RELATION OF MST ACTIVITY TO OPTIC FLOW AND HEADING

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INTRODUCTION

Visual stimulation from the whole visual field, as well as by objects within the field, can be accessed for the control of self-movement. One of the most important aspects of large field visual stimulations is the visual motion generated by self-movement referred to as optic flow (Gibson, 1950; Gibson, 1986). With forward movement, optic flow forms a radial pattern covering the entire visual field (Figure 1). The critical characteristics of the optic flow field include: the motion involves a large fraction of the visual field, expansion of the field from a center of motion (focus of expansion), and a gradient of motion speeds from the center to the periphery of the field.

Neuronal correlates of optic flow have been studied during the past several years (Andersen, Snowden, Treue and Graziano, 1990; Andersen, Treue, Graziano, Snowden and Quam, 1993; Wurtz, Yamasaki, Duffy and Roy, 1990; Duffy and Wurtz, 1991a; Duffy and Wurtz, 1991b; Duffy and Wurtz, 1995; Graziano, Andersen and Snowden, 1994; Orban, Lagae, Verti, Raiguel, Xiao, Maes and Torre, 1992; Lagae, Maes, Raiguel, Xiao and Orban, 1994; Saito, Yukie, Tanaka, Hikosaka, Fukada and Iwai, 1986; Tanaka and Saito, 1989). All have concentrated on area MST (the medial superior temporal area), an extrastriate region that lies in the superior temporal sulcus of the visual cortex of the macaque monkey. MST has a large fraction of cells that respond to moving stimuli and receives a direct projection from the other prominent motion area within the same sulcus, MT (the middle temporal area). Studies of the neural correlates of optic flow have concentrated on area MST rather than area MT for two major reasons. First the work of Tanaka, Saito and their collaborators (Saito et al., 1986) showed that cells in MST respond to rotating and expanding stimuli, whereas those in MT did not; MST therefore would seem to be a better candidate for the neuronal analysis of

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optic flow stimuli. Second, the size of the receptive fields in MST are large enough to include a substantial fraction of the optic flow pattern within their receptive fields. For example, Figure 1 shows the relative size of the receptive fields in V1, MT, and MST, and clearly the receptive field of the MST cell includes a larger fraction of the large field optic flow pattern. The MST cells whose field sizes are illustrated are found in a dorsal-medial region of MST (Tanaka, Hikosaka, Saito, Yukie, Fukada and Iwai, 1986; Komatsu and Wurtz, 1988) referred to by Komatsu and Wurtz as MSTd and it is on this region that we have concentrated.

Optic flow contributes to several behaviors including the determination of heading during self movement, the stability of posture, and the structure of the environment. In this brief summary we will concentrate only on the relevance of the optic flow to the determination of heading. Our discussion is based on more detailed reports published previously (Duffy and Wurtz, 1991a; Duffy and Wurtz, 1991b; Wurtz and Duffy, 1992; Duffy and Wurtz, 1993).
Figure 2 Neurons responding to optic flow stimuli in MSTd form a continuum of response specificity. The stimuli on which all MST neurons were first tested are shown across the top: 8 planar (directions at 45° intervals), 2 radial (inward and outward) and 2 circular (clockwise and counterclockwise) stimuli. Each box represents the 100° × 100° stimulus, and the arrows represent the direction of dot motion. A–C: Responses to each stimulus are shown for three neurons. Neuronal responses are represented by spike density plots averaging responses to 6 stimulus presentations. The vertical line on each plot marks stimulus onset and indicates a 75 spikes/sec discharge rate; the 1 s stimulus period is marked by the bold horizontal line. A: Example of a single component radial neuron which responded to outward radial motion (response shown in bold outline) but not to planar or circular motion. B: A double component neuron which responded to leftward planar and outward radial motion but not to circular motion. C: A triple component neuron which responded to rightward planar, outward radial, and clockwise circular motion. From Duffy and Wurtz 1993.

Neurons Respond to Optic Flow Components

In our experiments, we presented large field (100° × 100°), random dot, optic flow stimuli, while the monkey fixated in the center of the screen. These stimuli contain a limited set of optic flow cues: the size and shape of the dots do not change, and the dots all move in one plane. The only optic flow cue is motion which changes speed and direction as it would with forward motion of the observer. We concentrated primarily on two large field movements that would be generated by translational movements of an observer. The optic flow generated by forward (or backward) movement of the subject was simulated by using a radially expanding (or contracting) stimulus. Frontoparallel translation was represented by planar motion, using eight directions at 45° angle steps around 360°. We also included circular stimuli: clockwise and counter clockwise motion on the screen. For each
TRIPLE COMPONENT NEURON

