Feature attention for binocular disparity in primate area MT depends on tuning strength

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Ruff DA, Born RT. Feature attention for binocular disparity in primate area MT depends on tuning strength. *J Neurophysiol* 113: 1545–1555, 2015. First published December 10, 2014; doi:10.1152/jn.00772.2014.—Attending to a stimulus modulates the responses of sensory neurons that represent features of that stimulus, a phenomenon named "feature attention." For example, attending to a stimulus containing upward motion enhances the responses of upward-preferring direction-selective neurons in the middle temporal area (MT) and suppresses the responses of downward-preferring neurons, even when the attended stimulus is outside of the spatial receptive fields of the recorded neurons (Treue S, Martinez-Trujillo JC. *Nature* 399: 575–579, 1999). This modulation renders the representation of sensory information across a neuronal population more selective for the features present in the attended stimulus (Martinez-Trujillo JC, Treue S. *Curr Biol* 14: 744–751, 2004). We hypothesized that if feature attention modulates neurons according to their tuning preferences, it should also be sensitive to their tuning strength, which is the magnitude of the difference in responses to preferred and null stimuli. We measured how the effects of feature attention on MT neurons in rhesus monkeys (*Macaca mulatta*) depended on the relationship between features—in our case, direction of motion and binocular disparity—of the attended stimulus and a neuron's tuning for those features. We found that, as for direction, attention to stimuli containing binocular disparity cues modulated the responses of MT neurons and that the magnitude of the modulation depended on both a neuron's tuning preferences and its tuning strength. Our results suggest that modulation by feature attention may depend not just on which features a neuron represents but also on how well the neuron represents those features.

binocular disparity; feature attention; area MT

ATTENTION DIRECTED to a visual stimulus enhances the responses of sensory neurons that represent features of the attended stimulus, irrespective of the location of their receptive fields. Such a mechanism may facilitate visual search or difficult discriminations by enhancing the activity of relevant sensory neurons and suppressing that of irrelevant neurons (Martinez-Trujillo and Treue 2004). Early studies of feature attention in the middle temporal area (MT) of primate visual cortex have suggested that the extent to which feature attention modulates a neuron's responses depends on the match between the value of a feature of the attended stimulus and a neuron's tuning preferences for that feature—the so-called "feature-similarity gain" (FSG) model (Martinez-Trujillo and Treue 2004). Interestingly, and somewhat counterintuitively, this effect does not require that the animal perform a task that requires attention to the particular feature that is modulated. For example, when animals performed a speed change detection task, MT neurons exhibited feature-attention modulation based on the direction of motion of the attended stimulus, even though this feature was irrelevant to the task (Martinez-Trujillo and Treue 2004; Treue and Martinez-Trujillo 1999). The FSG model requires the existence of a mechanism that can globally modulate neurons with similar tuning preferences for a given feature. While many studies have found evidence for such modulation in the nonhuman primate brain (Bichot et al. 2005; Katzner et al. 2009; Khayat et al. 2010; Martinez-Trujillo and Treue 2004; McAdams and Maunsell 2000; Patzwahl and Treue 2009; Treue and Martinez-Trujillo 1999), the mechanism remains unknown (Maunsell and Treue 2006).

If one role of feature attention is to increase the selectivity of neuronal population responses to features of an attended stimulus, it would be advantageous to most strongly modulate the gains of the most selective neurons. Increasing the gain of neurons that were weakly tuned (or not selective at all) would only serve to render the population response noisier. We thus hypothesized that feature-attention modulation might be sensitive not only to the preferred and null stimulus values for a given neuron but also to the magnitude of the difference in the firing rates that those stimuli evoke, that is, to the neuron's "tuning strength." To explore this possibility, we measured feature-attention modulation of MT neuronal responses for both direction of motion and binocular disparity, a property for which nearly all MT neurons are selective (DeAngelis and Uka 2003; Maunsell and Van Essen 1983).

Our study uncovered several new properties of the way feature attention affects MT neurons. We found that in addition to being modulated by feature attention for motion direction (Treue and Martinez-Trujillo 1999), MT neurons are modulated by feature attention for binocular disparity—a tuning property that has a columnar organization in MT (DeAngelis and Newsome 1999), similar to that for direction of motion (Albright et al. 1984). We also found that feature attention for binocular disparity followed the prediction of the FSG model, that its presence did not require a perceptual judgment about binocular disparity, and that feature attention effects were not explained by bottom-up, stimulus-driven causes, such as influences from the receptive field surround (Allman et al. 1985). Finally, because of the variability of tuning strength for binocular disparity tuning in MT (DeAngelis and Uka 2003; Maunsell and Van Essen 1983), we were able to demonstrate the predicted relationship between a neuron's tuning strength and the magnitude of modulation by feature attention. Our results show that the mechanism underlying feature attention is

able to account for how well a neuron represents the features contained in an attended stimulus.

METHODS

The goal of our experimental paradigm was to test how attention directed to a stimulus placed far from a neuron's receptive field could modulate that neuron's response. To do this, we trained two adult male monkeys (*monkeys N and P*) to perform a speed change detection task that required them to detect a randomly timed, stepped speed increase in an attended moving visual stimulus by responding with a saccadic eye movement. Both monkeys had previously been trained to perform a speed change discrimination task where they signified the sign of a speed change by making a saccade to one of two targets (Price and Born 2010). The targets were removed, and both monkeys were trained, within one session, to saccade to the attended stimulus when its speed changed. No explicit instruction cue was provided to direct the animal to attend to the proper stimulus, and through the course of training for this study the animals were only ever rewarded for making saccades to the stimulus placed ipsilateral to our recording chamber and no speed changes ever occurred at the unattended stimulus location. Additional training was performed to ensure that the animals had stable performance across different stimulus locations, directions, binocular disparities ($-1.2°$ to $+1.2°$), reference speeds ($6-15°$/s), sizes ($4-12°$ diameter), and trial durations (up to 5,500 ms) and that they did not change their vergence when attending to stimuli at different binocular disparities.

Before electrophysiological recordings, each animal was implanted with a custom titanium head-post, two scleral search coils for monitoring eye positions, and a vertically oriented CILUX recording cylinder to protect a craniotomy centered posterior 3 mm and lateral 15 mm relative to ear bar zero. All animal procedures complied with the National Institutes of Health *Guide for the Care and Use of Laboratory Animals* and were approved by the Harvard Medical Area Standing Committee on Animals.

