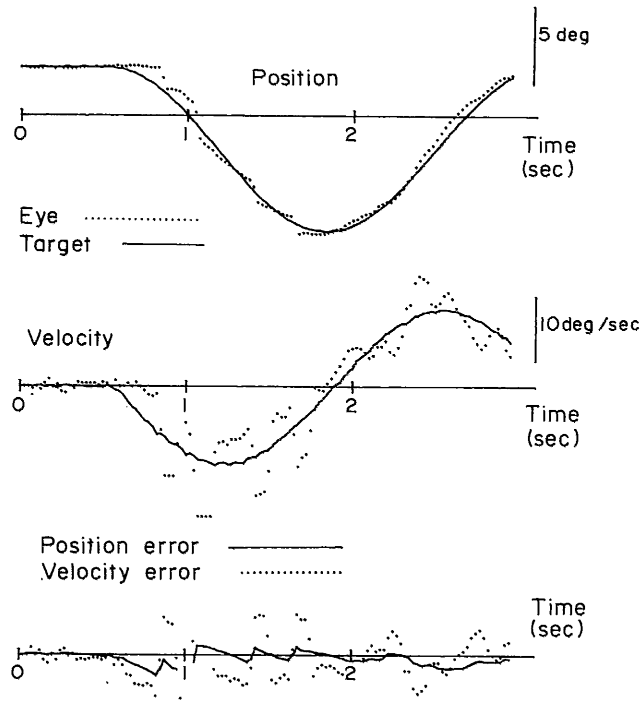

Fig. 5. Start-up transient for a sinusoid with unexpected initial phase and offset. The top two records are position and velocity as in Fig. 4. The bottom record shows position error (solid) and velocity error (dotted). The errors are large, particularly during the first half cycle. The pmse was 0.19 deg^2 and vmse was 16.7 deg^2/sec^2. Subject: J.K.

The parabolic target waveform

Because sinusoidal oscillation 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

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

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

The terms A and T are amplitude and period, respectively. The amplitude was fixed at 5 deg, but the period was varied from run to run.

Figure 6 shows excellent tracking of this parabolic target. The pmse for these data was 0.05 deg^2. Close comparison of the velocity records indicates that this subject tracked 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 Fig. 7. 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 between the disappearance of the target and the deviation of the smooth pursuit velocity from the previous target trajectory was 150 msec. The smooth pursuit velocity reached zero 420 msec after the disappearance of the target. Deflecting the laser behind the barrier meant that there was no error between the visual image and the output of the 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

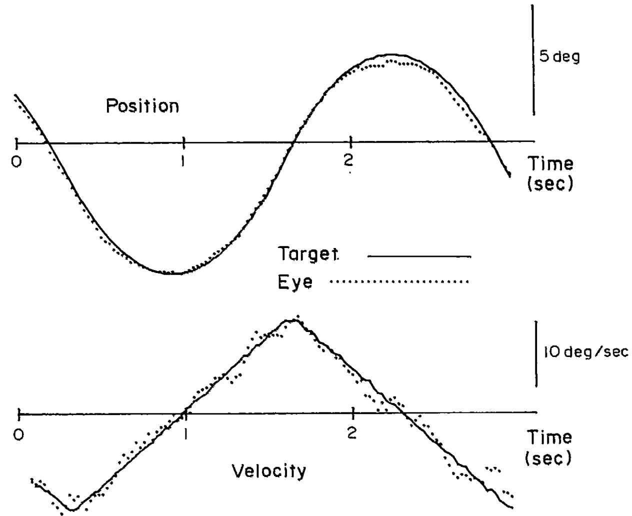

Fig. 6. Steady-state tracking of a parabolic target waveform. The clustering of the eye velocity dots about the target velocity line shows that the subject was using the correct waveform. Same display format as Fig. 4. The pmse was 0.05 deg^2 and vmse was 1.8 deg^2/sec^2. Subject: J.K.

