Neuronal Correlates of Optic Flow Stimulation

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INTRODUCTION

Optic flow fields are the patterns of visual stimulation generated by the movement of an observer through the environment. James Gibson emphasized that the structure of this flow field provides information to the observer regarding the observer's movement and the structure of the environment. More recently, psychophysical experiments have demonstrated a remarkable precision in judgment based on optic flow information. For example, the work of Warren and his collaborators has demonstrated using simulated optic flow fields that the observer can determine the heading of simulated self-motion to within a few degrees of arc. Such optic flow also contributes to stabilizing posture and can produce powerful illusory movements.

The neuronal basis for extracting information from optic flow stimuli has remained largely unknown. The critical characteristic of such neuronal mechanisms would seem to be sensitivity to motion over a large area of the visual field. In the monkey such visual areas as the primary visual cortex (striate cortex, or area V1) are responsive to motion but have minuscule receptive fields compared to the large-field stimulation of optic flow. However, several areas of extrastriate visual cortex have large receptive fields and are especially sensitive to visual motion. In particular, the middle temporal area (MT), which receives a direct projection from the striate cortex, has a high concentration of directionally selective cells, the sine qua non of visual motion processing. MT, in turn, projects to another area, the medial superior temporal area (MST), that also has a high proportion of directionally selective cells. For our present purposes, a key feature in this sequence along the pathway from V1 to MT to MST is the expansion in receptive field size. Figure 1 illustrates the approximate size of typical visual receptive fields found in these three areas of visual cortex with the receptive fields centered at 10° from the fovea. Superimposed on these mean receptive fields is an expanding optic flow field pattern with the center of expansion aligned with the point of fixation (FP). A V1 receptive field would subtend a negligible fraction of the optic flow field pattern, an MT receptive field substantially more but still a limited fraction, whereas the MST neuron would encompass a very large fraction of the optic flow stimulation.

Within the MST, Komatsu and Wurtz have identified functional subregions, one a lateral ventral region (MSTl), the other a dorsal medial division (MSTd). MSTl has a large fraction of cells that respond to the motion of small spots and frequently have small receptive fields. Damage leads to a deficit in the maintenance of pursuit eye movements. The relationship of this area to pursuit eye movements has been summarized elsewhere. The cells in the MSTd region have consistently large receptive fields (as illustrated in Figure 1) and in addition frequently prefer motion of large-field patterns rather than small spots of light. Receptive fields of MSTd...
neurons typically include or approach the fovea. Finally, MSTd cells not only respond to planar motion in front of the monkey, but also to rotation or looming of the visual stimulus. These characteristics make the MSTd neurons ideal candidates for the analysis of optic flow patterns, and for this reason we have investigated the responses of MSTd neurons to simulated optic flow stimulation. In this discussion we summarize our investigations of the response of MSTd neurons to optic flow stimulation that have been recently published. Work on the disparity sensitivity of MSTd neurons is considered elsewhere.

RESPONSE OF MSTD NEURONS TO COMPONENTS OF OPTIC FLOW

In our experiments on MSTd neurons, we used a set of translational and rotational stimuli from which all optic flow fields can be derived. These stimuli were
head centered and were designed to stimulate the components of optic flow that would be seen by subjects as they moved through the environment. The translational stimuli (FIGURE 2A) consisted not only of motion in the frontoplane plane, such as left–right, and up–down, but of radial expansion and contraction of the full-field stimulation that would occur as one moved in depth along the axis labeled in–out.

A Translation along axes

![Diagram of translation along axes]

B Rotation around axes

![Diagram of rotation around axes]

FIGURE 2. The basis set of motion components in head-centered coordinates. All motions in three-dimensional space (represented by the three axes, x, y, and z) consist of combinations of translation (as in A) and/or rotation (as in B) along or around these axes. In two cases rotation is very similar to translation: translation along the z-axis is similar to that for rotation around the x-axis; translation along the y-axis is similar to rotation around the z-axis and in these cases we tested only translation routinely. (From Duffy and Wurtz.)
Rotation could occur along any of the same axes (Figure 2B), but in our experiments we used only those along the axis into the frontal plane (z-axis) that produce clockwise and counterclockwise motion. We dropped the other four rotary motions because in preliminary experiments, we found that rotation around the axes labeled x and y approximated the response obtained with up-down or left-right motion, respectively. Our minimal test on all cells, therefore, consisted of four directions of frontal planar motion, in-out radial motion, and clockwise-counterclockwise rotary motion. Applying the same stimulus set (frequently expanded to include eight directions of frontal planar motion) allowed us to systematically investigate and compare the responses of all MSTd neurons.