Stimuli and Task

The stimuli consisted of moving dot patches and were presented on a black screen placed 410 mm from the animal with resolution $1,024 \times 768$ pixels (17.8 pixels/°) and refresh rate 100.1 Hz. The binocular disparity of each stimulus was created by drawing each dot twice, once in red and once in blue, and changing each dot pair's horizontal offset according to the specified disparity value. Dots at zero binocular disparity were drawn as a combination of the blue and red values, which appeared purple. The monkeys viewed the screen through monocular filters colored red or blue (Kodak gelatin filters nos. 29 and 47), so that only one set of dots was visible to each eye. Crossover between the two eyes, as viewed through the filters, was measured to be <3%. Dots were presented at a spatial density of 1.5 dots/$°^2$ with 150-ms lifetime and had 100% coherence (i.e., there were no noise dots, but the dots flickered because of their limited lifetime). Dots were drawn in a stationary circular aperture that either matched the full extent of the excitatory receptive field center of the neuron being studied or had a diameter equal to the eccentricity of the stimulus center, whichever was smaller. The two stimuli were always the same size.

The speed change detection task's trial sequence is shown in Fig. 1A. A trial began when the animal acquired fixation within an invisible square window that ranged from 0.7° to 1.6° per side and was centered on a small fixation spot. After 250 ms of stable fixation, two stationary random dot patches appeared on either side of fixation. One patch was placed in the receptive field of the neuron under study and the other in an equivalent position on the horopter in the opposite hemifield. The two stimuli were usually centered 15–25° away from each other. Both stimuli were always presented at the same elevation,

but when the receptive field of an MT neuron was relatively close to the vertical meridian, the attended stimulus was often placed 2–5° more laterally in the opposite hemifield. After an additional 250 ms, both dot patches began to move (*time 0* in Fig. 2B) for a duration of time that ranged between 500 and 5,500 ms until a stepped increase of speed occurred. To keep the speed change's hazard function relatively constant (Luce 1986), the length of the reference speed was randomly chosen from a truncated exponential distribution with a time constant of 2,000 ms. The magnitudes of the changed speed varied from 105% to 150% of the reference speed and were selected to ensure that the animals could correctly detect the change on roughly 70% of trials. Behavioral responses were assigned to one of four categories: *1*) correct, if a saccade was made to the attended stimulus 150–650 ms after the speed change; *2*) miss, if fixation was maintained for >650 ms after the speed change; *3*) false detection, if a saccade was made during the reference period or in the first 150 ms after the speed change; *4*) fixation break, if the eye position left a square fixation window with sides of length 0.7–1.6° but no saccade was made to the attended stimulus within 100 ms. Only correct trials were rewarded, and no speed changes occurred in the unattended stimulus. Psychometric functions were fitted with the "psignifit" toolbox version 2.5.6 for MATLAB (see **http://bootstrap-software.org/psignifit/**), which implements the maximum-likelihood method described by Wichmann and Hill (2001).

For each neuron, quantitative tuning data were collected for direction of motion, dot patch size, and binocular disparity while the animals were rewarded for fixating a central target (Fig. 2A). The preferred and null values for direction and binocular disparity derived from these data sets were used during the main experiment. The preferred direction was determined by the result of the mean vector calculation, and the null direction was set as the value 180° opposite of the preferred value. The preferred and null binocular disparity values were determined to be the maximum and minimum values from the tuning data, respectively. The two dot patches moved at slightly different speeds to discourage the animals from using the unattended stimulus as a reference for the detection task. For a given experimental session, a single speed for the attended stimulus was selected from a range of 6–15°/s while a single speed for the unattended stimulus speed was selected from a range between 4°/s and 20°/s and was usually 2–4°/s different, either faster or slower, than the attended stimulus. The speed of each stimulus was constant within a session, and the speed of the unattended stimulus was set at a value that drove the MT neuron optimally.

For the first experiment reported here, the unattended stimulus, which was placed in the receptive field of the recorded MT neuron, always moved in the neuron's preferred direction at its preferred disparity. The role of this stimulus was to drive the neuron under study, but it was not behaviorally relevant. To establish the presence of feature attention for binocular disparity and direction of motion, on any given trial a second, attended stimulus was presented in the opposite hemifield in one of four configurations: at *1*) the neuron's preferred direction and preferred binocular disparity, *2*) its preferred direction and null binocular disparity, *3*) its null direction and preferred binocular disparity, or *4*) its null direction and null binocular disparity.

The attended stimulus' direction and binocular disparity could change on every trial; therefore this design allowed for attentional modulation for each feature to be measured on interleaved trials. In the second experiment, additional conditions were used where the stimulus in the receptive field could also be presented at the preferred and null value of each of the two features (see Fig. 4, *A* and *B*). Additionally, during both quantitative tuning data collection and the task, dots drawn at zero disparity, called grounding dots (DeAngelis and Newsome 1999), were randomly placed in an annulus around the fixation target to aid the animal in maintaining vergence at the plane of fixation.