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. Whittaker and Eaholtz (1982) trained humans, and Eckmiller and Mackeben (1980) trained monkeys to continue smooth pursuit tracking of a 1 Hz sinusoidal target for more than a second. So, in summary, when the target disappears smooth pursuit stops, but not as

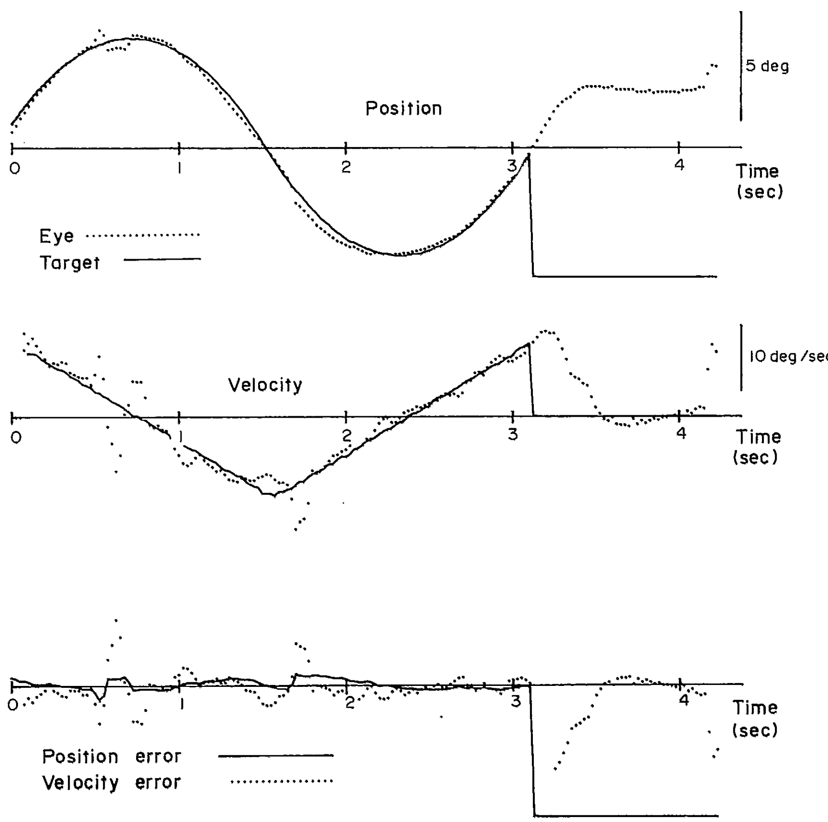

Fig. 7. End of tracking transient for a parabolic waveform. At 3.1 sec the target disappeared. The eye velocity then took 420 msec to decay to zero. Subject: J.K.

