Title: Responses of MST neurons to plaid stimuli

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ABSTRACT

The estimation of motion information from retinal input is a fundamental function of the primate dorsal visual pathway. Previous work has shown that this function involves multiple cortical areas, with each area integrating information from its predecessors. Compared to neurons in the primary visual cortex (V1), neurons in the middle temporal (MT) area more faithfully represent the velocity of plaid stimuli, and the observation of this pattern selectivity has led to two-stage models, in which MT neurons integrate the outputs of component-selective V1 neurons. Motion integration in these models is generally complemented by motion opponency, which refines velocity selectivity. Area MT projects to a third stage of motion processing, the medial superior temporal (MST) area, but surprisingly little is known about MST responses to plaid stimuli. Here we show that increased pattern selectivity in MST is associated with greater prevalence of the mechanisms implemented by two-stage MT models: Compared to MT neurons, MST neurons integrate motion components to a greater degree and exhibit evidence of stronger motion opponency. Moreover, when tested with more challenging unikinetic plaid stimuli, an appreciable percentage of MST neurons are pattern-selective, while such selectivity is rare in MT. Surprisingly, increased motion integration is found in MST even for transparent plaid stimuli, which are not typically integrated perceptually. Thus the relationship between MST and MT is qualitatively similar to that between MT and V1, as repeated application of basic motion mechanisms leads to novel selectivities at each stage along the pathway.

KEY WORDS

Motion integration
Vision
Electrophysiology
Perception
Cortex
INTRODUCTION

Motion perception is critical for a variety of tasks, from the moment-to-moment stabilization of gaze (Miles 1997) to successful performance in professional sports (Regan 1997). In the primate brain, motion processing is carried out by a collection of dedicated cortical areas, all of which receive direct or indirect input from the primary visual cortex (V1).

Although clear selectivity for stimulus motion is found in V1 (Hubel and Wiesel 1962), the ability of individual V1 neurons to estimate velocity for many types of stimuli is severely limited. Part of this limitation is due to the fact that V1 receptive fields are quite small, so that they only signal the motion of an object as it passes through a roughly 1° region of visual space. Thus in natural vision V1 neurons are generally able to provide only momentary information on a moving object’s velocity, and even this information is quite limited by the structure of the environment: Objects are usually comprised of edges for which local motion computations can only recover the component of motion perpendicular to the orientation of the edge (Wallach 1935). Because most V1 neurons are highly selective for such orientation cues, their outputs are in many cases ambiguous with respect to the velocity of the stimulus. Thus while V1 appears to be necessary for motion perception, its outputs are not sufficient to support accurate motion perception for the kinds of stimuli typically encountered in a natural environment.

Area V1 projects to a variety of extrastriate visual regions that are likely to be involved in motion perception. Here we will focus on the properties of the projection to the middle temporal (MT) area, which is highly specialized for motion processing. MT appears to be capable of overcoming many of the ambiguities present in the V1 output (Albright 1984; Movshon et al. 1985), and consequently it has inspired a number of two-stage models of motion processing. These models have converged on a number of key computational mechanisms for integrating motion signals (Rust et al. 2006; Simoncelli and Heeger 1998; Tsui et al. 2010). The first is a motion opponent mechanism that removes information about static orientation cues by subtracting the outputs of neurons that share the same motion preference but opposite motion directions (Adelson and Bergen 1985; Reichardt 1961; Rust et al. 2006; Simoncelli and Heeger 1998). The second is a pooling mechanism that incorporates information from multiple
motion components by summing the responses of V1 neurons tuned to different orientations (Rust et al. 2006; Simoncelli and Heeger 1998; Tsui et al. 2010). These models also contain nonlinear mechanisms that have been explored in detail elsewhere (Tsui et al. 2010).

These basic motion processing mechanisms can be probed with plaid stimuli (Figure 1a), which are comprised of two grating components, each of which moves in a different direction. Such stimuli are typically perceived by humans to be moving in a direction corresponding to neither grating, but rather to a velocity consistent with both of the one-dimensional grating components (Adelson and Movshon 1982). In contrast to these perceptual findings, V1 neurons generally respond to the individual component gratings (Movshon et al. 1985) and carry very little information about the motion of the plaid pattern. A subpopulation of MT neurons is capable of signaling the motion of the plaid pattern (Movshon et al. 1985), and this capability is associated both with stronger evidence of motion opponency and a broader integration of motion components (Rust et al. 2006).

Although these experimental and computational results suggest a clear distinction between areas V1 and MT, very little is known about the response of neurons in higher areas to plaid stimuli. Indeed a subsequent stage of motion processing, area MST, has primarily been studied with complex optic flow patterns (Duffy and Wurtz 1991b; Saito et al. 1986; Tanaka et al. 1986), so that its role in the basic integration of motion information is less clear. We have therefore recorded the responses of neurons in MST to a variety of plaid stimuli that have classically been used to study V1, MT, and visual perception. Our results indicate that area MST carries out some of the basic functions typically assigned to the second stage of the two-stage model. These include the suppression of information about static orientation (consistent with a motion-opponent mechanism) and the generalization of motion processing across one-dimensional components (pooling). Surprisingly, MST neurons are relatively insensitive to non-motion cues that are associated with perceptual transparency, suggesting that many neurons at higher levels of the dorsal hierarchy obligatorily integrate motion signals in a way that is not necessarily consistent with human perception.
Overall our results, while consistent with the hierarchical basis of two-stage models of motion processing, suggest a more general set of computations that are shared across all cortical areas. These include simple mechanisms for pooling of outputs across space and across feature selectivity and for suppressing irrelevant input signals. We speculate that these generic mechanisms, along with additional nonlinear mechanisms characterized elsewhere (Mineault et al. 2012) are likely to be at work in other parts of the visual cortex (Cadieu et al. 2007; Connor et al. 2007; Rust and Dicarlo 2010).
METHODS

Electrophysiological Recordings

Three rhesus macaque monkeys took part in the experiments. Prior to the experiments each animal underwent a sterile surgical procedure to implant a headpost and recording cylinder, and following recovery monkeys were seated comfortably in a primate chair (Crist Instruments) and trained to fixate a small red spot on a computer monitor in return for a liquid reward. Eye position was monitored at 200 Hz with an infrared camera (SR Research), and required to be within 2° of the fixation point in order for the reward to be dispensed. All aspects of the experiments were approved by the Animal Care Committee of the Montreal Neurological Institute, and in compliance with regulations established by the Canadian Council on Animal Care.

