Optic flow selectively activates neurons in medial superior temporal (MST) cortex. We find that many MST neurons yield larger and more selective responses when the optic flow guides a subsequent eye movement. Smaller, less selective responses are seen when optic flow is preceded by a flashed precue that guides eye movements. Selectivity can decrease by a third (32%) after a flashed precue is presented at a peripheral location as a small spot specifying the target location of the eye movement. Smaller decreases in selectivity (18%) occur when the precue is presented centrally with its shape specifying the target location. Shape precues presented centrally, but not linked to specific target locations, do not appear to alter optic flow selectivity. The effects of spatial precueing can be reversed so that the precue leads to larger and more selective optic flow responses: A flashed precue presented as a distracter before behaviorally relevant optic flow is associated with larger optic flow responses and a 45% increase in presented as a distracter before behaviorally relevant optic flow is larger and more selective optic flow responses: A flashed precue that guides eye movements. Selectivity can decrease by a third (32%) after a flashed precue is presented at a peripheral location as a small spot specifying the target location of the eye movement. Smaller decreases in selectivity (18%) occur when the precue is presented centrally with its shape specifying the target location. Shape precues presented centrally, but not linked to specific target locations, do not appear to alter optic flow selectivity. The effects of spatial precueing can be reversed so that the precue leads to larger and more selective optic flow responses: A flashed precue presented as a distracter before behaviorally relevant optic flow is associated with larger optic flow responses and a 45% increase in selectivity. Together, these findings show that spatial precues can decrease or increase the size and selectivity of optic flow responses depending on the associated behavioral contingencies.

Keywords: attention, extrastriate, MST, optic flow, vision, visual motion

Introduction

Moving observers are surrounded by the radial pattern of visual motion in optic flow (Gibson 1950). The retinal image of the flow field reflects the influences of self-motion direction and path as well as eye and head movements. The location of the radial center of motion in the retinal image of the optic flow field is a robust source of information about the observer’s self-motion and indicates heading direction, relative to the direction of gaze, during movement in a straight line. The utility of the heading information in optic flow is highlighted by its use in the active control of both ambulatory and vehicular self-motion (Lee 1980; Warren et al. 2001).

Dorsal extrastriate visual areas form a pathway for the sequential analysis of visual motion (Ungerleider and Desimone 1986b; Boussaoud et al. 1992) that contributes to spatial perceptual and cognitive processing (Mishkin et al. 1983). Dorsal medial superior temporal cortex (MSTd) occupies a central position in that pathway and contains neurons that respond to optic flow stimuli (Tanaka et al. 1986; Tanaka and Saito 1989; Duffy and Wurtz 1991b; Orban et al. 1992; Graziano et al. 1994) with selectivity for the radial center of motion that encodes heading direction (Duffy and Wurtz 1995; Lappe et al. 1996). MSTd’s optic flow responses are modulated by naturalistic sequences of heading directions that define paths of observer self-motion through the environment (Paolini et al. 2000; Froehlicher and Duffy 2002).

The dynamics of ongoing behavior modulate the responses of neurons in dorsal extrastriate cortex with well-documented effects on middle temporal (MT) neurons that precede MSTd in the dorsal processing chain (Seidemann and Newsome 1999; Cook and Maunsell 2004), and on posterior parietal neurons that follow MSTd in the dorsal processing chain (Steinmetz et al. 1994; Bisley and Goldberg 2003). The attentional demands of behavioral tasks have also been shown to alter MST’s neuronal responses with effects on the size, and possibly the selectivity, of responses to small patches of visual motion (Treue and Maunsell 1996; Treue and Martinez Trujillo 1999) and targets of pursuit eye movements (Recanzone and Wurtz 2000).

Optic flow stimuli activate a number of areas in human cerebral cortex, including the likely homolog of area MST (Greenlee 2000; Morrone et al. 2000; Dukelew et al. 2001; Peuskens et al. 2001). The pattern of optic flow activation revealed by functional imaging supports the recognition of a human dorsal stream processing pathway for visual motion related to self-movement (Vaina and Soloviev 2004). As in nonhuman primates, human MST cortical responses to optic flow show evidence of attentional modulation linked to the demands of ongoing behavioral tasks (O’Craven et al. 1997; Haug et al. 1998). Thus, previous studies support the view that MST is involved in visual motion processing for optic flow analysis related to self-movement perception and that this processing is modulated by the attentional demands of ongoing behavior.

