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# Visual Cortical Signals Supporting Smooth Pursuit Eye Movements

J.A. MOVSHON,* S.G. LISBERGER,† AND R.J. KRAUZLIS†

*Center for Neural Science and Department of Psychology, New York University, New York, New York 10003
†Department of Physiology, W.M. Keck Center for Integrative Neuroscience, and Neuroscience Graduate Program University of California at San Francisco, California 94143

The visual world is filled with moving objects, and it is therefore no surprise that the visual system contains special mechanisms for the analysis of motion (Hildreth 1983; Nakayama 1985). Visual motion processing has recently been the subject of vigorous neurobiological, psychophysical, and computational analysis. We now have a good understanding of the neuronal mechanisms that represent motion signals in the cerebral cortex (Maunsell and Newsome 1987) and sophisticated models of their function on a number of different levels (Hildreth and Koch 1987). Much interest in visual motion processing mechanisms has come from a desire to link psychophysical studies of motion analysis to their physiological substrate (Newsome et al., this volume). Other investigators have sought to relate computational approaches to motion sensing to biological mechanisms (Adelson and Bergen 1985; Watson and Ahumada 1985). Relatively little attention has been paid to the role that motion signals play in the generation of eye movements. Visual mechanisms that analyze form perform optimally only when the retinal image is stationary or slowly moving (see Graham 1990). One of the main roles of the oculomotor system is to steady the images of moving objects so that they can be properly seen; to perform this stabilization, the oculomotor system must have accurate information about retinal image motion. Signals about motion drive several kinds of eye movements, including the smooth pursuit eye movements that match the velocity of eye movement to the velocity of an attended moving visual target.

There is now good evidence for a cortical pathway specialized for the analysis of visual motion (Maunsell and Newsome 1987). This pathway originates in the M-type (broad-band) cells of the retina and the lateral geniculate nucleus (LGN), passes into the cerebral cortex through V1, and then courses through a complex set of cortical connections to the middle temporal area (MT or V5) and the medial superior temporal area (MST or V5a), which straddle the boundary between the occipital and parietal lobes. The link between the visual motion pathway and pursuit was suggested by the anatomical connections from these areas to the pontine nuclei and accessory optic system, and thence to regions of the cerebellum known to be involved in pursuit eye movements (Brodal 1978, 1979). Focal lesions of MT and MST selectively disrupt pursuit eye movements (Newsome et al. 1985; Dürsteler et al. 1986), producing deficits consistent with the idea that these areas are responsible for providing visual motion signals that support pursuit commands. Although these motion-analyzing neurons are at least six synapses away from the photoreceptors, and the motion information must traverse at least five more synapses to reach extraocular motoneurons, the study of visual motion processing and of the oculomotor system has narrowed the sensorimotor link to the cortico-ponto-cerebellar pathways.

Just as students of motion processing have typically paid little attention to the motor functions associated with motion signals, so those who study pursuit have largely ignored the consequences of visual processing for the kinds of signals available to control pursuit. For example, Robinson et al. (1986) offer a control-theory model of the pursuit system in which the role of the visual system is to produce a replica (delayed 50 msec) of the retinal motion signal. Because their model of visual processing is so simple, Robinson and his colleagues must attribute the dynamic features of pursuit to properties of the motor pathways. Recently, however, it has become clear that many features of pursuit may depend not on motor processing, but on the sensory analysis that precedes it (Lisberger and Westbrook 1985; Lisberger et al. 1987). These insights have come largely from studies that concentrate on analyzing the first "open-loop" phase of pursuit, during which the effects of the pursuit eye movement on retinal target velocity have not yet made themselves felt. Krauzlis and Lisberger (1989) analyzed many of these data and proposed a model with a more elaborate visual "front end." The properties of the visual processing in the model largely account for the dynamics of both open- and closed-loop pursuit, suggesting that much of the detail of the pursuit eye movement response might reflect constraints arising from visual processing, rather than motor output pathways.

The experiments reported in this paper seek to uncover the degree to which signals in the motion sensing pathway can *by themselves* explain the behavior of the pursuit system. Our approach was to study neurons at a high level in the cortical motion pathway, in area MT, with target motion profiles that reveal interesting features of the pursuit system. Our results show that neurons in MT carry signals having many features in

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common with pursuit, and they suggest that visual, rather than motor, processes may be the determinants of many features of smooth pursuit eye movements.

## METHODS

***Unit recording.*** We used conventional methods to record the activity of single isolated units in area MT of anesthetized, paralyzed macaque monkeys (*M. fascicularis*). Tungsten-in-glass microelectrodes (Merrill and Ainsworth 1972) were introduced hydraulically into MT through a craniotomy and durotomy placed over the overlying parietal cortex; unit activity was conventionally amplified and displayed; standard pulses triggered by each action potential were sent to a PDP11 computer for analysis and storage.

The monkeys were anesthetized with an opioid (sufentanil citrate, 4–12 $\mu$g/kg/hr) and paralyzed with a curariform muscle relaxant (vecuronium bromide, 0.1 mg/kg/hr), given together with isotonic lactated dextrose in Ringer's solution in intravenous infusion at 10.4 ml/hr. EEG, EKG, end-expiratory $P_{CO2}$, and body temperature were continuously monitored and maintained in a suitable state to verify that the animal remained properly anesthetized and in good physiological condition.

The corneas were protected with +2D clear contact lenses; supplementary lenses chosen by direct ophthalmoscopy and by optimizing the visual responses of visual units were used to make the retinae conjugate with a CRT display between 30 and 57 cm distant. Visual stimuli were generated on this display by the same PDP11 computer that monitored unit activity and controlled the sequence of stimulus presentations. In the experiments described here, the stimuli were always texture fields consisting of 300–500 randomly positioned bright dots on a dark background; the mean luminance of the display was 10 cd/m$^2$, and the frame rate was 250 Hz. Suitable motion targets were generated by moving all the dots in a selected region. For most cells, the entire field of dots (subtense: 10–18°) moved; for the minority of cells for which peripheral suppression was noticeable, the motion was confined to the excitatory receptive field, and the dots in the periphery remained stationary. We used extended texture stimuli rather than the single spots typically used in oculomotor work so that we would not need to be concerned in the design of experiments with the location and the timing of the movement of the target; it seems unlikely that this difference would have an important effect on our results. We first established the neuron's direction tuning for our targets; in all the experiments described here, the targets moved in the preferred direction.