We recorded from well-isolated single neurons in areas V1, MT, and MST. Single waveforms were sampled at 40 kHz, sorted online and then re-sorted offline, using spike-sorting software (Plexon, Inc). Area MT was identified based on anatomical MRI scans, the prevalence of direction-selective neurons, and on the correlation between receptive field size and eccentricity. Area MST was always found to be a few millimeters past MT during a posterior approach, with a gap in audible neural activity as the electrode tip passed through the superior temporal sulcus. MST cells generally had larger receptive fields that often extended into the ipsilateral visual field (Saito et al. 1986); many of these responded selectively to expanding and/or rotating stimuli in addition to the translating stimuli used in the tests of pattern selectivity. These neurons were analyzed in detail in a recent paper (Mineault et al. 2012).

It has been shown that both MT and the lateral/ventral portion of MST (MSTI) exhibit strong surround-suppression (Born 2000; Eifuku and Wurtz 1998), while MSTd neurons are generally not surround-suppressed. We generated area summation curves for many of the MT and MST neurons in our sample, based on responses to random dot stimuli moving at the preferred velocity for each neuron. To quantify these results, we used a surround-suppression index, which quantifies the extent to which a neuron is suppressed by stimuli which are presented beyond the size of its classical receptive field. In our data we found that the surround-suppression index of our MST sample was significantly lower than that of our MT sample (median surround-suppression index = 0.48 for MST vs. 0.64 for MT; p = 0.009; Student’s
However it has been shown that MSTl neurons exhibit surround-suppression which is on average greater than that of MT neurons (Eifuku and Wurtz 1998). Overall these results suggest that most of our recordings were from the dorsal, rather than the ventral, portion of MST, although this has not been verified histologically.

Local field potentials (LFPs) and single units (SUs) were recorded simultaneously on the same electrodes. LFPs were filtered using an analogue 2-pole low-cut (0.7 Hz) and a 4-pole high-cut (170 Hz) filter (Plexon, Inc) and were then digitized and sampled at 1 kHz. 60 Hz line noise was removed on-line using a software-switchable analog 2-pole low-cut filter (Plexon, Inc). However, the power spectra of a number of LFP traces still showed a peak at 60 Hz and its first harmonic. Thus we removed this noise off-line by applying a Gaussian notch filter (width = 5 Hz) whose peak corresponded to the peak of the line noise.

**Procedure and Visual Stimuli**

Stimuli were displayed at 85 Hz at a resolution of 1920x1200 pixels. The viewing area subtended 70° x 42° degrees of visual angle at a distance of 42 cm. Sinusoidal gratings were displayed on a gray background (luminance of 70.3 cd/m²); bikinetic plaids were constructed by superimposing two gratings of 50% contrast that differed in motion direction by 120°. Unikinetic plaids made use of the same grating components, but one component remained stationary throughout each trial. For the experiments involving transparent plaids, square wave gratings (luminance of 81 cd/m²) were displayed on a gray background (luminance of 106 cd/m²). Coherent plaids were then constructed by summing two gratings whose motion directions differed by 120°. We then tested each neuron again with similar square-wave gratings (luminance of 148 cd/m²) against a background of 248 cd/m². Transparent plaids were constructed by combining two gratings such that the luminance of the intersections was 88 cd/m², which effectively simulated conditions in which transparent gratings (transmittance ~60%) moved in front of a light source. Consequently they were well within the “transparency zone” defined by Stoner et al. (Stoner et al. 1990), and their appearance was judged informally to be transparent by human observers.
For all stimuli, spatial frequency, temporal frequency, and stimulus size were optimized for each cell. Motion direction was sampled in 30° steps. On each trial the animal was required to acquire and then maintain fixation for 250 ms, after which the stimulus appeared and remained stationary for 200 ms. The stimulus then moved at a constant direction and speed for 500 ms. Each stimulus was repeated 5 times in blockwise random order.

Data Analysis

Measurements of direction selectivity were taken from spikes averaged over a time period that spanned 120 to 500 ms after the onset of stimulus motion. This time period was chosen to exclude the early period when the component/pattern classification changes in many cells (Pack et al. 2001). From the resulting spike rate we subtracted the spontaneous activity measured during the 250 ms between the acquisition of fixation and the onset of the stimulus. Spike tuning curves were considered direction-selective if their directionality index (DI = preferred direction response / null direction response) was greater than two. We also fitted the direction tuning curves to a Gaussian function, using the Levenberg-Marquardt method in the Matlab optimization toolbox, and required the fit to be well characterized ($r^2 > 0.95$). Recordings that did not meet these criteria were excluded from further analysis. By optimizing the fit of each direction tuning curve to a Gaussian function, we obtained several parameters, including preferred direction, baseline firing rate, amplitude of response to preferred direction and variance. The bandwidths of the tuning curves were obtained by multiplying the standard deviation of the best-fitting Gaussian by $\sqrt{2\pi}$.

LFP responses were quantified by measuring their mean power, which was computed from the discrete Fourier transform function in Matlab (Mathworks, Natick, MA). We only included those LFP responses whose mean power for any given frequency bin was at least two standard deviations greater than the mean power of spontaneous activity.

To generate peri-stimulus time histograms (e.g., Figure 2), we used a 20 ms bin size. For the analysis of onset responses, we only considered neurons with an average motion response of > 10 spikes per second. The onset response was quantified as the maximum response in any 32 ms bin before stimulus motion onset. In other words it was the firing rate corresponding to the time bin which
contained the maximum response to the static stimulus. The motion response was defined as the average response of a neuron to grating motion 120 to 500 ms after motion onset. We also computed a static response index, which was defined as the ratio of the onset response to the motion response (Figure 3a). Thus, static response indices tended to be higher for those cells which had larger responses to static stimuli relative to moving stimuli.

Spike responses to gratings and plaids were classified according to the Z-transformed partial correlation coefficients between the data and the component and pattern predictions (Smith et al. 2005; Tinsley et al. 2003) using the following equations (shown for the z-transformed pattern correlation):

\[
Z_p = 0.5 \ln \left( \frac{1 + PC_p}{1 - PC_p} \right)
\]

(1)

where \( n \) corresponds to the number of motion directions (12 in our experiments) and \( PC_p \) is defined as follows:

\[
PC_p = \frac{RC_p - RC_c \cdot RC_{cp}}{\sqrt{(1 - RC_p^2)(1 - RC_c^2)}}
\]

(2)

Here \( RC_p \) and \( RC_c \) are the raw correlations between the data and the pattern prediction and component predictions, respectively, and \( RC_{cp} \) is the raw correlation between the two predictions. The Z-transformed component correlation \( (Z_c) \) can be obtained by exchanging \( PC_p \) and \( PC_c \), and the partial correlation \( (PC_c) \) between the component prediction and the data can be obtained by replacing \( RC_p \) with \( RC_c \) in the above equations. Each of the Z-transformed values was tested for significance according to the criterion of 1.28, equivalent to \( p = 0.10 \). The pattern index (PI) was defined for each cell as \( Z_p - Z_c \) and the component index was defined to be \( Z_c - Z_p \).