A

Fixate
250 ms

Stationary
dots 250 ms

Motion on
500 - 5500 ms
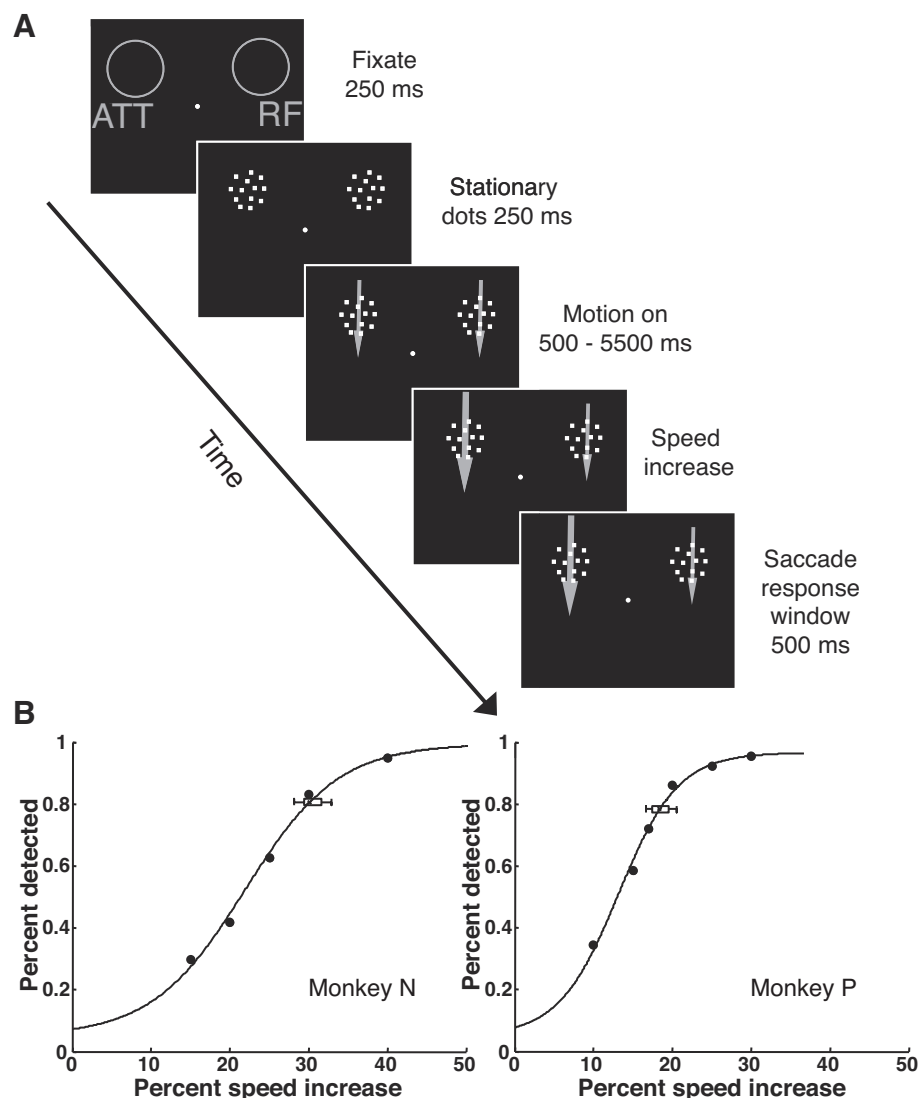
Speed
increase

Saccade
response
window
500 ms

Time

Fig. 1. Task design and stimulus configurations. *A*: illustration of behavioral task. ATT, attended; RF, receptive field. *B*: behavioral performance from example recording session from *monkeys N* (*left*) and *P* (*right*). Box plot signifies 95% confidence intervals (via bootstrap) of threshold estimation (at 80% detected).

B

Neuronal Data Set

We recorded from 207 single MT neurons with methods described previously (Price and Born 2010). Area MT was selected because its tuning properties are relatively well understood (DeAngelis and Uka 2003) and feature attention effects have been previously described for direction of motion (Treue and Martinez-Trujillo 1999). Neurons were identified as being within MT by a range of criteria including position of the electrode in the chamber judged relative to postsurgical magnetic resonance imaging; electrode depth relative to the dura; size of the spatial receptive field relative to the eccentricity; transitions between gray and white matter as the electrode was advanced; and amount of overlap of the receptive field into the ipsilateral hemifield. Typically, MT was encountered after the medial superior temporal area (MST), which was purposefully avoided because of larger receptive fields that may have been directly stimulated by the second, attended stimulus. Any neurons where spiking activity could be directly driven by placing a moving stimulus in the ipsilateral hemifield were rejected. Task data were only collected from neurons where a statistically identifiable preferred and null value for both direction and binocular disparity were found (paired *t*-test between maximum and minimum response, $P < 0.05$). Neurons with at least 80 completed trials from the first experiment were included in the population data. For the first experiment, 97 neurons from *monkey N* and 110 neurons from *monkey P* met these criteria. Included in those numbers

are 21 neurons from *monkey N* and 23 neurons from *monkey P* that contained the additional conditions shown in Fig. 4. Across the population, the median number of completed detection trials was 312 and the mean was 341. There were no significant differences between the effects observed in the two animals, so the data from both animals were combined.

Single-trial firing rates were calculated from spike counts that occurred in a 250-ms window of time that immediately preceded the speed change on correct trials. This was the interval during which we had the highest confidence that the animal was attending to the correct stimulus. Using other windows, including ones aligned to the stimulus onset, gave qualitatively similar results but did not allow for direct comparison with the control data described below. With these data, statistical tests and attentional indices for both direction and disparity feature attention were calculated. We calculated attentional modulation on trials when the other feature was at the neuron's preferred value. We used a standard attentional index, which we defined as $(\text{Resp}_{\text{AttPref}} - \text{Resp}_{\text{AttNull}})/(\text{Resp}_{\text{AttPref}} + \text{Resp}_{\text{AttNull}})$. This index is bound between -1 and 1, where 0 signifies that there was no modulation as a result of feature attention and positive values signify a larger response when the animal attended to the preferred value of a feature compared with when it attended to the null value. Spike density functions, which are for display purposes only (Fig. 2, *B–E*), were calculated by convolving spikes with a 50-ms Gaussian kernel.
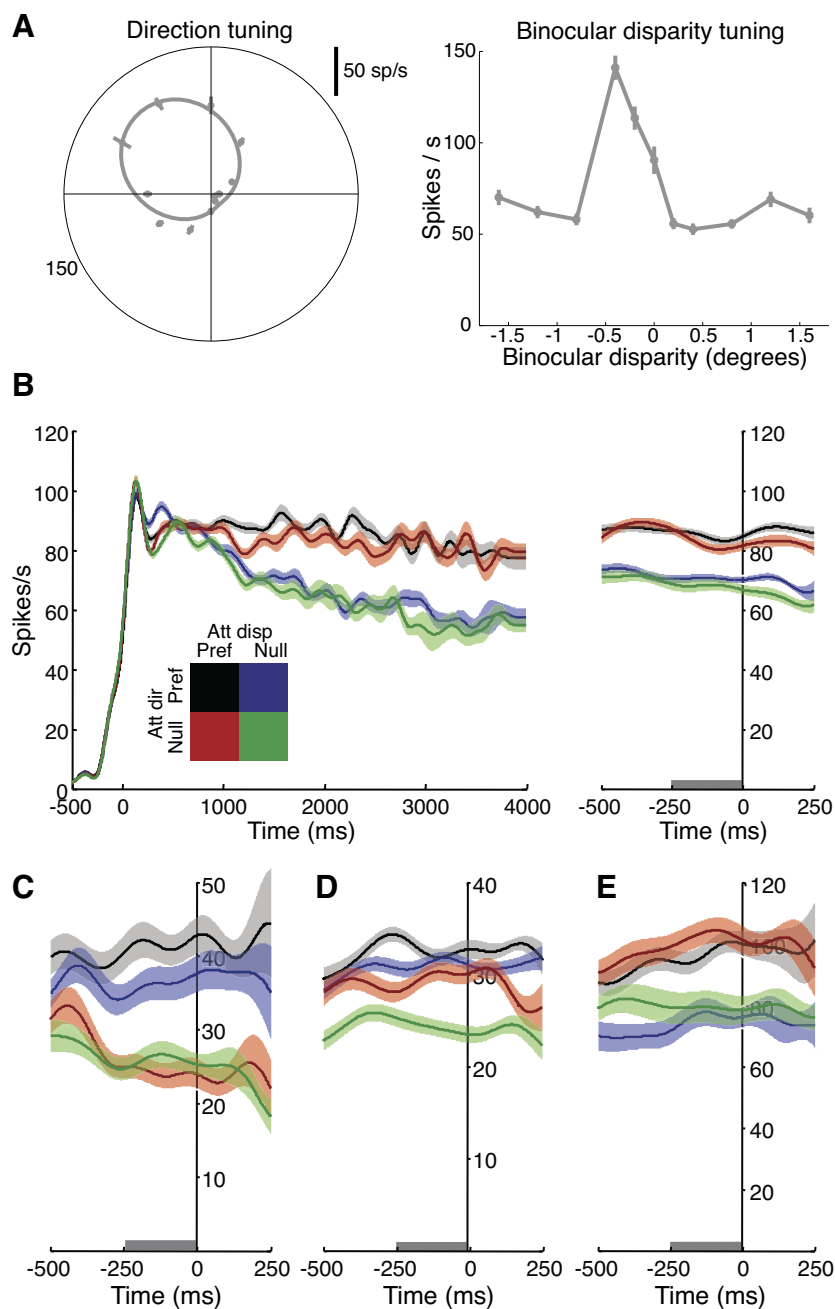
Fig. 2. Feature-based attention in middle temporal area (MT) for binocular disparity and direction of motion in single neurons. *A*: direction and binocular disparity tuning curves collected from an example neuron prior to the main task. Error bars are SE. *B, left*: spike density function aligned to stimulus motion onset from cell in *A*; shaded area is SE. *Inset*: the 4 attentional conditions. For each condition, the stimulus in the receptive field is moving in the preferred direction at the preferred binocular disparity. *Right*: same neuron but aligned to the time of correctly detected speed changes. Gray bar signifies the time window in which spikes were counted (250 ms prior to correctly detected speed changes). This cell exhibited large feature-based attentional modulation for binocular disparity (disparity index = 0.086; direction index = 0.017). *C–E*: 3 additional example cells, aligned to the time of the correctly detected speed change. *C*: disparity index = 0.077; direction index = 0.28. *D*: disparity index = 0.018; direction index = 0.04. *E*: disparity index = 0.12; direction index = −0.031.

