Linear responses to stochastic motion signals in area MST

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Abstract

The medial superior temporal area (MST) contains neurons with tuning for complex motion patterns, but very little is known about the generation of such responses. To explore how neuronal responses varied across complex motion pattern coherence, we recorded from single units while varying the strength of the global motion pattern in random dot stimuli. Stimuli were a family of optic flow patterns, consisting of radial motion, rotary motion, or combinations thereof (“spiral space”). We controlled the strength of the motion in the stimuli by varying the coherence -- the proportion of dots carrying the signal. This allows motion strength to be varied independently of stimulus size, speed, or contrast. Most neurons’ responses were well described as a linear function of stimulus coherence. While more than half the cells possessed significant nonlinearities, these typically accounted for little additional variance. Nonlinear coherence response functions could either be compressive (e.g. saturating) or expansive, and occurred in both the preferred and null direction responses. The presence of nonlinearities was not related to neuronal response properties such as preferred spiral-space direction or tuning bandwidth; however, cells with compressive nonlinearities in both the preferred and null directions tended to have higher response amplitudes and were more sensitive to weak motion signals. These cells did not appear to form a distinct subpopulation within MST. Our results suggest that MST neurons predominantly linearly encode increasing pattern motion energy within their RFs.

Keywords: receptive field, motion integration, global motion, heading, optic flow
Higher areas of the “motion pathway” in the visual cortex have large receptive field (RF) sizes with higher response complexity. These functional correlates of hierarchy result from summation over multiple afferent inputs. Area MST exemplifies both of these trends, but the mechanisms by which its receptive fields (RFs) are formed remain unknown. The RFs of MST neurons are much larger than those of MT, a predominant source of afferent input (Raiguel et al. 1997; Saito et al. 1986; Tanaka et al. 1986), and show increasingly complex response properties, including selective tuning for large global patterns of motion such as expansion, contraction or rotation (Duffy and Wurtz 1991a; Saito et al. 1986; Tanaka et al. 1986; Tanaka and Saito 1989). The large spatial scale and complex response preferences necessitates individual MST neurons integrating signals from many afferent inputs.

Several computational models have been used to explore candidate mechanisms generating the complex selectivities of MST neurons (Beardsley et al. 2003; Lappe et al. 1996; Perrone and Stone 1998; Wang 1995; Zhang et al. 1993). These models generally use a nonlinear function to govern the transformation from MT-like inputs to a representation like that observed in MST. The exact nature of the nonlinearity varies across different models, and none has received direct experimental support to date.

Similarly, responses in other visual cortical areas have been described using a linear-nonlinear (LN) model which contains an initial linear summation step followed by a static nonlinearity thought to be related to the process of spike generation (Rust et al. 2006). To demonstrate such nonlinearities, one would ideally use a family of stimuli which vary the energy associated with a specific stimulus, but while leaving as many other properties (area, contrast, etc.) unchanged. The stochastic motion stimuli now
widely used in both perceptual and physiological studies of sensitivity to weak motion are ideal for this purpose, since they selectively change the amount of a specified motion signal without changing other important visual parameters (Britten et al. 1993; Morgan and Ward 1980).

Previous physiological studies of MST cells have not directly addressed the linearity of response with respect to motion strength, but have focused on response changes due to area summation (Duffy and Wurtz 1991b; Lagae et al. 1994; Tanaka et al. 1989). Increasing stimulus size activates an unknown number of additional inputs, and may additionally recruit antagonistic surrounds (Raiguel et al. 1997) at any level up to and possibly within MST itself. Additionally, the space-averaged contrast will increase with the size of the stimulus, potentially engaging contrast gain control mechanisms (Gegenfurtner et al. 1997; Ohzawa et al. 1985). Thus, any observed nonlinearities in response could be due to nonlinear integration, varying the number of inputs, inhibition from surround activation, or gain control. Therefore, it seems useful to assess the linearity of MST responses with stimulus area and contrast held constant.

To address the question of linearity of the responses of MST neurons, we recorded from single units in area MST while varying the motion strength of specified complex motion stimuli. For each neuron, we determined the preferred and null complex motion patterns in “spiral space” (Graziano et al., 1994), and modulated response by varying the coherence of the motion pattern; this allowed us to vary stimulus strength directly. This manipulation changes the amount of energy associated with the specified pattern motion linearly, trading off “signal dots” for uncorrelated noise. We could
therefore ask how the response of MST cells varied as a function of stimulus strength without changing spatial scale or stimulus contrast.

