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A different approach to modelling pursuit eye movements

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Introduction

Previous models of pursuit eye movements have focussed on reproducing the smooth eye velocity of monkey and human subjects and have not attempted to reproduce the discharge of neurons within the visual and motor pathways for pursuit. For example, the initial model proposed by Young et al (1968) and formalized by Robinson (1971) drove pursuit with a neural signal related target velocity so that model eye velocity could match target velocity without going into large, undamped oscillations. In a more modern version of the pursuit model, Robinson et al (1986) employed a feedback mechanism like that introduced in the "bang-bang" saccade model (Zee et al 1976). Proper adjustment of the parameters of the model allowed its output to reproduce all the features of the eye velocity evoked by a step change in target velocity in humans. Model eye velocity reproduced both the rising phase of eye velocity at the onset of pursuit and the frequency and amplitude of the oscillations of eye velocity during pursuit of sustained target motion. The key feature of Robinson's pursuit model is that the eye velocity command is delayed, filtered, and added to a signal related to retinal image velocity to develop an internal representation of target velocity.

Krauzlis and Lisberger (1989) developed a model of a different class that was designed to reproduce the eye velocity evoked by steps of target velocity in monkeys. The input to their model, retinal image velocity, is processed in three parallel pathways that emit signals related to image velocity and two different versions of image acceleration. These three visual motion signals are summed and, as suggested by Lisberger et al (1981), Lisberger and Westbrook (1985), and Morris and Lisberger (1987), the sum is treated as a command for eye acceleration and is integrated to yield eye velocity. The strength of this model is that appropriate values of the parameters allow simulated eye velocity to reproduce the eye velocity evoked by steps of target velocity in either monkeys or humans (Krauzlis 1991). In addition, Goldreich et al (1992) demonstrated that the model of Krauzlis and Lisberger (1989) succeeds while the model of Robinson et al (1986) fails at reproducing the effect of changes in visual feedback delay on the frequency of oscillations during sustained pursuit. The successes of the model of Krauzlis and Lisberger (1989) suggest that the visual motion inputs for pursuit provide information about both the velocity and the acceleration of the target's image on the retina.

All previous models of pursuit share the common weakness that recordings of the intermediate signals within the model fail to reveal signals that match those recorded at various sites in the brain. For example, most models assume the intricacies of visual motion processing and take an input that is directly proportional to image velocity. However, signals proportional to image velocity are not found in the parts of the brain the process visual motion. Instead, most neurons are tuned so that they show a peak response at a preferred velocity and smaller responses for either higher or lower velocities (Maunsell and Van Essen 1983). In addition, it is

not known whether image acceleration is represented in the discharge of neurons in the visual motion pathways of the brain.

Our goal is to develop a model of pursuit (Figure 1) in which the visual inputs are derived from the responses of cells in the middle temporal visual area (MT). We chose to use MT to provide visual inputs to our model because of evidence that outputs from MT are needed to generate pursuit. Lesions of MT cause deficits in the use of image motion for the initiation of pursuit (Newsome et al 1985). The outputs from MT project to other cortical areas that are important for pursuit, such as the medial superior temporal visual area (MST), and to the dorsolateral pontine nucleus and the nucleus of the optic tract in the brainstem. Development of our model requires three steps: 1) record from cells in MT to obtain quantitative data about the representation of image velocity and acceleration; 2) develop a computer model that converts image velocity into the responses measured in MT; 3) determine a sensory-motor transformation that converts the outputs from MT into commands for the pursuit eye velocities evoked by a wide variety of target motions in monkeys. We now report on the first two steps in this process.