The stimuli in a particular experimental series were presented by the computer in a randomly interleaved sequence to attenuate the effects of response variability; average response histograms were calculated and viewed on-line, and the data were stored on disk for later off-line analysis.

We studied 45 neurons from five monkeys in sufficient detail to include in the analysis. All receptive fields were centered within 5° of the fovea. The position of each electrode track was marked with a small electrolytic lesion made by passing current through the electrode tip (2 $\mu$A, 2 sec, tip negative). At the end of each experiment, the monkey was killed with an overdose of thiopental sodium and perfused with 4% buffered paraformaldehyde. The region of cortex containing the electrode tracks was blocked, sectioned, and stained for Nissl substance and for myelin. All recording sites were verified to lie within the myeloarchitectural boundaries of MT (Van Essen et al. 1981).

***Eye movement recording.*** Oculomotor data were obtained from a trained rhesus monkey (*Macaca mulatta*), using methods described elsewhere (Lisberger and Westbrook 1985). During experiments, the monkey, with its head restrained, sat in a primate chair facing a tangent screen 114 cm distant, onto which visual targets were projected. The monkey was rewarded for keeping his eye position within 2° of a visual target whose motion was unpredictable from trial to trial; the target was a white spot 0.1–0.3° in diameter viewed against a dark background, and its intensity was set to be several hundred times the threshold of visibility for a human observer. Before the test portion of the trial began, a stationary red 0.1° fixation target of comparable intensity was presented for an unpredictable period of 600–900 msec.

Eye position was recorded using a magnetic search coil technique. Eye position signals were suitably low-pass-filtered, sampled at 1-msec intervals, and stored (along with other relevant timing information) by a PDP11 computer, which also controlled the stimulus display and the behavioral contingencies.

## RESULTS

It has long been known that the principal visual signal that drives pursuit is an encoded representation of target direction and speed. Recent analyses have suggested that in addition to signals purely related to speed, the pursuit system also makes use of information about target acceleration and also that its behavior depends on the time course of target presentation. To learn whether these kinds of information were usefully represented in the activity of MT neurons, we examined their responses to targets moving with controlled timings, speeds, and accelerations and compared the results with eye-movement data.

### Effects of Target Speed

***Representation of target speed.*** The most useful information on the effect of target speed on pursuit comes from studies using variants of the "step-ramp" paradigm introduced by Rashbass (1961). In experiments of this kind, a stationary visual fixation target simultaneously jumps and begins to move at a constant

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speed. The pursuit response to step-ramp stimuli consists of a rapid acceleration of the eye to a velocity approximating the target velocity; "catch-up" saccades designed to foveate the moving target can be eliminated by suitable choices of step and ramp parameters. Figure 1 shows pursuit data from a monkey working in a modified step-ramp task. The paradigm is indicated on the left (Fig. 1a): The fixation target was turned on to initiate the trial; then, after an unpredictable interval, the tracking target appeared, stood still for 300 msec, and then moved at a constant speed. The onset of target movement coincided with the offset of the fixation target, which cued the monkey to begin tracking. The traces in Figure 1b show averages of the monkey's eye speed for 400 msec following the beginning of the motion, for seven target speeds. Note that the pursuit response is graded with speed, becoming both more vigorous and more extended in time at higher target speeds.

Figure 1c shows an analysis of these traces to examine the effects of target speed on eye acceleration during the open-loop phase of pursuit. The value of eye acceleration is plotted for each target speed for an early interval (the first 40 msec of pursuit) and a later interval (the next 60 msec) in each averaged record. Both components of eye acceleration grow monotonically with target speed, with the earliest acceleration component (lower curve) saturating around 15°/sec. At much higher target speeds (in excess of 120°/sec, not shown), the later component of the pursuit response falls off (Lisberger and Westbrook 1985).