For the experiments involving transparent plaids, a transparency index was used to quantify the amount of transparency modulation for each cell. The transparency index was mathematically defined to be the component index obtained using the coherent plaid stimulus subtracted from the component index obtained using the transparent plaid. Higher values of the transparency index represent higher transparency modulation for a particular neuronal response.
To illustrate how the PI changes over time in MT and MST, we used a 10 ms bin size and analyzed neuronal responses incrementally, beginning at 60 ms after stimulus motion onset (see Figure 7). For example, the 1st bin used to calculate the PI was 60 – 70 ms while the 2nd bin was 60 – 80 ms. We considered a neuron to exhibit pattern (or component) selectivity when it remained pattern-tuned (or component-tuned) for 5 consecutive time bins. The emergence of pattern selectivity was considered to be the first of these time bins.

To determine the surround suppression index for each neuron, we first computed the ratio of the neuronal response evoked by the largest stimulus size to the largest neuronal response (for all the different stimulus sizes tested). This result was subtracted from 1 to generate the surround suppression index.

Models used to predict unikinetic plaid responses

We used two different methods to compute the component predictions for unikinetic plaids. In the first method (corresponding to Figure 5), we considered only the moving grating to compute the component prediction. For this model prediction we ignored the responses to the static grating under the assumption that these responses are generally much smaller than those elicited by a moving grating. However, a more accurate component prediction may be formed by considering the responses to the static grating as well, simply because a unikinetic plaid stimulus contains a static grating as one of its components. Estimates of the neuronal response to the static grating were taken from the period of each trial in which the grating remained stationary for 200 ms.

One problem with our approach to estimating the contribution of static orientation cues is that the response to the static grating is subject to contrast gain control, which varies over time and with the presence of the second grating of the plaid. Consequently it is difficult to isolate the contribution of static orientation cues to the responses to unikinetic plaids. To ensure that the variable gain of this response did not bias our results, we performed a second analysis in which the gain of the static grating response was treated as a free parameter, according to:
where CP is the component prediction, \( R_{GM} \) is the response to grating movement, \( R_{GO} \) is the response to grating orientation, and \( g \) is the free parameter corresponding to the gain of the static grating (orientation) response. By fitting this equation to the data obtained with unikinetic plaids, we obtained an upper bound on the validity of the component prediction for variations in the gain of the orientation response.

The pattern motion prediction for unikinetic plaids was generated by rotating the neuronal response to the grating stimulus clockwise by 30 degrees (Ferrera and Wilson 1990). This direction was along the orientation of the static grating and corresponded to the velocity that would be associated with the plaid if it were a single, rigidly moving object.
RESULTS

We recorded from a total of 335 neurons in areas V1, MT and MST of three alert macaque monkeys. All neurons were categorized according to their responses to the plaid stimuli shown in Figure 1a. These *bikinetic plaid* stimuli consist of two superimposed sinusoidal gratings, each of which moves in a different direction; these *component* directions are distinct from the *pattern* direction, which is the motion of the pattern as a whole. This distinction, along with standard statistical analysis (see Methods), permits a classification of each neuron according to its ability to integrate motion components. Neurons that respond predominantly to the motion of the plaid pattern are called pattern-selective, while those that respond to the motion components are called component-selective. As described in previous work (Khawaja, et al., 2009), we found that most (57%; 64/113) MST neurons were pattern-selective, while such selectivity was rarer in MT (30%; 31/103), and nearly absent in V1 (6%; 2/33). In addition to these standard measures, we report here the results of experiments involving other plaid stimuli designed to answer specific questions about the integration of motion information along the dorsal pathway.

Motion opponency

Most models of motion processing implement spatial filters that are selective for stimulus orientation, based in part on the finding that direction and orientation selectivity tend to be found in the same cells in V1 (Adelson and Bergen 1985). In the time domain, these filters are often rather broadly tuned, so that they respond to stimuli of the appropriate orientation, even in the absence of motion. Motion models typically remove such orientation signals by subtracting the outputs of detectors tuned for the same orientation but opposite motion directions. This *motion opponent* stage has the effect of increasing direction selectivity and suppressing the responses to non-directional noise, to which the early visual system is quite sensitive (Qian and Andersen 1994).

In our experiments each visual stimulus remained stationary for 200 ms in the receptive field of each neuron before moving. Many direction-selective neurons responded strongly during this period,
despite the fact that the stimulus was stationary. Others responded weakly or not at all, which is what is expected from the output of a motion-opponent computation. To study the prevalence of these onset responses along the dorsal hierarchy, we examined responses to static gratings across the populations of component, unclassified, and pattern cells for neurons in V1, MT, and MST. The results (Figure 2a-c) show a robust correspondence between responses to the static stimulus and pattern selectivity. The nine panels plot the mean time-course of the responses for each cell type (component, unclassified, or pattern) and brain region (V1, MT, and MST). The onset of motion in each plot is at $t = 0$ and the stationary stimulus appears at $t = -200$. The responses evoked by stationary stimuli are highlighted in gray.

Several trends are evident in the data. First, the selectivity for static orientation is lower in pattern cells than in component cells, as shown by the fact that on average, pattern cells respond nearly equally to orientations that are $90^\circ$ apart (blue and black lines). This result is not terribly surprising, given the link between pattern selectivity and motion tuning bandwidth (Rust et al. 2006; Tinsley et al. 2003) and the links between orientation and motion tuning in V1 and MT (Albright 1984). More interesting is the relationship between the amplitudes of the responses to static orientation and pattern selectivity. Pattern cells in V1 and MT respond relatively weakly to static orientation, and in MST there is virtually no response until the stimulus starts to move. Also evident in Figure 2 is the tendency of pattern cells from all three areas to have relatively small responses to the static orientation stimulus. These results are consistent with the suggestion (Qian and Andersen 1994; Rust et al. 2006) that motion opponency is important for pattern selectivity.