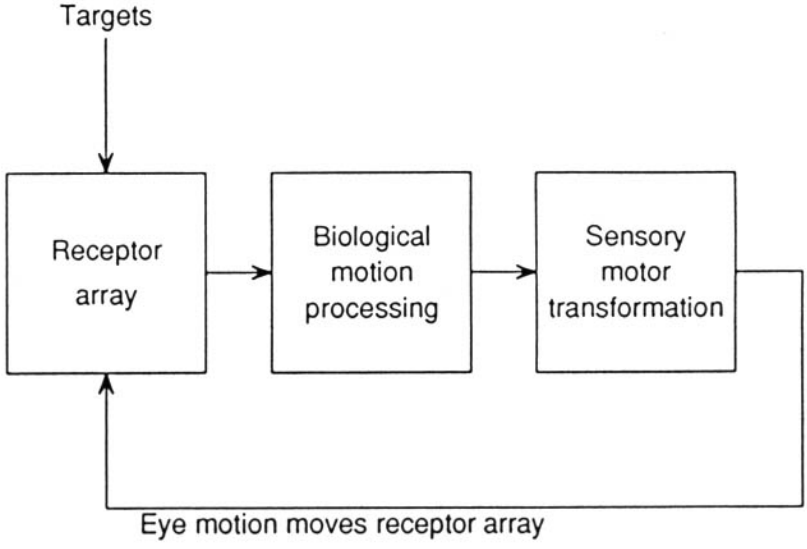

Figure 1. Outline of a biologically-based model of smooth pursuit eye movements. The "Receptor array" represents the retina, "Biological motion processing" converts visual inputs into outputs that reproduce the responses of MT cells, and "Sensory motor transformation" converts those outputs into commands for eye velocity.

Methods

We made extracellular recordings from cells in visual area MT in 6 anesthetized macaque monkeys (Macaca Fascicularis). The cortex was exposed over the intraparietal fissure on one side and the dura was reflected. Prior to the onset of recordings, the monkey was paralyzed and artificially ventilated. Its anesthetic status was monitored by displaying the EEG continuously on an oscilloscope. Metal microelectrodes were advanced through the cortex until we had isolated the action potentials of an individual MT cell, recognized by its relatively small receptive field and direction selective responses. Marking lesions were made at the end of each penetration and the location of the recordings in MT was confirmed after the experiment by reconstructing the penetrations in histological sections.

The visual stimulus consisted of a field of random dots that was placed over the receptive field of the cell under study. The dots were then moved across the receptive field so that dots were continually coming onto the receptive field from one side as they moved off on the other side. In about half the cells, the response to the dots was improved substantially by creating a window in the center of the dot pattern and moving only the dots that were under the window. For each cell, we attempted to achieve a strong response to motion of the dots before determining its response properties. Stimuli were presented on an oscilloscope screen so that they provided apparent motion with a temporal interval of 4 ms.

After we determined its preferred direction of motion, each MT cell was studied in three experiments 1) The dots were illuminated and stationary for 256 ms, underwent a step of speed to 0.6, 1.2, 2.4, 4.8, 9.6, 19.2, 38.4, 76.8, or 153.6°/s in the preferred direction of the cell under study, moved for 768 ms, and then disappeared. 2) The dots were illuminated and stationary for 256 ms, accelerated at a constant rate for 128 ms up to final speeds of 1.2 2.4, 4.8, 9.6, 19.2, 38.4, 76.8, or 153.6°/s^2, moved at the final speed for 640 ms, and then disappeared. 3) The dots appeared moving at the final speeds from the second experiment for 256 ms, decelerated at a constant rate for 128 ms until they were stationary, and remained on for 640 ms. Experiment 1 was run as one block of trials and experiments 2 and 3 were run together as a separate block of trials. Trials were interleaved by shuffling the entire list of stimuli, presenting them in the shuffled order, and repeating. Each stimulus was repeated 16 or 32 times and the responses of the MT cell were accumulated in histograms with a bin width of 4 ms. We then spliced the histograms from experiments 2 and 3 for each stimulus speed so that the data appeared as though a single trial had consisted of a ramp up to a given speed, a period of motion at that speed, and a ramp back down to 0°/s. Finally, the histograms were smoothed with a 3-point averaging algorithm.

Results

We present our data by showing two examples of MT cells that were at the extremes of the population of responses to steps and ramps of target velocity. The cell in Figure 2 appeared to respond almost purely to target velocity while the cell in Figure 3 provided information about target velocity and target acceleration. Our sample of 64 cells had response properties distributed between those shown by the two sample cells. Thus, all MT cells encoded information about target velocity while the population ranged across a broad continuum in the amount of information they encoded about target acceleration.