Figure 3  The response of a cell, which responds to planar, radial, and circular stimuli, varies with the position of a small stimulus within its receptive field. Top: The direction diagram shows responses to upward planar, clockwise circular and inward radial large-field stimulation. The diagrams are derived from the 400-1000 ms period after onset of the stimulus. Four planar responses are represented on horizontal or vertical axes, the direction of motion being represented relative to the center of the diagram (leftward stimulus is represented by line to left of center). Circular responses are represented as semicircles, the direction being indicated by arrowheads. Radial responses are represented on the oblique axis, inward from the right-upper corner, outward to the left-lower corner. The length of each line, and the diameter of each semicircle, is proportionate to the discharge activity rate as represented on the graph. The central activity rate is represented below the direction diagram on the same scale. Bottom: Direction diagrams for the small field studies 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. In all cases the monkey fixated on a point at the center of the large field. Modified from Duffy and Wurtz 1991b.
cell encountered we first determined its receptive field by hand and then determined the response of the cell to the standard set of planar, radial, and circular optic flow stimuli. A complete description of the procedures is given elsewhere (Duffy and Wurtz, 1991a; Duffy and Wurtz, 1995).

We found many cells that respond to these components of optic flow, but there were a variety of response types. Some neurons responded best to only a single visual motion stimulus, planar, circular or radial motion. Figure 2A shows an example of such a single component neuron; it responded to outward radial motion (darkened spike density plot). In contrast the neuron in Figure 2B responded to two of these motion stimuli — a double component neuron. Other neurons responded to planar, circular, and radial visual motion stimuli (Figure 2C) — a triple component neuron. We did not find discrete subpopulations of single, double, or triple-component neurons, but rather a continuum of response selectivity. In order to describe the distribution of cells, however, we classified each neuron according to the types of stimuli that evoked significant responses. In our most recent sample of 268 neurons (Duffy and Wurtz, 1995), we found all of these types to be substantially represented. A little less than 40% of the sample responded to all three components of the optic flow stimuli (planar, radial, and circular), slightly less than 30% to two stimuli (largely planar-radial and planar-circular), and a little less than 20% responded to only one of these components.

Thus, there are clear stimulus preferences in MST neurons for particular patterns of visual motion, simulating particular directions of self-movement through the visual environment. These preferences do not reflect a one-to-one correspondence between individual neurons and preferred optic flow fields. Rather, there is a continuum of relative preferences in the population of MST neurons.

Neurons Specific For Flow Components

One important issue is whether these MST neurons are sensitive to optic flow stimuli or whether they are simply responding to radial and circular motion because of the position of the stimulus on a receptive field sensitive to planar motion. For example, a cell that prefers upward planar motion might respond quite well to circular motion if that circular motion were positioned on the receptive field so that it provided primarily upward motion within the receptive field. We found this to be the case for some cells (Duffy and Wurtz, 1991b), and the cell shown in Figure 3 shows an example of this type of response. We first determined the response of the cell to full-field stimulation by optic flow stimuli, and then examined the response to smaller versions of the same stimuli presented in a subregion of the receptive field. The cell shown responded to planar, radial, and circular full field stimuli although for simplicity only the response to planar and circular stimuli are shown in Figure 4. Clearly the sensitivity of the cell to planar motion could underlie the neuron's response to the circular stimulus; the cell
**Figure 4** The response of a cell, which responds only to radial inward stimulus motion, continues to respond even as the position of a small stimulus within its receptive field is shifted. Same format as in Figure 3. In the small field experiments, selectivity for inward radial motion is maintained although it varies quantitatively across the field. Modified from Duffy and Wurtz 1991b.

responded to counterclockwise stimulation on the left of the field and to clockwise stimulation on the right side of the field, both of which would produce upward planar motion. This cell shows position dependence — the effect of the stimulus depends upon where the stimulus is located.

For other cells, the result is quite different, as illustrated in Figure 4. This figure shows an example of a neuron that responded only to a single optic flow com-
ponent, inward radial motion. The cell continued to respond to the inward radial stimulus at all of the positions in the larger field. This cell shows position invariance — the cell responds to the stimulus regardless of the position of the stimulus in the field. Note that the amplitude of the response does vary, a point to which we will return. Two other groups have done similar experiments and have also concluded that some but not all cells show this stimulus invariance (Graziano et al., 1994; Logue et al., 1994).