We also investigated potential relationships between our linearity measurements and the tuning properties of our sample of MST neurons. This allowed us to address whether cells with tighter tuning were more likely to exhibit nonlinear coherence-response functions, or if particular directions of complex flow patterns were more likely to be preferred by cells with nonlinear response functions. Finally, since MST neurons vary widely in their sensitivity to weak (low coherence) motion stimuli, we also related response nonlinearities to neuronal sensitivity to address whether improved discrimination of weak motion signals correlated with nonlinear responses.

**Methods**

The bulk of the physiological data in this paper are the same as those used in a previously published analysis of neuronal sensitivity in MST (Heuer and Britten 2004). These data include 7 cells discarded from the previous work because of poor psychophysical performance. The reader is referred to the report for additional details of the methods.

*Preparation.* Two adult rhesus macaques (*Macaca mulatta*) were used in this study (one male, one female). Prior to recording, each monkey was implanted with a stainless steel head restraint and a scleral search coil (Judge et al. 1980) to monitor eye position. A recording chamber was surgically placed over occipital cortex for a dorsal and posterior approach to area MST. At the beginning of each daily recording session, we inserted a stainless steel transdural guide tube at known locations within a plastic...
coordinate grid system (Crist et al. 1988). A tungsten microelectrode (Fred Haer Co.) was introduced through the guide tube and advanced using a stepping motor microdrive (National Aperture Instruments). We used physiological and anatomical landmarks to locate area MST on the anterior bank of the superior temporal sulcus (STS); these landmarks included receptive field size, transitions between gray and white matter, and recording depth. The transition from area MT to MST was ambiguous on a small number of penetrations. On these penetrations, we only included cells with large RFs that clearly included the fovea or were extensively ipsilateral (Desimone and Ungerleider 1986; Tanaka et al. 1986). Generally, these cells were found after an abrupt change or discontinuity in retinotopy, and they account for a small proportion (~4%) of our sample. The results from these cells do not noticeably differ from the rest of the population. From both location (dorsal relative to MT) and response properties (good responses to large dot fields), we believe the bulk of our data come from the dorsal subdivision, MSTd. However, histological confirmation of recording locations is not available, as both monkeys are alive and participating in other experiments.

We isolated and recorded single unit activity in MST using standard extracellular techniques. We used a window-discriminator (Bak Electronics) to isolate single units and convert action potentials to TTL pulses. We only included cells that passed strict isolation criteria, with spikes clearly distinct above background and a clear refractory period evident in their autocorrelogram. We recorded the time of stimulus events and action potentials with 1 ms resolution using the public domain software REX (Hays et al. 1982).

Receptive field mapping and stimulus optimization. Once we had a single neuron isolated, we determined the location and size of the RF qualitatively with handheld
moving bar stimuli and computer-generated moving dot patches. We assessed RF boundaries, which could be indistinct, both by positioning of the moving bar stimulus and with dot patches of varying diameter. We positioned the stimuli within the RF to maximize response. A minority of neurons showed sensitivity to eye position within the orbit, as previously reported (Squatrito and Maioli 1997; Squatrito and Maioli 1996); for these cells we attempted to jointly maximize response due to eye position and stimulus extent. Some RFs exhibited “hot spots” or regions of greater excitability; for these neurons, we placed the stimulus over the hot spot and may not have filled the entire RF. For the remaining cells, we placed the stimuli to maximize areal extent within the RF without extending past the RF edges (schematically illustrated in Figure 1A). When the RF of the neuron extended past the screen edge, the stimulus would reach the edge of the screen, but not completely fill the RF. This probably would not have a large effect because of the steep area-response summation curves exhibited by most MST neurons (Raiguel et al. 1997).

**Stimuli.** All stimuli were random dot patterns presented on a CRT with a viewing distance of 28cm. Pixel resolution was 1280 X 1024. The vertical refresh rate of the monitor was set at 80 Hz, corresponding to a frame duration of 12.5 ms. All stimuli were generated by custom software. Stimuli were white dots (60 cd/M² luminance) on either a neutral gray (10 cd/M²) or black (0 cd/M²) background, resulting in contrasts of 70% or 100%. For some cells, measurements were made with both contrasts; no significant difference was seen between the resulting data sets.

We used a subset of optic flow components termed “spiral space” by Graziano et al. (1994). As shown in Figure 1B, this stimulus space has been formalized as a set of
orthogonal axes; with radial (contraction-expansion) motion along one axis and rotary (clockwise-counterclockwise) motion along the other. Intermediate directions in this space consist of a combination of rotary and radial motion such as contracting counterclockwise or expanding clockwise spirals. For all patterns, the speed of motion increased proportionately with radial distance from the center of the pattern.