Figure 2 shows the responses of an MT cell with discharge that appeared to be related to target velocity but not to target acceleration during steps (A) or ramps (B) of target velocity. When the target was stationary the firing rate of the cell was near zero. Steps of target velocity in the cell's preferred direction caused the firing to increase without overshoot to a sustained level that was maintained during target motion. The sustained firing was tuned for velocity and reached a peak near 2.4°/s. Ramps of target velocity caused a similar response without overshoot when the final

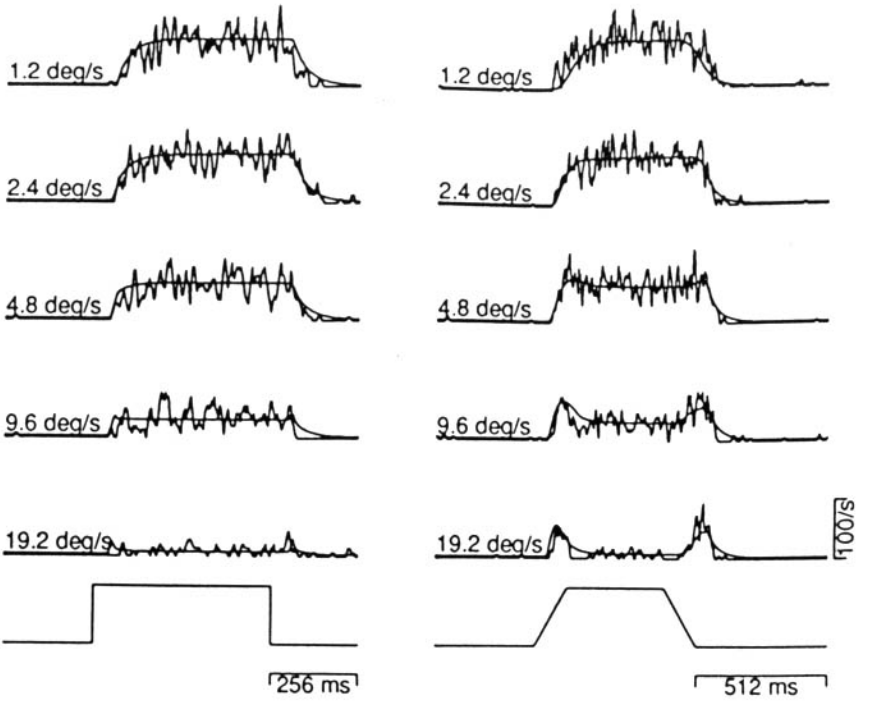

Figure 2. Responses of one MT cell discharged in relation to target velocity but not target acceleration for target motion in its preferred direction. A: Responses to steps of target speed. B: Responses to ramps of target speed. The bottom trace in each column shows the trajectory of target speed as a function of time. The noisy traces are the averaged and smoothed firing rate of the cell as a function of time. The smooth traces show the output of a model that was optimized to reproduce the responses of this cell. The numbers on each trace indicate the speed of the target during the constant-velocity portion of the stimulus.

target speed was less than the best speed for steps of target motion. For higher speeds, however, the cell showed a pulse of firing rate during both the ramp from zero to final speed and the ramp from final speed back to zero. The pulse was nearly symmetrical for target acceleration and deceleration and therefore does not provide information about target acceleration. Instead, it reflects the fact that firing rate increased as the ramp of target acceleration took target speed up through the best target speed and decreased as target speed continued to a final value above the best speed. The same pulse of firing occurs during the target deceleration because target speed traverses through the same sequence of speeds as it did during target acceleration.

