

A Control Systems Model of Smooth Pursuit Eye Movements with Realistic Emergent Properties

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Visual tracking of objects in a noisy environment is a difficult problem that has been solved by the primate oculomotor system, but remains unsolved in robotics. In primates, smooth pursuit eye movements match eye motion to target motion to keep the eye pointed at smoothly moving targets. We have used computer models as a tool to investigate possible computational strategies underlying this behavior. Here, we present a model based upon behavioral data from monkeys. The model emphasizes the variety of visual signals available for pursuit and, in particular, includes a sensitivity to the acceleration of retinal images. The model was designed to replicate the initial eye velocity response observed during pursuit of different target motions. The strength of the model is that it also exhibits a number of emergent properties that are seen in the behavior of both humans and monkeys. This suggests that the elements in the model capture important aspects of the mechanism of visual tracking by the primate smooth pursuit system.

1 Introduction

Computer models have advanced our understanding of eye movements by providing a framework in which to test ideas suggested by behavioral and physiological studies. Our knowledge of the smooth pursuit system is at a stage where such models are especially useful. We know that pursuit eye movements are a response to visual motion and that they are used by primates to stabilize the retinal image of small moving targets. Lesion and electrophysiological studies have identified several cortical and subcortical sites that are involved in pursuit (see Lisberger et al. 1987 for review), but the precise relationship between the visual motion signals recorded at these sites and those used by pursuit remain unclear.

We present a model that was designed to replicate the monkey's initial eye velocity response as a function of time for different pursuit target motions. The model emphasizes the variety of visual signals available for pursuit and minimizes the computations done by motor pathways. The structure of the model is based upon behavioral experiments which

have characterized how different aspects of visual motion act to initiate pursuit. In monkeys, the pursuit system responds not only to the velocity of retinal images, but also to smooth accelerations and to the abrupt accelerations that accompany the onset of target motion (Krauzlis and Lisberger 1987; Lisberger and Westbrook 1985). Therefore, the model includes three parallel pathways that are sensitive to these three aspects of visual motion.

2 Structure of the Model

Our model is drawn in figure 1. Within each pathway, a time-delayed signal related to the motion of retinal images ($\dot{T} - \dot{E}$, called retinal "slip") is processed by a nonlinear gain element derived from our behavioral experiments and a filter. The first pathway is sensitive to slip velocity (\dot{e}) and its gain is linear. The second and third pathways are both sensitive to slip acceleration (\ddot{e}), but in different ways. The impulse acceleration pathway is sensitive to the large accelerations that accompany step changes in target velocity, but has a dead zone in the gain element that renders it insensitive to smaller accelerations. The smooth acceleration pathway is sensitive to gradual changes in image velocity. The outputs of the gain elements in each pathway are low pass filtered to produce three signals with different dynamics ($\ddot{E}'_v, \ddot{E}'_i, \ddot{E}'_a$) that are then summed and integrated to give a command for eye velocity (\dot{E}'). The integrator makes our model reproduce the fact that the pursuit system interprets visual inputs as commands for eye accelerations (Lisberger et al. 1981). Eye velocity (\dot{E}) is obtained by passing the eye velocity command through a low pass filter that represents the eye muscles and orbital tissues.

The behavior of the model was refined by matching its performance under open-loop conditions to that of the monkey. We removed visual feedback by setting the value of feedback gain to zero, and compared the model's output to averages of the monkey's eye velocity in behavioral trials where visual feedback was electronically eliminated for 200 ms (methods in Morris and Lisberger 1987). First, we stimulated the model with steps in target velocity, which activate the slip velocity and impulse acceleration pathways. We adjusted the filters in these pathways to obtain the fit in figure 2A, where the rising phase of the model's output (dotted lines) matches the rising phase of the monkey's eye velocity (solid lines) during the open-loop portion of the monkey's response. Then, we stimulated the model with steps in target acceleration, which activates the slip velocity and smooth acceleration pathways, and adjusted the filter in the smooth acceleration pathway (Fig. 2B).

3 Emergent Properties of the Model

We tested the model by restoring visual feedback and providing steps of target velocity in closed-loop conditions. Figure 2C shows that the model matches the rising phase of the monkey's response and makes a realistic transition into steady-state tracking. Like the monkey, it reaches steady-state velocity at later times for higher target speeds. The contribution of each pathway to the initiation of pursuit can be assessed by setting its