In the current studies, we characterize the effects of 4 behavioral tasks on MST neuronal responses to optic flow using paradigms linked to constructs about spatial attention (Posner 1994). In the first 3 experiments, we compared neuronal responses to optic flow that is either relevant to the task or is designated as irrelevant by a preceding cue. We vary the nature of that cue to examine the impact of competing spatial information on optic flow stimulus selectivity. In the fourth experiment we test whether spatial cues that precede optic flow that is behaviorally relevant might also alter neuronal responses to those stimuli. Our goal is to test the hypothesis that optic flow responses are affected differently by the need to use the self-motion heading information in the stimulus to guide behavior, and by the presentation of competing spatial information in the task.

Methods

Animal Preparation

All procedures were approved by the University of Rochester Committee on Animal Research and were consistent with Society for Neuroscience policies. Bilateral recording cylinders were placed over trephine
holes in the parietal calvarium (anterior–posterior -2 mm, medial–lateral +/-15 mm, angle 0°) over MST.

**Optic Flow Stimuli**
The monkey sat fixating the center of a 90° tangent screen at a distance of 50 cm. The monkey viewed outward and inward radial optic flow stimuli while fixation was monitored using magnetic search coils. The optic flow had 1 of 8 centers of motion at 30° eccentricity at 45° intervals around the fixation point. The optic flow consisted of -1000 dots moving at an average speed of 40°/s (Tanaka et al. 1989). Our optic flow simulation modeled the approach of the observer to a black tangent screen centered with a random pattern of white dots (Duffy and Wurtz 1991b). As the observer underwent simulated movement toward the screen the dots moved in a radial pattern with a speed that was a sinθ function of eccentricity, where θ is the angle between the line of sight and each dot, and the dots accelerated as a 2 × cosθ × sinθ function (Nakayama and Loomis 1974; Lee and Young 1985; Hatsopoulos and Warren 1991). Each dot was 0.75° wide with a brightness of 1.8 cd/m^2 on a dark background having a brightness of 0.2 cd/m^2.

**Behavioral Tasks**
All 4 experiments compared responses in 2 types of block-wise interleaved trials: trials in which optic flow stimuli were relevant to the monkey’s behavioral task, and trials in which optic flow stimuli served as a behaviorally irrelevant distracter.

Flow-relevant trials began with centered fixation maintained for 2 s followed by optic flow for 1 s, and then a multiple choice array with targets arranged at 20° eccentricity spaced at 45° intervals around the fixation point. These trials required a saccade to the target corresponding to the center of motion in the preceding optic flow.

Flow-irrelevant (precued) trials began with centered fixation for 1 s, followed by a 1-s flash of a cue that indicated which of the choice array targets must be selected at the end of the trial, regardless of the intervening optic flow stimulus. These trials required a saccade, within 250 ms of choice array onset, to the target indicated by the precue stimulus that was presented before the behaviorally irrelevant optic flow.

In both types of trials, the monkey’s response saccade was required within 250 ms of choice array onset. The monkeys generated single saccade responses more reliably using the target eccentricity of 20° rather than targets that exactly matched the 30° eccentricity of the radial centers of motion. Successful completion of a trial resulted in a water reward.

**Neural Recording**
Tungsten microelectrodes (Frederick Haer, Inc., Bowdoin, ME) were passed through transdural guide tubes into cortex to record single neuron spikes using a dual window discriminator and the REX experimental control system. Receptive fields were hand-mapped by neuron spikes using a dual window discriminator and the REX system. Receptive fields were hand-mapped to patterned visual motion than to moving bar or spot stimuli. Many of the more transient responses recorded in MSTd (Duffy and Wurtz 1991b) that rather than targets that exactly matched the 30° eccentricity of the radial centers of motion. Successful completion of a trial resulted in the payment of a reward.

**Statistical Analysis**
All of our analyses used the 50- to 300-ms response interval after optic flow onset. Inspection of averaged response profiles had revealed that this early phase of the responses showed the most consistent differentiation of the task conditions. In some neurons, later phases showed larger effects but also included greater response variability. We used a 250-ms averaging period because we have found it to be a reliable averaging period for MSTd responses (Logan and Duffy 2006) with shorter intervals having greater variance and longer intervals obscuring many of the more transient responses recorded in MSTd (Duffy and Wurtz 1997).

Neuronal responses to the preferred outward or inward optic flow were entered into repeated measures 2-way analyses of variance (ANOVs) with main effects of task (relevant vs. irrelevant optic flow stimuli) and center of motion (8 radial centers, each presented in 8 successful trials) in the flow relevance comparison. In data from flow-irrelevant (precued) trials, we conducted an additional analysis with main effects of the distance between the precise location and the radial center of motion (far vs. near) and the radial centers of motion (8, with 3 repetitions) in the precue comparison. These ANOVAs included all neurons with significant flow-relevance effects (P < 0.05) and all neurons that have similarly sized far/near precue effects. We took this approach because far/near precue comparisons rely on fewer than half as many trials. The approach of maintaining the same effect size criterion is equivalent to using a significance cut-off of P < 0.1 (Cohen 1988).