Figure 3a shows the correlation between the magnitudes of the onset responses to stationary stimuli (relative to motion responses) and the pattern index, a scalar value that captures the extent to which the responses conform to the pattern prediction (see Methods for mathematical definition). These values are shown for neurons in V1 (blue circles), MT (green Xs), and MST (red crosses). There is a significant correlation between these measures in MT ($p < 0.05$) and MST ($p < 0.01$) but not in V1 ($p = 0.18$); this latter result is likely due to the smaller sample size in V1. The slopes of the regression lines
relating the magnitude of the onset response to the pattern index were not significantly different across areas (ANCOVA, p>0.60). In contrast the y-intercepts of these regression lines were significantly different between V1 and both MT and MST (ANCOVA, p<0.001), with a marginally significant difference between MT and MST (ANCOVA, p<0.07). Thus on a cell-by-cell basis, there is a relationship between the responses to stationary stimuli and the degree of pattern selectivity, and this relationship is similar across visual areas. This is consistent with the idea that the incorporation of onset transient mechanisms improves pattern selectivity in roughly the same way at all levels of the dorsal visual hierarchy. At the same time, for a given strength of onset response, pattern selectivity was stronger at higher levels of the dorsal visual hierarchy, suggesting that other factors are involved in increasing pattern selectivity in higher-level areas.

One such factor is preferred speed, which on average increases, which on average increases along the pathway from V1 to MT (Mikami et al., 1986; Churchland et al., 2005; Pack et al., 2006) and from MT to MST (Lagae et al., 1994; Churchland et al., 2007). Previous work (Palanca and DeAngelis 2003) has shown that some MT neurons prefer stimuli moving at speeds very close to zero, which could be related to the onset response to a non-moving stimulus. To examine this point, we estimated the preferred speed for 40 MT neurons and 46 MST neurons. There was no significant correlation between preferred speed and pattern selectivity for either MT (p>0.36) or MST (p>0.14). Thus at the single neuron level we find that the static onset response was a better predictor of pattern selectivity than preferred speed.

As an alternative to the static response measure, we also calculated the neuronal responses to motion in the anti-preferred direction. In this case a motion opponent mechanism should produce suppression of the response below the level of spontaneous firing, as has typically been observed in MT (e.g., Mikami et al., 1984). For our sample we calculated a null-direction suppression index, which is the normalized difference between the spontaneous firing rate and the anti-preferred direction firing rate. Consistent with previous models of pattern-motion processing (Rust et al. 2006; Simoncelli and Heeger 1998), there is a significant correlation between the anti-preferred direction suppression index
and pattern index for both MT (p<0.01) and MST (p<0.05). Thus both measures of motion opponency suggest that this mechanism is more effective in cells that exhibit greater pattern selectivity.

Examination of the local field potentials (LFPs) recorded simultaneously with the single-neuron responses revealed a robust response to stimulus onset, even in area MST, where onset responses were largely absent in single neurons. Figure 4a shows the mean LFP time-course, along with the mean spiking response (right panel), for all recording sites in MST. Here the difference between the LFP and single-neuron responses was particularly striking for the low-gamma ($\gamma_L$) frequencies (compare the middle and right panels of Figure 4a). The peak onset response (highlighted in gray) that occurs before $t = 0$ is comparable in amplitude to the peak motion response, as observed for many single-unit responses in V1 and MT (Figure 2). Onset responses in MST were present but somewhat reduced in the high-gamma ($\gamma_H$) LFP frequencies (Figure 4a, left).

On average the onset responses for LFPs in MT and MST were generally similar to single-unit responses in lower-level areas (Figure 4b), with stronger responses being found in the $\gamma_L$ band than in the $\gamma_H$ band. These results suggest that onset responses are stronger in the input to a given area than in the (spiking) output, as reported previously for component selectivity (Khawaja et al. 2009). One plausible explanation for both results is then that the motion opponent mechanism, and by extension pattern selectivity, relies on lateral inhibitory connectivity, to which the LFPs are thought to be particularly sensitive (Henrie and Shapley 2005).

**Bandwidth of motion integration**

The previous section suggests that responses to static stimuli decrease along the dorsal pathway, and that this decrease is predictive of pattern selectivity. Another measure of motion selectivity that tends to change along the motion processing hierarchy is the bandwidth of direction tuning. Neurons in V1 are quite narrowly tuned for motion direction (Gizzi et al. 1990; Hubel and Wiesel 1968; Tinsley et al. 2003), whereas those in MT and MST are more broadly tuned (Albright 1984; Duffy and Wurtz 1991a;
Maunsell and Van Essen 1983). This feature would seem to be important for pattern selectivity, which requires the integration of information from motion components that move in very different directions.

Figure 3b shows the correlation between the tuning bandwidths (measured with gratings) and the pattern index for neurons in V1, MT, and MST. There was a significant correlation between motion tuning bandwidth and pattern selectivity in each area (p < 0.01 for MST; p < 0.001 for MT and p < 0.01 for V1). As shown above for motion onset responses, the slopes of the regression lines relating tuning bandwidth to pattern selectivity were not significantly different across areas (ANCOVA, p>0.12). The y-intercepts of these regression lines were significantly different between V1 and both MT and MST (ANCOVA, p<0.001), and marginally significant between MT and MST (ANCOVA, p<0.08). Thus increases in tuning bandwidth were associated with similar increases in pattern selectivity in each area, and for a given tuning bandwidth, pattern selectivity was stronger in MT and MST than in V1. Although the same tendency was present between MT and MST, it did not reach statistical significance, as would be expected had we obtained a larger sample size (Lagae et al., 1994). These results, along with those related to static motion responses, are consistent with the idea that the computation of pattern selectivity relies on similar mechanisms in each area. By both measures, however, the overall differences between V1 and MT were greater than those between MT and MST.

**Processing of unikinetic plaids**

As shown in Figures 2 and 3, the responses to static orientations decrease at each stage along the dorsal visual pathway. However, previous theoretical and psychophysical work has shown that, under some circumstances, a static grating can be used to constrain the interpretation of motion. This results from the fact that a static grating is locally consistent with motion in a direction parallel to the grating’s orientation (Albright 1984; Dobkins et al. 1998; Ferrera and Wilson 1990; Gorea and Lorenceau 1991). A clear example of this effect occurs with a *unikinetic* plaid, in which a stationary grating is
superimposed on a moving one (Ferrera and Wilson 1990). In that case one perceives motion parallel
to the grating orientation, even though the static grating contains no time-varying information. Thus one
might expect higher levels of the motion processing hierarchy to exhibit direction-selective biases to
stimuli that contain stationary gratings, even though the responses to these stimuli presented in isolation
decrease sharply at each stage.

