Receptive Field Dynamics Underlying
MST Neuronal Optic Flow Selectivity

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ABSTRACT

Optic flow informs moving observers about their heading direction. Neurons in monkey medial superior temporal (MST) cortex show heading selective responses to optic flow and planar direction selective responses to patches of local motion. We recorded MST neuronal responses to a $90^\circ \times 90^\circ$ optic flow display, and to a $3 \times 3$ array of local motion patches covering the same area. Our goal was to test the hypothesis that the optic flow responses reflect the sum of the local motion responses. The local motion responses of each neuron were modeled as a mixture of Gaussians, derived using a genetic algorithm, and then used to predict that neuron’s optic flow responses. Although some neurons showed good correspondence between the local motion model and the optic flow responses, others showed substantial differences.

We then used the genetic algorithm to modulate the relative strength of each local motion segment’s responses to accommodate multiplicative interactions during their co-activation by the global patterns of optic flow. These gain modulated models showed uniformly better fits to the optic flow responses, suggesting that co-activation of receptive field segments alters neuronal response properties. We tested this hypothesis by simultaneously presenting local motion stimuli at two different sites. These two-segment stimulus studies revealed that interactions between response segments have direction and location specific effects that can account for aspects of optic flow selectivity. We conclude that MST’s optic flow selectivity reflects dynamic interactions between spatially distributed local planar motion response mechanisms.
INTRODUCTION

Dorsal MST (MSTd) neurons respond to the large-field patterns of optic flow (Tanaka and Saito, 1989; Saito et al., 1986) encoding self-movement heading direction (Duffy and Wurtz, 1995; Bremmer and Lappe, 1999). Many MSTd neurons are responsive to planar, radial, and circular patterns in a manner that is consistent with a planar directional mechanism in the peripheral visual field. Others show either planar and radial or planar and circular responsiveness, consistent with an eccentric planar response mechanism that is selectively activated by either radial or circular patterns that contain orthogonal motion throughout the stimulus. The most selective neurons show only planar, or radial, or circular responsiveness with yet unclear relations to planar response mechanisms (Duffy and Wurtz, 1991a and b). This spectrum of response selectivities is compatible with a range of MSTd neuronal response properties in a 3D pattern direction space (Graziano et al., 1994).

The view that planar motion sensitivity is the basis of optic flow analysis was undermined by evidence that human heading estimation is unaffected by concurrent pursuit eye movements that distort retinal motion patterns (Warren and Hannon, 1990). These findings were interpreted as supporting computational models of optic flow analysis that avoid the distorting effects of eye rotation by deriving separate rotational and translational components from the optic flow field (Longuet-Higgins and Prazdny, 1980; Prazdny, 1981). A number of biologically plausible models of optic flow component decomposition have augmented these views by the consideration of the combined contributions of direction and speed tuning (Heeger, 1987; Perrone, 1992; Dyre and Andersen, 1997; Barraza and Grzywacz, 2005). Emphasis on the
role of planar motion sensitivity in optic flow analysis was bolstered by evidence that non-visual signals about pursuit eye movements are required for heading estimation during eye rotation (Royden et al., 1992; Banks et al., 1996). Thus, the influence of pursuit signals on MSTd’s neuronal responses supported the notion that these cells might process optic flow by combining planar motion responses with oculomotor signals (Bradley et al., 1996; Page and Duffy, 1999; Page and Duffy, 2003).

In the current studies, we examined the role of planar motion response mechanisms in optic flow analysis by recording responses to both local planar motion and large-field optic flow during visual fixation. We modelled MSTd’s planar motion responses as a mixture of Gaussians because our experience with the highly variable shape of their planar direction response functions suggested that simpler models were inadequate (Duffy and Wurtz, 1991b; Duffy and Wurtz, 1997). We used a genetic algorithm to optimize the mixture of Gaussians models, guided by response magnitude and selectivity error functions. We use these dual criteria to avoid response function biases and accrue greater resistance to local minima encountered in the fitting process (Bleeck et al., 2003; Van Geit et al., 2008). By combining data from various stimulus paradigms we incrementally refined our model of MSTd neuronal responses to identify factors that might shape planar motion mechanisms so that they are more specifically suited to optic flow analysis.
METHODS

Animal preparation

Rhesus monkeys were accommodated to the laboratory routine, and then underwent surgery in preparation for single neuron recording. Surgical procedures were preceded by sedation with Ketamine (15 mg/kg im) and Robinul (0.011 mg/kg im), followed by venous catheterization, endotracheal intubation, and general anesthesia using inhaled Isoflurane. Continual verification of the surgical plane of anesthesia was maintained while measuring heart rate, core temperature, $O_2$ saturation, and end-expired $CO_2$.

We excised a 3 cm X 4 cm section of scalp, debrided the exposed calverium and inserted 16 to 24 dental pins around the edge of the exposed bone to stabilize the implant. We placed bilateral scleral search coils by peri-limbotomy, tunneling the leads to connectors within the area of excised scalp (Judge et al., 1980). A head holder socket was placed over the frontal midline and bilateral recording cylinders were placed over 2 cm trephine holes above area MSTd (AP –2mm, ML+/-15mm, angle 0). The dental pins, coil connectors, head holder, and recording chambers were then encased in a dental acrylic cap.

Postoperatively, the animal was returned to its home cage when it could maintain postural stability and coordinate its limb movements. Close monitoring of its behavior guided analgesia with Banamine (1 mg/kg im) as judged appropriate by the veterinary staff. Daily cleaning of the excised scalp edge and of the recording chambers was maintained thereafter. All protocols were approved by the University of
Rochester Committee on Animal Research and complied with U. S. Public Health Service and Society for Neuroscience policy on the care of laboratory animals.

When the animals had fully recovered from surgery, they were trained to maintain visual fixation during visual stimulus presentation as confirmed by eye position monitoring using the magnetic search coils (Robinson, 1963). Trials began with a stationary, red fixation point centered at eye height directly in front of the animal. The monkeys were required to maintain fixation (+/-3°) throughout the trials while patterns of optic flow stimuli were presented. Successful completion of a trial was accompanied by the sounding of an auditory tone and the delivery of a liquid reward. Single neuron recording sessions were begun after the animal consistently completed >90% of the stimulus presentation trials.