This sort of monotonically graded response to target

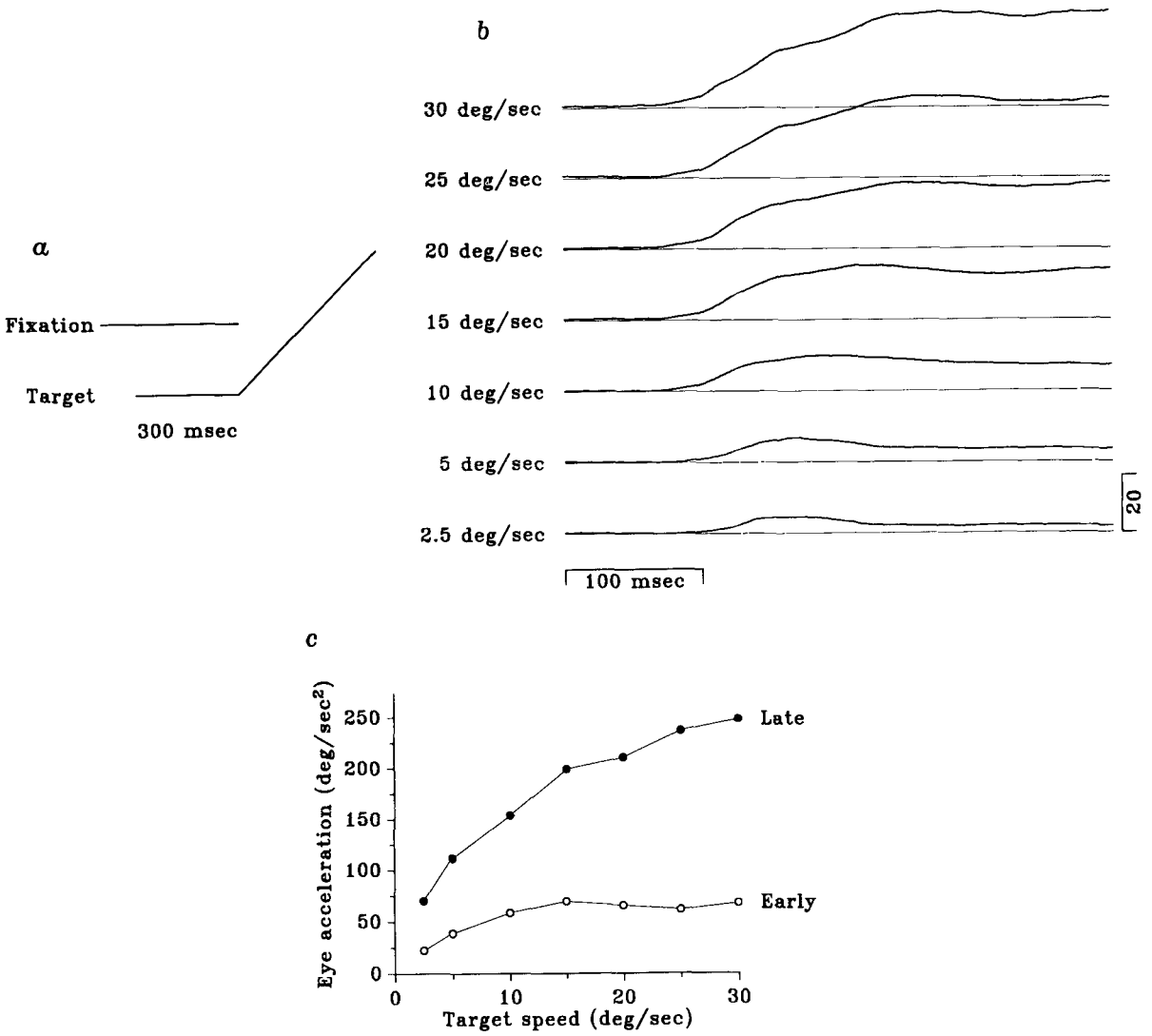


**Figure 1.** Pursuit eye movement responses to targets moving at different speeds in a modified step-ramp task. (*a*) The monkey viewed a central fixation target before the beginning of each trial. After an unpredictable interval of 600–900 msec, the pursuit target appeared; 300 msec later, the fixation target disappeared and the pursuit target began to move, signaling to the monkey the beginning of the pursuit task. (*b*) Averaged eye-speed traces from trials of the type shown in *a*, for leftward pursuit. Each trace is the average of between 10 and 20 responses. The vertical calibration next to the bottom record is 20°/sec. (*c*) Eye acceleration values derived from the records shown in *b* and similar data for rightward pursuit. The curve marked "early" plots acceleration in the first 40 msec of pursuit; the curve marked "late" plots acceleration in the following 60 msec.

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speed has led to the notion that the visual representation of target speed might be similarly graded (see, e.g., Robinson et al. 1986; Krauzlis and Lisberger 1989). Interestingly, the representation of target speed by MT neurons is not graded in this way but is instead based on a multiple-channel strategy in which each neuron is selective for a range of speeds, and neurons having different speed preferences are intermingled (Maunsell and Van Essen 1983). Thus, the visual motion signal driving pursuit responses to different target speeds cannot come from a single neuron or pool of neurons but must derive instead from separate groups of speed-tuned neurons. This transformation of signals from an array of speed-tuned channels to a pursuit command remains unexplored.

***Latency dependence on speed.*** Pursuit responses to targets of different speeds are graded, but responses to low and high speeds are not scaled replicas of one another—there is a systematic effect of target speed on pursuit latency. Inspection of the traces in Figure 1b shows that pursuit begins with a shorter latency for higher target speeds. Figure 2 shows an analysis of this effect, plotting the latency of pursuit against the inverse of target speed; the dependence of latency on speed is approximately linear when represented in this way. The intercept of the plotted regression line is the expected pursuit latency at high target speeds, and the slope may be thought of as the distance through which the target must move before pursuit signals arise. The values for the data shown are 81 msec and 4.1 min of arc, respectively. We were interested to determine whether the onset responses of MT neurons depended on latency in a way that could be related to this aspect of pursuit.

Figure 3 shows data obtained from a single MT neuron. Figure 3a shows averaged response histograms

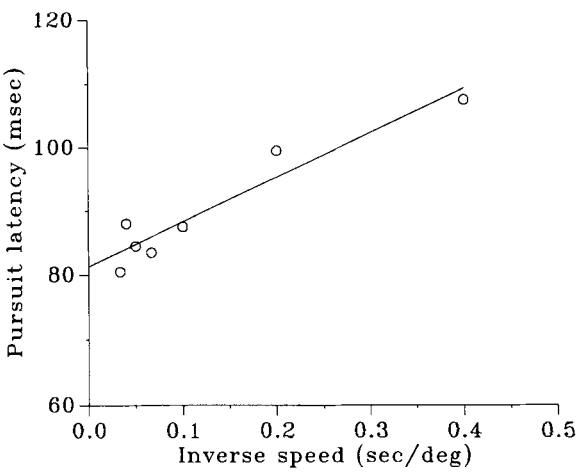


**Figure 2.** Influence of target speed on pursuit latency (derived from the data shown in Fig. 1b). Latency was determined by identifying the first point in averaged eye-speed records at which speed exceeded the resting value. Speed is plotted on an inverse scale. When represented in this way, the relationship between latency and speed is roughly linear; the solid line is the least-squares regression through the data. The intercept of this function is 81 msec, and its slope is 4.1 min of arc.

to a target that remained stationary for 256 msec after it was turned on, and then began to move with the speed indicated under each histogram at the time indicated by the speed trace (bottom) and vertical line. The speed tuning of the cell is evident in the dependence of response magnitude on speed (Fig. 3b). It is also clear that response latency decreased systematically with increasing target speed. This relationship is plotted (again representing speed on an inverse axis) in Figure 3c. The intercept in this case is 49 msec, and the slope is 1.8 min of arc.

Figure 4 compares the derived slope and intercept parameters for 32 MT neurons with the values obtained from the monkey (Fig. 2). The distribution of the value of latency/speed slope for the MT neurons varies fairly widely, but it is centered on the value obtained for the monkey. The shortest asymptotic latencies in the MT cell population are 25–30 msec shorter than the behavioral asymptotic latency, but this difference should be interpreted with caution because of the somewhat different conditions of visual stimulation in the two sets of experiments.