For the purpose of displaying overlaid standard error, both the spike density functions and their standard errors were low-pass filtered with a 1st-order Butterworth filter with a cutoff frequency of 0.1, which serves to smooth out jumps in the spike density function and its standard error as trial numbers change because of different trial lengths.

A 2 × 2 ANOVA was performed on square-root transformed firing rates for each neuron to test for main effects of attending to either its preferred or null direction and binocular disparity as well as the interactions between these main effects. Wilcoxon signed-rank tests were performed to determine whether population distributions were significantly different from zero; Wilcoxon rank sum tests were performed to determine significance for individual neurons on population plots (Fig. 3 and Fig. 4).

To test whether attentional modulation for each feature combined additively or multiplicatively, we predicted the response during one condition (the attend to the null direction and null disparity condition)

using the mean observed responses to the other three conditions. The multiplicative model took the form

$$\text{Predicted}_{\text{NullNull}}$$
$$= \text{Obs}_{\text{PrefPref}} \times \left(\text{Obs}_{\text{PrefNull}}/\text{Obs}_{\text{PrefPref}}\right) \times \left(\text{Obs}_{\text{NullPref}}/\text{Obs}_{\text{PrefPref}}\right)$$

while the additive model took the form

$$\text{Predicted}_{\text{NullNull}} = \text{Obs}_{\text{PrefPref}} + \left(\text{Obs}_{\text{PrefNull}} - \text{Obs}_{\text{PrefPref}}\right)$$
$$+ \left(\text{Obs}_{\text{NullPref}} - \text{Obs}_{\text{PrefPref}}\right)$$

We then compared the predicted Predicted$_{\text{NullNull}}$ value to the observed value. This process was repeated separately to predict the PrefPref condition using the other three conditions, and similar results were observed.

With the quantitative tuning data, the preferred and null values for each feature were determined and a tuning index of the form (Resp$_{\text{Pref}}$ − Resp$_{\text{Null}}$)/(Resp$_{\text{Pref}}$ + Resp$_{\text{Null}}$) was calculated. This index was effec-

tively bound between 0 and 1 because the preferred value was, by definition, always larger than the null value. Larger values signified stronger tuning modulation for that feature.

To test whether the presence of the second, attended stimulus (which was outside the neuron's receptive field) led to direct, bottom-up neuronal responses that could be misattributed to feature attention, we collected additional data immediately before the task in 199 of our 207 recordings. Both stimuli were simultaneously flashed for 250 ms each in the exact positions and configurations in which they would occur during the main task, while the animal was rewarded for maintaining fixation. Indices were calculated and an ANOVA was performed with these data, which had the same sensory input as during the task but were collected during a condition where the animal had no incentive to attend to either stimulus and, because of the brief presentation, could not switch its attention between the stimuli during their presentation.

RESULTS

Psychophysical Performance

The monkeys performed a reaction time task in which they made a saccade to indicate that they detected a randomly timed increase in the speed of the cued (attended) stimulus (Fig. 1A). A speed change detection task was used because it ensures that the animal is attending to the stimulus, but the feature itself is not directly related to the two features for which we are investigating neural effects of feature attention. Previous work has shown that task relevance is not necessary to observe feature attention effects in sensory neurons (Katzner et al. 2009; Martinez-Trujillo and Treue 2004; Treue and Martinez-Trujillo 1999); therefore, this design allowed us to probe the relationship between feature attention effects and tuning strength without using a task that would bias effects in favor of one feature over the other. As previously described (Price and Born 2010), performance during this task depended on the Weber fraction, which is the ratio of the changed speed to the reference speed. Smaller speed ratios were associated with more frequent missed changes and longer reaction times. The magnitude of the speed increase was randomly selected from a small range of values in order to encourage the animal to work hard and maintain performance near 70% correct. Figure 1B depicts detection performance as a function of percent change in speed for an example recording session from monkeys N and P, respectively. Psychophysical thresholds were defined as the speed change amount that led to an 80% detection rate. The thresholds from the two example sessions were a 30% speed increase for monkey N (Fig. 1B, left) and a 19% speed increase for monkey P (Fig. 1B, right). The median threshold during recording sessions was a 30% (SD = 9.3%) speed increase for monkey N and a 20% (SD = 4.4%) increase for monkey P. For the two animals, fixation breaks (13% for monkey N, 11% for monkey P) and early responses (12% for monkey N, 14% for monkey P) accounted for an average of 25% of trials across sessions. Of trials where the speed change occurred, it was correctly detected 71% of the time (69% for monkey N, 73% for monkey P) while the remaining 29% of speed changes failed to be detected and were classified as misses.

To confirm that the animals did not rely on the unattended stimulus as an aid in detecting the speed change, we measured detection performance and reaction times as a function of the relationship between the attended stimulus's direction, disparity, and reference speed differences. We found that nothing about the relationship between the two stimuli was predictive of the monkeys' behavioral performance, whether that of probability of detection or reaction time, which suggests that the animals properly allocated their attention to the correct stimulus.