**Visual Stimuli**

After the isolation of responses from a single neuron, its receptive field characteristics were mapped using a hand-held projector presenting varying size bars and random dot patterns. We then began the automated presentation of optic flow stimuli generated by a personal computer driving a television projector (Electrohome ECP4100) at 60 Hz to cover the central visual field (90° x 90°) for 2 s. The optic flow stimuli simulated the self-movement scene for 16 different heading directions. The 16 directions were presented in a pseudo-random sequence until each had been presented during 6-8 successful fixation trials. Each optic flow stimulus consisted of 500 white dots (0.19° at 2.61 cd/m²) on a black background (.18 cd/m²) stimulating the central 90° x 90° of the visual field. All dots were replaced by lifetime expiration (33 to 1000 ms) or by a smoothing algorithm that maintained a uniform and consistent dot
density across the stimulus in all frames. Dots for these radial patterns accelerated as a sine X cosine function of their distance from the focus-of-expansion maintaining an average speed of 40°/s.

In other blocks during the recording session, the visual stimulus was subdivided into nine, non-overlapping, 30° x 30° screen segments (Figure 1a). Planar motion in the four cardinal directions was presented in each segment separately (Fig.1b). Trials began with the monkey fixating a central target followed by the presentation of a random series of the nine locations and four planar motion directions shown for 500 ms each. Each stimulus interval presented either motion in a single segment or in two independently selected segments. The pre-selection of locations for the paired stimulus presentations was based on the review of receptive field characteristics to identify the most responsive segments of the display area. The segment and direction of motion, and the presentation of single or paired stimulus segments, were all interleaved pseudo-randomly.

**Neural recording and data handling**

In these studies, single neuron responses were recorded from three cerebral hemispheres of two rhesus monkeys. Tungsten microelectrodes (Microprobe, Inc.) were passed through a trans-dural guide tube to record neuronal activity (Crist et al., 1988). A dual window discriminator digitized discharges that were stored with event markers on the REX experiment control system (Hays et al., 1982). MSTd was identified by determining that the recording sites contained neurons having large receptive fields (>20°²) that include the fixation point, with direction selective responses, preferring pattern to bar motion (Komatsu and Wurtz, 1988a) (Duffy and
Wurtz, 1991a). When these experiments were completed, we placed electrolytic marking lesions at selected sites in the recording region. Subsequent histological analysis confirmed that our recording sites were in the anterior bank of the superior temporal sulcus, overlapping with the heavy myelinated zone that is associated with MSTd. In our preliminary data analysis, neuronal spikes were convolved with a 20 ms Gaussian to produce spike density functions that were averaged over the six to eight presentations of each visual stimulus.

**Genetic Algorithmic Modeling**

In these experiments, the visual display area was divided into a 3 X 3 array of nine spatial segments (Figure 1A). We developed a generative model in which the responses of each segment was modeled as a mixture of two Gaussian functions (Fig. 2A). We then simulated the presentation of optic flow stimuli to the nine segment composite model, combined as the linear sum of the individual segment responses, to predict that neuron's responses to optic flow (Fig. 2B).

Four parameters were estimated for each of the Gaussian functions in each screen segment’s mixture of Gaussians model of the neuronal firing rate responses:

$$G(\theta, c, p, \mu, \sigma)_{ij} = c_{ij} \cdot p_{ij} \cdot \exp\left(-\frac{(\theta - \mu_{ij})^2}{2\sigma_{ij}^2}\right)$$

where $\theta$ is the motion direction, $c$ is the gain constant modulating the magnitude of the Gaussian, $p$ is the polarity of the excitatory or inhibitory response function, $\mu$ is the mean angular direction of the segment’s preferred visual motion, $\sigma^2$ is the variance around the preferred direction, $i$ represents the stimulus screen segment ($i = 1,2,\ldots,9$), and $j$ represents the two Gaussians within each screen segment ($j = 1,2$).
Thus, there were 8 parameters estimated for each of the nine segments. The complete local motion model of responses, with nine stimulus segments, required the estimation of 72 parameters. In consideration of the risk of over-fitting, we tested the local motion models with independent data from the same neurons, acquired using optic flow stimuli. To do so, the output of each Gaussian, relative to that neuron’s baseline firing rate (during fixation without visual motion stimulation) was summed across all nine segments and then summed with the baseline firing rate to predict the firing rate response to the full-field optic flow stimuli. In later versions of these models, the relative gain of each segment was independently adjusted, matching the gain factors of the two Gaussians in each segment’s model. When each of the individual Gaussian response mechanisms was assigned an independent gain, the gains were modulated independently.

Several different approaches might be used to estimate the mixture of Gaussians parameters. In this work, we use a computational genetic algorithm. Genetic algorithms are a class of computational methods that seek to solve an optimization problem. The problem is formulated in terms of an initial population, a fitness function, a selection method, and crossover and mutation methods used to produce successive generations in the population. Here, we first randomly created an initial population of 1300 individuals. Each parameter in Equation 1 was represented by a binary string: 10110101 00110101 00011111………. where each set of eight bits represents a parameter value with the number of bytes per parameter depending on the upper bound of that parameter’s values.
Evaluation of Computational Models

The genetic algorithm searched the parameter space to minimize error in predicting neuronal responses. The quality of a potential solution is determined by the fitness function. In our application, we are seeking a set of parameters that minimize the difference between the model’s firing rate and that of the neuron recording in the neurophysiological experiment. In evaluating the success of each candidate model, the genetic algorithm combined two equally weighted error functions to recursively assess the mixture of Gaussians models’ fit to the mean firing rates evoked by local motion stimuli.

The first error function was the total error, the sum of the differences between a model’s predicted firing rate responses and the observed averaged, normalized firing rates evoked by each of the stimuli, weighted by the firing rate standard error from the responses to each presentation of that stimulus:

\[ d_e = \sum_{i=1}^{n} \frac{|r_{m_i} - r_{n_i}|}{se_i} \quad (2) \]

where \( d_e \) is the total error, \( r_{m_i} \) is the model’s firing rate response, \( r_{n_i} \) is the neuron’s firing rate response, \( se \) is the standard error of the neuron’s firing rate response, and \( i \) is the index value across the number of stimuli in that stimulus set (36 for local motion, 16 for optic flow).