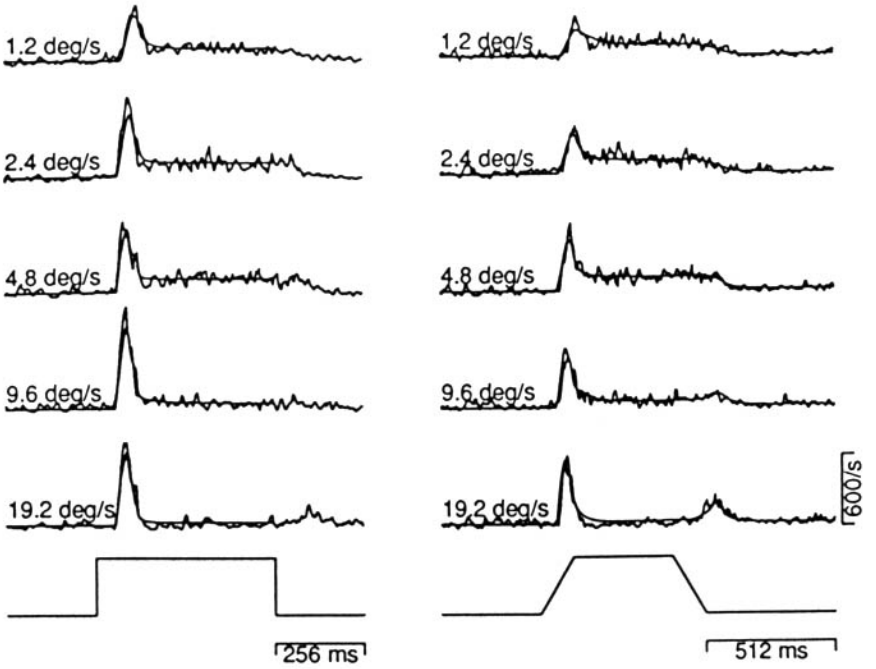

Figure 3. Responses of one MT cell that discharged in relation to both target speed and target acceleration. A: Responses to steps of target speed. B: Responses to ramps of target speed. The bottom trace in each column shows the trajectory of target speed as a function of time. The noisy traces are the averaged and smoothed firing rate of the cell as a function of time. The smooth traces show the output of a model that was optimized to reproduce the responses of this cell. The numbers on each trace indicate the speed of the target during the constant-velocity portion of the stimulus.

Figure 3 shows the responses of an MT cell that provided information about both target speed and target acceleration. Steps of target speed (A) caused this cell to emit a large transient burst of firing followed by sustained firing that was largest when target speed was 1.2°/s. Ramps of target speed (B) caused a the cell in Figure 3 to respond in a way that was qualitatively different from the cell illustrated in Figure 2. As target speed accelerated from zero to any sustained speed the cell emitted a large transient surge in firing rate followed by sustained firing rate. As target speed decelerated, firing rate showed either a small transient surge or simply decreased to resting firing rate. The large asymmetry between the responses to target acceleration and deceleration provides information about the direction of target acceleration. One of the long-term goals of our research is to determine whether the output of MT cells also provide information about the magnitude of target acceleration that can be used to help guide pursuit eye movements.

A model of the firing of MT cells

Because we recorded from MT cells in anesthetized, paralyzed monkeys, our target movements were presented under open-loop conditions and we therefore obtained information about the responses of MT cells for only a discrete sampling of target speeds and target accelerations. To develop a model that uses the responses of MT cells as its visual input and that reproduces the closed-loop pursuit of monkeys, it will be necessary to develop a way to simulate the responses of MT cells for combinations of target acceleration and speed we did not present. Because of the complex temporal sculpting of the responses of MT cells, we elected to develop a model that could be fitted to the responses of our cells. Such a model, if prevented from operating as a table-lookup, would be able to interpolate between the stimuli we used and would provide good estimates of how the MT cells would have responded during closed-loop pursuit.

The output of our model MT cells, shown by the smooth solid lines in Figures 2 and 3, followed the trajectory of actual firing rate closely. The model was fitted to the responses of each MT cell by using the "stepit" optimization algorithm (Chandler 1965) to choose the values of the parameters. The model for each cell consisted of two or three modules that had the structure illustrated in Figure 4. Each module