In order to vary the strength of these stimuli, we used a technique previously applied to simpler translating stimuli (Britten et al. 1992; Celebrini and Newsome 1994). Stimulus strength was determined by the percentage of dots that are re-plotted each frame in a manner consistent with the specified direction pattern. We varied this percentage, and thus the motion strength, by setting the probability that each dot would be repositioned in this way. We refer to the proportion of dots that carry the specified motion pattern as the % coherence. A fully coherent stimulus had all the dots re-plotted with the appropriate spatial and temporal offsets to produce an apparently smooth motion pattern. The opposite extreme, the 0% coherence stimulus, contained only dots that are randomly repositioned, forming spectrally “white” motion noise. This technique allowed us to smoothly vary the strength of our spiral space stimuli. A schematic example can be seen for 3 levels of coherence in Figure 1C. For each cell, we selected at least 5 coherence levels, spaced logarithmically, based on the sensitivity of the neuron and of the monkey to the specific geometry in use. The levels were chosen to span enough of the cell’s dynamic range to bring it from negligible response difference (preferred-null; these were often both well elevated above baseline firing rates) to where the two distributions were non-overlapping. In our sample, this resulted in maximum coherences of 64% (45
cells), 32% (41 cells) and 16% (11 cells). All experiments also included 0% coherence stimuli.

**Data Analysis.** We made three related sets of measurements: spiral space tuning, coherence-response functions, and neuronal sensitivity. Methods specific to each measurement will be described briefly below. For all analyses, we calculated the response as the total number of spikes in a time window equal to the stimulus duration, delayed 50ms after stimulus onset to allow for latency. Spike count was then converted to firing rate (spikes/sec), and averaged across the multiple repetitions of each unique stimulus condition. For all measurements, we performed fits using maximum likelihood estimation with an iterative fitter (“STEPIT”, Chandler 1965); all likelihoods were estimated based on the empirically measured standard error.

**Spiral Space Tuning.** To assess the tuning properties of the cells in our sample, we presented eight evenly spaced directions in spiral space. We determined stimulus size, speed, and location during the initial qualitative map of the RF and adjusted these if necessary to optimize the stimulus for maximal response. For the tuning measurements, we used highly coherent (75% correlation) motion patterns. Typically, these stimuli were 500 ms in duration, and were presented in a pseudo-random order. Trials usually consisted of three stimuli, with 500 ms of blank screen intervening between stimuli. We discarded any presentation where the animal broke fixation. A minimum of five repetitions per stimulus condition was required for inclusion in our data set. The average responses for each cell were then fit with a Gaussian function to determine preferred spiral space direction, bandwidth, and response amplitude.
Coherence-response functions. After determining the preferred spiral space direction of the cell under study, we measured the response of the neuron to motion strengths along the cell’s preferred-null axis in spiral space. For the coherence-response measurements, each stimulus was presented for 1 s. We used the stimulus speed, size and location determined by our initial tuning measurements. Typically, we collected data at 5 or 6 motion strengths (1-2% to 32-64%), as well as responses to pure noise (0% coherence).

We assessed the linearity of the coherence-response functions by fitting the data for each direction with first- or second-order polynomials of the form:

\[ R = a_1(\text{coherence}) + a_2(\text{coherence})^2 + b \]  

Hereafter, we will refer to the fits with and without a free \( a_2 \) parameter as linear and quadratic, respectively. We treated preferred direction responses independently from the null direction; both data sets contained the non-directional responses to the incoherent (0%) stimuli. To examine whether there was significant improvement when the data were fit with the quadratic function compared to the linear function, we used nested log-likelihood analyses (Hoel et al. 1971). We transformed the likelihoods obtained from each fit by

\[ \lambda = -2\ln(L(\text{data|linear})/L(\text{data|quadratic})) \]

\( \lambda \) is distributed approximately as \( \chi^2 \), with 1 degree of freedom. If \( \lambda \) did not exceed the critical value (3.841), we concluded that the quadratic fit did not provide a significantly better account of the data. Similarly, we used this approach to test whether responses were significantly different from the mean (\( b \) in Eq. 1) alone; this allowed us to evaluate whether responses were significantly modulated by changing coherence. Only
cells with significant coherence modulation in at least one direction were included in the sample.