The second error function was the sum of the differences in response classification based on a three group k-means cluster analysis. The three group cluster analysis was independently applied to the model’s firing rate responses and the observed firing rate responses of the corresponding neuron. The k-means cluster cutting yielded two varieties of clusters that were approximately equally represented in
the sample of neurons: 1) excitatory responses, non-responses, and inhibitory responses and, 2) large and small excitatory responses and non-responses. We then summed the cluster classification differences across all of the visual motion stimuli presented in that study as:

\[ d_g = \sum_{i=1}^{N} | \text{kmc}(r_{m_i}, k) - \text{kmc}(r_{n_i}, k) | \]  

(3)

where \( d_g \) is the group error, \( r_m \) and \( r_n \) are as in (2) and kmc \((x, k)\) is the k-means clustering of the \( x^{th} \) responses, across the \( i^{th} \) stimulus in that stimulus set. The two fitness functions were independently used to rank each model from best to worse fit to the corresponding neuron’s firing rate data, resulting in two ordered lists. The best 25 individuals from each list were chosen to be parents. Each of the 25 lowest total firing rate error individuals were then crossed-over with each of the 25 lowest group classification error individuals, and each parent produce two offspring.

The four offspring from each pair of parents was generated by cleaving the bit sequence of each at a random location within a selected parameter’s gene. This split that variable bit string into two pieces that were then combined: left piece from parent 1 to left piece from parent 2, left piece from parent 1 to right piece from parent 2, right piece from parent 1 to left piece from parent 2, and right piece from parent 1 to right piece of parent 2. If any of the resulting crossed-over variables contained an invalidly high number, it was set to the maximum value allowed. The resulting total offspring of 1250 was combined with the 50 parent individuals to populate the next generation for successive application of the genetic algorithm.

To prevent convergence of the population to a local minimum, 5% of the individuals in each generation underwent a toggling of randomly selected bits from
their parameter bit strings, a process that is intended to mimic the occurrence of mutations in biological evolution. We terminated the algorithm after a fixed number of generations to avoid having different numbers of generations for different neurons. The number of generations for each condition was determined by reviewing the error gradients from test runs of the algorithm. As a result, the algorithm was terminated after 75 generations for the local motion models, 50 generations for the gain modulated models, and 25 generations for the dual stimulus interaction models.

At the completion of the relevant number of generations, the model with the smallest total error score was selected as the final model for that neuron. The modeling of the local motion responses was repeated ten times with independently selected random starting parameters to assess the impact of those parameters and minimize the risk of the final model's reflecting local minima in the error functions.

In evaluating the success of these modeling efforts, we used the final values of the total and group error functions, as well as a measure that was independent of the modeling algorithm. In the latter case, we ordered the local motion responses by increasing average firing rate and compared them to the model's corresponding firing rate predictions using a linear regression model (SPSS Inc., 2007).
RESULTS

We studied the responses of 52 neurons from two hemispheres of two Rhesus monkeys using three stimulus sets presented during centered fixation: single site local planar motion, two site local planar motion, and large-field optic flow. All neurons were recorded in guide tubes that yielded characteristics typical of MSTd neurons (Komatsu and Wurtz, 1988a; Komatsu and Wurtz, 1988b): large receptive fields that include the fovea, preferring pattern motion to moving bars, and showing strong direction selectivity. Subsequent histological examination of the recording sites confirmed that they were in the dorsal-anterior bank of the superior temporal sulcus in the region associated with the medial superior temporal area.

Modeling Responses to Local Motion

We presented a randomly interleaved series of 36 local motion stimuli to each neuron. These stimuli were limited to one of nine 30° X 30° screen segments juxtaposed to cover the same 90° X 90° stimulus area of the previously presented optic flow stimuli (Figure 1A). At each of the nine sites we presented four different planar motion directions: left, right, up, and down (Fig. 1B). These stimuli revealed a diverse array of local motion direction selectivities across the stimulus area, typically including both excitatory and inhibitory responses to different directions of motion (Fig. 1C). This combination of responses yielded distinctly different directionality profiles in different stimulus segments.

To characterize the local motion responses, we derived separate mixture of Gaussians models of the responses evoked for each of the nine stimulus segments. This was achieved by using a genetic algorithm to simultaneously optimize the fit of
the averaged responses to the four directions of local motion in each segment using
free parameters of the direction (0-359°), magnitude (spikes/s), and sign (excitatory or
inhibitory) of the model responses for each of the two Gaussians (Figure 2A). Ten
independent models were calculated for each neuron to assess the intrinsic variability
of the genetic algorithm and its dependence on its randomly assigned starting values.

We assessed the success of each model using the model’s two equally
weighted error functions of total firing rate error and k-means (k = 3) cluster analysis
classification error. In addition, we derived a measure of the model’s effectiveness
that was independent of the modeling process, using a linear regression of the
ordered set of observed firing rate responses and the model’s predicted firing rates.

The genetic algorithm achieved excellent fits to the local motion, with the
model’s responses closely matching the local motion responses in all neurons (Figure
2B). The ten models for each neuron yielded comparable fits to the recorded data,
reflected in the low variance of the fitting error across the ten models: mean total error
= 6.03 spks/s, mean group error = .17 classes, mean $r^2 = .90$.

To test the similarity of the ten models generated for each neuron, we
correlated each model’s prediction of the local motion responses to those derived from
each of the other models of that neuron. We averaged the $r^2$’s for all combinations of
the ten models of each neuron, and then averaged across neurons to derive a net $r^2 = .88$ with a mean standard deviation of the $r^2$’s across neurons of +/- .06. These results
suggest that the ten models for each neuron yield highly similar predictions of the local
motion responses, implying convergence of the modeling process across multiple
trials seeded with randomly selected starting conditions.
Local Motion Models of Optic Flow

The activity of these neurons was also recorded during the presentation of large-field (90° X 90°) optic flow stimuli during centered fixation. We randomly interleaved 16 optic flow stimuli including eight directions of planar, six radial, and two circular patterns (Figure 3A). Combinations excitatory and inhibitory responses to planar, radial, and circular stimuli were encountered, as previously described (Duffy and Wurtz, 1991a). These responses were characterized as the mean firing rate during the 1 s stimulus interval of 6-8 repetitions of each stimulus and compared to the mean firing rate during blank screen fixation trials (Fig. 3B).