To examine this issue, we recorded the responses of MT and MST neurons to bikinetic (Figure
1a) and unikinetic (Figure 1b) plaid stimuli. Again the responses were quantified according to standard
techniques (see Methods) that classify neurons as “component”, “pattern”, or “unclassified” (Ferrera
and Wilson 1990; Movshon et al. 1985; Smith et al. 2005). For unikinetic plaids, the component
prediction is formed by adding together the responses of the moving grating and the static grating (see
Methods) (Figure 5). The pattern prediction for the direction of unikinetic plaids is based on the
velocity-space intersection of the two components, which corresponds to a clockwise rotation of the
single grating tuning curve by 30 degrees.

Figure 5 provides examples of MT and MST direction tuning curves for gratings as well as
bikinetic and unikinetic plaids. Two typical MT neurons are illustrated (Figure 5a, b) along with one
typical MST neuron (Figure 5c). The polar plots show the observed responses in black, the component
predictions in blue, and the pattern predictions in red. Below each tuning curve is shown the
corresponding classification. The first and second columns show the responses and predictions to
gratings and bikinetic plaids, respectively, while the third column corresponds to unikinetic plaids.

The first example neuron shown for MT (Figure 5a) is categorized as “unclassified” (pattern
index = 0) when stimulated with bikinetic plaids (Figure 5a second column); however, it exhibits
significant component selectivity when tested with unikinetic plaids (pattern index = -1.66; Figure 5a,
third column). The MT neuron shown in Figure 5b is categorized as a pattern cell when bikinetic plaids
are used (pattern index = 3.24), but it is statistically unclassified for unikinetic plaids (pattern index =
0.25; Figure 5b third column). Thus pattern selectivity decreases when both MT neurons are tested with
unikinetic plaids. In contrast the MST neuron, which is classified as pattern-selective when stimulated
with bikinetic plaids (pattern index = 5.08), also exhibits pattern selectivity when tested with unikinetic plaids (pattern index = 2.17; Figure 5c third column).

Figure 6 plots the distributions of cell types for the MT (a) and MST (b) populations in response to bikinetic (column 1) and unikinetic (column 2) plaids. As reported previously (Khawaja et al. 2009), pattern selectivity for bikinetic plaids was greater in MST than in MT (Figure 6a, b third column; p < 0.05; Student’s t-test), and a similar difference is found for unikinetic plaids (Figure 6a, b fourth column; p < 0.05; Student’s t-test). As illustrated in the third and fourth columns of Figure 6, pattern selectivity was significantly lower in both MT and MST when unikinetic plaid stimuli were used (MT mean PI = 0.002 ± 0.35 for bikinetic plaids vs. -1.36 ± 0.32 for unikinetic plaids, p < 0.01; MST mean PI = 1.31 ± 0.25 for bikinetic plaids vs. -0.24 ± 0.27 for unikinetic plaids, p < 0.001; paired student’s t-test). Similar results were obtained when we allowed for potential changes in the gain of the response to the static orientation during the motion period (MT mean PI = -1.61 ± 0.35 for unikinetic plaids, p < 0.01; MST mean PI = -0.65 ± 0.32 for unikinetic plaids, p < 0.001; see Methods for model).

The fifth column of Figure 6 plots the pattern indices for the responses to bikinetic and unikinetic plaids in MT and MST. As suggested from the fourth column of Figure 6, many neurons that are classified as pattern-selective for bikinetic plaids are either classified as component-selective or belong to the unclassified category when tested with unikinetic plaids (11/12 (92%) for MT and 15/22 (68%) for MST). The decrease in the frequency of pattern selectivity is likely to be due in part to the difficulty of distinguishing between the pattern and component predictions, which are necessarily very similar for unikinetic plaids (Figure 5). Because of the nature of the partial correlation coefficient used to define pattern selectivity, even slight departures from the component and pattern predictions will cause neurons to be labelled as unclassified. However, the substantial increase in significant component selectivity in both MT and MST is not likely to be a consequence of this procedure, suggesting that responses to unikinetic plaids are genuinely less pattern-selective in both areas. Overall, these areas appear to be different in their ability to integrate unikinetic plaids, as MST contains a significantly larger percentage of cells that are pattern-selective for both types of plaid stimuli (Figure 6b, fifth
column top right box of both the top and bottom panels (7/22 (32%) in MST vs. 1/12 (8%) in MT; 
p<0.01, binomial test). Thus, although pattern selectivity is generally weaker for unikinetic plaids, area 
MST appears to be unique among the areas we examined in having an appreciable proportion of 
neurons capable of robustly signalling pattern motion for different types of stimuli.

In contrast to our results with bikinetic plaids, there was no relationship between unikinetic 
pattern selectivity and the response to stationary stimuli in MST or MT (linear regression, $r^2 = 0.07$; p = 
0.28 for MST and $r^2 = .008$; p = 0.69 for MT). Indeed, as mentioned above, responses to these static 
stimuli in MST were very low in amplitude and largely unselective, even though information about 
orientation is necessary to estimate the motion of the unikinetic plaid. Similarly there was no clear 
relationship between tuning bandwidth and unikinetic plaid pattern selectivity in MT or MST (linear 
regression, $r^2 = 0.04$; p = 0.23 for MST and $r^2 = 0.04$; p = 0.16 for MT).