***Motion onset delay.*** Krauzlis and Lisberger (1987, 1989, and unpubl.) have studied an additional factor that influences both the latency and the briskness of pursuit eye movement responses to step-ramp targets: the duration of illumination of the pursuit target before it begins to move. Figure 5 shows the nature and magnitude of this effect. Figure 5a shows a schematic representation of the oculomotor paradigm. At the beginning of a trial, the fixation light was illuminated. The pursuit target then was illuminated; after an unpredictable delay (dashed line), the fixation light was extinguished and the pursuit target began to move at 5°/sec. The monkey was obliged to maintain fixation on the fixation target until it disappeared.

The traces in Figure 5b show averaged eye speed records for the series of delay values indicated beside each histogram. The beginning of each record corresponds to the onset of target motion. The eye-speed records all have the same general form: a rapid rise in eye speed to or slightly beyond the target speed, followed by a more gradual approach to the 5°/sec target speed. Inspection of the records reveals that the onset of the response is delayed and the initial eye acceleration is reduced when the motion onset delay is less than 100 msec or so. This impression is confirmed by Figure 5c, which plots the eye acceleration during the first 40 msec of pursuit as a function of the delay of motion onset from target onset.

Krauzlis and Lisberger (1989) interpreted these data in the context of a mechanism that signals transient acceleration by differentiating an internal representation of target speed, but it is also possible to view this effect in more basic visual terms. When a target flashes on, the transient spreads spatiotemporal energy over the entire range of speeds and directions. If the target starts moving as soon as it appears, one might imagine that accurate information about motion would be

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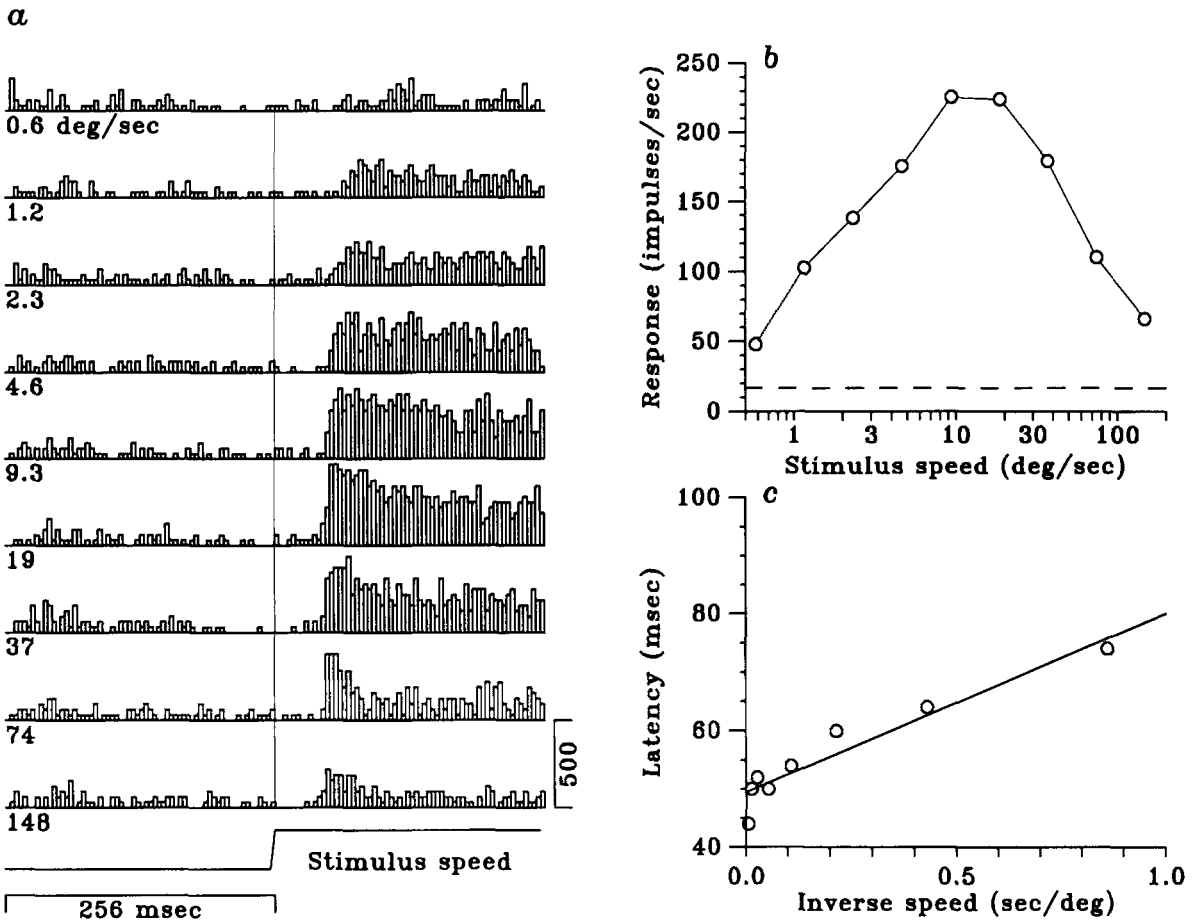


**Figure 3.** Influence of target speed on the response of a single MT neuron. (*a*) Average response histograms showing the responses to the onset of motion at different speeds (indicated under each histogram). At time 0 (the left end of each histogram), a stationary field of random dots appeared on a previously dark screen. After 256 msec (step in the speed trace at bottom, line through the histograms), the dots began to move at the indicated speed. The vertical calibration beside the bottom histogram is 500 impulses/sec. (*b*) Speed tuning curve for the same neuron, derived from measurements of the neuron's steady-state responses to dot fields drifting at different speeds. The dashed line indicates the maintained discharge measured in the presence of a stationary random dot field. (*c*) Relationship between the latency of neuronal response and stimulus speed, derived from the histograms shown in *a*. As in Fig. 2, speed is plotted on an inverse scale, and the solid line is the least-squares regression line. The intercept in this case is 49 msec, and the slope is 1.8 min arc.