**Gaussian Fits**
To characterize flow-relevance and precue proximity effects we used Matlab curve fitting algorithms to fit Gaussians to response amplitudes for the 8 radial center of motion locations presented in the optic flow stimuli. We used response amplitudes derived by averaging the neuronal firing rate across the 50- to 300-ms response interval for each stimulus type. The Gaussian fits yielded amplitude, baseline, tuning width, and preferred radial center of motion parameters describing those fits. The Gaussian width is the sigma (square root of the variance) derived as the minimum variance unbiased estimation of the sample variance based on Matlab’s least squares fit to the data. The goodness of fit was measured as an F-ratio of the residuals in the best Gaussian versus best linear fit; only neurons that showed fits with P < 0.05 were accepted (McAdams and Maunsell 1999b).

**Anatomical Distribution of Recorded Neurons**
Continuation of microelectrode penetrations to greater depths confirmed MSTd recording by then encountering the response characteristics of MT neurons. After penetrobarital euthanasia and transcardiac formalin perfusion, histological analysis confirmed recording on the anterior bank of the superior temporal sulcus (STS). Both gross sulcal anatomy and Cresyl Violet and sectional anatomy confirmed that all recording sites were within the anterior bank of the STS. Silver staining for myelinated fibers confirmed that almost all recording sites were within the densely myelinated zone that serves as a landmark for area MST (Ungerleider and Desimone 1986a). A few penetrations extended in an infero-medial direction but the neurons encountered remained consistent with MST as defined by the previously cited physiological criteria (Komatsu and Wurtz 1988; Duffy and Wurtz 1991b). These cells typically had very large receptive fields, about a quadrant of the 90° display screen plus the adjacent visual meridians, with larger responses to patterned visual motion than to moving bar or spot stimuli.

**Results**
We recorded the optic flow responses of 410 MSTd neurons from the cerebral hemispheres of 2 rhesus monkeys. The behavioral relevance of the optic flow stimuli was manipulated in a series of 4 experiments each of which included the direct comparison of responses to behaviorally relevant versus irrelevant optic flow. These experiments are presented here in the order in which they were conducted.

In experiment 1, a competing task marked irrelevant optic flow using an exogenous spatial cue the location of which specified the location of the saccade target. In experiment 2, a competing task marked irrelevant optic flow using a centrally placed endogenous spatial cue the shape of which specified the location of the saccade target. In experiment 3, a competing task marked irrelevant optic flow using a centrally placed nonspatial cue the shape of which specified the shape of the saccade target. In experiment 4, a valid or invalid exogenous spatial stimulus precued the monkey about the saccade target to be specified by the task-relevant optic flow stimulus.
All 4 experiments were analyzed using the same approach to identifying the subset of MST neurons that showed significant behavioral effects and then quantifying those effects on optic flow response size and selectivity. First, we used ANOVA to identify neurons that were responsive to behavioral relevance, either as a main effect of relevant versus irrelevant optic flow or its interaction with radial center of motion. Second, we fit Gaussian functions to those neuron’s radial center tuning curves to find those neurons with good fits in both behavioral relevance conditions. Third, fit parameters in both behavioral conditions were compared on a neuron-by-neuron basis and by averaging parameters across neurons.

**Experiment 1: Exogenous Spatial Cueing**

Our first goal was to determine if MSTd’s optic flow responses are influenced by the need to use the stimulus to guide behavior. We recorded the responses of 135 neurons from one hemisphere in each of 2 monkeys while presenting identical optic flow stimuli that were either relevant or irrelevant to a memory guided saccade task.

This experiment presented 2 types of trials that were interleaved in blocks of 8 trials (Fig. 1A): Flow-relevant trials were those in which the optic flow specified the location of the target for the subsequent saccade. These trials began with centered fixation followed by optic flow with a 30° eccentric radial center of motion at 1 of the 8 locations distributed at 45° intervals around the fixation point. After the optic flow was extinguished, we presented a choice array containing 8 potential saccade targets. The monkey was then required to saccade to the target at the location corresponding to the radial center of motion in the preceding optic flow (Fig. 1A, top left).

Flow-irrelevant (precued) trials were those in which the target for the subsequent saccade was specified by the location of a small square flashed at the same location as of 1 of the 8 radial centers of motion in optic flow. The precue was followed by 1 of the 8, independently selected, optic flow stimuli that were irrelevant to the saccade task. That is, the location of precue specified saccade target was unrelated to the radial center of motion in the intervening optic flow (Fig. 1A, bottom left).