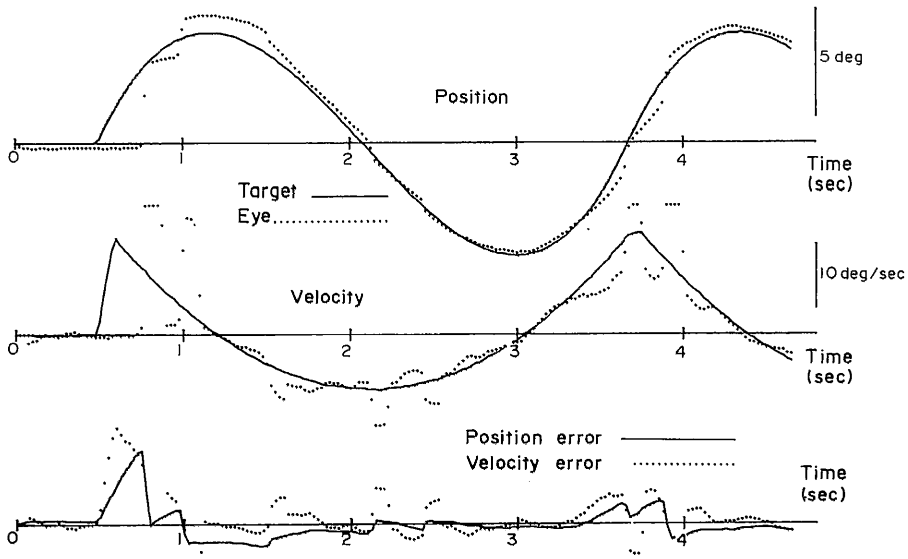

Fig. 8. The first cycle of cubic tracking for an inexperienced subject. Eye velocity between 1.5 and 2.5 sec is the same as between 3 and 4 sec, indicating that the subject has not yet learned that the target velocity is asymetrical. The pmse was 0.52 deg² and vmse was 37.6 deg²/sec². Subject: G.B.

fast as when a visible target stops. However, we could not predict the behavior of any subject on any given run because this behavior depended upon uncontrolled conditions.

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 satisfied the requirements $r(0) = 0$, $r(T/2) = 0$, and $r(T) = 0$, is

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

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

Figure 8 displays the results of the first encounter of a naive subject with the cubic waveform. Performance improved with practice. After observing the cubic waveform for several minutes, spread over a few days, most subjects had learned the waveform sufficiently to track with great fidelity as shown in Fig. 9.

We recorded the eye movements of two members of the Pittsburgh Baseball Club to see if experienced athletes were more adept at tracking targets. The data shown in Fig. 10 were recorded while a member of the Pittsburgh Baseball Club tracked the cubic target after having seen this waveform for only 13 sec previously. This baseball player learned the cubic waveform much faster than our graduate students; it took our best graduate students several minutes before they could track with such small error.

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 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 Fig. 3 shows this waveform.

A subject's first encounter with this target waveform produced corrective saccades every 200 msec, which is typical of poor tracking. The subject's velocities were widely dispersed from the target velocity. This waveform was the most difficult to learn. It took our subjects several minutes, spread out over several sessions, to learn this waveform. Our best subject learned this waveform in a little over 2 min. The data

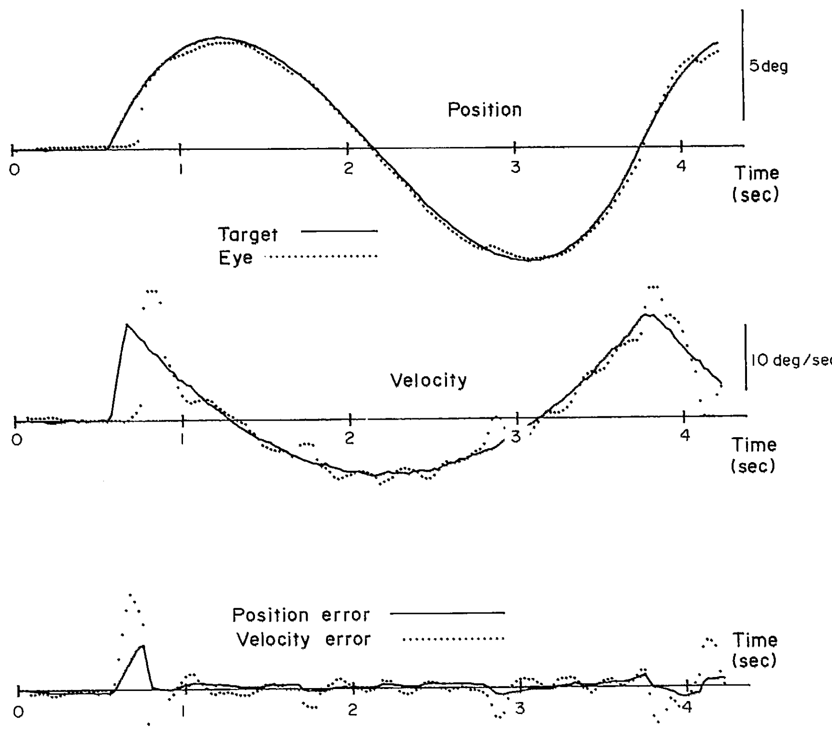

Fig. 9. Start-up transient and subsequent zero-latency tracking of a cubic target waveform. The eye velocity dots cluster around the target velocity line indicating that the subject has learned the waveform. The pmse was 0.13 deg^2 and the vmse was 15.4 deg^2/sec^2. Subject: J.K.

of Fig. 11 show excellent tracking of this pseudo-random acceleration target waveform after the subject had observed this waveform for 135 sec in a 20 min 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.