Analysis of Neuronal Activity

Feature attention for binocular disparity modulates responses of single MT neurons. The responses of a single neuron from correct trials during the task are shown aligned to the onset of stimulus motion (Fig. 2B, *left*) and to the time of the speed change (Fig. 2B, *right*). The spike density functions depict the neuron's response to the same unattended stimulus in its receptive field, which was a random dot patch moving in the neuron's preferred direction at its preferred binocular disparity. The differences between the traces can therefore be attributed to the animal's attention to the distant stimulus, which was presented in one of four possible combinations of the preferred and null directions and binocular disparities (color-coded *inset* in Fig. 2B).

The example neuron in Fig. 2B responded more when the animal attended to distant stimuli that most closely matched its tuning preferences. The neuron responded most strongly when the animal attended to the distant stimulus in which both features were presented at the neuron's preferred values and most weakly when both were null values. Intermediate levels of response occurred for the two preferred/null combinations: attending to a stimulus moving in the neuron's null direction at its preferred binocular disparity yielded only a slightly lower response than the preferred/preferred combination, and attending to a stimulus moving in the neuron's preferred direction at its null disparity yielded a much lower response than when attending to the preferred/preferred combination. Thus this neuron's firing rate was more strongly modulated by attention directed to a stimulus containing the preferred disparity compared with the null disparity than it was when the attended stimulus moved in the preferred relative to the null direction. These same data are shown aligned to the time of the speed change in Fig. 2B, where the same pattern of attentional effects is apparent. Feature attention indices for every neuron were calculated using spike counts during a 250-ms window prior to correct speed change detections. For the example neuron in Fig. 2B, the attentional index for binocular disparity was 0.086 and the attentional index for direction was 0.017. An ANOVA on the data revealed a significant main effect of attending to a stimulus that contained the preferred relative to the null binocular disparity ($P < 0.05$).

Figure 2, C–E, show the responses of three additional single neurons aligned to the time of the speed change to demonstrate the heterogeneity in the population. Figure 2C depicts a neuron that exhibits larger attentional modulation when attention is directed to a stimulus moving in the preferred relative to the null direction of motion than for the same difference for binocular disparity (feature attention for disparity index = 0.077; feature attention for direction index = 0.28; significant main effect of attention directed to the preferred relative to the null binocular disparity, $P < 0.05$). This was the most common pattern in the population. Figure 2D depicts a neuron with somewhat comparable feature-attention modulation for both direction of motion and binocular disparity (feature attention for disparity index = 0.018; feature attention for direction

index = 0.04; significant main effect of attention directed to both the preferred relative to null binocular disparity and direction of motion, both $P < 0.05$). Figure 2E shows an example neuron with positive attentional modulation directed to the preferred binocular disparity compared with the null but negative attentional modulation for attending to the preferred compared with the null direction of motion (feature attention for disparity index = 0.12; feature attention for direction index = −0.031; significant main effect of attention directed to the preferred relative to null direction of motion, $P < 0.05$). This example cell highlights the observation that the attentional effects for each feature could be of either sign.

Figure 3 depicts the distribution of attentional indices for attention directed to the preferred compared with the null binocular disparity (Fig. 3A) and for attention directed to the preferred compared with the null direction of motion (Fig. 3B) for all 207 neurons. Both distributions are significantly shifted to the right (binocular disparity attention index mean = 0.014, approximately a 3% modulation, Wilcoxon signed-rank test

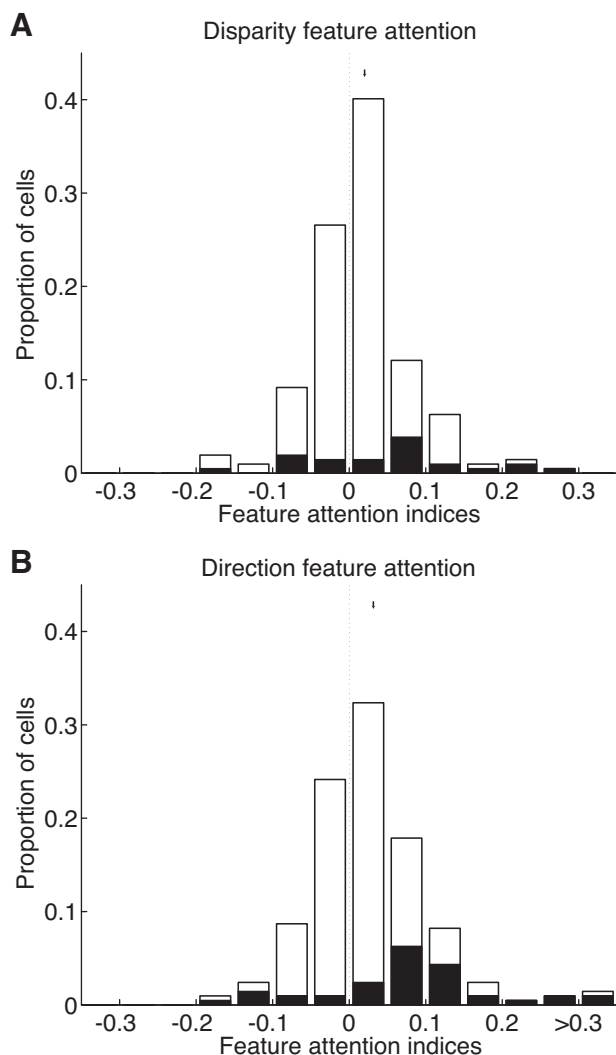**A** Disparity feature attention

B Direction feature attention

Fig. 3. Population feature-based attentional modulation for binocular disparity and direction of motion. Attention indices for each feature: binocular disparity (A), direction of motion (B). Arrow on each plot signifies the population mean; black portions signify significant cells as determined from Wilcoxon test. $n = 207$.

$P < 0.005$; direction of motion attention index mean = 0.026, approximately a 5% modulation, $P < 0.001$), demonstrating an increase, on average, in the firing rate of MT neurons as a function of attending to the preferred relative to the null value of each feature. The population's feature attention indices for direction are significantly larger than the indices for binocular disparity (Wilcoxon paired signed-rank test $P < 0.05$). The observation of feature attention effects for direction of motion in MT replicates previous work done by Treue and Martinez-Trujillo (Martinez-Trujillo and Treue 2004; Treue and Martinez-Trujillo 1999); feature attention effects for binocular disparity have not been previously described.

While the population average attention effects were highly significant, a minority of individual neurons exhibited significant feature attention effects. A 2×2 ANOVA on square root-transformed firing rates revealed a significant main effect of attention to direction in 57 neurons (28%) and to binocular disparity in 44 neurons (21%). Twelve neurons (5.8%) exhibited significant main effects for both features, which is what would be expected if the two effects occurred independently within our population of 207 neurons and only co-occurred by chance ($P > 0.05$, χ^2-test). Seventeen cells (8.2%) showed a significant interaction between attention to direction and binocular disparity.