In the flow-irrelevant trials, the location of the square precue and the optic flow’s radial center of motion was both randomly assigned to 1 of the 8 target locations. Consequently, the location of the precue had a varying spatial relationship to the location of the radial center in the subsequent optic flow.

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**Figure 1.** Experiment 1: The effects of exogenous spatial cueing on neuronal responses. (A) Left: In relevant optic flow trials (red), centered fixation is followed by optic flow visual motion with 1 of 8 eccentric radial centers-of-motion and then an 8 spot array requiring a saccade to the remembered location of the radial center. In irrelevant optic flow trials (blue), a flashed square preceded the optic flow and a saccade was required to the remembered square location. Right: Precue effects were seen in the irrelevant optic flow condition by comparing trials in which the precue was nearby (green) versus far from (light blue) the radial center. (B) Left: Spike density histograms (SDHs) of responses to 8 radial center stimuli in relevant optic flow (red) and irrelevant optic flow (blue) trials for 1-s optic flow stimulus period (vertical bar = 100 spikes/s). This neuron prefers the right-upper radial center with larger responses in relevant optic flow trials (red shading). Right: SDHs for the near (green) and far (light blue) precue trials in a neuron preferring the lowest radial center with larger responses in near precue trials (red shading). Behavioral task effects were concentrated in the first 300 ms of the neuronal responses.
a result, some of the trials presented precues that were near the subsequent radial center of motion. Other trials presented precues that were far from the subsequent radial center of motion (Fig. 1A, right). This allowed a secondary analysis in which we compared optic flow responses from trials in which the precue location was near versus far from the radial center of motion in the optic flow.

A total of 27% (36/135) of the neurons showed significant differences in their responses to optic flow that was presented in the different types of trials (Fig. 1B): 21% (28/135) showed differences between responses to relevant versus irrelevant optic flow (Fig. 1B, left); 8% (11/135) showed differences between responses to irrelevant optic flow that was presented after a precue that was near the radial center, versus a precue that was presented far from the radial center (Fig. 1B, right); 3 neurons showed both effects.

The great majority of neurons (86%, 31/36) with significant effects of behavioral relevance on their optic flow responses were reasonably characterized by significant Gaussian fits to their radial center tuning curves for both relevant and irrelevant optic flow (Fig. 2). Relevant optic flow evoked larger responses than irrelevant optic flow with an average magnitude difference of 21% ($P = 0.0006$) based on the Gaussian amplitude measures. Relevant optic flow also evoked greater radial center selectivity than irrelevant optic flow with significantly narrower averaged tuning width for the radial center of relevant optic flow (tuning width difference of 32%, $P = 0.008$) (Fig. 3A).

Figure 2. Effects of exogenous cueing on single neuron radial center tuning profiles. (A) Neuronal responses (mean ± standard error of the mean) and Gaussian fits to relevant (solid red) and irrelevant (dashed blue) optic flow showing greatest differences at the preferred radial center. (B) Neuronal responses to irrelevant optic flow in near (solid green) and far (dashed light blue) precue trials showing largest near precue associated increases in response amplitude at the preferred radial center.

Figure 3. Effects of exogenous spatial cueing on averaged neuronal tuning profiles. (A) Average tuning profiles of neurons with significant differences between responses to relevant (solid red) and irrelevant (dashed blue) optic flow and with good fits in the relevant and irrelevant conditions. The responses of each neuron were normalized to the amplitude of its largest radial center response. These curves show a larger magnitude (21%) and narrower tuning curve width (32%) in response to relevant optic flow. (B) Average responses of neurons with significant precue proximity effects and with good fits in the near (solid green) and far (dashed light blue) conditions. There are nonsignificantly larger responses and narrower tuning to optic flow following precues that were nearer to the subsequent radial center.
We also compared responses with irrelevant optic flow depending on whether it was preceded by a precue that was near to, versus far from, the radial center in the subsequently presented irrelevant optic flow. This comparison revealed a tendency toward larger responses after precues that were near the location of the subsequent radial center. The magnitude of these effects was comparable with the differences between responses to relevant and irrelevant optic flow. However, the near/far differences were not significant (radial center × near/far interaction $F_{1,450} = 1.0$, $P = 0.43$), potentially because the near/far comparisons were based on half as many trials as the relevant/irrelevant comparisons (Fig. 3B).

We conclude that optic flow stimuli evoke larger and more selective responses from MSTd neurons when the optic flow provides an exogenous spatial cue that guides subsequent behavior. However, behaviorally irrelevant optic flow is not devoid of behavioral effects, with a tendency toward larger and more selective responses when the precue that makes it irrelevant is near the subsequent radial center.