Sensitivity. The final measurement is the sensitivity of MST neurons to spiral space motion. We used the neuronal responses to varied coherence levels to determine the neuron’s threshold for discriminating opposite spiral space directions. We applied “neurometric analysis” (Britten et al. 1992). For each coherence, we compiled two distributions of these responses: one for stimuli in the preferred spiral space direction and a separate distribution for anti-preferred (null) stimuli. We then compared the distributions using receiver operator characteristic (ROC) analysis (Green and Swets 1966), allowing us to evaluate the discrimination performance for each level. We fit the resulting ROC values data with a modified Quick (Quick 1974) function:

\[ p = 1 - 0.5 \exp\left[-\frac{\text{coherence}}{\alpha}\right]^{\beta} \] (6)

where \( \alpha \) indicates the neuron’s threshold – the motion strength level where the ROC area is 0.825, indicating that an ideal observer could correctly identify the direction of motion correctly 82.5% of the time. The parameter \( \beta \) describes the slope of the function. We used \( \alpha \) as our measure of sensitivity, which allowed us to ask whether cells with greater sensitivity were more likely to exhibit nonlinearities in their coherence-response functions.

Results

For the majority of our sample of 97 MST neurons, responses could be well described as a linear function of stimulus coherence. To test for this, we fit each direction (preferred and null) independently with a simple linear equation, as described in the
Methods. Figure 2 shows 6 example cells with best-fit lines; median parameter values for the linear fits are shown in Table 1. Across our sample, linear fits explained 93.4% of the variance for preferred direction responses and 66.8% for null direction responses (median values). For some neurons, response was unaffected by coherence for one direction (n = 4 preferred, n = 35 null). When we excluded these neurons, the median amount of variance explained increased to 94.2% for preferred (93 cells) and 83.3% for null (65 cells) directions. Thus, for the majority of cells in our sample, a simple linear function was largely sufficient to explain the dependence of the neuronal response on stimulus strength.

Although linear coherence-response functions generally provided a very good account of the data, the responses of many cells (54/97; 56%) were significantly better described by including a quadratic nonlinearity for one or both directions (Figure 3). Of cells with significant nonlinearities, 19 showed this for only the preferred direction, 14 for just the null direction, and 21 were nonlinear in both directions. Thus, the frequency of joint nonlinearity is higher than expected by chance (chi-square = 6.79, df=1, p = 0.0092). If one assumes that preferred and null direction responses arise from activity in different sets of inputs, then this suggests that the mechanism(s) underlying these minor nonlinearities lie in the cell or column in MST, rather than being inherited from the afferents.

For most cells, the improvement in fit was quite modest when data were fit with a quadratic rather than a linear function. Figure 4A shows the comparison of variance accounted for by the quadratic and linear functions for the preferred direction. The same comparison is seen in Figure 4B for the null direction. For the preferred direction, the
quadratic function captured a median of 1.9% additional variance compared to the linear function; for the null direction, median improvement in variance explained was 5.4%. When we considered only those cells with significantly nonlinear coherence response functions, the variance explained increased by a median of 4.7% and 16.7% for the preferred and null directions respectively. Note that the improvement was bounded; cells whose variance was already well-explained by a linear function could only improve slightly. However, this slight improvement was frequently significant when examined with our nested log-likelihood test.

Given the prevalence of modest improvements for nonlinear fits, we examined the type of nonlinearities to see if there was a consistent pattern that might suggest a functional role. For either direction, the nonlinearity could be considered expansive or compressive. We defined compressive nonlinearities as ones where the quadratic term pulled the response towards the baseline firing rate (defined as the response to 0% coherence). Conversely, an expansive nonlinearity accelerated the response away from baseline.

For the preferred direction, both types of response nonlinearity occurred with nearly equal frequency. Compressive nonlinearities for the preferred direction (Figure 3A and B) were significant for 23/97 cells. Expansive nonlinearities, such as the ones demonstrated in Figure 3C and D, were seen for 17/97 cells. An intuitive measure of the effects of the quadratic term on the response function is the ratio of the quadratic term (Q) from the second-order polynomial to the slope (L) of the first-order polynomial function (Figure 5A). This “Q/L” ratio shows the impact of the quadratic term on the overall shape of the function; more extreme values indicate a greater degree of curvature.
in the response function. The distribution of ratios is centered near 0, confirming that the
great majority of cells are predominantly linear in their coherence-response function. We
compared the distributions of "Q/L" ratios for cells with maximum coherences of 32%
and 64% and found no significant difference between them (not shown), suggesting that
the apparent linearity is not due solely to the coherence ranges explored.