How are attentional effects to multiple features combined? We created two models that attempted to determine whether the attentional effects observed in these data were best described as combining additively or multiplicatively. Both models attempted to predict a neuron's response during the condition when the animal attended to the stimulus that contained the null value of both features using the responses from the other three conditions. In one model, the effects of attention were combined multiplicatively; in the other model, the effects of attention were combined additively. Across the population, the model that combined attentional effects multiplicatively was significantly better than the additive model at predicting the response during the fourth condition (Wilcoxon paired signed-rank test of the prediction error from each model, $P < 0.001$). Despite this statistical significance, the absolute differences between the predictions of the two models were quite small. In fact, the difference between the two models' predictions was, on average, <1 spike in the 250-ms time window evaluated (median = 0.11, mean = 0.36). This small difference in the predictions of each model is due to the overall small size of feature attention effects observed in the population. Therefore, these results should be cautiously interpreted. Similar results were obtained when the models predicted the responses to the stimulus that contained the preferred value of each feature using the three remaining conditions. Treue and Martinez-Trujillo (1999) found, on average, that an additive model better explained how feature and spatial attention effects combine in MT neurons. While the differences in the prediction of our additive and multiplicative models are quite small, our results show that feature attention for binocular disparity combines with feature attention for direction of motion in a way that is slightly more consistent with a multiplicative model. However, further work will be required to more conclusively address this issue.

Interestingly, both models predicted the response during the null/null condition to be lower than was actually observed. The median prediction from the multiplicative model was 1.9

spikes lower than was observed, while the median prediction from the additive model was 2.1 spikes lower than the observed response. The population distributions of these small differences between the prediction and the observed data were significantly different from zero (Wilcoxon rank sum, $P <$ 0.01) and suggest that there may be a small nonlinear component when feature attention effects for different features are combined. Again, similar results were obtained if the models were designed to predict the responses to the stimulus that contained the preferred value of each feature using the three remaining conditions.

Does feature attention for binocular disparity support the feature-similarity gain model? Because the unattended stimulus in the receptive field moved in the neuron's preferred direction at its preferred binocular disparity, there are two potential explanations for the feature attention effects that were observed. The first is that the attentional modulation is the result of enhancement due to the fact that the attended and unattended stimuli are identical. This is called feature matching (FM), and this hypothesis suggests that a match between the features contained in the attended stimulus and the features of the unattended stimulus in the neuron's receptive field is important for feature attention (Motter 1994). The other potential explanation is that the unattended stimulus in the receptive field is irrelevant for feature attention and, instead, the relationship between the value of a feature of the attended stimulus and a neuron's tuning preference for that feature is critical for attentional modulation. This latter possibility is formalized in the FSG model (Martinez-Trujillo and Treue 2004; Maunsell and Treue 2006).

To test which of these hypotheses best explains the results for feature attention to binocular disparity, we performed a second experiment on 44 neurons (21 from *monkey N*) in which the stimulus in the MT neuron's receptive field could be presented at either the preferred or null value of its direction and binocular disparity tuning curves while the attended stimuli also were presented at either the preferred or null value. This allowed us to directly discriminate between the two hypotheses. If the FM model is correct, the response to a null stimulus in the receptive field should be enhanced when the animal attends to the corresponding null stimulus relative to when the animal attends to the preferred stimulus, whereas the predicted pattern is opposite under the FSG model.

Figure 4 shows the population attention indices when the null value of each feature was presented in the receptive field. Positive attentional indices mean that the important factor in feature-attention modulation is the relationship between the feature of the attended stimulus and the neuron's tuning preference for the feature (FSG model), whereas negative indices indicate that it is the match between the attended stimulus and the stimulus in the receptive field that is most important (FM model). While we observed individual neurons whose activity supports each model, the preponderance of the data supports the FSG model, with both population means shifted to the right. The mean feature attention index for binocular disparity (Fig. 4A) did not reach significance with this smaller sample (mean = 0.019, Wilcoxon signed-rank test $P < 0.3$) but was close to the value observed in the larger population (overall population mean = 0.014; see Fig. 3A). The mean feature attention index for direction of motion was significantly shifted to the right (mean = 0.15, Wilcoxon signed-rank test $P <$
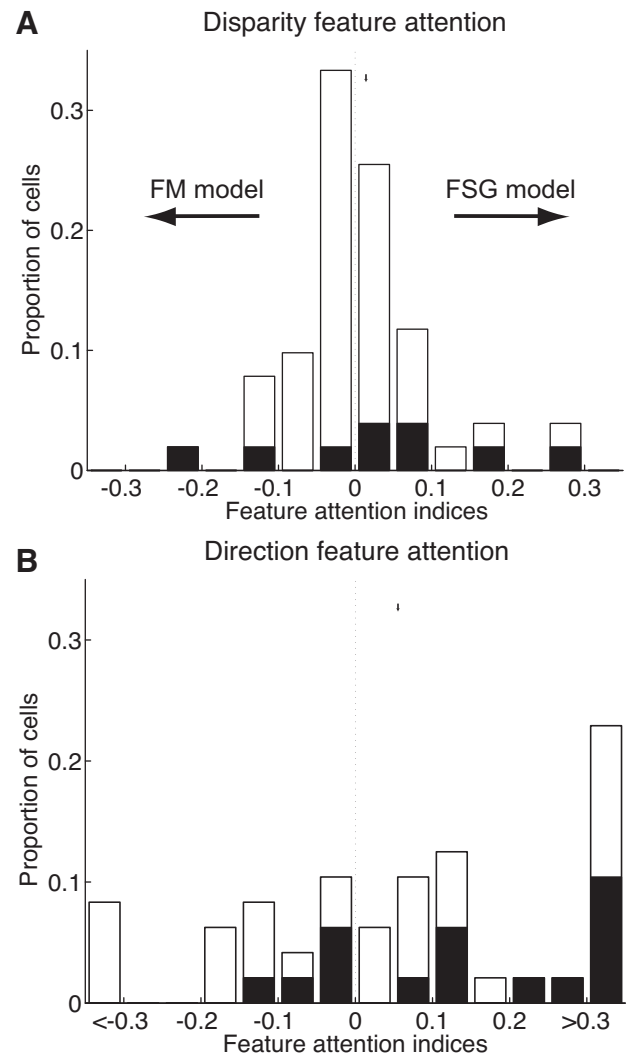

Fig. 4. Population attention indices testing the feature-similarity gain (FSG) model for feature-based attention for binocular disparity and direction of motion. Attention indices for each feature: binocular disparity (*A*) and direction of motion (*B*) calculated with the null value of each feature in the receptive field. Arrow on each plot signifies the population mean; black portions signify significant cells as determined from Wilcoxon test. A shift to the left would provide support for the feature matching (FM) model; a shift to the right would provide support for the FSG model. $n = 44$.