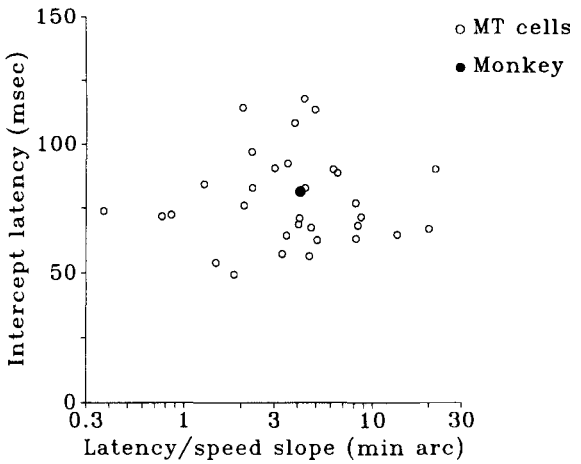


**Figure 4.** Distributions of the slope and intercept parameters derived from regression fits (Figs. 2 and 3c) for 32 MT neurons (○) compared with the data for the monkey (●).

masked or attenuated by the spatiotemporal "splatter" produced by the flash. If, on the other hand, enough time elapsed between target onset and motion onset for this transient signal to die away, the beginning of target motion could produce an unmasked response. With this explanation in mind, we decided to examine the responses of MT neurons as a function of the delay between target onset and motion onset.

Figure 6 shows the responses of the same MT neuron whose data were shown in Figure 3 to the onset of the motion of a random-dot target that was illuminated for a variable period before it began to move. The extent of the stationary foreperiod is indicated by the leftward extension of each histogram before the time (deflection in the bottom trace) at which target motion began. Clearly, the neuron's response shows an effect of varying motion onset delay that is qualitatively similar to that shown in the eye movement data of Figure 5,

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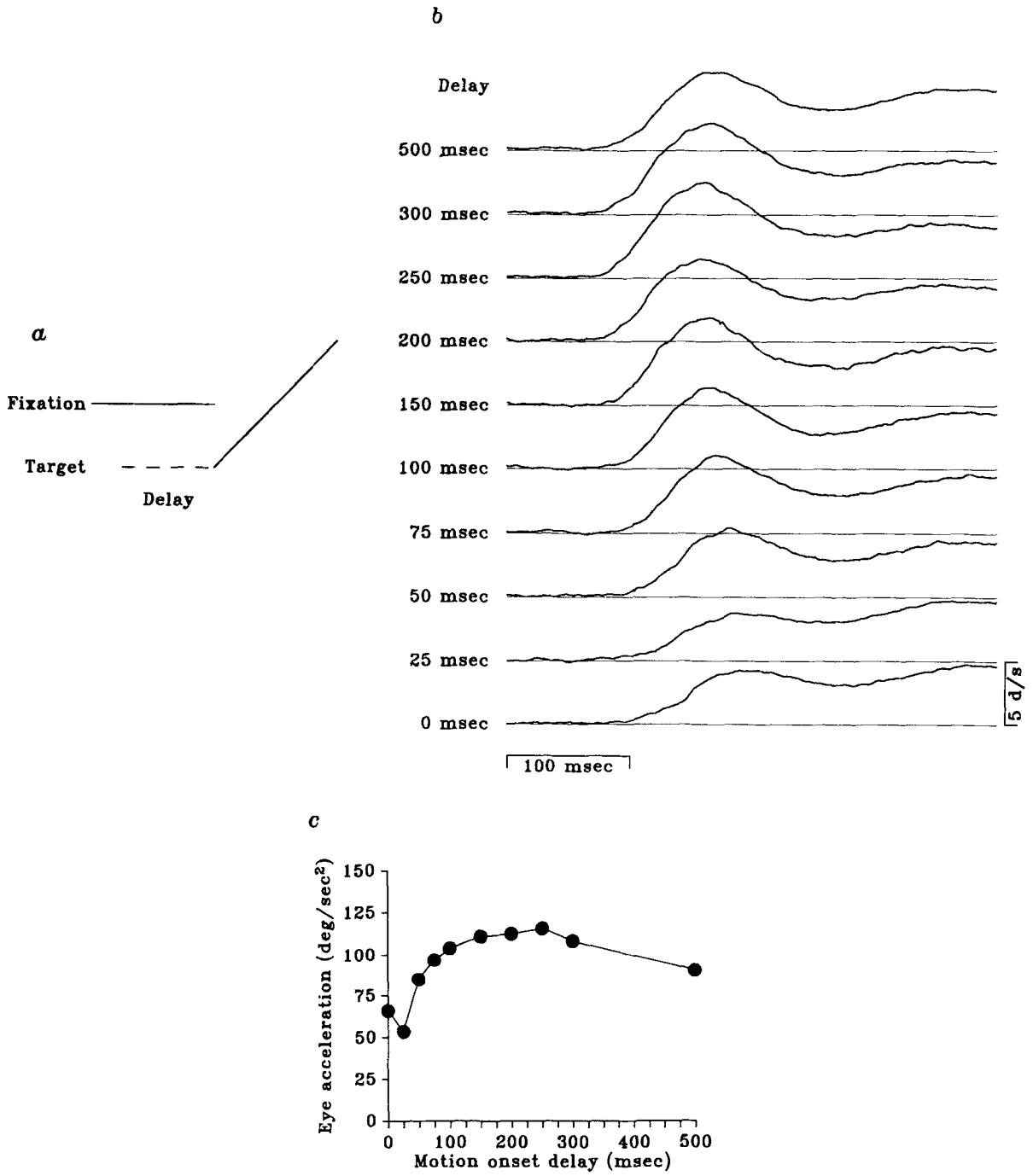


**Figure 5.** Pursuit eye movement responses to targets whose motion onset was delayed by different amounts. (*a*) Monkey viewed a central fixation target before the beginning of each trial. After an unpredictable interval of 600–900 msec, the pursuit target appeared; a variable delay later, the fixation target disappeared and the pursuit target began to move at 5°/sec. (*b*) Averaged eye-speed traces from trials of the type shown in *a*, for leftward pursuit. Each trace is the average of between 10 and 20 responses. The vertical calibration next to the bottom record is 5°/sec. (*c*) Eye acceleration values during the first 40 msec of pursuit, derived from the data shown in *b*, and from other data for rightward pursuit.

becoming brisker and shorter in latency as the motion onset delay is increased.