For those cells with significant compressive nonlinearities in the preferred
direction, the curvature of the coherence-response function suggests response saturation.
Approximately 25% of our sample showed preferred direction compressive nonlinearities
in response to increasing stimulus coherence; these functions were generally consistent
with response saturation at higher coherences. The quadratic function captured the data
extremely well for these functions (median variance explained: 98.1%).

One possible explanation for saturation would be a sigmoidal coherence-response
function, like the typical contrast response functions seen in visual cortex (Albrecht and
Hamilton 1982; Sclar et al. 1990). A sigmoidal coherence response function should show
an expansive nonlinearity at low coherences, followed by response saturation at moderate
to high stimulus strengths. We did not observe this. We examined the residuals from the
quadratic fits to see if the quadratic function over-estimated the data at low coherences as
would be expected if the data were sigmoidal. There was no systematic deviation in the
residuals for the quadratic functions (not shown). This suggests that the flattening of the
functions that we observed is due to “hard” rate saturation rather than a sigmoidal
response function.

In our sample, expansive nonlinearities were nearly as common for the preferred
direction as were compressive ones, further suggesting that the nonlinearities form a
continuum of response functions with the majority being linear in nature. However, linear
functions were worse descriptions of the cells whose functions were compressive than of
those with expansive nonlinearities. The median difference in the percentage of variance
explained between the linear and quadratic fits was 7.0% for the compressive fits and
3.8% for the expansive cases. Therefore, compressive nonlinearities appear more
pronounced than expansive ones. We will see that this observation is also correlated with
neuronal sensitivity, below.

In contrast to the preferred direction responses, null direction compressive
nonlinearities (Figure 3A and D) were much more common than expansive nonlinearities.
Only four cells showed expansive nonlinearities in the null direction. Again, the
curvature of the nonlinear functions was modest; the Q/L ratios were quite small for the
majority of cells. There was a slight but non-significant shift towards negative values of
the Q/L ratio (Figure 5B). One simple explanation for the apparent compressive curvature
of many null direction responses would be a “floor effect” resulting from complete
inhibition. Some cells showed complete inhibition while others did not. For cells with
compressive nonlinearities in the null direction, the minimum response rates ranged from
a non-response of 0.3 spikes/sec to a fairly vigorous response rate of 41 spikes/sec
(median 5 spikes/sec). Thus, some cells appeared to saturate due to a floor effect, while
for others, the compressive nonlinearities appear to reflect a more general nonlinearity in
the response unrelated to absolute firing rate.

*Relationship to Tuning Properties.* We were naturally interested in whether the
presence or absence of demonstrable nonlinearities predicted any other observable
neuronal response properties. The first pass at this analysis involved categorizing neurons
into linear or nonlinear groups, and analyzing whether there were any significant category differences in other properties. We wished to use categories that jointly considered both stimulus type and the nature of the nonlinearity. Accordingly, we categorized each response function (preferred, null) into linear, expansive, or compressive (L, E, C) to form nine possible groups. The first letter of the group code describes the preferred direction characteristic; the second captures the null. Table 2 shows the median slope (L) and quadratic coefficient (Q) for each group. Note that group CE contains of only one cell, and no cells showed expansive nonlinearities in both directions (EE).

We were principally interested in relating nonlinearity to the tuning properties of neurons in spiral space, as previously described (Graziano et al. 1994). The tuning functions of our sample were typical of MST for these stimuli. We fit the tuning data with Gaussian functions (Figure 6A) which allowed us to determine amplitude, bandwidth of tuning, and the neuron’s preferred direction in spiral space coordinates. Distributions of these parameters for the population were consistent with previous reports (Figure 6B-D).

Nonlinearities in the coherence-response functions were not associated with a particular direction in spiral space. We used contingency table analysis to investigate whether cells with a particular preferred direction (e.g. expansion) were more likely to exhibit curvature in their coherence-response functions. Cells were classified as preferring expansion, contraction, counter-clockwise, or clock-wise rotation; while there was a strong anisotropy with a bias in favor of expansion selectivity (Figure 6B), this was unrelated to the linearity of the response to varying motion strength. Finer gradations of
preferred direction were difficult due to the imbalance of preferred directions but did not suggest a relationship between preferred direction and response linearity.

We also investigated whether cells with preferred directions near a cardinal axis (radial or rotary motion) were more likely to exhibit nonlinearities than intermediate directions. We classified cells with preferred directions in a 45-degree range (22.5° to either side) of each axis as “cardinal” and the remaining cells as “intermediate”. This allowed us to assess whether cells which would probably be classified as “single-component” (Duffy and Wurtz 1991) were more likely to be nonlinear than those which responded most strongly to a combination of rotation and radial motion. There was no difference in the distribution of nonlinearities between the two groups; cells which were tuned for pure radial or rotary motion were no less linear than those tuned for spiral patterns.