We used the mixture of Gaussians model of the local motion responses of each neuron to predict that neuron’s responses to the 16 full-field optic flow stimuli. First, for each neuron, we calculated each of the nine stimulus segments’ responses to each of the 16 optic flow stimuli. This was achieved for each stimulus segment by determined the firing rate that would be expected from its trained mixture of Gaussians model when shown the local motion that would cover its screen segment during the presentation of each optic flow stimulus. Second, for each neuron, we summed the firing rates for each of the nine stimulus segments to predict a net response of that neuron to each of the 16 optic flow stimuli. Finally, we used the net responses of each neuron to create an optic flow response profile for that neuron and compared that profile to the observed firing rates profile obtained from that neuron’s responses to the 16 optic flow stimuli.

We assessed the local motion models’ ability to predict the optic flow responses using the same three metrics used to assess the local motion fits: 1) The
differences in the predicted and observed normalized firing rates summed across the
16 optic flow stimuli, 2) the sum of the differences in response classification based on
a three group cluster analysis of the optic flow responses, and 3) r²'s derived from an
ordering of optic flow responses by increasing amplitude and comparing them to the
corresponding predicted response amplitudes.

Three salient points emerged from our examining the local motion model's
predictions of the optic flow responses using all three response metrics (Figure 4):
First, across the sample of neurons, there is a wide range of accuracies in predicting
optic flow responses. The best fits are highly accurate, whereas some other neurons
yielded fits that are up to five times worse by the error metrics. Second, all three fit
metrics yield similar orders of model accuracy across the sample of neurons; neurons
that yield the best model fits do so by all three measures. Third, in individual neurons,
the ten independent local motion models yielded similar fits to the responses. There
was less variability in the quality of the fit across the ten models of any neuron, than
across the sample of neurons.

These findings suggest that the optic flow response selectivities of some
neurons are adequately explained by the summation of simple planar motion
responsiveness distributed across MSTd neuronal receptive fields. In many other
neurons, optic flow responses have not been readily predicted as the sum of local
planar motion responses.

Weighted Local Motion Models of Optic Flow

The common failure of local motion models to predict optic flow responses
prompted us to consider the hypothesis that the relative influence of various receptive
field segments might be altered during their co-activation by optic flow. To assess this possibility we used the genetic algorithm to adjust the relative influence of the nine screen segments and optimize each model’s fit to that neuron’s optic flow responses. First, we randomly assigned a multiplicative gain to the mixture of Gaussians model of each of the nine screen segments. Then, the genetic algorithm modified these nine weightings to minimize the total and group errors for each of the ten models of each of the neurons. This approach does not alter the direction specificity of the nine segments, but modifies the strength of each segment’s influence on their composite prediction of optic flow responses.

The resulting segment gain modulated models yielded a substantial improvement of the fit to optic flow for many neurons. The neuron illustrated in Figure 5 yielded a local motion model (Fig. 5A) with an excellent fit to the recorded local motion data (Fig. 5B) but not to optic flow. In this example, the local motion model inconsistently predicted the responses to the eight directions of planar motion and the radial and circular optic flow patterns (Fig 5C). The segment gain modulated model (Fig. 5D) showed substantial and systematic changes from the parent local motion model. These changes are shown as segmental gains that increase the influence of the middle segment and decrease the influence of the segments on the right side of the display area (Fig 5E). When tested with optic flow stimuli, the segment gain modulated model showed a substantially better fit to the recorded optic flow responses (Fig. 5F).

We explored the hypothesis that interactions between local motion responses during large-field optic flow stimulation might act on the direction selective
mechanisms modeled as the 18 Gaussian filters in the nine stimulus segments. To test this hypothesis, we allowed the genetic algorithm to independently modify the relative weighting of the 18 Gaussians filters in the local motion models of each neuron. The resulting changes in the response gains of the 18 Gaussians can modify the composite direction selectivity of each of the nine stimulus segments, as well as their relative weight, potentially altering the spatial distribution of response directionality and strength.

Figure 6 illustrates the mixture of Gaussians models of a single neuron derived from local motion stimuli, and modified by segment and response gain modulation. This neuron showed a variety of models Gaussians across its nine stimulus segments (Fig. 6A) with an excellent fit to the local motion responses (Fig. 6B) but a poor fit to the optic flow responses (Fig. 6C). Segment gain modulation substantially changed the nine models (Fig. 6D) and resulted in lower segmental gains in the upper left segment and on the right, with higher segment gains elsewhere (Fig. 6E) and a better fit to the optic flow responses (Fig. 6F). Response gain modulation substantially changed the 18 Gaussians (Fig. 6G) with lower gains in the center segment and higher gains in the lower segments (Fig. 6H) that resulted in an excellent fit to the optic flow responses (Fig. 6I).

The models’ predictions of the optic flow responses were compared to the actual responses from each neuron using a least squares regression fit to quantify model accuracy. This measure was used to compare the results of the original local motion models of each neuron to the results of that neuron’s models after segment gain (Figure 7A) and response gain (Fig 7B) modulation. Both gain modulated models
yielded substantially better fits than the local motion models, as illustrated by almost all points being above the unity lines shown in those plots. The segment gain modulation resulted in a mean $r^2$ increment $= .18$ over local motion models. Response gain modulation resulted in a mean $r^2$ increment $= .28$ over local motion models. Improvements with segment gain modulation demonstrate that changing only the relative influence of the nine screen segments enhances the fits to optic flow. Greater improvements with response gain modulation imply that changes in the relative contributions of the mixture of Gaussians models yields additional benefit, still without changing the individual Gaussians’ directionality derived from the local motion studies.

**Impact of Local Motion Weightings**

Our use of gain modulation to optimize the composite fit of local motion models to optic flow data had several other effects. Across all neurons, there was a roughly equal balance of total excitatory and inhibitory Gaussian response amplitude in the original local motion models (3.3% greater excitation) and in the segmental gain modulated models (2.1% greater excitation). In contrast, response gain modulated models showed greater net inhibitory amplitude (14.4% greater inhibition). Thus, response gain modulation more closely fit the optic flow data using a preponderance of inhibitory effects.