**Experiment 2: Endogenous Spatial Cueing**

In experiment 2 we tested the hypothesis that the larger and more selective responses to relevant versus irrelevant optic flow, seen in experiment 1, might reflect our placement of precues in different parts of the visual field to mark a subsequent stimulus as irrelevant. We used an endogenous spatial cueing task to test this hypothesis, presenting differently shaped precues at the center of the display to mark the subsequent stimulus as irrelevant. Relevant optic flow had 1 of 8 radial centers followed by a target array requiring a saccade to the location of the preceding radial center with 4 orthogonal alternatives presented in each trial. Precued trials flashed 1 of 4 shapes at the center of the screen, which was followed by behaviorally irrelevant optic flow. The 4 shapes were then presented in a fixed array, presenting the same arrangement in all irrelevant optic flow trials, and prompting the monkey’s saccade to the target shape (Fig. 4A).

Significant behavioral effects on optic flow responses were seen in 31% (27/86) of the neurons (Fig. 4B). In 17% (15/86), the relevance of the optic flow significantly altered the responses. In another 19% (16/86), the distance from the target location implied by the shape precue to the radial center in the optic flow (far vs. near) significantly affected the responses. Four neurons showed both effects.

Most neurons (87%, 27/31) with significant behavioral effects on optic flow responses also yielded significant Gaussian fits to
tuning curves for the radial centers. Behavioral effects on the Gaussian fit parameters were in the same direction as those seen in experiment 1 with exogenous spatial cueing. Responses to relevant optic flow were larger than those to irrelevant optic flow (magnitude difference of 16%, \( p = 0.004 \)) with relevant optic flow yielding greater radial center selectivity (tuning width difference of 18%, \( p = 0.03 \)) (Fig. 5A). The comparison of responses with irrelevant optic flow preceded by shape precues that implied far versus near target locations again yielded somewhat smaller responses in the far precue condition but again these effects did not attain statistical significance (interaction \( F_{7,1520} = 1.65, p = 0.12 \)) (Fig. 5B).

Thus, the larger response magnitudes and the narrower radial center selectivity tuning curves seen with relevant versus irrelevant optic flow do not depend on the precue being presented at different locations in the visual field. Similar changes in magnitude, but smaller changes in selectivity, occur with endogenous precueing by centrally presented shapes that have a learned correspondence to different locations.

**Experiment 3: Nonspatial Cueing**

Our shift from exogenous spatial cueing in experiment 1 to endogenous spatial cueing in experiment 2 resulted in smaller tuning width effects in relevance-irrelevance comparisons and smaller differences between near and far precue trials. In experiment 3 we considered that if these effects are linked to each other, using nonspatial precueing might eliminate both effects. We created a nonspatial variant of the endogenous cueing task by eliminating the shape precue’s learned correspondence to specific target locations. Nonspatial shape precueing was used to manipulate the behavioral relevance of optic flow while recording 88 MSTd neurons in 2 monkeys.

As in both the exogenous and endogenous spatial cueing experiments, relevant optic flow was followed by a target array requiring a saccade to the location of the preceding radial center with 4 orthogonal alternatives per trial. Precued trials flashed 1 of 4 shapes at the center of the screen followed by irrelevant optic flow, and then the 4 precue shapes in an arrangement that was randomized across trials. In these irrelevant optic flow trials, the monkey’s task was to saccade to the shape that had preceded the optic flow. Each of the 4 shape target arrays appeared with equal probability, dissociating precue shape from location (Fig. 6A).

Nonspatial precueing resulted in significant effects of behavioral relevance on optic flow responses in 23% (20/88) of the neurons (Fig. 6B). Most of those neurons (60%, 12/20) also yielded significant Gaussian fits to tuning curves for the radial center of optic flow. Relevant optic flow evoked larger responses than the irrelevant optic flow (magnitude difference of 25%, \( p = 0.002 \)) without a significant change in radial center selectivity (tuning width difference of 2%, \( p = 0.45 \)) (Fig. 6C).

Because cue location information was not available during optic flow stimulation, no near–far effects could be obtained.

This study shows that relevant optic flow stimuli evoke larger responses than irrelevant stimuli regardless of whether the stimulus that cues the irrelevance contains information about the target location. However, the absence of spatial information in the precue stimuli presented in this experiment appears to have resulted in the absence of a significant tuning width effect in the comparison of responses to relevant and irrelevant optic flow. This suggests the spatial information conveyed by the precue is linked to tuning width effects on radial center of motion selectivity.

**Experiment 4: Spatial Cueing of Relevant Optic Flow**

The preceding 3 experiments suggest that precueing decreases the size of neuronal responses to subsequent optic flow stimuli. In experiment 4 we tested whether precueing effects might be reversed by manipulating the behavioral significance of the precue. That is, can precues be manipulated so that they increase the size and selectivity of optic flow responses?

