

TIGHT CORRELATION BETWEEN THE TIME COURSE OF SENSORY AND MOTOR ESTIMATES OF TARGET DIRECTION IN SMOOTH PURSUIT.

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Abstract: The sensory task of the smooth pursuit system is to extract an estimate of target velocity from image motion on the retina, and its motor task is to accelerate the eyes to match target velocity. We quantified the directional accuracy of early pursuit eye movements and relate this to the sensory signals in cortical area MT likely to mediate the behavior. We computed the signal-to-noise ratio as a function of time in primate eye velocity responses to visual targets whose trajectories differ by small angles. We found that about 80% of the final directional accuracy of the eye movement is achieved within its first 100ms. In experiments in anesthetized macaques, we measured the responses of single MT units to stimulus motion differing by small angles. Computing the time course of direction information available in MT responses, we found that neurons also provide about 80% of their maximal information within the first 100ms of their responses. Therefore, target direction information can be extracted from single units as quickly as behavioral performance requires it. Individual MT neurons were much less directionally accurate than the eye movement itself, necessitating a mechanism for pooling information from many neurons to achieve the observed behavioral accuracy.

Summary:

In smooth pursuit eye movements, primates move their eyes continuously to track the motion of a target across the visual field. The smooth eye movement is specific to the speed and direction of motion of the target, and it depends on an estimate of the vector velocity of the target. Because the retina is attached to the moving eye, the visual input to the brain is image velocity rather than target velocity, which varies as tracking is initiated and refined. Indeed, the latency from visual input to smooth eye movement output dictates that the visual motion signals for pursuit vary on a time scale of about a hundred milliseconds. The sensory-motor system that drives pursuit must be able to extract reliable estimates of image direction and speed over this time scale. In two sets of experiments and analyses, we examine the time course of directional accuracy of pursuit behavior and the information about target motion direction available from single neurons in the pursuit system.

In the first part of this project we investigate the directional accuracy of pursuit eye movements as a function of time. We recorded the horizontal and vertical components of eye velocity of several rhesus macaques pursuing visual targets that stepped away from a central fixation point then moved at constant speed in a randomly chosen direction. The set of directions used for each experiment differed by intervals of 1 to 3 degrees. We can think of the eye velocity signal, observed in a time window from 0 to T , as being a vector of points $\vec{s} = \{s_i\}$, where the index i marks the different samples

in time (1ms intervals) and the different components of motion, horizontal and vertical. For each direction of target motion, θ , we can compute the average signal across trials, subtract this from the eye velocity on each trial to form an eye velocity noise vector, $\delta\vec{s} = \vec{s}(\theta) - \langle \vec{s}(\theta) \rangle$, and then compute the covariance matrix for these noise vectors,

$$C_{ij} = \langle \delta s_i \delta s_j \rangle_{\theta} \quad (1)$$

where i and j index points in time and $\langle \dots \rangle_{\theta}$ denotes an average over all trials with target motion in direction θ . For these small changes in direction, the covariance matrix does not depend on θ , so we obtain a better estimate by lumping together all the trials. To a very good approximation the fluctuations δs_i are distributed as Gaussian random variables and so this covariance matrix provides a complete description of their statistics. From the mean signals, $m_i(\theta) = \langle s_i(\theta) \rangle$, and the covariance matrix of the noise, we can define the signal-to-noise ratio for discrimination between two different target directions θ and θ' :

$$\Delta m_i(\theta, \theta') = m_i(\theta) - m_i(\theta') \quad (2)$$

$$SNR(\theta, \theta'; T) = \sum_{i=1}^{2T} \sum_{j=1}^{2T} \Delta m_i(\theta, \theta') (C^{-1})_{ij} \Delta m_j(\theta, \theta') \quad (3)$$

where C^{-1} denotes the inverse of the covariance matrix. The difficulty in using this equation to analyze experimental data is that small amounts of noise in vectors and matrices of very high dimensionality can lead to large errors. We deal with this problem in two ways. First we assume that the component of the eye velocity along the average direction does not provide any significant signal to the discrimination. For example, if the directions of motion are small angles near horizontal, say -4, -2, 0, +2, and +4 degrees, the vertical component of the eye velocity would carry most of the signal to discriminate target direction. This reduces the dimensionality of the covariance matrix by half. Second, we find that the variance is dominated by fluctuations in two directions, corresponding to the two largest eigenvalues of the covariance matrix. We can therefore take the total signal-to-noise ratio as the sum over the contributions from each of the two largest eigenvalues, and this result should be a conservative estimate of the monkey's performance that is more robust to against artifacts and the finiteness of the data set.

We find experimentally that the signal-to-noise ratio for pairs of angles θ, θ' scales as $SNR(\theta, \theta'; T) \propto (\theta - \theta')^2$, as expected theoretically. Thus we can rewrite the signal-to-noise ratio as an effective threshold for reliable discrimination of target direction, which is the difference in direction $|\theta - \theta'| = \Delta\theta_{thresh}(T)$ that would generate $SNR = 1$ (equivalent to 69% correct). From preliminary data from three animals, the minimum threshold for reliable direction discrimination ranges from 3.0 to 5.9 degrees, with a mean of 3.9 and a median of 3.5 degrees. The minimum threshold does not depend on the average direction of target trajectories within 45 degrees of horizontal.