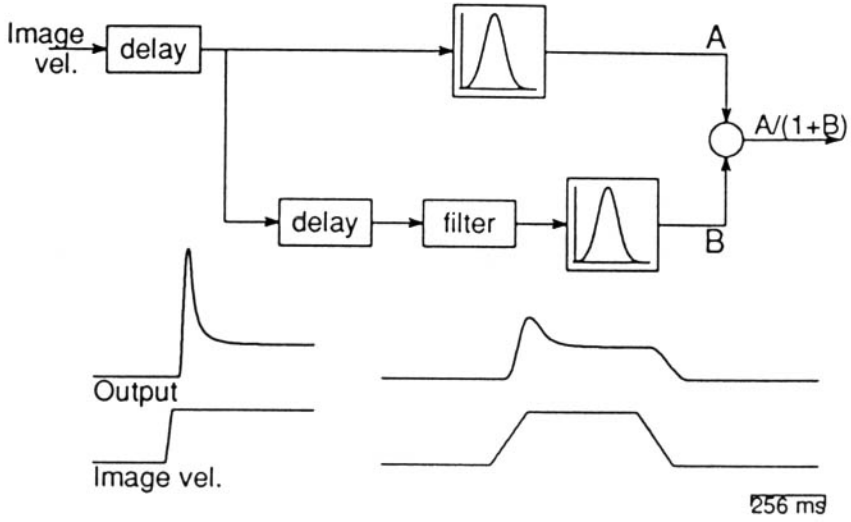

Figure 4. A model that reproduces the responses of MT cells to steps and ramps of target speed. A: Configuration of a module of the model. The pathway labeled "A" is the direct pathway, while that labeled "B" is the gain-control pathway. The Gaussian function in each pathway is a non-linearity that takes delayed/filtered image velocity as its input and produces an output that is tuned for image velocity. Each cell was modelled as the sum of the outputs from 1 to 3 such modules. B: Response of one module to a fast ramp of target speed, approximating a step of target speed. C: Response of one module to a ramp increase and decrease in target speed.

consisted of a direct pathway that produced the output labeled "A" and a gain-control pathway that produced the output labeled "B". The net output from each module was computed as A/(1+B). Each pathway in each module contained a tuned non-linearity (graphs inside large square boxes) that transformed the delayed/filtered image velocity input into signals that peaked for a preferred target velocity and were smaller for velocities that were above or below the preferred velocity. The two example traces at the bottom of Figure 4 illustrate how the model worked. Because of the extra delay in the gain-control pathway, the initial response of each module was determined by the direct pathway, so that the tuned non-linearity in the direct pathway determined the relationship between the amplitude of the transient response and the amplitude of the step of target speed. The delay in the gain-control pathway determined the duration of the transient response, the filter determined the time course of the decay toward sustained firing. Finally, the relationship between the amplitude and tuning of the non-linearities in the direct and gain-control pathways determined the relationship between sustained firing rate and target speed. For ramps of target speed, the gain-control pathway also determined the asymmetry between the response to smooth target acceleration and deceleration. If the gain control pathway was not included, then B was zero for both target acceleration and deceleration and the output of the model was related purely to target velocity; this is how we modeled the responses of the cell in Figure 2. If the gain control pathway had a non-zero gain, then the value of B would be zero during target acceleration but would be positive during target deceleration. The model would emit a large pulse of firing for target acceleration but a smaller pulse or no pulse during target deceleration. This is how we modeled the responses of the cell in Figure 3.

Discussion

We have demonstrated that many cells in visual area MT have responses to smooth target motion that contain information about both target speed and target acceleration. However, it may not be correct to say that the output of area MT "encodes" target acceleration because the firing of MT cells in relation to target acceleration is so tightly linked to their firing in relation to target velocity. In data not presented here, we have shown that the same smooth change in target velocity produces responses that depend strongly on the initial target speed. Thus, target acceleration from zero to the preferred speed causes a large response and target acceleration from the preferred speed to twice the preferred speed causes no response or even some inhibition of firing (Movshon et al 1990).

The finding of firing related to both target acceleration and target speed in area MT provides a potential neural substrate for the visual processing in the pursuit model of Krauzlis and Lisberger (1989). The model postulated that commands for pursuit eye acceleration would be provided by visual motion signals related to both image velocity and image acceleration. Although we have found such signals in MT, they are completely different from the signals used by the model of Krauzlis and Lisberger (1989) and we have demonstrated only that MT cells provide information about the direction of target acceleration. Thus, it is not possible at this time to say if the signals recorded in area MT also provide information about the magnitude of target acceleration or whether the output of MT can be used in the way envisaged by Krauzlis and Lisberger (1989). Our next goal will be to resolve this issue by using the models that described the responses of our MT cells to provide distributed visual motion signals as inputs for a model of closed-loop pursuit. We are currently exploring a variety of biologically-plausible functions to determine the nature of sensory-motor transformations that would convert the output of MT cells into command signals for pursuit eye velocity.

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