Naive subjects

To linearize our recording system, the photodiodes and amplifiers were adjusted while the subjects tracked targets moving sinusoidally. Consequently, none of our subjects had been recorded during their first cycle of sinusoidal tracking. Therefore, for one subject with no

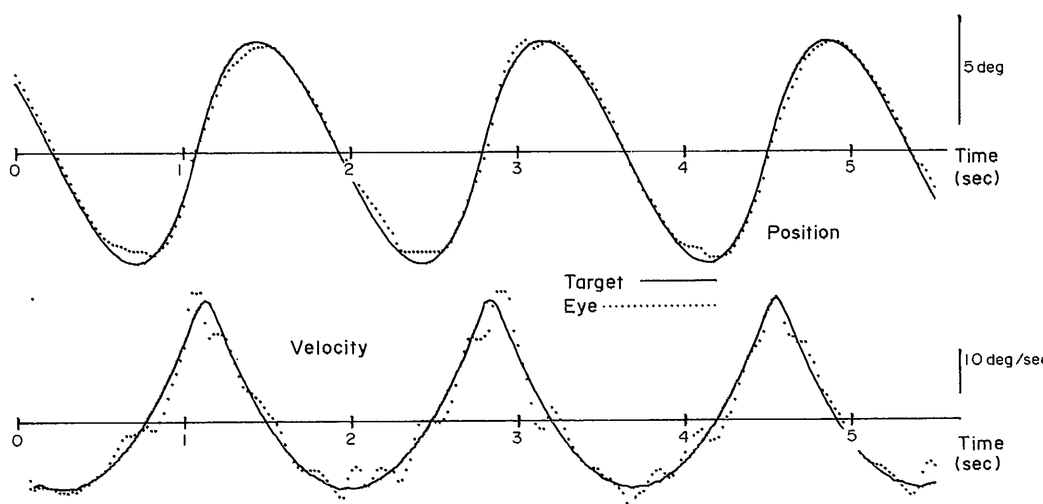

Fig. 10. Zero-latency tracking of a cubic target waveform by a baseball player after only 13 sec of exposure to such a waveform. The position errors on extreme left gaze (the bottom) are artifacts due to a soft saturation of the instrumentation system. The pmse was 0.11 deg^2 and the vmse was 8.6 deg^2/sec^2. Subject: J.O.

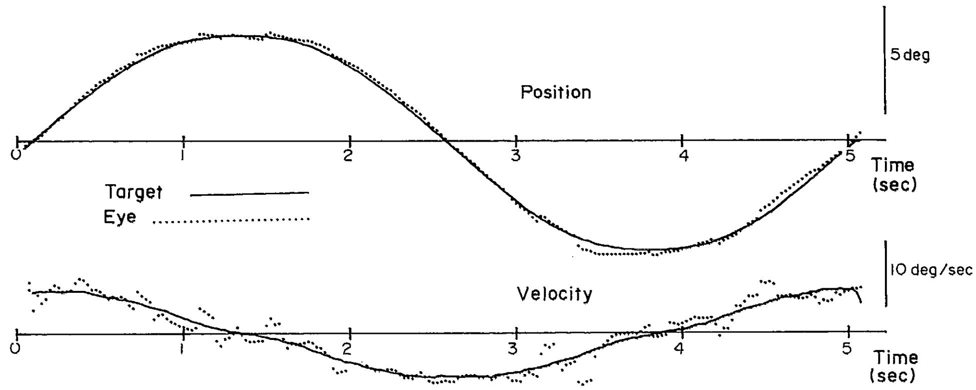

Fig. 11. Zero-latency tracking of a pseudo-random acceleration target waveform. The target velocity line is slightly flattened at the zero velocity and at maximum velocity. The eye velocity dots also reflect this flattening. The pmse was 0.04 deg^2 and vmse was 1.8 deg^2/sec^2. Subject: J.L.