To test this hypothesis, we presented a precue that indicated that the subsequent optic flow was behaviorally relevant; that is,
it must be used to guide the eye movement response. In these trials, the behaviorally relevant optic flow was preceded by a precue optic flow stimulus. The use of optic flow, rather than a shape, as the spatial precue in relevant optic flow trials avoided confusion with the shape precues presented in irrelevant optic flow trials.

The precue optic flow in relevant optic flow trials randomly presented either the same or the opposite radial center as in the subsequent, behaviorally relevant, optic flow (Fig. 7A, top). As in the previously described nonspatial paradigm, the irrelevant optic flow trials were precued by a shape stimulus presented at the center of the display (Fig. 7A, bottom). This new paradigm was created to optimize the chances of reversing the previously obtained decreases in optic flow response amplitudes by a preceding precue stimulus.

In this experiment, 43% (43/101) of the neurons showed significant differences between responses to the relevant and irrelevant optic flow, the highest percentage obtained in all of these studies. Most of these neurons (51%, 22/43) also had significant Gaussian fits to tuning curves for the radial center of the optic flow. There were no significant differences between the responses to optic flow presented as a precue before relevant optic flow, and the responses to the irrelevant optic flow presented in the shaped precued trials (Fig. 7B), neither of which required a behavioral response. In contrast, responses to relevant optic flow were substantially larger than responses to the shape precued irrelevant optic flow (Fig. 7C).

Averaged responses to precue optic flow were not significantly larger (3%, \( P = 0.28 \)) than responses to irrelevant optic flow in shape precued trials but the precue optic flow did show significantly narrower tuning width (35%, \( P = 0.006 \)) (Fig. 8A). In contrast, relevant optic flow evoked stronger responses than irrelevant optic flow (15%, \( P = 0.01 \)) with a still greater narrowing of tuning width (45%, \( P = 0.0005 \)) (Fig. 8B). This narrowing of tuning width for the radial center in optic flow was not associated with a difference in responses to the relevant optic flow that followed same versus opposite radial centers in the precue versus relevant optic flow comparison (Fig. 8C).

This study shows that a precue signaling the behavioral relevance of an upcoming optic flow stimulus can lead to larger and more selective responses to that behaviorally relevant optic flow. Together, these studies suggest that the presentation of a behaviorally relevant precue can lead to either smaller or larger optic flow responses depending on the associated behavioral contingencies.

**Discussion**

**Behavioral Relevance Enhances Optic Flow Responses**

We manipulated the behavioral relevance of optic flow stimuli that activate the large receptive fields of MSTd neurons (Duffy and Wurtz 1991a; Lagae et al. 1994) and support radial center of motion selectivity for specific directions of self-motion.

Figure 6. Experiment 3: The effects of nonspatial endogenous cueing on neuronal responses. (A) In relevant optic flow trials (red), centered fixation is followed by optic flow visual motion with 1 of 8 radial centers and then a 4 spot array requiring a saccade to the remembered location of the radial center. In irrelevant optic flow trials (blue), a flashed shape (a circle, square, triangle or "x") preceded the irrelevant optic flow and a saccade was required to that shape within an array of targets presented after the optic flow. In contrast to the endogenous spatial cueing task, the 4 shape targets were presented in 1 of 4 randomly selected arrangements removing the spatial information in the shape precue. (B) Single neuron responses (mean ± standard error of the mean) to optic flow with Gaussian fits to relevant (red) and irrelevant (blue) optic flow showing larger responses to relevant than irrelevant optic flow. (C) Average tuning profiles of neurons with significant effects of optic flow relevance and with good fits in the relevant and irrelevant conditions. As with exogenous and endogenous spatial cueing, relevant optic flow evoked larger responses (25%) than irrelevant optic flow. However, there was no significant difference in the width of these tuning curves.
Duffy and Wurtz 1995; Lappe et al. 1996). All 4 behavioral paradigms yielded ~20% larger responses to relevant optic flow in ~25% of the neurons.

In experiment 1, exogenous spatial precueing of irrelevant optic flow by a spot flashed at 1 of 8 locations (Fig. 1A) yielded responses to subsequently presented optic flow that were 21% smaller than the responses evoked by relevant optic flow in 27% of the neurons (Fig. 3A). In experiment 2, endogenous spatial precueing of irrelevant optic flow by centrally placed shapes indicating the location of target stimuli (Fig. 4A) yielded responses that were 16% smaller than those evoked by relevant optic flow in 31% of the neurons (Fig. 5A). In experiment 3, nonspatial precueing of irrelevant optic flow by shape stimuli indicating the shape of target stimuli (Fig. 6A) yielded responses that were 25% smaller than those evoked by relevant optic flow in 23% of the neurons (Fig. 6C). In experiment 4, the nonspatial precueing of irrelevant optic flow applied in experiment 3 was supplemented by the spatial precueing of relevant optic flow (Fig. 7A) with the combined effect of 15% larger responses to relevant optic flow in 43% of the neurons (Fig. 8B). We conclude that behaviorally relevant optic flow yields larger responses than behaviorally irrelevant optic flow, regardless of how the relevance of the optic flow is signaled.