This level of performance develops rapidly within the pursuit eye movement. Within 100 ms of the onset of the eye movement, the direction threshold is within 71 to 91% of its minimal value (mean 78% and median 80%).

In the second series of experiments, we investigate the neural basis of the directional accuracy of smooth pursuit behavior by measuring the time course over which information about target motion is represented in the primate visual system. Previous work has implicated extrastriate area MT as a major source of the visual signals that control pursuit eye movements. MT provides a major cortical projection, via the pontine nuclei, to the parts of the cerebellum that control smooth pursuit. Further, neurons in MT have response properties that seem appropriate for guiding pursuit: they are selective for moving stimuli and are tuned for the direction and speed of motion. However, the question remains open whether MT neurons can provide reliable guidance about target direction and speed on the hundred-millisecond timescale needed by pursuit.

To ask how target direction could be decoded on this time scale, we have calculated the time course of Shannon information from spike count about motion direction in individual MT neurons recorded extracellularly in anesthetized primates (*Macaca fascicularis*). Stimuli were random dot patterns, stepped from stationary to the preferred speed of the cell for 256 ms, in a direction randomly chosen with 7.5 or 15-degree increments. Each stimulus direction was repeated ~150 times, enabling us to measure the distribution of spike count n at time T conditioned on the motion direction θ , $P_T(n|\theta)$. The mutual information between spike count and motion direction as a function of time is defined as:

$$I_{count}(T) \equiv I_T(n; \theta) = \sum_{\theta} P(\theta) \sum_n P_T(n|\theta) \log_2 \left[\frac{P_T(n|\theta)}{P_T(n)} \right] \quad (4)$$

$I_{count}(T)$ measures in bits the amount of information that a single observation of the spike count n provides about the direction of motion θ . Note that $P_T(n)$ is the total probability of observing n spikes after counting over a time interval T , averaged over all stimuli. In our case all stimuli occurred with equal probability.

All methods of analysis indicate that the majority of information about motion direction is encoded early during the onset of the response when the cells have fired only a few spikes. Information calculated from cumulative spike count rises rapidly, reaching ~80% of its maximal value in the first 100 ms of the neural response (range 50-97%, mean 78% and median 79%, $n=26$ cells encoding at least 0.2 bits of information). After this initial period, direction information from the cumulative spike count rises much more slowly during the remaining 156 ms of our motion stimulus. Thus, continuing to integrate neural responses to constant motion beyond this time window does not substantially improve the estimation of motion direction. This is true no matter when in the response we start counting spikes, so it is not strictly a property of MT units' onset responses, although spikes during the onset transient do contribute slightly more information per spike than during the later portion of the response. Rather, this time limit is imposed by the presence of temporal correlations that cause fluctuations in the spike

count to be correlated within a trial on a ~ 100 ms time scale. These cause the variance of the count to increase more rapidly than the mean with the size of the averaging window. Hence, averaging the firing rate or count across the whole response does not substantially improve the estimate of the stimulus direction. While absolute values for the information about direction are not large under these stimulus conditions (maximum bit values range from 0.04-1.3 bits, $n=36$, mean 0.49 median 0.43 bits out of 3.7 bits possible for 13 stimulus directions), this population of cells responds near the maximum entropy limit for their firing rates. We conclude that almost all available directional information could be extracted from the first few spikes of the neuron's response, on a time scale comparable to the initiation of smooth pursuit eye movements.

The previous analysis summarizes the time course of direction information but does not assess the directional acuity of the neurons in a manner we can compare to the behavior. MT units have symmetric directional tuning curves, such that spike rate varies with motion direction with a Gaussian or half-cosine profile around a preferred direction. We have the intuitive expectation that any given MT neuron will discriminate a pair of directions better on the steeper flanks of its tuning curve, where the mean responses are more separated, than it will a pair straddling its peak, where the mean responses are similar. To compare the direction discrimination thresholds of the MT units to the animal's behavior, we compute the mutual information for each pair of stimulus directions (7.5 or 15 degree increments), again from the cumulative spike count, which we can express as an equivalent choice probability for an ideal observer discriminating one direction from the other (e.g. 0.11 bits is equivalent to 69% correct). We find that the neurons match our expectation in the sense that they encode more information about pairs of directions that both fall on the flanks of their tuning curves. The difference between the information encoded on the flank and at the peak (relative to the information on the flank) ranges from 28% to 97% (mean 74%, median 79%, $n=22$ reached 69% correct) for 60 degree separated stimulus pairs. But the neurons do not match our expectation in the sense that the smallest discriminable pair (reaching 69% correct) does not vary with distance from the preferred direction. The population mean neural directional threshold is about 30 degrees both near the preferred direction and at 60 degrees away. The average shift in threshold is only 4 degrees between the two locations on the tuning curve ($n=20$ reached 69% correct). To compute the average directional threshold for a unit, we take the mean of the neural direction threshold (at 100 ms) within +60 and -60 degrees of the preferred direction. This ranges from 7.5 to 68 degrees across 34 units, with a mean of 34 and a median of 33 degrees. We conclude that the average directional acuity of individual MT neurons is about a factor of ten worse than that of pursuit behavior. Therefore the pursuit system must pool responses across MT neurons to improve the estimate of target direction in order to produce the observed behavioral accuracy.

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