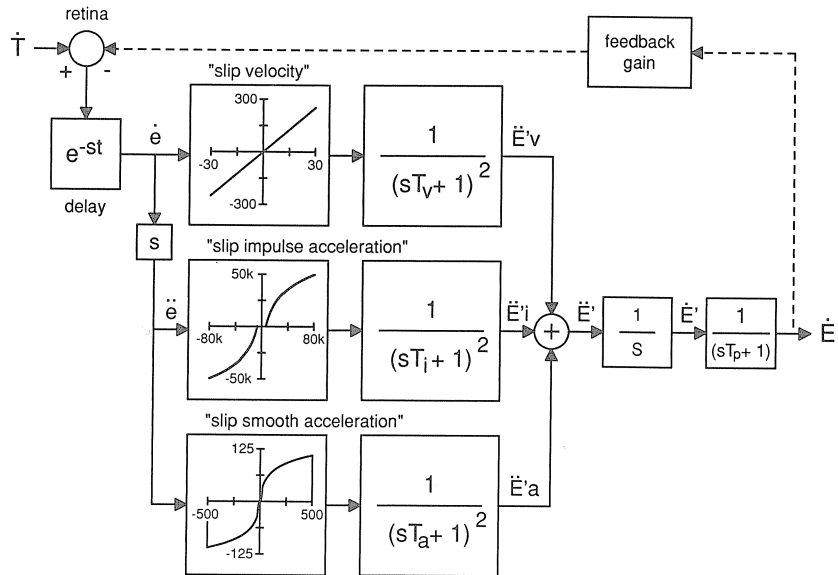


Figure 1: Model of smooth pursuit eye movement system. Boxes contain transfer functions expressed in Laplace notation. Abbreviations: \dot{T} , target velocity; \dot{e} , slip velocity; \ddot{e} , slip acceleration; $\ddot{E}'v$, output of slip velocity pathway; $\ddot{E}'i$, output of slip impulse acceleration pathway; $\ddot{E}'a$, output of slip acceleration pathway; \ddot{E}' , eye acceleration command; \dot{E}' , eye velocity command; \dot{E} , eye velocity. Parameters used: $t = .065$; $T_v = 0.030$; $T_i = 0.020$; $T_a = 0.010$; $T_p = 0.015$. Functions for gain elements: Slip velocity pathway: $y = ax$; $a = 8.3$. Slip impulse acceleration pathway: for $x > c$, $y = a \log(bx + 1)$; $a = 17500$, $b = .00015$, $c = 3000$. Slip smooth acceleration pathway: for $d > x > e$, $y = a \log(bx + 1)$; for $x < e$, $y = (cx^2)a \log(bx + 1)$; $a = 28$, $b = .1$, $c = .0016$, $d = 500$, $e = 18.5$. Equations given for impulse and smooth acceleration pathways apply for $x > 0$. For $x < 0$, equivalent odd functions are used.

gain to zero, effectively "lesioning" that limb of the model. When the slip impulse acceleration pathway is lesioned, the rising phase is delayed and more sluggish, but the transition to steady-state tracking is unchanged (Fig. 2D, open arrow). This pathway contributes exclusively to the initial 25–50 ms of the response to steps in target velocity and allows the model to reproduce the observation that the earliest component of the pursuit response is sensitive to target direction, but relatively insensitive to target speed (Lisberger and Westbrook 1985). When the smooth acceleration pathway is eliminated, the rising phase is unchanged, but there is a large overshoot in the transition to steady-state tracking (Fig. 2D, filled arrow). Thus, the smooth acceleration pathway normally decelerates the eye as eye velocity approaches target velocity. This is an emergent property of the model, since this pathway was tuned by adjusting its contribution to the acceleration of the eye as shown in figure 2B.

The model rings at a relatively high frequency, 5 Hz, in response to steps in target velocity (solid lines in figure 3A). Similar oscillations are seen in the behavior of both humans and monkeys (Goldreich and Lisberger 1987; Robinson et al. 1986). If the model is driven at this resonant frequency, the output lags target velocity by 180 degrees (Fig. 3B, filled arrow), an effect that is also seen in the monkey's behavior (Goldreich and Lisberger 1987). The high frequency properties of the model depend upon the presence of the smooth acceleration pathway. If this pathway is eliminated, the spontaneous oscillations still occur, but now at only 1.6 Hz (Fig. 3A, open arrow), and the phase lag in the response to sinusoidal inputs increases (Fig. 3B, open arrow).

4 Discussion

An important property of our model is that it allows independent control over the initiation and maintenance phases of pursuit. The rising phase is determined mainly by the slip velocity and impulse acceleration pathways. The steady-state behavior is determined primarily by the smooth acceleration pathway. Since the differentiator in the smooth acceleration pathway introduces a phase lead, the steady-state behavior of the model has a higher frequency response than the rising phase. The exact frequency of ringing depends upon the total delay around the smooth acceleration pathway. For example, if the delay in the visual input is increased by 30 ms, the model will ring at 3.8 Hz, similar to what is normally observed in humans (Robinson et al. 1986) or in monkeys when the delay in visual feedback is increased (Goldreich and Lisberger 1987). The amount of ringing depends upon the gain element in the smooth acceleration pathway. Lowering the gain dampens or eliminates the ringing, increasing the gain produces persistent ringing. Such variations are also seen on individual trials in the monkey's behavior.