The monkey in our experiments faced a tangent screen 50 cm in front of it, onto which the 100° × 100° stimuli were projected. It was rewarded for maintaining fixation on a spot, usually at the center of the screen, for the duration of the stimulus presentation. Since all receptive fields included or closely approached the fovea, and since that is the visual area of greatest responsiveness, we usually centered the stimuli over the fovea.

We studied over 200 single neurons in the MSTd and obtained a variety of response profiles to the optic flow stimuli. Some neurons gave selective responses to either planar, circular, or radial motion, and Figure 3 shows an example of neurons responsive to each of these stimuli. In each column of Figure 3, the eight types of visual stimuli are shown down the edge of the column and the response of the cell to that stimulus is adjacent to it. We have used a spike-density display that shows the averaged response for between 6 and 12 presentations of each stimulus. The stimulus duration of 1500 ms is represented by the dark bar; the vertical line indicates the onset of the visual stimulus. We found that many MSTd neurons gave a relatively nonselective early phasic discharge followed by a sustained selective response, and we have therefore concentrated our analysis on the more selective tonic response. In Figure 3, the response of the cell in the left column is clear for leftward motion, that in the middle column is clearest for counterclockwise circular motion, and that in the right column clearest for inward radial motion. While these neurons responded primarily to just one component of the visual stimulus, most MSTd neurons responded to a combination of these motion components. Some neurons responded to planar and circular motion, or to planar and radial motion. In these cases, however, the motion selectivity was to one type of circular or radial motion or one direction of planar motion, not an indiscriminate response to all planar, circular, or radial motions. For example, a cell responding to planar and circular motion responded to counterclockwise motion only and to leftward motion only. Other neurons responded to planar, circular, or radial motion. We quantified the tonic response of
these neurons by requiring a statistically significant response of the neuron above the firing rate when the monkey fixated but no visual stimulation appeared. Using Student's t-test to make the distinction \( p < 0.01 \), we found that 23% of the neurons responded to only a single component of optic flow (planar, circular, radial), 34% responded to two components (planicircular or planoradial), and 22% responded to three components. In our sample we did not find cells that gave a significant response to both circular and radial stimulation without having a significant response to planar motion. Further analysis showed that these categories were not discrete groupings of cell types, but rather points along a continuum ranging from responsiveness to a single component of the optic flow stimulation at one end of the continuum to responsiveness to all three components of the optic flow stimulation at the other end of the continuum.

This categorization of the cells was based on the excitatory response of the neurons, but as can be seen from Figure 3, some optic flow components produced an inhibitory response in these cells. We found that the frequency of these inhibitory responses also varied along the continuum of the neurons. Single-component neurons had an average of about 3 inhibitory responses per neuron for the set of eight stimuli that we tested, double-component neurons had an average of about 1 inhibitory component response per neuron, and triple-component neurons had only 0.4 inhibitory response per neuron. Thus, as we move along the continuum from single-component neurons to triple-component neurons, the frequency of both excitatory responses and inhibitory responses varied: the single-component neurons appeared to be the most selective, they had limited excitatory responses to one component of the stimuli we used and the clearest inhibition to other components.

In considering the relation of these neurons to optic flow, it is equally important to consider what stimulus factors did not influence these cells. On a smaller sample of cells, we found that most were responsive to a wide range of stimulus speeds over the range of 10° to 80°/second. The response of the cell was remarkably independent of dot density, responding not only to our usual density of 350 dots/100°, but continuing to respond even when this density was reduced to 25 dots/100°.

In summary, cells in MSTd do respond to the components of optic flow stimulation and their insensitivity to dot density and to speed make them ideal candidates for response to large-field optic flow stimulation. However, there is not one cell type in the MSTd, but rather a continuum ranging from highly selective single component neurons to less-selective multiple-component neurons.