Response gain modulation’s emphasis on inhibitory mechanisms was still more evident in the spatial distribution of gain modulation effects. In general, there was a great deal of variation in the patterns of gain modulation across neurons. We identified trends across the sample by combining the segmental gain modulation data from all models of all neurons in a two-way ANOVA with main effects of horizontal and
vertical segments. Using the segmental gain modulation data, this analysis yielded significant main effects of horizontal position (F2, 2789 = 7.26, p = .001) but not vertical position (p < .31) or their interactions (p = .26), with post-hoc tests distinguishing the midline from the contralateral side (Tukey's HSD, p < .05). Selecting for gain modulated models with higher r²'s, or with higher r² increments over the local models, by median split, yielded the same pattern of results but somewhat larger and more significant effects (Figure 7C). Thus, using segmental gains to fit optic flow responses resulted in an overall relative decrease in the weight of vertical midline and ipsilateral segments.

We took the same approach to the response gain modulation data, separately considering changes in the gains of excitatory and inhibitory Gaussians. The analysis of excitatory Gaussians yielded significant main effects of horizontal (F2, 2825 = 8.14, p < .001) but not vertical (p = .35) position, and no significant interactions (p < .51), with post-hoc tests distinguishing the ipsilateral side from the midline and contralateral side (Tukey's HSD, p < .05). The analysis of inhibitory Gaussians yielded significant main effects of horizontal (F2, 2876 = 4.63, p = .01) and vertical (F2, 2876 = 8.38, p < .001) position, and their interactions (F4, 2876 = 5.62, p < .001), with post-hoc tests distinguishing the ipsilateral from the contralateral sides, and distinguishing the lower segments from the middle and upper segments (Tukey's HSD, p < .05). Again, selecting for gain modulated models with higher r²'s, or with higher r² increments over the local models, by median split, yielded the same pattern of results but somewhat larger and more significant effects (Figure 7D). Thus, using response gains to fit the optic flow responses resulted in an overall relative decrease in the midline segments.
We considered that gain modulation might have improved the fit to the local motion data and only secondarily improved the fit to the optic flow. To test this hypothesis we used the gain modulated models to predict the responses of each of the nine stimulus segments to the local motion data. In all but one neuron, the gain modulated models showed poorer fits to the local motion data than was achieved by the original local motion models (Figures 7E and 7F). This suggests that gain modulation captures some differences between the response mechanisms activated by local motion versus optic flow.

Several points summarize the impact of segment and response gain modulation: First, both approaches improved fits to optic flow responses in all neurons, somewhat more so with response gain modulation, but neither approach resulted in perfect fits in all neurons. Second, the spatial distribution of effects resulted in an overall increase in the relative weighting of the contralateral hemi-field. Third, the gain modulated model’s poorer fits to the local motion data implies that some effects that are not captured in the local motion data must contribute to optic flow selectivity.

**Interactions between Local Motion Stimuli**

The response interactions implied by the success of the gain modulated models was assessed by presenting dual, simultaneous local motion stimuli. The four directions of local motion evoked different direction selectivities at different sites within the visual field. When two local motion stimuli were presented together they revealed a variety of direction and location specific interaction effects. These interactions are illustrated in Figure 8. In this neuron, two non-adjacent screen segments yield
substantially different net direction selectivities (Fig. 8A). When these two segments were both activated at the same time, with varying directions of motion, we saw direction specific response interactions: rightward motion in the upper left corner evoked upper and rightward response preferences from the lower right screen segment (Fig. 8B). Thus, response interactions across non-adjacent screen segments can modify the direction selectivities of MSTd neurons.

We recorded two-segment local motion responses across a variety of stimulus segments. Figure 9 depicts findings from a neuron in which we placed left- or rightward motion in either the upper-left (fixed direction site A) or upper-middle (fixed direction site B) segments and combined those stimuli with the four different cardinal directions of motion in the other stimulus segments. Two examples are illustrative: 1) Center segment response interactions: Local motion in the center segment alone showed leftward and upward direction preferences, with no response to downward motion (black diamond). However, when downward motion in the center segment was combined with rightward motion in upper-left segment (Site A) it evoked the largest responses recorded in this neuron (red diamond). 2) Middle-left segment response interactions: Local motion in the middle-left segment alone showed a moderate response to upward motion (black diamond). However, when upward motion in the middle-left segment was combined with the small responses to rightward motion in the upper-middle segment (Site B), it evoked large responses (orange diamond); when upward motion in the left-middle segment was combined with the large responses to leftward motion in the upper-middle segment, it evoked small responses (green diamond).
This example suggests several points: First, two-segment stimulation evoked non-additive interactions across stimulus segments. Second, those interactions are idiosyncratically direction selective. Third, these idiosyncratic direction selective interactions differ across different pairs of stimulus segments. These findings support the notion that large-field patterns of optic flow might activate response interactions that impart properties that are not evident in responses to local motion stimuli.

Comparison across the other two-segment combinations supports the impression that the directional specificity of response interactions is not homogenous across the stimulus area. Thus, response interactions across stimulus segments are both highly non-additive, within a pair of stimulus segments, and highly variable across different pairs of stimulus segments.

These findings led us to consider that response interactions across stimulus segments might account for differences between neuronal responses to optic flow and those that are predicted by the local motion models. To test this hypothesis we used the two-segment responses to modify local motion models to account for response interactions across stimulus segments.

Figure 10 depicts findings from a neuron in which we used the center and upper-middle segments as set stimulus locations. Again, two examples are illustrative: 1) When leftward motion filled both test locations, the resulting combined local motion data was best fit by a model that predicted the moderate firing rate that would result from uniform leftward optic flow, an effect not captured by the single stimulus local motion models or its gain modulated variants. 2) When upward motion filled the upper-middle test locations, with the center segment remaining blank, the
resulting combined local motion data was best fit by a model that predicted the high firing rate that would result from outward radial optic flow, also an effect not captured by the single stimulus local motion models or its gain modulated variants.