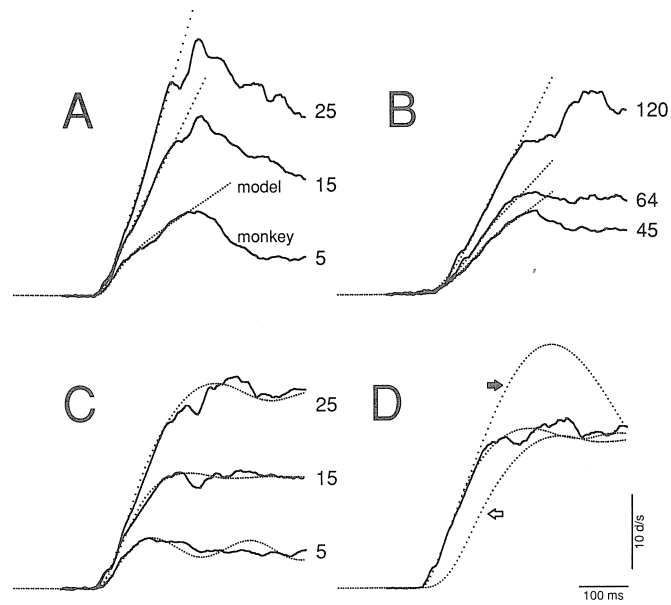


Figure 2: Comparison of the eye velocity output from the model and the monkey. In all panels, dotted lines show the model's output and solid lines show the monkey's eye velocity. A: Steps in target velocity of 5, 15, and 25 d/s under open-loop conditions. The monkey's open-loop response lasts for the first 200 ms of his response. B: Steps in target acceleration of 45, 64, and 120 d/s^2 under open-loop conditions. C: Steps in target velocity of 5, 15, and 25 d/s under closed-loop conditions. D: Effect of lesioning either acceleration pathway on the model's response to a step in target velocity of 20 d/s. Open arrow, model's response when gain in slip impulse acceleration pathway is set to zero. Closed arrow, model's response when gain in slip smooth acceleration pathway is set to zero.

The strength of our model is that it uses open-loop behavioral data to embody the pursuit system's sensitivity to different aspects of visual motion. Although it was designed to replicate the dynamics of the initiation of pursuit, the model also serendipitously solves a problem noted by Robinson (Robinson et al. 1986), namely, that the rising phase of pursuit is sluggish compared to the frequency of its ringing. The emergence of realistic steady-state properties in the model indicates that the visual elements in its pathways capture important aspects of signal processing within the smooth pursuit system. Our model does not include a sensitivity to position errors, which can affect steady-state tracking in monkeys (Morris and Lisberger 1987). It also does not include the topographic organization of the visual system and therefore cannot reproduce the retinotopic deficits in the initiation of pursuit or the directional deficits

in the maintenance of pursuit which are seen after lesions of cortical areas MT and MST (Dursteler et al. 1987; Newsome et al. 1985). However, it should be possible to embed the dynamics of our model within a topographic structure that would account for these effects.

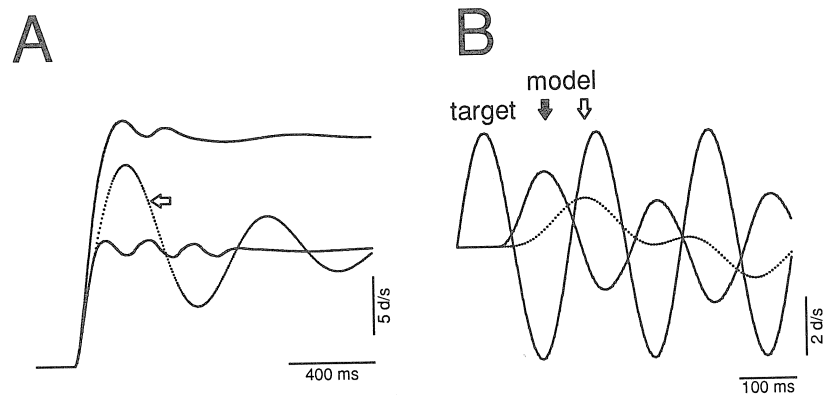


Figure 3: Ringing and frequency response of the model. A: Solid lines, model's closed-loop response to steps in target velocity of 10 and 20 d/s, viewed on larger time scale than in figure 2C. Dotted line, model's response to step in target velocity of 10 d/s when gain in smooth acceleration pathway is set to zero. B: Driving the model with sine wave target velocity at 5.0 Hz under closed-loop conditions. Filled arrow, the intact model's response lags target motion by 180 degrees. Open arrow, model's response when gain in smooth acceleration pathway is set to zero. Phase lag is now 325 degrees.

Acknowledgments

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