To analyze this similarity, we took each histogram, aligned it to the motion onset, and then calculated the difference between the response and the response measured with no onset delay (the bottom record in Fig. 6). We then calculated the peak of this difference firing rate function as a function of delay. The results of this analysis are shown in Figure 7. Figure 7a shows data from the neuron whose responses are illustrated in Figure 6; Figure 7b shows data from a second neuron that was studied over a wider range of delays. Plainly, both neurons show an effect of motion onset delay that is similar in time course to the effect of such delays on

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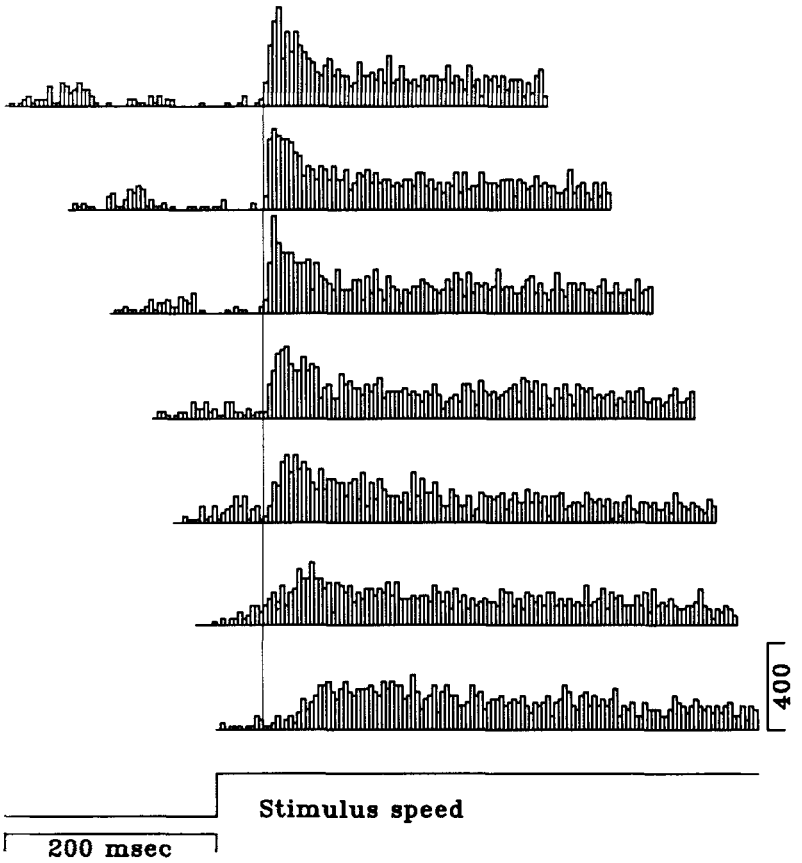


**Figure 6.** Responses of an MT neuron to target motion beginning with a variable delay after target onset. The target appeared at the beginning of each average response histogram; the histograms have been shifted so that they are aligned on the subsequent onset of target motion (speed trace at bottom). The vertical line marks a time 44 msec after motion onset to facilitate comparison of latency across the histograms. The vertical calibration on the bottom histogram is 400 impulses/sec; the speed for all targets was 37.1°/sec.

eye acceleration (Fig. 5). All the neurons we studied in this way showed similar effects of motion onset delay, although the time course of the effect varied slightly from neuron to neuron.

### Effects of Target Acceleration

The data and simulations of Krauzlis and Lisberger (1987, 1989) suggested that the pursuit system might have access to information about both the speed and acceleration of visual targets. We therefore explored the responses of MT neurons to targets whose speed and acceleration varied.

Figure 8 shows the responses of the same MT neuron (data shown in Figs. 3 and 6) to a series of target accelerations and decelerations. The histograms on the left show responses to a 128-msec acceleration pulse that produced a ramp of target speed, from a base speed of 0 (bottom trace). The histograms on the right show responses to a similar deceleration pulse that brought target speed from some value down to 0. The acceleration values are shown under the left-hand histogram of each pair, and the terminal speeds (for acceleration trials) or initial speeds (for deceleration trials) are given under the right-hand histogram. For low acceleration values, the neuron responded with a simple increase or decrease in firing (for acceleration and deceleration, respectively), suggesting that only speed-related signals were present. When the acceleration values increased, however, the neuron's response developed a distinct pulse coinciding with the period during which speed changed. This response pulse could represent the kind of acceleration-related signal needed to account for the sensitivity of the pursuit system to target acceleration.

Note that the acceleration-related responses do not suggest any particular tuning for acceleration on the part of the neuron. For example, response pulses were evident both for target acceleration and deceleration. Inspection of the data, in combination with the speed tuning of the neuron (Fig. 3b), suggests that these acceleration-related responses could arise as a simple consequence of the neuron's speed tuning. Notice that acceleration-related response pulses occur when the stimulus speed ramps between values that straddle the neuron's optimal speed (roughly 15°/sec; Fig. 3). This response pattern could arise because the stimulus' speed traverse begins at a low (or high) speed ineffective for the neuron, changes to an intermediate value that is more effective, and then ends at a high (or low)

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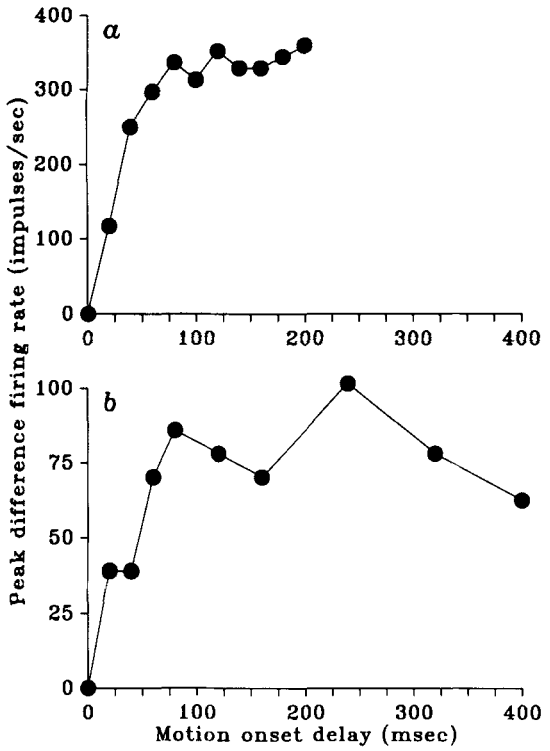


