Integration of Motion Signals for Smooth Pursuit Eye Movements

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How does the brain combine *local* motion measurements to form an accurate description of *object* motion? For example, if a vertically oriented bar moves upward and rightward at a constant velocity, a neuron with a small receptive field positioned along the length of the contour can measure only the rightward component of motion, since the upward component provides no time-varying information within its receptive field. In contrast, cells positioned at the endpoints of the contour can measure motion direction accurately. Because direction-selective neurons early in the visual pathways have small receptive fields, the visual system is constantly faced with this "aperture problem."[1] And since they provide the sole input to subsequent stages of cortical visual processing, which in turn inform the premotor circuitry used for making eye movements, the error in measuring local velocity could be perpetuated. How are these conflicting motion signals—the potentially erroneous signals measured along a contour and the correct signals originating from terminators—ultimately resolved in the visual cortex?

Microelectrode recordings from neurons in the middle temporal visual area (MT) of alert monkeys have shown that the earliest directional responses, beginning about 80 msec after the onset of stimulus motion, primarily encode the component of motion *perpendicular* to the orientation of a contour. That is, they are strongly affected by the ambiguous contour signals. However, the later responses (>140 msec after motion onset) encode the true direction of motion, irrespective of contour orientation. Thus the responses of MT neurons reflect the solution of the aperture problem for motion over a period of about 60 msec.[2]

Given the evidence that MT neuronal signals are important for the initiation of smooth pursuit eye movements,[3–5] we asked whether the time-evolving signals we observed in MT neurons had a behavioral correlate. We had subjects (monkeys and humans) track the center of a single moving bar whose orientation was varied with respect to its direction of motion. The bar was dim green (4.2 cd · m^{-2}; $u' = 0.28$, $v' = 0.59$), and its center was indicated by an isoluminant, red gaussian blob

(4.2 cd · m^{-2}; $u' = 0.64$, $v' = 0.34$). The subject had to track the blob to within $\pm 3°$ while eye movements were monitored using a scleral search coil. Eye position and velocity (analog differentiator: low pass, -3 dB at 50 Hz) were digitized at 1 kHz and stored to disk for off-line analysis.

In agreement with previous studies of both human perception[6] and the human ocular following response,[7] the initial direction of pursuit deviated in a direction *perpendicular* to the orientation of the bar, regardless of the true direction of bar motion. We then asked how the relative amounts of contour and terminator information affected the behavior by varying the *length* of the bar on randomly interleaved trials. Increasing bar length had the expected effect of increasing the magnitude of the deviation, as measured by the initial eye acceleration perpendicular to the direction of target motion. This effect of bar length was decreased if the targets were presented eccentrically, consistent with the predicted effects of larger receptive field sizes with increased eccentricity (magnification factor).

To study such scaling effects more thoroughly, we next used long bars of varying *widths*, which had the effect of symmetrically displacing the ambiguous contour signals various distances from the fovea. The "bars" for these experiments were actually parallelograms (i.e., end contour parallel to direction of bar motion), chosen so that we did not introduce potentially disambiguating contour signals at the ends of the bar. These results showed the same effect described above (i.e., smaller deviations with greater eccentricities) and also afforded us the opportunity to examine longer periods of pursuit uninterrupted by saccades. Interestingly, the earliest period (0 to 40 msec from the onset of pursuit) showed a relatively shallow, nearly *linear* decrement in perpendicular eye acceleration as a function of eccentricity, whereas the later period (40 to 80 msec) showed a much steeper, *exponential* decline. This differential sensitivity to eccentricity is reminiscent of a similar difference found for initial eye acceleration as a function of target position[8] and supports the idea that the early phase of pursuit initiation is driven by inputs that de-emphasize the central visual fields,[9] or, alternatively, have uniformly large receptive fields across the representation of visual space—such as those from the accessory optic system.[10] In this scheme, the later phase of pursuit initiation would be driven by the cortical pathway involving area MT, which inherits a considerable emphasis on foveal vision from the striate cortex and thus exhibits an exponential decline in magnification factor.[11]

Finally, given the robust nature of the "bottom-up" contour effects on pursuit, we thought it would be interesting to pit these signals against more "top-down" signals based on the predictability of target motion. We performed two types of experiments in both monkeys and humans. In the first, target motion on any given trial could be in one of four possible directions, but, on half of the trials, target onset was preceded by a cue that indicated the direction of motion of the upcoming target. In the second type of experiment, the direction of motion was exactly the same on every trial. For the monkeys, neither one of these manipulations affected the magnitude or timing of the contour-induced deviation; however, we as yet have no independent evidence that the monkey made use of the predictive signals. For human observers, predictability reduced the effect by about 50%.

In sum, our results indicate that the primate pursuit system initially derives a rough estimate of direction by *averaging* local motion signals obtained from neurons with relatively small receptive fields. The same effect of ambiguous contour motion

has been observed in human perception,[6] the human ocular following response,[7] and the responses of MT neurons.[2] The initial integration takes place over a remarkably large spatial range—up to 35°—further blurring the distinction between smooth pursuit and other smooth eye movements, such as ocular following and the optokinetic response. The efficacy of spatial integration depends on both eccentricity and the period of pursuit measured, perhaps constituting a signature of early, subcortical influences followed by later, cortical signals. Lastly, in humans top-down signals, such as prior knowledge of true target direction, can clearly reduce the earliest contour-induced effect, but they cannot eliminate it completely.

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