Unikinetic Plaid Temporal Dynamics

Previous work has shown that the pattern selectivity of MT neurons for bikinetic plaids generally 
increases during the early phases of the response (Pack et al. 2001; Pack and Born 2001; Smith et al. 
2005; Solomon et al. 2012). Perceptually, the perceived direction of plaid stimuli approximates a vector 
average (or sum) of the motion components for brief presentation durations (Yo and Wilson 1992), with 
longer durations leading to the perception of pattern motion. The vector average and pattern direction 
are identical for bikinetic plaids, but for unikinetic plaids the two directions differ by the angle between 
the grating components. This difference has been exploited in ocular following experiments, which 
show that the initial eye movement responses to unikinetic plaids exhibit a clear temporal transition in 
both humans and monkeys (Barthelemy et al. 2010; Masson and Castet 2002). Specifically, these 
 studies show that eye movement responses to a unikinetic plaid stimulus initially follow the moving 
grating and only incorporate the static grating after a delay. Consequently the latency for initiating 
accurate tracking movements for unikinetic plaids is somewhat longer than that for tracking gratings or 
bikinetic plaids.
To investigate the temporal dynamics of neural responses to unikinetic plaids, we plotted the mean pattern index as a function of time for both MT and MST. In these plots the pattern index accumulates across time (Smith et al. 2005) (see Methods). Figure 7a shows that, for bikinetic stimuli, the average time required for pattern-selective neurons to become statistically pattern-selective is similar for MT (red line; mean = 143 ± 12 ms; n = 12) and MST (black line; 150 ms ± 11.33 ms; n = 12) (p = 0.68; Student’s t-test). Consistent with the results on ocular following, pattern selectivity emerges substantially later for unikinetic plaids, with a delay that is similar for the two areas (Figure 7b) (PI mean time = 225 ± 71.90 for MT (n = 4) vs. 255 ± 67.07 for MST (n = 24); p = 0.77; Student’s t-test). To emphasize this difference, Figures 7c and 7d replot the time-course of pattern selectivity for unikinetic plaids and for bikinetic plaids in MT and MST, respectively. In MT, the latency of pattern selectivity was longer for unikinetic than for bikinetic plaid stimuli, although this difference did not reach significance (p = 0.14; Student’s t-test). In MST the computation of pattern selectivity for unikinetic plaids lagged that for bikinetic plaids, and this difference was statistically significant (p < 0.05; Student’s t-test). The results we have observed in MST are thus consistent with previous studies which show that eye movement responses to unikinetic plaids initially correspond to the moving grating and incorporate the static grating later in time (Masson and Castet 2002).

**Correlates with perceptual transparency**

Our results up to this point suggest that MST neurons are more pattern-selective than neurons in previous areas for both bikinetic and unikinetic plaids. This is consistent with the idea that neuronal responses at higher stages are more strongly correlated with visual perception than are those at lower levels (Williams et al. 2003). However, an alternative interpretation is that the higher-level neurons are simply more effective at integrating motion signals, as evidenced by the increase in receptive field size and tuning bandwidth at successive stages along the pathway. These two possibilities (greater integration versus correlation with perception) lead to the same outcome when the stimulus is a coherent bikinetic or unikinetic plaid, but they predict divergent results for other types of stimuli.
A particularly interesting example is the transparent plaid stimulus introduced by Stoner et al. (Stoner and Albright 1992; Stoner et al. 1990). This stimulus is similar to the plaid stimuli described in the previous section, except that the plaid is displayed against a bright background, and each of the component gratings is made to appear translucent. Thus where the gratings intersect, the luminance is no longer additive, but instead conforms to the laws of transparency (Metelli 1974). Mathematically the non-additivity of the intersections can, under certain assumptions, introduce motion signals in the pattern direction, but perceptually the resulting motion is more consistent with the motion of the components. That is, observers perceive the two gratings to be sliding over each other, rather than seeing a single pattern moving coherently (Stoner et al. 1990).

The transparent plaid stimulus allows us to dissociate two possible explanations for the increased pattern selectivity observed in MST with both unikinetic and bikinetic plaids. The responses of MST cells that have outputs that are most similar to human perception should become more component-like for transparent stimuli, and this modulation should be stronger than that observed in MT. On the other hand, if MST cells are simply integrating motion components indiscriminately, then we should see little effect of the transparent manipulation. We tested these possibilities on 37 V1 cells, 52 MT cells, and 69 MST cells.

Each cell was tested with an additive square-wave plaid (which is perceptually coherent), and a non-additive, perceptually transparent, plaid. Figure 8a plots the values of the pattern index for the two different kinds of plaid tested on each cell. For area V1 (Figure 8a), these values tend to fall along the unity line, indicating no modulation by perceptual transparency. For MT (Figure 8b), consistent with previous results (Stoner and Albright 1992), the points tend to fall below the unity line, suggesting that these responses are modulated by depth cues associated with transparency. Surprisingly, there is on average little modulation by transparency in MST, as the points in Figure 8c tend again to fall along the unity line.

To quantify the degree of transparent modulation in each neuron, we defined a transparency index (TI) by subtracting the component index obtained in the coherent condition from that obtained in
the transparent condition. Thus more negative values of TI indicate greater modulation by transparency. Transparency modulation significantly increases from V1 to MT (mean of 0.02 in V1 and -0.67 in MT; p < 0.05; Student’s t-test), but a similar increase is not observed in the comparison between MT and MST (mean of -0.67 in MT to 0.02 in MST; p < 0.01; Student’s t-test). Out of the three areas tested, transparency modulation was significantly different from zero only in MT (p < 0.001; Student’s t-test). Indeed there is little overall modulation by transparency in the MST population (mean TI = 0.02), consistent with the hypothesis that MST cells integrate motion components indiscriminately.

One possible explanation for these results is that our recordings targeted dorsal MST (MSTD), rather than ventral MST (MSTV). This is entirely possible, as many of the neurons described here came from a previous study aimed at examining optic flow processing (Mineault et al. 2012), which is a key function of MSTD. In contrast MSTV is thought to be involved in object motion processing, a task which may require the use of information about transparency (Britten 2008). Although we have no definitive method of identifying the anatomical locations of the neurons from which we recorded, previous work has shown that MSTV neurons exhibit greater surround suppression than MSTD neurons (Eifuku and Wurtz 1998). However, we found no correlation between the TI and a measure of surround suppression in MST (linear regression; p > 0.74).
DISCUSSION

In this work we have characterized the responses of MST neurons to visual stimuli that have classically been used to study motion selectivity in earlier cortical areas, such as V1 and MT. Previous research on pattern motion selectivity in these areas has led to the notion of a two-stage model, in which the projection from V1 to MT is largely responsible for estimates of object velocity that are invariant to other stimulus parameters, notably orientation. Our results, while generally consistent with the hierarchical aspect of these models, suggest that the relevant computations involve additional areas, including MST. Indeed our results with unikinetic plaids provide an example of a pattern motion computation that is unlikely to be carried out fully at the level of MT. For these stimuli the relationship between MT and MST is qualitatively similar to that between V1 and MT for bikinetic plaids: MT neurons are generally selective for the motion components, while a minority of MST neurons is capable of signalling pattern motion.