Studies of dorsal (Bushnell et al. 1981) and ventral (Fuster and Jervey 1982; Reynolds et al. 1999) stream neurons have linked the behavioral relevance of stimuli within a neuron’s receptive field to spatial attention. Attentional modulation may enhance MT and MST neuronal responses to local motion (Treue and Maunsell 1996) in a manner consistent with multiplicative gain effects without changes in the selectivity of the responses (Treue and Martinez Trujillo 1999). Such gain effects might underlie the response amplitude changes in our studies when behavioral relevance focuses attention on optic flow.

However, our rapid, sequential presentation of a precue near the location of the subsequent radial center of motion may have created a situation more like that seen when 2 nearby stimuli are presented simultaneously. In the case of nearby simultaneously presented stimuli, but not distant simultaneously presented stimuli, attention appears to suppress responses to the stimulus that is less relevant to the behavioral task (Chelazzi et al. 1993; Luck et al. 1997). That suppression has been interpreted as supporting a biased competition model of attentional effects in which interactions between the cortical representations of nearby stimuli are modulated by top-down attentional mechanisms so that the more relevant stimulus suppresses responses to the less relevant stimulus (Reynolds et al. 2000; Reynolds and Desimone 2003). The interactions we observed between precue stimuli and nearby radial centers of motion separated by only 250–500 ms may trigger similarly biased competition.

**Spatial Cueing Narrows Response Tuning**

Our studies revealed behavioral task effects on the width of Gaussian fits to averaged tuning curves for the radial centers of motion in optic flow. Precueing behavioral irrelevance by exogenous spatial cues in experiment 1 showed 32% narrower

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**Figure 7.** Experiment 4: The effects of spatial cueing of relevant optic flow on neuronal responses. (A) In relevant optic flow trials (red), centered fixation is followed by optic flow with 1 of 8 radial centers and then the random selection of a second optic flow with either the same radial center or the radial center on the opposite side of the fixation point. The irrelevant optic flow trials (blue) are the same as those in the nonspatial paradigm (Fig. 6A). (B) Single neuron responses (mean ± standard error of the mean) to optic flow with Gaussian fits to the optic flow presented as the precue in the relevant optic flow trials (red) and to the irrelevant (blue) optic flow stimulus showing slightly larger magnitude and narrower tuning width in response to relevant optic flow. (C) Single neuron responses to the relevant optic flow (red) and the irrelevant (blue) optic flow showing substantially larger magnitude and narrower in response to relevant optic flow.

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tuning to relevant versus irrelevant optic flow (Fig. 3A). Endogenous spatial cueing in experiment 2 yielded an 18% effect (Fig. 5A) showing that tuning width effects do not depend on residual sensory activation from a peripherally placed precue. Combined with the finding that nonspatial cueing in experiment 3 yields only a 2% effect (Fig. 6C), these studies suggest that tuning effects are linked to the strength of spatial information in the precues.

Spatial precue effects on optic flow tuning width might be mediated by a stored representation of the precued location. The stored precue location could interact with MSTd neurons to enhance responses encoding radial centers near that location or suppress responses to radial centers far from that location. This view is consistent with the near–far precue proximity effects seen under conditions that resulted in significant tuning width changes: exogenous spatial cueing in experiment 1, greater than endogenous spatial cueing in experiment 2, and greater than nonspatial cueing in experiment 3. Top-down response modulation by a stored representation of the precued location might have different effects than competing stimuli which do not show effects of stimulus proximity (Seidemann and Newsome 1999).

In experiment 4, the nonspatial paradigm that did not yield significant tuning effects was supplemented with the addition of an optic flow precue in the behaviorally relevant optic flow trials (Fig. 7A). The optic flow precue provided a 50% valid and 50% invalid cue regarding the location of the target radial center in the subsequently presented 100% valid relevant optic flow. In this paradigm we observed significant narrowing of the tuning curves for both the optic flow precue (35%) (Fig. 8A) and for the relevant optic flow (45%) (Fig. 8B).

One explanation of the tuning width effect on responses to precue optic flow is that the random presentation of valid and invalid precues increases the spatial demands of the task and that this effect results in narrower tuning curves. This is consistent with the similarity of responses to relevant optic flow presented after the same and opposite precue optic flow stimuli (Fig. 8C).