0.01). This mean is considerably larger than the value reported for the first experiment (overall population mean = 0.026; see Fig. 3B); however, this, along with the non-Gaussian shape of the distribution, was likely an effect of the low firing rates produced by a null direction stimulus in the receptive field. Because our index divides by the firing rate of the cell, small modulations on top of extremely low stimulus-driven firing rates can lead to relatively large index values (note several cells with very large attentional indices).

These results suggest that MT neurons exhibit feature attention effects for both features that are consistent with the FSG model (Martinez-Trujillo and Treue 2004). The results of this study extend the FSG model by demonstrating that feature attention effects can be found in neurons for multiple features including those to which they are not most strongly tuned (i.e., not just for direction of motion in MT). This conclusion is supported by studies demonstrating that neurons in V4 exhibit

task-related feature attention effects for orientation, spatial frequency, shape, and color (Bichot et al. 2005; Cohen and Maunsell 2011).

Feature attention and tuning strength. We hypothesized that because attentional modulation depends on a neuron's tuning preferences (its preferred and null direction and disparity), it should also be sensitive to its tuning strength (the differences in its responses to preferred and null stimuli). We found that MT neurons are more strongly tuned for direction than they are for binocular disparity, as has been previously reported (DeAngelis and Uka 2003) (Fig. 5, *A* and *B*). In addition to neurons being more strongly tuned for direction than for binocular disparity, there was also considerably larger variance for binocular disparity tuning. This greater range of tuning strengths allowed us to test for a relationship between the

A Disparity tuning strength

B Direction tuning strength

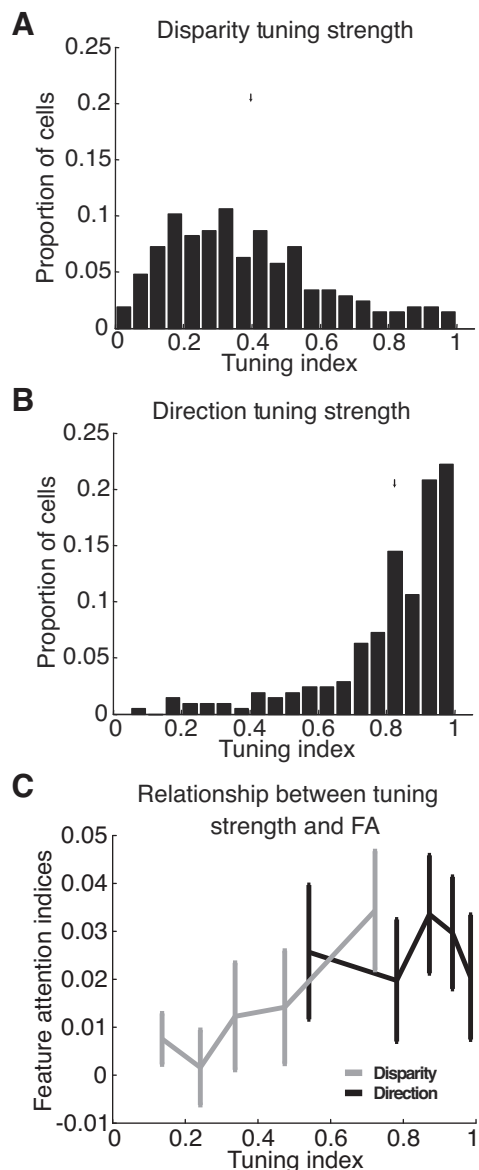**C** Relationship between tuning strength and FA

Fig. 5. Relationship between tuning strength and feature attention. *A*: population binocular disparity tuning strength. *B*: population direction tuning strength. Arrows signify population means. *C*: relationship between tuning strength (binned by quintiles of tuning strength) and feature attention (FA) for both binocular disparity (gray line) and direction (black line). Each quintile is plotted at the median tuning strength value for its respective bin.

strength of tuning for a feature and the amount of observed feature-attention modulation. All of the cells included in our analyses had statistically significant differences ($P < 0.05$) in firing rate between the preferred and null values of each feature, as determined during quantitative tuning data at the beginning of each recording session (see METHODS). The tuning strengths of each neuron, as measured by a tuning modulation index [(Pref − Null)/(Pref + Null)], for both binocular disparity and direction, are shown in Fig. 5, *A* and *B* (binocular disparity mean index = 0.38; direction mean index = 0.81). As a point of reference, with a different modulation index that incorporates spontaneous firing rate [(Pref − Null)/(Pref − Spontaneous)], our population mean for binocular disparity was 0.61, which is lower than the 0.73 measured by DeAngelis and Uka (2003).

Figure 5*C* shows the feature attention values for each neuron plotted against their tuning modulation index for both binocular disparity and direction. The data are binned into quintiles as determined by the population's tuning strength for each feature. As tuning strength increases, feature attention effects in the population tend to be larger. The cells from the largest bin of binocular disparity tuning strength exhibited significantly larger feature-attention modulation for binocular disparity than did neurons in each of the two most weakly tuned bins (Wilcoxon rank sum test $P < 0.05$ for each). There were insufficient numbers of weakly direction-tuned cells in the population to reveal a similar relationship for direction of motion. Interestingly, despite there being overall larger feature attention effects for direction than for binocular disparity, these differences disappeared when we compared bins with overlapping tuning strength. These results suggest that the difference between the feature attention effects for the two features in our data can be attributed to the differences in tuning strength for the respective features. Importantly, variability in cognitive factors such as arousal and motivation across days, which were undoubtedly present in our experiments, make it more difficult to identify this relationship between attentional modulation and tuning strength. Thus we believe that the relationship we have measured represents a lower bound on the true effect of tuning strength.

The relationship between tuning strength and feature attention is not an artifact of the binning procedure, as a significant correlation was observed for the relationship between tuning strength and binocular disparity (Spearman correlation $\rho = 0.18$, $P < 0.01$; 95% confidence interval 0.036–0.31). The relationship between feature attention for direction of motion and tuning strength was not significant (Spearman correlation $\rho = 0.021$, $P = 0.76$), but the observed range of tuning strengths for direction of motion was much smaller (Fig. 5, *B* and *C*).

With this relationship between tuning strength and feature attention in mind, the binocular disparity data presented in Fig. 4 were revisited. Using just the neurons with binocular disparity tuning indices > 0.5 (only 10 neurons in our population) the mean for binocular disparity was tested to determine whether these more selective neurons alone displayed feature attention effects consistent with the FSG model. The mean feature attention values for binocular disparity in this subset of neurons were significantly shifted to the right and thus also support the FSG model (disparity mean = 0.085, Wilcoxon signed-rank test $P < 0.05$).