**MECHANISMS OF RESPONSE SELECTIVITY**

The response of MSTd neurons to radial and circular motion over a large part of the visual field could indicate that these neurons are carrying out sophisticated higher-order analyses of visual motion. Alternatively, these responses might result from stimulation of parts of the receptive field of a cell that is essentially sensitive to planar motion. For example, Figure 4 shows how a circular response and a radial response might result from a neuron that had only sensitivity to planar motion. A neuron with sensitivity to downward planar motion (Figure 4, upper half) might respond to counterclockwise motion if it just overlapped the right side of the planar-sensitive field, or to clockwise motion if the stimulus overlapped the field on the left. Similarly, a receptive field sensitive to rightward planar motion (Figure 4, lower half) might respond preferentially to inward radial motion if that motion
overlapped the receptive field of the cell on the right side, and to outward radial motion if it overlapped the receptive field on the left side.

We investigated this issue by determining first the response of a single neuron to the large-field stimulation, and then its response to the same stimuli placed in smaller subregions of the stimulus field. If the responses of the cell were dependent upon the position of the stimulus, then we would expect that the stimulation in

![Diagram showing response to circular and radial stimuli](image)

**FIGURE 4.** Response to circular (top) and radial (bottom) stimulation explained by the sensitivity of the hypothetical neuron to planar motion. See text for description.

different subregions of the field would produce different responses as in **FIGURE 4**. On the other hand, if the responses were position independent, then the same stimulus in different parts of the field would produce the same responses. **FIGURE 5** shows the results of such an experiment. **FIGURE 5A** shows the response of the cell to full-field stimulation. In this figure we show the response to the planar, circular, and radial stimuli using a schematic vector summary diagram. Response to planar motion is indicated by the lines to the left, right, up, and down with the amplitude of the line.
FIGURE 5. A triple-component, planocircular radial neuron showing substantial response variability to small-field stimuli. A: The direction diagram shows responses to upward-planar, clockwise-circular, and inward-radial large-field stimulation (100° × 100°). B: Direction diagrams for the small-field studies (33° × 33°) showing variation in planar direction selectivity with strong upward selectivity in the right-lower segment and strong rightward selectivity in the middle-upper segment. Circular direction selectivity reverses from strong clockwise selectivity in the right-lower segment to strong counterclockwise selectivity in the left-upper segment. Radial selectivity is maintained but varies quantitatively, being strongest in the right-upper segment and weakest in the left-lower segment. In all cases the monkey fixated on a point at the center of the large field. (From Duffy and Wurtz.)
indicating the magnitude of the response. Circular motion is indicated by the
hemicircles with the diameter of the hemicircle indicating the size of the response.
Inward radial motion is shown by the arrow running from upper right to center, and
outward motion by the arrow running from the center to lower left with length again
indicating amplitude of response. An arrowhead indicates that the response was
statistically significant at the p = 0.01 level (Student’s t-test). Figure 5B shows the
same stimuli applied to a fraction of the 100° x 100° field (33° x 33° stimuli). The
upward planar sensitivity was present throughout the field; the rightward sensitivity
varied considerably as did the amplitude of the inward radial response. The response
to the circular stimulus varied dramatically, being clockwise for stimuli on the right
side and counterclockwise for stimuli on the left side, and the response of this neuron
to circular stimulation therefore could be explained on the basis of the upward
planar motion using the logic illustrated in Figure 4. Thus, the responses are
position dependent varying with the position of the stimulus within the field.
We obtained a very different result in a similar study on the single-component
radial neuron illustrated in Figure 6. The response of this neuron to full-field
stimulation (Figure 6A) indicated a clear response to radial-inward motion. The
response to stimulation in the small fields continued to show this same inward-radial
selectivity. While the amplitude of the response varied, the neuron basically showed
a position-independent response to inward-radial motion. The response of this
neuron is not easily explained on the basis of its minimal planar response, and its
visual sensitivity is more likely to result from higher-order visual processing.
We compared the response of 160 neurons to the large-field stimulation and to
stimulation within subregions of the field and found a variety of results ranging
between those illustrated in Figures 5 and 6. The salient point was that neurons that
had sensitivity to multiple components of optic flow, such as the triple-component
neuron in Figure 5, were more likely to have a response that could be in large part
explained by planar sensitivity. In contrast, neurons that were sensitive to single
components of optic flow stimulation (such as the neurons sensitive primarily to
inward-radial stimulation in Figure 6) were the least likely to be understood on the
basis of any sensitivity to planar motion. The continuum of selectivity that we have
observed in these neurons seems to be related to the structure of their visual
receptive fields.19

RESPONSE TO COMBINATIONS OF OPTIC FLOW COMPONENTS

Using components of optic flow stimulation has been a useful first step in
determining the response of the population of cells in MSTd, and has allowed initial
experiments on the selectivity of these neurons. However, movement of an observer
through the environment nearly always produces combinations of these optic flow
components, and in the next step in our experiments we are investigating the effect of
combining optic flow components on the single neuron’s response.