Across the sample of neurons, 74% (14/19) of the neurons with the poorest performance of their local motion models (group error > 9) showed better fits with interactions models. Neurons that were well fit by their local motion models, or by the gain modulated variants of those models, less clearly benefitted from the consideration of two-segment stimulus interactions. This suggests that some neurons may have more substantial interactions than others, although we can not reject the possibility that our arbitrary selection of test locations might not have included locations with substantial interactions in all neurons. Nevertheless, these studies demonstrate that response interactions evoked by the co-activation of two stimulus segments can explain some of the observed inadequacies of local motion models’ abilities to predict neuronal responses to optic flow stimuli.
DISCUSSION

Local Motion Mechanisms of Optic Flow Selectivity

Neuronal optic flow selectivity may reflect the composite effects of spatially distributed planar motion sensitivities, or specific sensitivity to distributed properties of optic flow fields. Early studies showed that optic flow selectivity in some MSTd neurons might reflect converging planar directional input from MT (Saito et al., 1986) (Tanaka et al., 1989). Later studies found that many of these responses were maintained despite changes in the size and position of the stimuli, suggesting a role for distributed response sensitivities (Duffy and Wurtz, 1991b). These findings suggest a spectrum of optic flow selectivities in MSTd. At one end are neurons with planar, circular, and radial responses that can be explained by local planar directional mechanisms confined to a segment of the visual field. At the other end are neurons with either circular or radial responses and greater position invariance and little or no underlying planar directionality (Duffy and Wurtz, 1991a) (Graziano et al., 1994).

We have now tested relations between local motion responses, recorded at nine segments across the central visual field, and optic flow responsiveness by developing mixture of Gaussians model of MSTd receptive field mechanisms. We assessed the performance of the modeling process using the error criteria imbedded in the model (total firing rate error and response classification error), as well as an independent criterion ($r^2$s), all of which produced the same pattern of results (Figure 4). We used these models to predict neuronal responsiveness to optic flow, finding substantial variation in success of this approach.
These findings reinforced our impression that the optic flow responses of some neurons reflect local planar motion mechanisms, whereas other neurons may respond to more fundamental attributes of optic flow. One such attribute is the increasing divergence of visual motion elements that define the outward radial pattern seen during forward self-movement (Koenderink and van Doorn, 1975) (Koenderink and van Doorn, 1981), potentially implemented by a normalization of motion properties across a segment of the visual field to derive the affine motion of elements in that segment (Beusmans, 1993). As an alternative, we considered that dynamic interactions between planar motion response mechanisms might account for optic flow selectivity. This view prompted our combining computational and experimental approaches to characterize planar motion response interactions in MSTd neurons.

**Gain Modulation by Optic Flow**

We used a genetic algorithm to explore the possibility that the simultaneous co-activation of different response mechanisms might alter their relative influence on neuronal responses. We randomly assigned a .1x to 10x multiplier to the relative amplitude of the local motion models using two approaches: First, we treated the nine stimulus segments as spatially defined response mechanisms and assigned a single weight to each segment. Second, we treated the 18 Gaussians as separate response mechanisms and assigned independent weights to each Gaussian.

Gain modulation accessed the optic flow responses to direct their improvement across successive generations (Figures 5 and 6). As expected, the net effect is improved fits to optic flow with the response gain approach yielding larger average $r^2$ increments than the segment gain approach (Fig. 7A and B). Both approaches
yielded significant spatial distributions of gain changes reflecting the lowering of the relative influence of segments in the vertical midline and on the ipsilateral side of the visual field (Fig. 7C and D). Thus, co-activation of all nine stimulus segments by optic flow induces a spatially selective decline in responsiveness that emphasizes the influence of the contralateral hemi-field. These effects may be viewed as a large-field version of lateral inhibition in which one part of the receptive field deactivates others.

We verified that gain modulation was not simply creating better fits to local motion data to secondarily improve fits to optic flow. When the gain modulated models were back fit the local motion responses we found that they do not fit the local motion as well as the original local motion models (Fig. 7E and F). Thus, gain modulation incorporated aspects of optic flow responsiveness that are not available in the responses to local planar motion stimuli presented separately.

The success of local planar motion models in predicting the optic flow responses of some neurons is consistent with neuronal template models (Perrone and Stone, 1994). The incremental enhancement of our models with changes in the relative influence of receptive field segments supports the view that MSTd is optimized for optic flow selectivity by the adjustment of weightings on the inputs to each neuron (Wang, 1995), possibly through Hebbian shaping guided by heading direction feedback (Zhang et al., 1993). This optimization might use MSTd’s co-activation by signals from object motion (Zemel et al., 1998) (Royden and Hildreth, 1999) (Logan and Duffy, 2006) and vestibular input (Duffy, 1998) (Page and Duffy, 2001) (Gu et al., 2006) about self-movement.
One can think of the nine mixture of Gaussians local motion models as reflecting separate inputs from neurons projecting to MSTd, potentially from adjacent area MT’s planar motion selective neurons (Zeki, 1980) (Felleman and Kaas, 1984) (Ungerleider and Desimone, 1986) (Boussaoud et al., 1990) (Boussaoud et al., 1992). Co-activation of distinct inputs can result in non-additive interactions yielding increases or decreases in neuronal firing (Holt and Koch, 1997) (Doiron et al., 2001). MT sub-population projections to MSTd might form dendritic compartments to create a substrate for response interactions (Hausser and Mel, 2003) (Rabinowitch and Segev, 2006). Dendritic compartment mediated response interactions can be expected to have gain modulation effects that can activate or inactivate the effects of an input on neuronal firing (Larkum et al., 2009) (Larkum et al., 2004). The gain modulation effects we have modeled in MSTd are consistent with effects on dendritic compartmentalized local motion inputs from MT.

**Co-activation Dependent Directionality**

We assessed interactions between local planar motion response mechanisms by simultaneously presenting two local motion stimuli in different segments of the visual field. These studies revealed substantial changes in the net directionality of co-stimulated areas compared to that seen with the isolated stimulation of either area (Figures 8 and 9). These effects accounted for many of the differences observed between local motion models and optic flow responses in MSTd, including those that were not accounted for by adding gain modulation to the models (Figure 10).