Mechanisms of motion integration

The estimation of object motion is often characterized as a two-stage process, in which the second stage infers the velocity of the object from first-stage measurements that are individually ambiguous. The ambiguity results in part from the fact that motion-selective neurons in areas such as V1 will respond to a stationary stimulus nearly as strongly as they respond to one that moves in their preferred motion direction (see for example Figure 2A). Such responses are obviously problematic for an organism that relies on these neurons to estimate motion. In theory this problem can be solved by subtracting the outputs of two neurons tuned to opposite motion directions (Adelson and Bergen 1985; Reichardt 1961; van Santen and Sperling 1985), as the portion of the response due to the stationary stimulus will on average be equal in both cells. The process that carries out the subtraction is called a motion opponent mechanism.
A similar ambiguity exists for moving stimuli. For a stimulus comprised of multiple contours, the response of a neuron in V1 will generally depend on the shape of the object as well as its velocity. This confound results from the fact that neurons with small receptive fields only receive information about the component of motion perpendicular to the orientation of a contour passing through their receptive fields (Wallach, 1935). One way to resolve this problem is to implement a second stage that integrates over the outputs of multiple first-stage neurons that prefer different motion directions (Rust et al. 2006; Simoncelli and Heeger 1998; Welch 1989).

Our results, consistent with previous findings (Qian and Andersen 1994; Rust et al. 2006), indicate that both the strength of opponent motion processing and the bandwidth of integration are greater in MT than in V1. We also find that both mechanisms are stronger in MST than in MT, suggesting that these fundamental aspects of motion integration are carried out in at least three stages along the dorsal visual hierarchy. A comparative analysis of our data from V1, MT, and MST (Figure 3) indicates that the increases in motion opponency and tuning bandwidth are not by themselves sufficient to account for the increased pattern selectivity seen at higher-level areas of the cortex. Rather pattern selectivity is generally greater in MST than in MT and in MT than in V1, even when the increase in the mean tuning bandwidth and decrease in responses to static stimuli are taken into account (Figure 3).

**Implications for motion models**

Both the mechanisms discussed above (opponent motion and integration) can be modeled as linear operations, in which the inputs of one stage are added or subtracted to generate the output of the next stage. While these linear operations are incorporated to some degree into virtually all models of motion processing, recent models also include a nonlinear operation that transforms the outputs of each of the neurons at one stage prior to their summation at the next stage. Thus for example, an MT neuron can effectively be modeled as receiving input from a number of V1 neurons, with each input being transformed by a nonlinear function prior to summation at the MT stage. Generally the nonlinear transformation is captured by a compressive function, which causes the contribution of each neuron to
saturate (Nishimoto and Gallant 2011; Rust et al. 2006; Tsui et al. 2010). Interestingly the same
nonlinearity was recently shown to be essential to account for the transformation of optic flow
selectivity between MT and MST (Mineault et al. 2012). Thus a generic model that makes use of
similar linear and nonlinear mechanisms seems capable of accounting for selectivity in both MT and
MST for various stimuli including plaids (Rust et al., 2006; Tsui et al., 2010), optic flow (Mineault et
al., 2012), and natural scenes (Nishimoto and Gallant, 2011).

One departure from this generic modeling framework concerns the mechanisms underlying the
processing of unikinetic plaids. From a theoretical standpoint, these stimuli are particularly challenging
because they require the estimate of motion direction to take into account information from non-moving
stimuli that by themselves elicit little neuronal response. In the case of the unikinetic plaid the velocity
of the pattern is perceived to be parallel to the non-moving grating component. In our data (Figure 6),
pattern selectivity for unikinetic plaids was most common in area MST, where responses to such static
stimuli were negligible. Thus models that rely entirely on the mechanisms discussed above (motion
opponency, integration across motion directions, nonlinear transformations of firing rates) are unlikely
to account for this selectivity. Instead the existence of cells that are pattern-selective for both unikinetic
and bikinetic plaids would seem to require more specialized mechanisms, such as an intersection-of-
constraints calculation (Simoncelli and Heeger 1998) or a mechanism for integrating second-order
motion signals (Ferrera and Wilson 1990). Although limited evidence for both mechanisms has been
found in MT (Albright 1992; Nishimoto and Gallant 2011; Priebe et al. 2003), they remain largely
unexplored in MST.

**Transparency**

As mentioned above in the context of unikinetic plaids, the interpretation of visual motion can be
strongly influenced by visual cues that contain no time-varying information. One important example
credits depth cues, such as retinal disparity (Duncan et al. 2000; Shimojo et al. 1989), occlusion (Pack
et al. 2004; Vallortigara and Bressan 1991), and transparency (Stoner et al., 1990; Stoner et al., 1992).
The influence of the latter cue is particularly evident when luminance conditions are used to manipulate the apparent depth arrangement of the components of a plaid stimulus (Stoner et al. 1990).

Consistent with previous results (Stoner and Albright 1992), we have found a neuronal correlate of these perceptual findings in MT. Our results further suggest that modulation of neuronal responses by transparency is lacking in V1 (Figure 8), where neurons generally respond to the individual component gratings even for perceptually coherent plaids. These results together might suggest that neurons further along the dorsal pathway combine motion and depth signals in a manner that is more consistent with perception, but we found little evidence for this idea. Indeed, the responses of the MST population to transparent plaids were similar to those of the V1 population. This would seem to contradict previous findings that MST responses are more consistent with visual perception (Williams et al. 2003); here we consider a number of possible ways to interpret this result.

The first possibility is that the perception of transparent plaid stimuli may involve pathways that do not include the MST neurons in our sample. Indeed, as mentioned in the Results, our recordings targeted area MSTd, which is often assumed to be associated with self-motion, rather than object motion processing (Tanaka et al. 1993). We consider this to be an unlikely explanation, because computational results have shown that MSTd neurons are in fact capable of estimating object motion (Mineault et al. 2012; Zemel and Sejnowski 1998). Moreover, transparency cues are likely to improve estimates of self-motion and to modulate the responses of MSTd neurons (Upadhyay et al. 2000).

A second possibility is that the stimuli used in our experiments were not perceptually transparent. Although we selected stimulus parameters that induced strong percepts of transparency in humans (Stoner et al., 1990), we did not attempt to optimize them for the monkeys in our study. Although one previous report suggests that the perception of transparent plaids is similar between macaques and humans (Thiele and Stoner 2003), there are considerable technical problems associated with training monkeys to report their percepts of these stimuli. Thus we cannot rule out this possibility completely.
A third possible explanation for our results is that transparency modulation is present in MST, but not apparent at the single-unit level. This would result if the neural correlate of transparency population involved synchrony among neurons (Castelo-Branco et al. 2000) or if it involved a more specialized readout of the neuronal population (Treue et al. 2000). The former is theoretically possible, although a direct test of the relationship between stimulus transparency and synchrony in the awake monkey failed to find the predicted result (Thiele and Stoner 2003). The other possibility, that transparency perception results from the precise shape of the overall distribution of responses in a population (Treue et al. 2000), remains entirely possible. Indeed the broad tuning of individual MST neurons for motion direction and spatial position would seem to necessitate additional processing to extract the motion of multiple, independently moving objects.