Similarly, there was no evidence that coherence-response linearity was related to tuning bandwidth. The majority of cells showed fairly tight tuning for spiral space stimuli: the median bandwidth, as determined by the sigma term of the Gaussian fit, in our sample was 46 degrees (Figure 6C). There was no main effect of linearity on tuning width (ANOVA, p>0.05; Figure 7A), nor were any pair-wise comparisons significant. Thus, nonlinear coherence-response functions did not correspond to a subset of tightly tuned neurons.

Finally, the amplitude of the neuron’s tuning in spiral space was not obviously related to the linearity of the response functions. There was a weak but non-significant trend for cells with compressive nonlinearities in both directions to have higher response amplitudes (Figure 7B); this can be attributed primarily to the greater slopes in both
directions for these cells; this is more sensitively characterized by the sensitivity analysis, below. The lack of significant outcome from this relatively coarse but sensitive categorical analysis precludes the need for more detailed examination of how nonlinearity relates to tuning properties.

**Sensitivity.** Another possible role for the extensive spatial summation in these large RFs is the detection of weak signals in noise. Nonlinearities might help to boost such weak signals and improve neuronal detection or discrimination thresholds. We have previously used receiver-operator characteristic (ROC) analysis to analyze neuronal sensitivity in these same MST neurons, and will only briefly describe the approach as this work is published (Heuer and Britten 2004). We used an opponent formulation to estimate neuronal thresholds, where each neuron’s response would be compared against a similar but oppositely tuned neuron. Current models of sensory decision-making frequently employ such opponency, and place the opponency downstream from sensory areas like MT or MST (Ditterich et al. 2003). To estimate thresholds, we compiled two distributions of responses (one for preferred, one for null) for each coherence level for each cell. This allowed us to calculate for each coherence level how well the firing rate of the neuron distinguished between the alternative directions. This type of ideal-observer analysis has been previously described in greater detail elsewhere (Britten et al. 1992; Celebrini and Newsome 1994; Heuer and Britten 2004).

An example of the resulting ROC values is shown for a single cell in Figure 8. We then fit these data with a Quick function as described in the Methods to obtain the neuronal threshold. We used the threshold ($\alpha$) as our measure of neuronal sensitivity; this parameter indicates the coherence at which the ROC value would reach 0.825.
Cells with compressive nonlinearities in both directions were significantly more sensitive to weak motion signals than were other categories. We used the same eight categories of cells for this analysis as above, and log-transformed $\alpha$ to obtain an approximately normal distribution. There was a strong effect of group (ANOVA, $p=.0002$; Figure 9); post hoc tests (Bonferroni-Dunne) indicated that the significant differences lay between the CC group and the CL and LL groups ($p<0.0003$). Therefore, a compressive nonlinearity in only the preferred direction was not sufficient to predict increased sensitivity. The increased sensitivity of cells with compressive nonlinearities in both directions reflects the steep slopes of these functions at low coherences and thus more rapid divergence of the preferred and null responses.

**Discussion**

Our results indicated that neurons in MST are generally linear in their responses to weak motion stimuli. Although many cells showed modest nonlinearity in their coherence response function for either the preferred or null direction, these nonlinearities were not systematic in sign, and generally small in magnitude.

**Stimulus considerations.** We chose a limited subset of possible complex motion patterns because it has been extensively employed by physiologists and psychophysicists, and because it can be parametrically varied in useful ways. Of course, many other mathematically possible patterns were not tested – most notably shear and deformation (Koenderink and van Doorn 1987). It is possible that MST contains a subset of highly tuned, nonlinear detectors for a specific set of patterns that we might have missed because of inescapable limitations in the range of stimuli we used. We think this unlikely. First, there is no single complex pattern, analogous to faces for form vision, which stands
out in terms of its behavioral significance. If any such bias exists in natural scenes, it would favor expansions and rotations which are covered by our stimulus set. Secondly, it seems non-parsimonious to suggest that fundamental mechanisms of receptive field formation would vary greatly with the pattern being detected. We can thus use any representative set of patterns to investigate such general mechanisms. While the stimuli we used were potentially not optimal for many neurons in our sample, this is true of most studies of any higher-order stimulus processing and is unavoidable.