**Figure 7.** Response enhancement produced by delaying the onset of target motion in two MT neurons. Response histograms like those shown in Fig. 6 were aligned to motion onset and subtracted; the value plotted is the peak of the resulting difference histogram and represents the degree of response enhancement produced by motion onset delay. (*a*) Responses of the neuron whose data are shown in Fig. 6. (*b*) Responses of a second neuron studied over a wider range of delays.

value that is again ineffective. Thus, the "pulse" arises not from a specific sensitivity to acceleration, but from the fact that the stimulus traverses the neuron's speed tuning curve in a way that produces a pulse of excitation. We have attempted to account quantitatively for response waveforms like those shown in Figure 8 by synthesizing predicted responses from the neuron's magnitude and latency of response to different speeds (Fig. 3). In some cases, including the neuron whose data are shown, these predictions are reasonably accurate, but they do not account for the observed asymmetry between responses to acceleration and deceleration. It seems to be necessary to add an additional dynamic stage in order to account properly for the shape of the response, which often includes a markedly greater response to target acceleration than to deceleration.

Another way to determine whether MT neurons are especially sensitive to target acceleration is to try to learn whether their acceleration-related responses are invariant when other stimulus conditions change. Figure 9 shows data (again for the same neuron as in Figs. 3, 6, and 8) from an experiment of this kind, in which we studied the effect of varying the base speed on acceleration-related responses. The left-hand histograms show responses to target accelerations whose durations were adjusted so that speed increased from a base speed of 0°/sec to 18.5°/sec (a value close to optimum: Fig. 3c). The right-hand histograms show responses to an identical acceleration series, but with a base speed of 18.5°/sec and a terminal speed of 37.1°/sec (above optimum). It is clear, first, that base speed

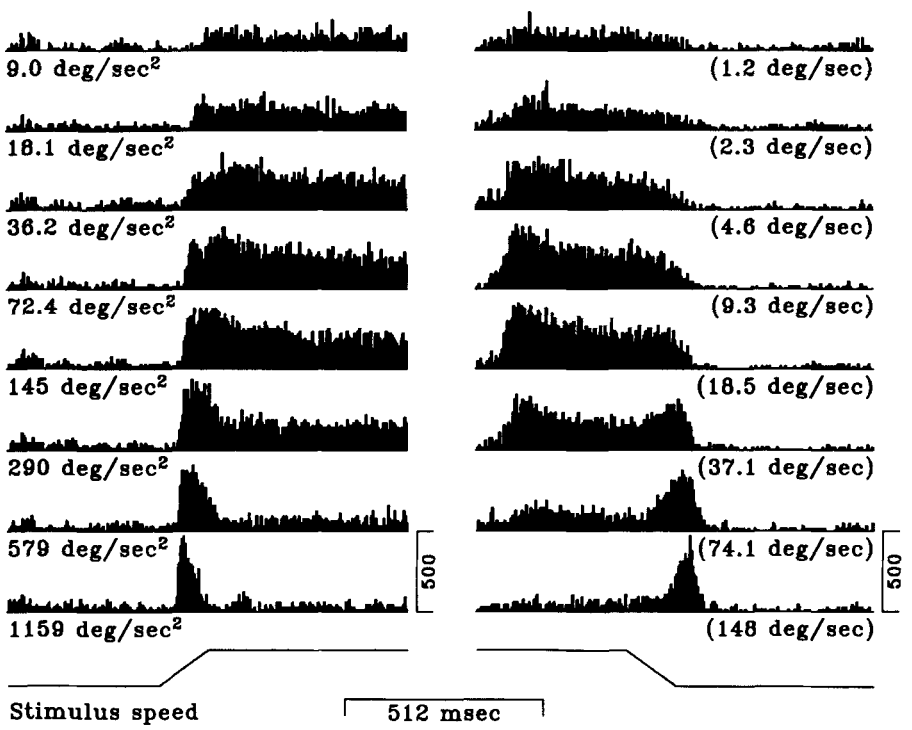


**Figure 8.** Responses of an MT neuron to target acceleration (*left*) and deceleration (*right*). The trace at the bottom of each column gives the time course of stimulus speed throughout the trial; acceleration or deceleration occurred in a 128-msec interval delayed 384 msec from stimulus onset. Stimulus acceleration (or deceleration) is given under the left-hand histogram of each pair; the terminal (or initial) target speed is given under the right-hand histogram of each pair. The initial speed for acceleration trials was 0°/sec, as was the terminal speed for deceleration trials. The calibration next to the bottom histograms is 500 impulses/sec.