While such effects might be intrinsic to MST, we must consider that MT’s direction selective inputs to MST might include such conditional modifications. The
two-stage orientation and coherence selectivities model of MT, reflecting sequential processing in V1 and MT, created fixed neuronal direction preferences (Adelson and Movshon, 1982). However, surround effects defining non-classical receptive fields of some MT neurons (Allman et al., 1985) with potent center-surround antagonism (Tanaka et al., 1986) highlighted the potential for winner-take-all interactions adding complexity and flexibility to MT neuronal responses (Bulthoff et al., 1989). Integrating the idiosyncratic spatial distributions of direction and speed sensitivities of these neurons can promote the segmentation of complex scenes into objects and surfaces (Mikami et al., 1986) (Nowlan and Sejnowski, 1994) (Xiao et al., 1995). The rectification and normalization of these responses, possibly through divisive inhibitory response interactions, would refine population responses and favor particular response mechanisms (Simoncelli and Heeger, 1998) in a manner that might be disproportionate to their spatial summation based on the spatial extent of visual stimuli (Britten and Heuer, 1999).

Rather than viewing response interactions as being obligatorily and antagonistic, we should accept that different MT neuronal sub-populations might show fundamentally different center-surround interactions with some altering response directionality while others do not (Huang et al., 2008). This more elaborate view of MT neuronal responses is consistent with the cascade model of MT response processing that incorporates both linear and non-linear processing in the V1 to MT transformation (Rust et al., 2006). The range of MT responses might provide a basis for differential processing in the transformation to MSTd that could support optic flow selectivity (Tohyama and Fukushima, 2005).
The extensive connections between MT and MSTd are paralleled by neurophysiological and functional homologies. The planar motion response properties of MT neurons range from simple direction selectivity to dynamically interacting directionalities (Albright et al., 1984) (Movshon et al., 1986) (Rodman and Albright, 1989) that define sub-populations that respond to either the components of two superimposed directions or to their composite pattern (Movshon and Newsome, 1996) (Kohn and Movshon, 2004) (Bair and Movshon, 2004) with related illusory perceptions of plaid pattern motion (Welch, 1989) (Beutter et al., 1996). Similarly, the planar motion response properties of MSTd neurons range from direct correspondence to optic flow selectivities to the spatio-directional dynamic relations evident in our two-stimulus interaction studies (Figure 9) that may correspond to sub-populations with distinct responses to overlapping planar and radial motion (Duffy and Wurtz, 1997) that create illusory transformations of optic flow (Duffy and Wurtz, 1993) (Lappe and Rauschecker, 1995). The anatomical connections and functional similarities between these areas suggest a continuum of dorsal extrastriate response properties from MT, to MSTI, MSTd, and 7a in which visual motion response mechanisms are preserved across increasing spatial scale from receptive field segments in MT to visual hemisphere representations in 7a.
ACKNOWLEDGEMENTS

We gratefully acknowledge Dr. David J. Logan's role in the design and execution of the single neuron recording experiments and Ms. Sherry Estes' assistance in monkey care and surgery. This work was supported by National Eye Institute grants R01-EY10287 and P30EY01319.
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Tanaka K, Saito H (1989) Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial


FIGURE LEGENDS

Figure 1. Local planar motion stimuli evoke direction and location selective responses in MSTd neurons. A. The 90° X 90° stimulus screen was divided into 9 equal 30° X 30° stimulus segments. B. Four directions of planar moving dot stimuli were presented in each segment with remaining segments remaining blank. C. The neuronal spike density histograms for a neuron showing the responses to planar motion in each of the corresponding screen segments (dashed line boxes) and motion direction (up, left, right, down).

Figure 2. Mixture of Gaussians local motion models of nine screen segments recorded in one neuron. A. Model used either excitatory (red) or inhibitory (blue) vectors to match the neuronal responses. Vector direction and amplitude (length of vector) indicate the tuning of each of the two Gaussian functions in each of the nine segments. B. The mixture of Gaussians model created highly accurate fits (red) for the responses to the 36 local motion stimuli (blue). The ten models generated for this neuron yielded consistently excellent fits to the local motion data: mean total error = 2.72 spks/s, mean group error = .03 classes, mean r² = .98

Figure 3. Optic flow stimuli evoke heading direction selective responses in MSTd neurons. A. Sixteen optic flow stimuli were presented in a pseudo-random sequence with each stimulus repeated 6-8 times. Schematic plots (boxes) indicate optic flow pattern on screen along with corresponding spike density histograms. Dashed vertical line indicates the start of the trial. B. Responses of an MSTd neuron to the 16 optic flow stimuli along with variance (+/- sem). The icons along the abscissa indicate the optic flow stimulus evoking the corresponding firing rate response.
**Figure 4.** Local motion mixture of Gaussians model fits to responses to 16 optic flow stimuli. The neuronal responses to the optic flow stimuli were compared to the model predictions by three methods: normalized total errors (A), normalized group errors (B) and the $r^2$ regression fits of the model prediction to the neuronal response data (C). In all panels the neuron number (abscissa) was maintained in the order of increasing total error to facilitate comparisons between the three metrics.

**Figure 5:** The transformation of a neuron’s mixture of Gaussians models by segmental gain modulation. A. Mixture of Gaussians model derived from local motion responses in the nine stimulus segments. B. Corresponding fit of the local motion model to neuronal responses to the 36 planar stimuli (format as in Fig. 3). D. Corresponding fit for the local motion model (red) to the 16 optic flow patterns showing a poor model fit to the neuronal responses (blue). D. Mixture of Gaussians model after segmental gain modulation. E. Segmental gain changes that were implemented by the model to modulate the weight of the mixture of Gaussians model in each of the nine segments (increases, green; decreases, brown; full-scale +/- 10x). F. Fit of the segment gain modulated model to the 16 optic flow patterns shows a substantial improvement for all optic flow stimuli compared to that of the unmodulated local motion model shown in C.

**Figure 6.** The transformation of a neuron’s mixture of Gaussians models by response gain modulation. A-F format as in Figure 5. G. Mixture of Gaussians model after response gain modulation. H. Response gain changes that were implemented by the model to modulation the weight of each of the 18 Gaussians (increases, above line; decreases, below line; excitatory Gaussians, red; inhibitory Gaussians, blue; full-scale
Fit of the response gain model to the 16 optic flow patterns shows a substantial improvement for all optic flow stimuli compared to both the unmodulated local motion model (C) and the segment gain modulated model (F).