An alternative explanation focuses on the fact that the precue optic flow and the task relevant optic flow in experiment 4 both provide important spatial information about the location of the saccade target in that trial. The precue optic flow reduces the number of alternative targets from 8 to 2 and allows the monkey to increase the probability of a correct choice from 0.125 to 0.5. Likewise, the subsequent, task-relevant optic flow stimulus allows the further increase of the probability of a correct choice from 0.5 to 1. From this perspective, both stimuli have similar spatial cueing significance and the similarity of the effects on

![Figure 8](image.png)

**Figure 8.** Averaged responses to the spatial cueing of relevant optic flow. (A) Average responses of neurons with significant differences between tuning curves to optic flow presented as the precue in the relevant optic flow trials (solid red) and as the irrelevant (dashed blue) optic flow and with good fits in the precue and irrelevant conditions. There is only a nonsignificant difference in magnitude but there is significantly narrower tuning width (35%) with precue optic flow (solid red) versus irrelevant optic flow (dashed blue). (B) Average responses of neurons with significant differences between tuning curves to relevant (solid red) versus irrelevant (dashed blue) optic flow and with good fits in the relevant and irrelevant conditions. There is both substantially larger magnitude (15%) and substantially narrower tuning width (45%) with relevant (solid red) versus irrelevant (dashed blue) optic flow. (C) Average responses of neurons with significant differences between tuning curves to relevant versus irrelevant optic flow and with good fits in the same and opposite conditions. Comparison of responses with the relevant optic flow stimulus when it was preceded by precue optic flow that had either the same (solid orange) versus the opposite (dashed brown) radial center of motion. There are no significant differences of magnitude or tuning width between these response profiles.
their tuning widths is consistent with our hypothesized tuning effects of spatial cuing.

Further experiments are needed to fully characterize these effects. For our purposes, the main point is that experiment 4 shows how alterations in the behaviorally relevant trials can result in the same types of tuning effects as was seen with alterations in the behaviorally irrelevant trials in the first 3 experiments.

**Relationship of Magnitude and Tuning Effects**

All 4 studies suggest that response magnitude and tuning width effects are independent. In the first 3 studies, magnitude increases of 21%, 16%, and 25% were seen with width decreases of 32%, 18%, and 2% showing no systematic relationship. In the fourth study, the spatial precueing of relevant optic flow resulted in magnitude increases of 3% for precise optic flow and of 15% for relevant optic flow with decreases in tuning width of 35% and 45%. Thus, neither the direction nor the size of magnitude effects were linked to tuning width effects, even in responses from the same neurons with comparisons from within the same trials.

Narrower tuning for attended stimuli has been seen in the orientation selectivity of V4 neurons during a discrimination task (Spitzer et al. 1988). Match-to-sample paradigms in V4 also show tuning effects: Some suggest tuning when the stimulus matches the cue (Motter 1994a,b) and others suggest that featural similarity has a graded effect (Haenny and Schiller 1988; Haenny et al. 1988; Maunsell et al. 1991). In contrast, Gaussian fits to the responses of MT, MST (Treue and Andersen 1996; Treue and Martinez Trujillo 1999), and V4 (McAdams and Maunsell 1999a, 2000) neurons have not shown tuning effects of featural or spatial attention. However, featural attention may enhance direction selectivity in MT’s population responses (Martinez Trujillo and Treue 2004).

We found dissociable effects of behavior on response amplitude and tuning width in MSTd neuronal responses to optic flow. Response amplitude was linked to the behavioral relevance of the stimulus: Relevant optic flow evoked larger responses than irrelevant optic flow. This may reflect the activation of a neuronal population devoted to a particular task in a manner consistent with the multiplicative gain control of responses (Treue and Maunsell 1996), in this case activating MST when the task requires optic flow heading discrimination.

In contrast, task effects on tuning width for the heading of self-motion in optic flow were linked to spatial information in the competing task: Exogenous spatial cues evoked stronger tuning effects than endogenous spatial cues, which evoked stronger effects than nonspatial cues. This may reflect the differential activation of neurons within a population to represent a particular stimulus attribute, possibly by engaging local competitive interactions within that population (Reynolds et al. 1999), in this case favoring MST neurons devoted to a particular heading direction.

Thus, behavioral context might induce amplitude or tuning effects in MST related to demands placed on optic flow analysis and the spatial attributes of the task. Our experiments do not prove that amplitude and tuning effects rely on separate mechanisms. However, the dissociable effects of behavior on response amplitude and tuning are consistent with separate top-down influences on MST. Top-down influences yielding response amplitude modulation might be linked to greater yielding of one cortical area over others, whereas influences yielding tuning width modulation might be linked to greater activation of one group of neurons with others within an activated area.

**Notes**

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