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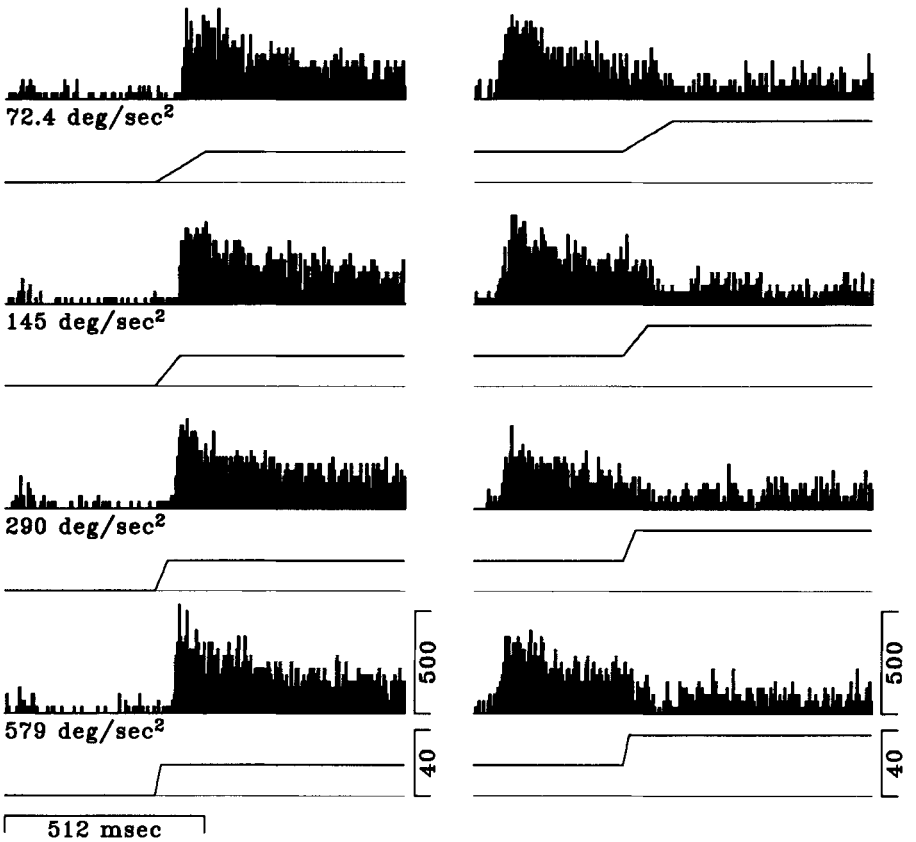


**Figure 9.** Effect of base speed on acceleration-related responses in an MT neuron. The trace under each histogram shows stimulus speed throughout the trial. For the histograms on the left, the initial speed was 0, and the acceleration duration was adjusted so that the terminal speed was 18.5°/sec. For the histograms on the right, the initial speed was 18.5°/sec and the terminal speed was 37.1°/sec. The acceleration for each pair of histograms is given under the left-hand member of the pair. The calibrations on the lowest histograms and speed traces are 500 impulses/sec and 40°/sec, respectively.

had an important effect on the response. When the target accelerated from 0 to near optimal speed, there was a brisk response including a modest acceleration-related pulse. However, when the target accelerated from near optimal speed to a much higher speed, there was a mild decrease in response. Second, the specific acceleration value had little influence on the response—all the histograms on the left or on the right are rather similar. This pattern of results can again be predicted from the neuron's simple speed tuning (Fig. 3b), by noting that the left-hand histograms show responses to speed modulation between two speeds of very different effectiveness, whereas the right-hand histograms show responses to speed modulation between two speeds of roughly similar effectiveness.

These experiments suggest that MT neurons are not "acceleration-tuned" in the same sense that they are direction- or speed-tuned, because direction and speed tuning depend very little on other stimulus parameters. However, all the neurons we studied showed brisk acceleration-related discharge pulses for suitable choices of base speed and acceleration. These response pulses might well serve the purpose of providing signals like those hypothesized by Krauzlis and Lisberger's (1989) model, in which acceleration signals serve mostly to enhance pursuit commands when retinal velocity changes. They could not serve, however, as the basis for a comprehensive representation of target acceleration in MT.

## DISCUSSION

The experiments in this paper were designed to explore the notion that many of the dynamic features of pursuit eye movements are a consequence of fundamentally visual, rather than motor, processes. The results reveal that the response properties of neurons in area MT do indeed have many features in common with the pursuit command signals inferred from studies of the open-loop phase of pursuit in monkeys. In particular, the dependence of MT response latency on target speed is similar to the dependence of pursuit latency on target speed; the effects of introducing delays between the onset of a target and the onset of its motion are similar for MT responses and for pursuit; MT neurons produce acceleration-related responses that may provide the target acceleration signal inferred from analysis of the pursuit system.

A natural question about these results is whether the interesting features of MT responses arise in MT or whether they might be present even earlier in the visual pathway. We have not studied the responses of neurons in V1 to the kinds of stimuli used in these experiments, but it is reasonable to suppose that neurons there might give similar responses. Supporting this is evidence from a series of simulations in which we explored the response of a modified version of the motion energy sensor model of Adelson and Bergen (1985) to motion profiles of the kind used in our experiments. Adelson

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and Bergen's model is an idealized model of directional mechanisms in primary visual cortex (cf. Emerson et al. 1987). Interestingly, the motion energy simulation seems to capture the dependence of response latency on target speed (Fig. 3) and to generate acceleration-related response pulses under conditions similar to those used to collect the data shown in Figures 8 and 9. The motion energy model does not, however, seem to show any effect of motion onset delay (Fig. 6). Our suggestion that the effect of motion onset delay might arise through interference from transiently elicited signals in sensors having other preferred speeds and directions suggests that interactions among motion sensitive neurons—not included in the Adelson and Bergen model—might be necessary to account for this effect.

A second question concerns the nature of the further processing needed to transform the visual motion signal provided by MT into pursuit commands. Our results suggest that relatively little transformation of the neural signal would be required, other than the transformation from the channel-based representation of speed in MT into the monotonic representation needed to drive eye acceleration (Figs. 1 and 3). A major component of pursuit control, however, is its dependence on conscious decision and motivational processes. For example, the pursuit system must select the components of the visual image that are the target to be tracked and exclude signals related to the movement of other targets or the background. Pursuit also depends strongly on the alertness and attentional state of the animal. Studies of the discharge of cortical neurons during pursuit initiation suggest that few signals of this kind are present in MT neurons. It is possible to imagine that the visual motion signals from MT are combined with or gated by decision-related signals arising elsewhere in the cerebral cortex, to provide suitably formulated signals passing into the ponto-cerebellar pathways, and thence into the cerebellum and brainstem to form motor commands. This scheme would place MT just on the sensory side of the sensory-motor link, and the ponto-cerebellar pathways at the beginning of a set of fundamentally motor pathways. It would appear that by continuing to study visual motion processing in the areas associated with MT, in combination with the decision-related processes arising elsewhere in the pursuit pathways, we can come in time to a full account of the sensory-motor interactions that give rise to this basic class of visuomotor behavior.

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