**Comparison with previous work.** Our variable-strength random dot stimuli allow us to investigate the response of MST neurons to a linearly varied signal, proportionate to motion energy (Britten et al. 1993). Increasing coherence improves the signal in the specified direction and decreases the proportion of dots moving in non-specified directions. Several types of nonlinearity might be seen in the coherence response functions. One type would be a sigmoidal, saturating nonlinearity, similar to the contrast response functions reported for visual cortex (e.g. Albrecht and Hamilton 1982; Sclar et al. 1990). A sigmoidal nonlinearity would suggest that the mechanisms which controlled response gain for contrast also functioned to normalize response as a function of motion strength. We did not observe such a sigmoidal dependence on stimulus coherence. A modest proportion of our cells (~25%) did show response saturation at high motion strengths, but were not consistent with a sigmoidal function at lower coherences. This suggests that the saturation we observed was due to a rate saturation, and not to gain control mechanisms similar to those observed for stimulus contrast.

Similarly, it was possible that neuronal responses would show expansive nonlinearities as a function of motion strength. A multiplicative or cooperative interaction
either among the input neurons or among similarly-tuned MST neurons would result in an accelerating nonlinearity. Previous work (Tanaka et al. 1989) has suggested that multiple vectors cooperate to produce responses in MST neurons. When a small number of stimulus vectors are presented, the response is only a small fraction of that when a higher number of vectors forms the pattern, and the relationship is often dramatically nonlinear. This could be interpreted as a static “threshold” nonlinearity, or as a multiplicative interaction between responses to the different vectors. Our stimuli are different in that the total number of input vectors and spatial extent were held constant; only the distribution of vectors changed across conditions. Either consistent thresholds or multiplicative nonlinearities should manifest themselves in our results, but neither did. We observed only modest expansive nonlinearities, and these were just about as prevalent as were compressive ones. Therefore, our results are inconsistent with a multiplicative nonlinearity between inputs representing preferred direction motions. Similarly, our data do not show clear threshold nonlinearities. Thus, it seems likely that the nonlinearities in the Tanaka study were largely related to spatial summation and not a motion pattern detection mechanism.

Instead, our data revealed a predominantly linear response as a function of stimulus coherence. This is consistent with observations in extrastriate area MT, a major source of input to MST (Baizer et al. 1991; Boussaoud et al. 1990; Maunsell and Van Essen 1983). The responses of MT cells varied linearly with the coherence of translational motion patterns (Britten et al. 1993). The RFs of MST cells are quite large, and encompass the RFs of many afferent neurons. If we assume that the coherence-
response functions of the afferent structures are linear, as suggested by the results in MT, then we can conclude that MST is not imposing a novel nonlinearity.

Underlying mechanisms. Our observations allow us to gain insight into response generation in MST neurons. Most models of MST receptive field formation generally have relied on either intrinsic nonlinearities (Saito et al. 1986; Tanaka et al. 1989) or linear summation mechanisms followed by a nonlinear transform to scale responses (Duffy and Wurtz 1991; Lappe et al. 1996; Lappe and Rauschecker 1993; Perrone and Stone 1998; Zhang et al. 1993) The present observations cannot be used to critically test such models as the models do not make clear predictions for our family of stimuli.

However, we can speculate about how a linear coherence-response function might be generated. At low coherence, a very large number of afferents, representing a wide range of speeds and directions, are all modestly active. Unlike a low-contrast stimulus, this is not a low-input regime; presumably both excitatory and inhibitory inputs are active to some degree. As coherence rises, the pattern of activity collapses onto just those inputs which represent the chosen direction pattern (preferred or null for the MST neuron under study). Presumably, this shift in activity both increases excitation and decreases inhibition on the cell. The cell then integrates these varying inputs (the linearity of this process is a matter of active debate) and also imposes some degree of static nonlinearity due to the spike generation process (Chichilnisky 2001; Rust et al. 2006).

With so many nonlinearities available, the fact that most MST neurons are approximately linear against coherence seems remarkable. While we cannot say with certainty how it happens, we speculate that two forces might be particularly important. First, the relatively high-input regime in which we work avoids simple threshold
nonlinearities to a large extent, and enables a large fraction of the network to be active. Secondly, normalization mechanisms, such as those demonstrated in other cortical areas (e.g., Britten and Heuer 1999; Carandini et al. 1997; Simoncelli and Heeger 1998), should help keep the neurons in their linear operating range. Direct testing of these ideas with a targeted recording and modeling approach seems very likely to be rewarding.