In our sample of cells, we found a tendency for single component cells to show the most position invariance and for triple component neurons to show the least. We showed this by a consistency analysis which compared the frequency with which a cell gave a significant response to the same stimuli in each of the nine subfields as it did when the same stimuli were presented in the full field. A cell that responded to exactly the same stimuli in each of the nine subfields as it did in the full field would be 100% consistent with the full field stimulus. We found clear differences between cells that responded to single optic flow components and those that responded to all three components. Those that responded to only one component (as in Figure 4) had a consistency between large and small field stimuli of 84% whereas those that responded to all three components (as in Figure 3) had a value of 60%. Therefore, in our sample of cells, the greatest stimulus invariance was among the cells that responded only to one of the stimulus components.

In net, just as we saw a continuum among cells with respect to the number of optic flow components, we now also see a continuum of specificity for the position invariance of optic flow stimuli. Since many cells do show such invariance, it seems most likely that these cells are selectively responding to the components of optic flow.

Neurons Selective for Center of Motion

So far, we have considered the response of the neurons to radial or circular stimuli when the center of motion of these stimuli are in the center of the visual field where the monkey is fixating. But critical information might be conveyed by the location of the center of motion in the receptive field. Therefore, we have studied the response of these cells to full-field radial and circular stimuli when the center of motion is shifted to different regions of the visual field. Here we will consider only the response to the shifted centers of radial motion because it is this type of stimulation that is relevant to observers as they translate through the visual environment.

Figure 5A shows the distribution of the centers of motion we used. Each of the 17 boxes represents the 100° square stimulus, the arrows represent the direction of dot motion, and the dots represent the center of motion. The order of the stimuli in Figure 5A places the stimulus with centered motion in the middle and
Figure 5  Three neurons that respond best to optic flow stimuli with centers of motion in different parts of the field. A: The 17 stimuli used with neurons that responded to outward radial motion. Each box represents the 100° × 100° stimulus, the arrows within each box represent the directions of visual motion, and the circles indicate the center of motion. The outer ring of boxes represent planar stimuli, their outward centers of motion can be regarded as being 90° from the center, off the screen in these stimuli. The inner ring of boxes represent stimuli with shifted centers of motion, their outward centers of motion are 45° from the center, near the edge of the screen in these stimuli. The center box represents the outward radial stimulus with its center of motion at the center of the screen. B–D: Spike density histograms showing the responses of three neurons to the stimuli occupying the same positions as the stimuli illustrated in A. The darkened histograms are those that were not significantly different from the largest response (t-test, p < 0.01). B: A neuron that responded best to the stimulus with its center of motion at the center of the screen. C: A neuron that responded best to stimuli with eccentric centers of motion. D: A neuron that responded best to a planar stimulus with a peripheral center of motion. From Duffy and Wurtz 1995.
Figure 6  Centers of motion in all parts of the visual field are represented in the sample of MSTd cells A. Distribution of centers of motion that evoked the strongest response for neurons that exhibited inward or outward motion. The 17 segments of the circular plot represent the 17 stimuli, with each segment representing the center of motion stimulus depicted at the corresponding position in Figure 5A. Each dot represents a neuron, and they are plotted in the segment which corresponds to the stimulus that evoked the largest response from that neuron. All tested centers of motion are preferred by at least one neuron. B: The relative distribution of the preferred centers of motion. The graph shows the percentage of neurons that had the strongest response to center, eccentric, or peripheral centers of motion stimuli. Stimuli having eccentric centers of motion were most commonly preferred, but the stimulus with the center of motion in the center of the screen was the single stimulus preferred by the largest number of neurons. From Duffy and Wurtz 1995.

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those with shifted centers of motion more eccentrically. Responses to planar motion are shown at the edge of the figure reflecting the location of their centers of motion in the far periphery. We found some neurons that responded best to each of these three types of motion; those with their strongest responses to centered, eccentric, or peripheral centers of motion. Figures 5B–D show the responses of three neurons as spike density histograms located in the positions occupied by the stimuli which evoked them, as shown in Figure 7A. All three neurons responded to outward radial motion. The darkened responses are the best responses, or the responses that were not significantly different from the best responses. The neuron shown in Figure 5B responded best to the center of motion stimulus. The best responses in Figure 5C are to an eccentric center of motion stimulus, and in Figure 5D the best responses are to a planar stimulus — one that can be regarded as having a peripheral center of motion.