prior experience in eye movement experiments, the equipment was carefully calibrated using only square wave target waveforms and linear ramps. The first encounter of this subject with the sinusoidally moving target produced the records shown in Fig. 12. After one-fourth of a cycle the subject's velocity had already begun to take on a sinusoidal form and the zero crossings indicated zero-latency. This naive subject also learned the parabolic target quickly. After tracking 7 cycles of the parabolic target waveform, his pmse was 0.07 deg^2 and his vmse was 3.6 deg^2/sec^2.

Database averages

The figures in this paper show some of the best tracking that we have observed for each particular waveform. 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 many saccades and occasional periods of off-foveal tracking, see for example Fig. 4 of Bahill and McDonald (1983). It is unusual to have more than a cycle without at least a microsaccade. To provide a metric indicating typical performance, we have summarized the data from seven subjects tracking targets moving with frequencies between 0.2 and 0.6 Hz. For 1506 sec of data covering 46 experiments, including the start of tracking and end of tracking transients, the average pmse was 0.43 deg^2 with a standard deviation of 0.27 deg^2, and the average vmse was 16.8 deg^2/sec^2 with a standard deviation of 15.8 deg^2/sec^2. For the 1059 sec of steady-state tracking, without

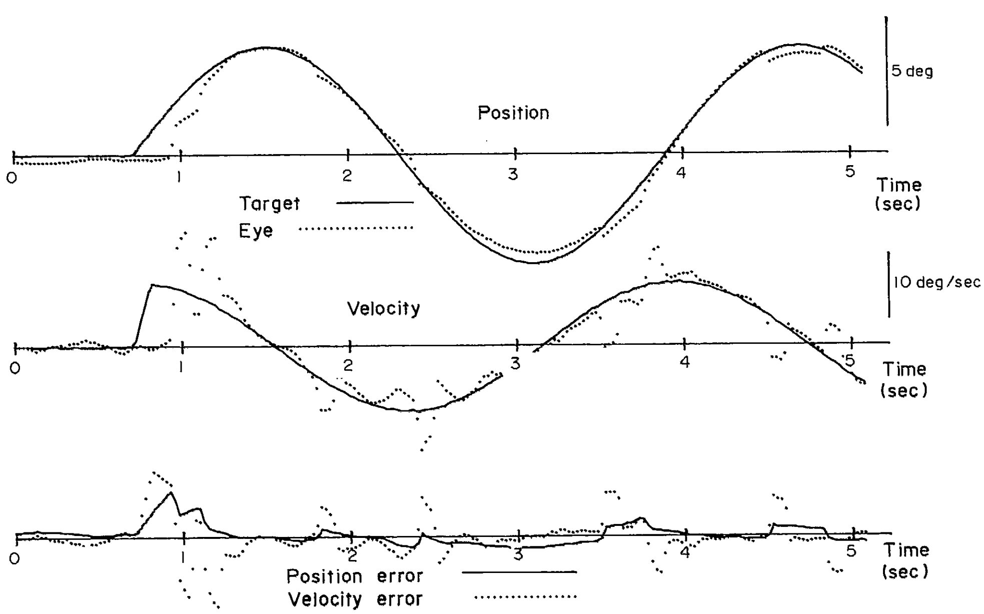

Fig. 12. The first cycle of sinusoidal tracking for a naive subject. The velocity waveform seems appropriate although there are many position correcting saccades. The pmse was 0.23 deg^2 and vmse was 9.5 deg^2/sec^2. Subject: D.A.

starting and stopping transients, the average pmse was 0.32 deg^2 with standard deviation 0.28 deg^2, and the average vmse was 5.8 deg^2/sec^2 with standard deviation 5.7 deg^2/sec^2. Over the long term, humans track in a manner similar to that of Figs 8 and 12. In the short term (much as a sprinter can perform optimally for short periods of time) a human can track accurately as shown in Figs 4, 6, 9, 10 and 11.