One of the simplest combinations would be that of radial and planar stimulation.
Such stimulation would occur as an observer moves forward but drifts to the side, as
for example in the case of the observer in a row boat looking straight ahead while
drifting sideways. This combination of radial and planar motion could also be taken
as an approximation for the addition of radial and rotatory motion if the scene were
at a substantial distance from the observer.

Figure 7 shows the stimulus when planar motion in 4 of the 8 directions tested
was combined with radial motion (shown in the center). We applied these stimuli to
neurons that were sensitive to radial motion, and in our initial experiments, we have
found once again that not all neurons respond to such combined stimulation in the same way. For example, the response of the single component neuron to full-field stimulation (FIGURE 8A) was substantial to radial-outward motion. In FIGURE 8B, the response was reduced when this radial motion was combined with one of the 8 directions of planar motion (indicated by the eight lines). In contrast, the triple-component neuron shown in FIGURE 9A had a large response to large-field outward-radial motion, to planar motion to the right and down, and counterclockwise circular
motion. Combining radial motion with the eight directions of planar motion (FIGURE 9B) produced little effect for certain directions and an increase in the discharge rate for other directions. Our sample of neurons in this experiment is relatively limited, but there is again a tendency for single-component neurons and triple-component neurons, as two ends of the continuum within the population, to respond to the combinations of optic flow stimuli in different ways.

Clearly the combination of optic flow stimuli alters the response of some of the MSTd neurons. Exploring these combinations using stimuli that would actually occur with movement of the observer through the environment should yield a better understanding of the role of MSTd neurons in the cortical analysis of optic flow fields.

SUMMARY AND CONCLUSION

Neurons in a region of monkey extrastriate cortex, MSTd, respond to the components of optic flow stimulation. Some of these neurons (single-component

![Diagram](image)

**FIGURE 7.** Effect of combining radial motion alone (center drawing) with each of four sample directions of the eight planar motion directions used (surrounding drawings). Note that the combination shifts the focus of expansion in each of the combination cases.
neurons) are selective for a single type of motion such as inward- or outward-radial motion. Other neurons respond to multiple types of rotation, for example, rightward planar, clockwise circular, and inward radial. Rather than forming discrete groups, we think these neurons represent a continuum covering the range from single-component sensitivity to multiple-component sensitivity. By combining the optic flow...
stimuli, we have also been able to recognize that such combinations alter the response of cells in the continuum to varying degrees.

At this point, while our evidence is consistent with the hypothesis that cells in area MSTd contribute to the processing of optic flow stimuli, we do not know whether these neurons do in fact serve this function. As in all single-cell recording

![Diagram A]

CONTROL 22 spikes/sec

![Diagram B]

CONTROL 23 spikes/sec

**FIGURE 9.** Combined radial and planar motion has little impact on the response of a triple-component neuron. A: Response to full-field stimulation showing a response to planar-circular and radial-outward motion. B: Response to the combined radial and planar motion for the same neuron. The response to the radial motion alone is indicated by the circle. Same notation as in **FIGURE 8.**
experiments, even those in awake animals performing tasks closer to real-world tasks than we have succeeded in emulating here, the activity of the cell in relationship to the visual stimulation is simply a correlate of the optic flow stimulation and may or may not contribute to the processing of optic flow stimulation upon which behavior depends. Further information on a number of characteristics of these cells might clarify their role. Information on such factors as whether heading in the environment is conveyed by individual neurons, or whether this property is more likely to be conveyed over a population of neurons, and the role of changes in the point of fixation of the eyes are critical points. Generation of behavior on the basis of the optic flow stimulation and determination that this behavior is modified by selective lesion of MSTd would also strengthen the argument that visual motion processing in this area is related to analyzing optic flow information.

REFERENCES