All regions of the field are represented by some cells, as indicated in Figure 6 which divides the field into the same segments as in Figure 5. In our sample
Figure 7 The center of motion fields of MSTd neurons have substantial structure and broad response gradients. The centers of motion of the set of 33 outward radial stimuli are distributed at 10° intervals along four axes, similar but more extensive than in Figure 5A. Responses of a neuron are represented by ovals at positions which correspond to the relative position of the centers of motion. Response amplitude of the ovals at each position is proportionate to the length of the oval and is derived from the spike density histograms as described in Figure 3. Activity during unstimulated control trials is represented below each plot. The responses of the neuron indicate preferred stimuli having centers of motion in the lower left corner of the screen, with decreasing response amplitude graded towards the center. B: The responses of another neuron that shows a preference for stimuli having centers of motion nearer the center of the screen, with the greatest responses to stimuli in which the center of motion was at the center of the screen. From Duffy and Wurtz 1995.
Figure 8  The continued response of the cells showing stimulus invariance to small field stimuli is consistent with the large area of the visual fields over which cells respond to shifted centers of motion. A: The neuronal responses of the neuron shown in Figure 4 and identified as one showing relatively large response invariance as the position of the stimulus was changed. The responses are replotted using the same diagram as in Figure 7. B: Response of the same neuron as in Figure 7B for comparison. Both neurons show a preference for centers of motion in one region of the field, but that region can be quite large.
amplitude of the response in both experimental conditions. We conclude that the relatively small shifts of the small field stimuli can be regarded as movements across the graded preference for centers of motion revealed by our large field stimuli. Thus, under some conditions, MSTd neurons could provide information related to heading.

Based on these observations, our hypothesis of the organization of MSTd for the determination of heading is as follows. We suggest that each of the MSTd neurons can be regarded as having a center of motion field. The responses of individual neurons would be graded according to the proximity of the center of motion of a stimulus to the preferred center of motion for the neuron, just as other visual cortical neurons have graded preferences for the direction of planar motion or for the location of a spot of light.

Our notion is that there is an orderly arrangement of MSTd neurons with each region of the visual field being represented by a set of neurons whose center of motion falls in that region of the field. The population of neurons would have a gradient in the density of the centers of motion with those near the middle of the visual field more highly represented and responding to centers of motion over a more limited area of the visual field. While an orderly anatomical arrangement remains to be established, an organization based on the functional criteria of center of motion preference would be an interesting shift in organization from the retinotopy of adjacent area MT.

The role of MSTd neurons in interpreting optic flow fields would be one of responding to visual motion according to the degree of match between the visual input and the preferred optic flow field of the neuron. In the experiments we have described we have eliminated as many cues as possible from the optic flow stimuli, and have simulated motion toward a single plane during visual fixation of a stationary target. Our physiological observations would be particularly relevant to determining heading in the circumstance in which the point of fixation is at a distance. The forward view from an airplane during landing, used by Gibson (1986) to illustrate flow patterns, closely approximates this condition since there is radial flow with little rotation. In the example shown in Figure 9, the MSTd neurons studied with the dense array of center of motion stimuli (Figure 7) have motion sensitivity that might permit these neurons to differentiate between going where the observer is looking versus going in another direction. Figure 9A and 9B illustrate this by the comparing the flight path leading towards the landing strip, which would be detected by a neuron with a preferred center of motion in the center of the field, with a flight path leading to the lower left corner, which would be detected by a neuron with the preferred center of motion off to the side. This is a limited and highly specific example of the use of the center of motion structure of these MSTd cells, but it indicates the type of heading information that the population of these neurons could provide.

Our ideas concerning the potential contribution of individual neurons to the determination of heading is remarkably similar to ideas about the activity of
Figure 9  The potential application of elements in the map of center of motion preference.
In this illustration, the observer is utilizing optic flow in piloting an approach to an airport
(drawings after Gibson, 1966). The observer’s field of view is represented by a series of
concentric circles to mark eccentricity. The shaded areas within these fields represent
regions of center of motion responsiveness of MST neurons, with darker shading depicting
subregions of greater responsiveness. These idealized response fields reflect findings
illustrated in Figure 7. A: A peaked pattern neuron would respond best when the center
of motion is over the fixation target on the landing strip when the pilot is looking where
he is going. B: A graded pattern neuron would respond best when the center of motion
is in the periphery, to the left of the landing strip. From Duffy and Wurtz 1985.
neurons within the superior colliculus before the generation of saccadic eye movements. A recent report estimated that more than a quarter of the neurons in the colliculus are active before each saccade regardless of the amplitude of the saccade (Munoz and Wurtz, 1995); only which neurons are active changes from saccade to saccade. The population code in MSTd might be like that in the superior colliculus: to make a specific center of motion discrimination which could contribute to a heading determination, many neurons would be active.

Finally, it is worth noting that these MSTd cells all fall in one of the visual processing streams in the extrastriate visual cortex. These extrastriate regions are thought to be grouped into two processing streams: a ventral one regarded as determining what an object is or more closely related to perception, and a dorsal one indicating where an object is or more closely related to control of movement.

The relation of optic flow to movement fits nicely with this notion of the dorsal visual pathway and the control of movement.

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