DISCUSSION

This demonstration of zero-latency tracking of predictable target waveforms by the human smooth pursuit system is unique. It cannot be derived from published literature, because it requires the superposition of low-noise target and eye velocity waveforms in addition to the use of target waveforms with unique velocity profiles.

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. These waveforms required a learning period before zero-latency tracking could be attained. The purpose of these experiments was not to study the time-course of learning. Therefore, we can only make general statements about how fast each waveform was learned. The cubic waveform required 13 sec to 5 min, and the pseudo-random acceleration waveform required 2 to 10 min. We do not know how long the subjects retained the information. We will presently conduct a study that will enable us to model the time course of learning, forgetting, and relearning.

There are other questions about the smooth pursuit system that cannot be answered by studying our data. By studying the position error as a function of time we found that all saccades were not position correcting. Those that were position correcting varied in amplitude, indicating that there was no sharp threshold that triggered position correcting saccades. We also found no evidence that the left, right, dominant, or nondominant eye tracked with smaller error.

For steady-state tracking the cross-correlation function is an indicator of tracking delay. The cross-correlation of target and eye position was computed for the unpredictable target waveform of Fig. 2. The peak value of cross-correlation function was 0.916, and it occurred at a time-lag of 95 msec. This implies that the time delay during steady-state tracking was 95 msec. The cross-correlation function is a good indicator of time delay when no feature of the data is available to distort the computation. However, saccades can distort the computations. For example, we computed the cross-correlation between eye and target position three ways for the data of Fig. 12. For the data from 0 to 1 sec, the peak correlation was 0.992 at a delay of 190 msec, which agrees with an intuitive visual inspection of the start-up record. For the data from 0.42 to 1.42 sec, the peak correlation was 0.989 at a delay of 165 msec. The saccade influences the correlation function. For the data from 0.84 to 1.84 sec, the peak correlation was 0.994 at a delay of 130 msec. These differences were caused by the effects of the saccade. When saccades are present the time of maximum correlation only gives a rough approximation of the time delay of the smooth pursuit system.

The routine recording of position mean square errors around 0.1 deg^2 is a demonstration of the accuracy of our photo-electric instrumentation. These mean square errors represent the sum of instrumentation noise, biological noise, nonlinearities, drift, and human tracking errors. If the instrumentation system were not accurate, such small errors would not be possible; also, if the human were not capable of accurate tracking, such small errors would not be possible.

The human smooth pursuit eye movement system has a large internal time delay. However, when the target is predictable, a control signal is generated that causes the smooth pursuit system to track with zero-latency and unity-gain. Within certain frequency, velocity and acceleration limits, humans can learn to track any predictable waveform that is smooth and periodic.

Acknowledgements—We thank Branch Rickey, Joe Orsulak and Nelson Della Rosa of the Pittsburgh Baseball Club for being subjects, and Susan B. Dunkle of Carnegie-Mellon University for reading our manuscript. Research was supported by National Science Foundation grant ECS-8121259.

REFERENCES

Bahill A. T. (1981) *Bioengineering: Biomedical, Medical and Clinical Engineering*. Prentice-Hall, Englewood Cliffs, NJ.

Bahill A. T. and McDonald J. D. (1981) Adaptive control model for saccadic and smooth pursuit eye movements. In *Progress in Oculomotor Research* (Edited by Fuchs A. F. and Becker W.), pp. 551–558. Elsevier/North-Holland, Amsterdam.

Bahill A. T. and McDonald J. D. (1983) Frequency limitations and optimal step-size for the two-point central difference derivative algorithm with applications to human eye movement data. *IEEE Trans. Biomed. Engng* **BME-30**, 191–194.