**Figure 7:** Comparison of fits to neuronal responses derived from the local motion models (abscissas) and the two approaches to the gain modulation of those models (ordinates). The $r^2$ values are from linear regression fits of each neuron’s observed firing rate responses to each model’s predicted responses (each data point represents one neuron). A-B. The $r^2$’s for the correlation between observed and predicted responses to the 16 optic flow stimuli. Both segmental gain (A) and response gain (B) modulated models yielded better fits to the neuronal responses than did the original local motion model, as indicated by the points being above the unity line. C-D. The spatial distribution of gain modulations combined across all models for the nine stimulus segments. The size of each arrow is scaled to reflect relative gains across segments in the models yielding higher $r^2$ increments, downward arrows reflect decreased gains. The distributions for left hemisphere neurons were reversed to match the majority right hemisphere orientation. C. Segmental gain modulation resulted in greater declines in the influence of vertical midline more than ipsilateral segments with little effect on contralateral segments. D. Response gain modulation resulted in declines in midline excitatory Gaussians (filled arrows) with widespread increases in inhibitory Gaussians (open arrows). E-F. The $r^2$’s for the correlation between observed and predicted responses to the 36 local motion stimuli. Both segmental gain (E) and response gain (F) modulated models yielded poorer fits to
local motion neuronal responses than did the original local motion response models, as indicated by the points being below the unity line.

**Figure 8.** An example of a two-segment stimulation study that reveals neuronal response interactions between local motion stimuli presented at the set location or the test location. A. Left: Spike density histograms (SDH) of responses to local motion at the fixed-direction location, indicating a preference for right-downward planar motion (open arrow). Right: SDHs of responses to local motion at the probe location, indicating a preference for left-downward planar motion. B. Responses when local motion was presented simultaneously at both the fixed-direction and probe locations. Left: When leftward motion was presented at the fixed-direction location (green arrows), the direction preference for stimuli at the probe location (SDHs) yielded little net direction selectivity. Right: When rightward local motion was presented at the fixed-direction location (blue arrows), the direction preference for stimuli at the probe location (SDHs) yielded strong right-upward selectivity, a $180^\circ$ change from the probe location’s original directionality.

**Figure 9:** Site and direction specificity of response interactions as revealed by simultaneous stimulation at two different locations. The spatial location of the two stimuli, and their directions of motion, interacted to produce a variety of idiosyncratic responses. Responses to motion at the fixed direction sites presented alone are shown as colored asterisks. Responses to motion at the probe sites alone are shown as black diamonds. Two-segment responses are plotted in the probe location’s segment as colored diamonds with the color corresponding to that used for the fixed direction component.
Figure 10. Example of transformation of mixture of Gaussians models by local motion interaction effects. A. The local motion model fails to predict the neuronal response to optic flow in this neuron (recorded responses, blue; predicted responses, red which overlaps the axis to indicate predicted net firing rate of zero for all optic flow stimuli). B. The response gain model improved the fit to several of the optic flow stimuli, but failed to predict the neuronal response to many others. C. The local motion interactions model yielded much better fits to the optic flow responses (lower middle). The five frames show the mixture of Gaussians models used for each of the five optic flow patterns indicated by the black arrows. In each model, the segments outlined in red were the set sites and their red arrows were the set site directions, used to probe local motion interactions. These experiments yielded unique mixture of Gaussians models for each combination of set site directions, those set site directions specifying the optic flow stimulus to which that model might correspond best. The interactions related to optic flow responsiveness: rightward planar optic flow (lower-left frame), upward planar optic flow (upper-left frame), leftward planar optic flow (upper-middle frame), outward radial optic flow (upper-right frame), and clockwise optic flow (lower-right frame). The differences between the mixture of Gaussians models derived from local motion stimuli in the context of each set site direction provided the basis for the improved predictions of optic flow responses.
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Figure 1

A  Nine Sites of Local Motion Stimuli

B  Four Directions of Local Motion

C  Single Neuron Local Motion Responses
A  Mixed Gaussians Model of Local Motion Responses

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B  Firing Rate Error of Model Fit to Local Motion

**Neuron 819R64**

- **Recorded Data**
- **Model Fit**

Total Error = 1.83
Group Error = 0
\( R^2 = .99 \)
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Figure 3

A  MST Neuronal Responses to Optic Flow Stimuli

B  Neuronal Firing Rates Evoked by Optic Flow

Neuron 819R64

Optic Flow Stimulus

Firing Rate (100 sp/s)
Local Motion Model Prediction Of Optic Flow Responses

A
Average Normalized Firing Rate Error

B
Average Group Error

C
Goodness of Fit (R²)

Neurons (from best to worst fit)
### Local Motion Model Segment Gains Model

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#### C

**Optic Flow Stimulus**

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**Optic Flow Stimulus**

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Figure 6

Local Motion Model

Segment Gains

Response Gains

Optic Flow Stimulus

Firing Rate (spk/s)
Figure 7

A. Gain Modulated Fit to Optic Flow Data
Segment Gain vs. Local Motion

B. Gain Modulated Fit to Optic Flow Data
Response Gain vs. Local Motion

C. Gain Modulated Spatial Transformation
Segment Gain (↓ gain decrease)
Gain Change from Local Motion Model (full height = 3.25x)
contralateral ipsilateral
contralateral ipsilateral

D. Gain Modulated Spatial Transformation
Response Gain (↑ excit., ↑ inhib.)
contralateral ipsilateral
contralateral ipsilateral

E. Gain Modulated Fit to Local Motion Data
Segment Gain vs. Local Motion

F. Gain Modulated Fit to Local Motion Data
Response Gain vs. Local Motion
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Figure 8

A  
Single Site Stimulation
One Site X 4 Directions

B  
Dual Simultaneous Stimulation
2 Set Spot Directions X 4 Test Spot Directions
Response Interactions at Two Test Sites

Fixed Direction Site A
- Left Motion
- Right Motion

Fixed Direction Site B
- Left Motion
- Right Motion

Neuron 819R10
- Site A Left + Probe
- Site B Left + Probe
- Site A Right + Probe
- Site B Right + Probe
- Probe Site Alone

100 spk/s
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Figure 10

A  Local Motion Model

B  Response Gain Model

C  Local Motion Interaction Models

Neuron 819R32