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Figure Captions

**Figure 1.** Experimental stimuli. *A*, Examples of bikinetic stimuli used in our experiments. Cells were stimulated with both a single grating (left, center) and a plaid stimulus (right) formed by summing two gratings with orientations that differed by 120°. Arrows represent the direction perceived by human observers. *B*, Unikinetic plaid stimuli in which only one of the gratings moves (left) while the other remains stationary (center). The perceived direction is parallel to the orientation of the stationary grating (arrow; right). *C*, Transparent plaid stimuli (right) consisting of two square gratings (left and centre). The motion of both gratings is typically perceived (arrows; right).

**Figure 2.** Mean peri-stimulus time histograms (PSTHs) for V1 (n=33), MT (n=103) and MST (n=113). *A*, PSTHs for V1 showing mean spike responses evoked using grating stimuli for the group of component (left), unclassified (middle) and pattern (right) neurons in our sample. Preferred (blue), null (red) and perpendicular (black) directions are shown. Gratings were presented at -200 ms, remained stationary for 200 ms, and then began moving at 0 ms. The response evoked by the stationary stimulus is highlighted in gray. *B*, PSTHs for MT. *C*, PSTHs for MST.

**Figure 3.** Correlations of pattern index vs. static response index and tuning width for V1, MT and MST. *A*, Scatter plot showing the correlation between pattern index and static response index for V1 (blue circles), MT (green Xs) and MST (red crosses). Solid lines show the linear fits obtained with an ANCOVA model. *B*, Scatter plot illustrating the correlation between pattern index and motion tuning bandwidth for V1 (blue circles), MT (green Xs), and MST (red crosses).

**Figure 4.** Summary of LFP and spike responses to stationary stimuli. *A*, Mean peri-stimulus time histograms (PSTHs) illustrating the change in response for the population of MST $\gamma_H$ sites (left column), $\gamma_L$ sites (middle column), and spikes (right column) elicited by sinusoidal gratings. Preferred (blue), null (red) and perpendicular (black) directions are shown. Gratings were presented at -200 ms, remained stationary for 200 ms, and then began moving at 0 ms. The response evoked by the stationary stimulus is highlighted in gray. *B*, Summary of the mean static response index (see Methods) for $\gamma_H$ (red), $\gamma_L$ (black) and spike responses (blue) for the population of V1, MT and MST sites.
Figure 5. Example spike responses of MT and MST neurons to bikinetic and unikinetic plaid stimuli. 

Polar plots showing examples of grating (left), bikinetic plaid (centre) and unikinetic plaid (right) direction tuning curves obtained from single recordings for $A$, an MT cell which is unclassified for bikinetic plaids but component-tuned for unikinetic plaids, $B$, an MT cell which exhibits pattern selectivity with bikinetic plaids and is categorized as unclassified with unikinetic plaids and $C$, an MST cell which is pattern-selective with both bikinetic and unikinetic plaids. Neuronal responses are shown in solid black, direction-tuning curve fits in dashed black, component predictions in dashed blue and pattern predictions in dashed red. The category (i.e. component, unclassified or pattern) of each response for bikinetic and unikinetic plaids is provided below the corresponding polar plots.

Figure 6. Pattern and component selectivity in MT and MST for bikinetic and unikinetic plaids. Scatter plots showing $Z$-transformed component correlations vs. $Z$-transformed pattern correlations (first two columns) for the population of spikes recorded from $A$, MT (n=46) and $B$, MST (n=50). Cells were classified as pattern-selective (red) and component-selective (blue) according to the $Z$-partial correlation coefficients between the data and the component and pattern predictions (see Methods). Cells which could not be assigned to either category were labelled unclassified (black). Histograms (third and fourth columns) showing a significantly smaller mean pattern index when unikinetic plaids are used for MT ($A$; $p < 0.01$) and MST ($B$; $p < 0.001$). The mean pattern index is greater for the MST population compared to the MT population when both bikinetic ($p < 0.01$) and unikinetic plaids ($p < 0.05$) are used. The fifth column shows a scatter plot comparing the distribution of pattern indices for MT ($A$) and MST ($B$) for bikinetic vs. unikinetic plaids. MST contains a greater percentage of neurons that exhibit pattern selectivity for both types of plaid stimuli.

Figure 7. Temporal dynamics of component and pattern selectivity. $A$, Temporal dynamics of the mean pattern index when bikinetic plaids are used for the set of MT component (blue) and pattern (red) neurons and for MST pattern neurons (black) in our sample. Dashed black lines demarcate the threshold of pattern index used to consider a neuron as component (-1.28) or pattern-selective (+1.28). $B$, Average temporal response profile of MT component (purple) and pattern (light brown) neurons, as well as of MST component (gray) and pattern (green) neurons. $C$, Mean time-course of MT component
and pattern selectivity for bikinetic and unikinetic plaids. \(D\), Mean time-course of MST component
and pattern selectivity for both bikinetic and unikinetic plaids.

**Figure 8.** Pattern selectivity of the population of V1, MT and MST neuronal responses to coherent vs.
transparent plaids. Comparison of the distribution of pattern indices measured for V1 (37 cells) \((A)\), MT
(52 cells) \((B)\) and MST (69 cells) \((C)\) neuronal responses to coherent (x-axis) vs. transparent (y-axis)
plaids. The mean transparency index (TI) for V1 is significantly smaller than that for MT \((p < 0.05)\),
which is significantly larger than that found in MST \((p < 0.01)\).


Rust NC, and Dicarlo JJ. Selectivity and tolerance ("invariance") both increase as visual information propagates from cortical area V4 to IT. *J Neurosci* 30: 12978-12995, 2010.


a) Tuning width (deg) vs. Static response index

b) Tuning width (deg) vs. Pattern index

Legend:
- V1
- MT
- MST
MT vs. MST bikinetic

MT vs. MST unikinetic

MT bikinetic vs. unikinetic

MST bikinetic vs. unikinetic
a) 

V1

mean TI = 0.02

n = 37

b) 

MT

mean TI = -0.67

n = 52

c) 

MST

mean TI = 0.02

n = 69