*A role in detection?* While we did not observe any consistent relationship between particular nonlinearities and most tuning measurements, we did find that more sensitive neurons tended to have compressive nonlinearities to both preferred and nonpreferred patterns. There are two ways to think about this observation, which are mechanistically distinct. There could be specific circuit mechanisms designed to bolster responses at low signal-to-noise ratios, because of the importance of specific visual patterns (like looming stimuli, for which MST cells are frequently tuned). These would presumably involve some kind of cooperative (multiplicative) interactions between inputs. Alternately, these are simply neurons with particularly high-gain, linear responses, which, because of their response gain, are more likely to saturate at high rates or “hit the floor” when inhibited by anti-preferred stimuli. This would lead to compressive nonlinearities and high sensitivity, from what is essentially a simple linear mechanism. Because of its parsimony, we favor the latter interpretation, and believe that the bulk of our data support the view that MST is largely linear in its responses. This is most noticeable under conditions when contrast is constant and only the distribution of motion energy in the scene is changing. This simple view is also supported by the fact that neuronal sensitivity was not related to what stimuli a neuron preferred (Heuer and Britten 2004). If there were dedicated circuits tuned to particular patterns, e.g. expansion, then these might be expected to show systematically
distinct nonlinearities which are not present in our data. We think that the dominantly linear responses in MST can signal the amount of particular motion patterns in a stable and reliable way under most circumstances found in the course of normal visually guided behavior.

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**References**


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**Figure and Table Legends**

Figure 1. A. Schematic representation of stimulus geometry in the RF. + is the fixation point; thick dashed line indicates stimulus aperture and thin dashed line shows RF boundaries. B. Spiral space (Graziano et al., 1994). Intermediate directions are combinations of rotary and radial motion. C. Schematic illustration of stimulus coherence for a contracting stimulus. Coherence increases from left to right.

Figure 2. Example coherence-response functions. Data in the left column are from one monkey; data in the right are from the other. Error bars indicate SEM. Bold open symbol on the y-axis indicates response to 0% coherence stimuli. Different ranges of coherence were used for each cell to maximize the number of trials in each condition while also adequately covering each cell’s dynamic range.

Figure 3. Nonlinear coherence response functions. Thick lines indicate best quadratic fit; thin lines indicate best linear fit. Error bars indicate SEM. Panel titles indicate type of coherence response function (compressive, expansive or linear) for the preferred and null directions respectively.

Figure 4. Percentage of variance explained by linear and quadratic fits. The variance explained is calculated by the expression: \( \% \text{variance} = 100 \frac{1-(\text{model-data variance})}{\text{data variance}} \). A. Preferred direction. Right-hand panel is an enlargement of the left to show improvement for high-quality fits. B. Null direction.
Figure 5. Ratios between the quadratic and linear terms of the quadratic fits. A. Preferred direction ratios. B. Null direction ratios. E: significant expansive nonlinearity; C: significant compressive nonlinearity; L: linear functions.

Figure 6. Spiral space tuning properties. A. Single cell responses to spiral space stimuli and resulting Gaussian fit. B. Distribution of preferred directions: Rose diagram. Each bin represents 15 degrees in spiral space; the length of each wedge indicates the number of cells in the bin. C. Distribution of tuning bandwidths. D. Distribution of response amplitudes.

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Figure 8. ROC analysis. Single cell example. Solid line is best-fit Quick equation. Dashed lines indicate the motion strength level at which the threshold (82.5%) is reached; for this cell the threshold is 8.27%.

Figure 9. Distribution of thresholds (log-transformed) for each group. Error bars indicate SEM. Pairwise comparisons (Bonferroni-Dunne corrected) indicate group CC to have significantly lower thresholds than groups CL and LL (p<0.0003).
Table 1. The medians were calculated for the full sample of MST neurons. The same data were either fit with linear (first-order) or quadratic functions.

Table 2. Median parameter values calculated for subsets of our sample, defined according to the nature of the (non)linearity of each response function. The first digit in the category code denotes the preferred direction nonlinearity, and the second the null direction. C = compressive; E = expansive; L = linear
Table 1. Median parameters for first and second order polynomial fits by stimulus direction.

<table>
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<th>Direction</th>
<th>First order (Linear)</th>
<th>Second order (Quadratic)</th>
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<td>Intercept</td>
<td>Slope (L)</td>
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<tr>
<td>Null</td>
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<td>-0.053</td>
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Table 2. Median parameters for each linearity category

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<tr>
<th>Category</th>
<th>Count</th>
<th>PD L</th>
<th>PD Q</th>
<th>ND L</th>
<th>ND Q</th>
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<td>0.222</td>
<td>0.002</td>
<td>-0.019</td>
<td>0.0002</td>
</tr>
</tbody>
</table>
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