Bahill A. T., Iandolo M. J. and Troost B. T. (1980) Smooth pursuit eye movements in response to unpredictable target waveforms. *Vision Res.* **20**, 923–931.

Bahill A. T., Kallman J. S. and Lieberman J. E. (1982) Frequency limitations of the two-point central difference differentiation algorithm. *Biol. Cybernet.* **45**, 1–5.

Baloh R. W., Kumley W. E., Sills A. W., Honrubia V. and Konrad H. R. (1976) Quantitative analysis of smooth pursuit eye movements. *Ann. Otol. Rhinol. Lar.* **85**, 111–118.

Dallos P. J. and Jones R. W. (1963) Learning behavior of the eye fixation control system. *IEEE Trans. Autom. Control* **AC-8**, 218–227.

Davson H. (1976) *The Physiology of the Eye*. Academic Press, New York.

Eckmiller R. (1981) A model of the neural network controlling foveal pursuit eye movements. In *Progress in Oculomotor Research* (Edited by Fuchs A. F. and Becker W.), pp. 541–550. Elsevier/North-Holland, Amsterdam.

Eckmiller R. and Mackeben M. (1980) Pre-motor single unit activity in the monkey brain stem correlated with eye velocity during pursuit. *Brain Res.* **184,** 210–214.

Fuchs A. F. (1967) Saccadic and smooth pursuit eye movements in the monkey. *J. Physiol.* **191,** 609–631.

Greene D. F. and Ward F. E. (1979) Human eye tracking as a sequential input adaptive process. *Biol. Cybernet.* **33,** 1–7.

Jurgens R. and Becker W. (1975) Is there a linear addition of saccades and pursuit movements. In *Basic Mechanisms of Ocular Motility and Their Clinical Implications* (Edited by Lennerstrand G. and Bach-Y-Rita P.), pp. 525–529. Pergamon Press, Oxford.

Lanman J., Bizzi E. and Allum J. (1978) The coordination of eye and head movement during smooth pursuit. *Brain Res.* **153,** 39–53.

Mack A., Fendrich R. and Wong E. (1982) Is perceived motion a stimulus for smooth pursuit. *Vision Res.* **22,** 77–88.

Miller J. M., Ono H. and Steinbach M. J. (1980) Additivity of fusional vergence and pursuit eye movements. *Vision Res.* **20,** 43–48.

Rashbass C. (1961) The relationship between saccadic and smooth tracking eye movements. *J. Physiol.* **159,** 326–338.

Robinson D. A. (1964) The mechanics of human saccadic eye movement. *J. Physiol.* **174,** 245–264.

Schalen L. (1980) Quantification of tracking eye movements in normal subjects. *Acta otolar.* **90,** 404–413.

Stark L., Vossius G. and Young L. R. (1962) Predictive control of eye tracking movements. *IRE Trans. Hum. Fact. Electron.* **HFE-3,** 52–57.

Steinbach M. (1976) Pursuing the perceived rather than the retinal stimulus. *Vision Res.* **16,** 1371–1376.

Westheimer G. (1954) Eye movement responses to a horizontally moving visual stimulus. *AMA arch. Ophthalmol.* **52,** 932–941.

Whittaker S. G. and Eaholtz G. (1982) Learning patterns of eye motion for foveal pursuit. *Invest. Ophthal. visual Sci.* **23,** 393–397.

Williams R. A. and Fender D. H. (1979) Velocity precision in smooth pursuit eye movements. *Vision Res.* **19,** 343–348.

Winterson B. J. and Steinman R. M. (1978) The effect of luminance on human smooth pursuit of perifoveal and foveal targets. *Vision Res.* **18,** 1165–1172.

Yasui S. and Young L. (1975) Perceived visual motion as effective stimulus to pursuit eye movement system. *Science* **190,** 906–908.

Young L. (1977) Pursuit eye movements—what is being pursued. In *Control of Gaze by Brain Stem Neurons* (Edited by Baker R. and Berthoz A.), pp. 29–36. Elsevier/North-Holland, Amsterdam.