Can sensory factors be disguised as attention? Although we took care to position the attended stimulus far away from the receptive field of the MT neuron under study (see METHODS), the modulatory surrounds of MT neurons can extend for some distance and have been shown to include parts of the ipsilateral hemifield for some neurons (Albright and Desimone 1987; Desimone and Ungerleider 1986; Maunsell and Van Essen 1987). In such cases, it is conceivable that the attended stimulus engaged the MT neuron's surround and produced the changes that were observed in a bottom-up manner and not via top-down modulation as has been proposed. When isolating neurons for the present study, we placed moving dot stimuli at the attended stimulus location while the animal fixated to ensure that the second stimulus would not directly elicit visually driven spikes. Furthermore, we collected separate data (for 199 of 207 neurons) in which both stimuli were repeatedly flashed on and off for 250 ms in all of the configurations used during the main experiment, while the animal was rewarded for simply fixating. Because each stimulus was presented very briefly, there was insufficient time for the animal to change its focus of attention, and thus these control experiments should isolate any purely visual modulation due to the second stimulus.

We calculated mock attention indices using the data collected during the rapid presentation of these stimuli by comparing responses when different stimuli were positioned outside the neuron's receptive field. These indices reflect the influence of the different stimuli outside the receptive field on the neurons' firing rates. These mock attention indices were much smaller than the attention indices we calculated during the change detection task (binocular disparity mean = 0.0051, Wilcoxon signed-rank test $P = 0.45$; direction mean = -0.00039, $P = 0.13$), indicating that the attention effects observed during the task were not the result of direct stimulation. In addition, we performed an ANOVA for each individual neuron. Only 15 neurons had a significant main effect of having the second stimulus at the preferred versus null binocular disparity, 7 of which had a positive effect and 8 a negative effect. Thirty neurons had a significant main effect of the second stimulus moving in the preferred versus null direction, 12 of which had a positive effect and 18 a negative effect. A total of 4 neurons had a significant main effect for binocular disparity during both the control experiment and the main attentional task (1 positive, 3 negative), while 11 neurons had a significant main effect for direction of motion during both the control experiment and the main attentional task (6 positive, 5 negative). Excluding cells with a significant main effect from both this control experiment and the task before calculating population feature attention indices resulted in population mean values similar to those reported for the entire data set (binocular disparity index mean = 0.0135, Wilcoxon signed-rank test $P < 0.005$; direction index mean = 0.0231, $P < 0.0001$). Excluding all neurons with a significant main effect during the control experiment from the main task data resulted also in mean population feature attention values that were nearly identical to those reported for the entire population (binocular disparity index mean = 0.0131, Wilcoxon signed-rank test $P < 0.005$; direction index mean = 0.0231, $P < 0.0001$).

These data show that the presence of the distant attended stimulus may have led to direct stimulus effects in a small number of neurons in the population but that it cannot account for the feature attention effects observed for either binocular disparity or direction of motion. The other results presented in this report do not change significantly if any of the subsets of cells highlighted by these data are excluded.

Possible artifacts. A potential concern about the interpretation of these results is that either the attention effects or the tuning strength indices may depend on a neuron's firing rate. To address this possibility, we tested the relationship between observed firing rates and these measures. The absolute firing rates of MT neurons during the task were not correlated with the feature attention effects that were observed for either feature (binocular disparity, Spearman $\rho = -0.1$, $P = 0.15$; direction, $\rho = 0.01$, $P = 0.89$; data not shown). Additionally, tuning strength indices were not significantly related to overall firing rate (binocular disparity, Spearman $\rho = -0.02$, $P = 0.77$; direction, $\rho = 0.029$, $P = 0.68$; data not shown), suggesting that the firing rate of MT neurons was not a critical factor in the effects described in this study.

DISCUSSION

We measured how the effects of feature attention on MT neurons depend on the match between the features of an attended visual stimulus and the neuron's tuning for those features. We manipulated the binocular disparity and direction of motion of a distant attended stimulus while monkeys performed a speed change detection task that required attention to the distant stimulus. We found that the relationship between the binocular disparity of the attended stimulus and the tuning of an MT neuron led to changes in the firing rate of the neuron in a way that is similar to the effect previously described for direction of motion (Treue and Martinez-Trujillo 1999). Furthermore, the magnitude of feature-attention modulation for binocular disparity depended both on the neuron's tuning preferences and on its tuning strength. We also found that the modulation in MT did not require an explicit perceptual judgment about the feature of interest and that feature attention effects in MT did not result from bottom-up stimulus drive. Our results suggest that modulation by feature attention depends not only on which features a neuron represents but also on how well the neuron represents the features of an attended stimulus, thus revealing previously unknown specificity of feature-attention modulation.

What Constitutes a "Feature"?

Thus far we have treated binocular disparity as a "feature" to which MT neurons are tuned, similar to other features thought to be explicitly represented in visual cortex, such as color or orientation. But binocular disparity is a critical cue to depth, which is the third spatial dimension, so one might wonder whether we have really been studying a form of spatial attention (He and Nakayama 1995). However, it is important to note that we did not assess effects within the restricted three-dimensional volume that was the animals' spatial locus of attention for the speed change task—something that would be necessary in order to interpret the results as due to spatial attention.

In fact, our results for binocular disparity support a more general idea of attention, captured by the FSG model, in which attentional modulation reflects similarity between any feature

of an attended stimulus and any matching feature for which a neuron is selective, with "space" being considered as just another feature (Patzwahl and Treue 2009). From this perspective, the distinction between spatial and feature-based attention is largely a semantic one. However, it is still important to note that, by positioning the attended stimulus a large distance ($>15°$) from the recorded neuron's receptive field, we rendered a spatial interpretation of our results highly unlikely. It is possible that had we required the animals to attend to different depth planes within the recorded neuron's receptive field we would also have revealed a spatial component of attention in depth. While we believe our results are better explained in the framework of feature attention, it is worth noting that we cannot rule out the possibility of surface-based attention contributing to our results (Treue and Katzner 2007; Wannig et al. 2007).

The fact that we were able to demonstrate a spatially remote form of attention to binocular disparity is particularly interesting, because it suggests that what matters most is the nature of the cortical organization and corresponding connectivity underlying the representation of a given feature. Whereas two-dimensional retinotopy is a feature of most early cortical visual areas, including MT, we find that the third dimension—at least in MT—is represented more like other nonspatial features, as a system of distributed columns (DeAngelis and Newsome 1999), similar to the representation of direction of motion (Albright et al. 1984). This sort of distributed columnar organization may be a necessary condition for feature attention (Maunsell and Treue 2006), as it would potentially facilitate "like-to-like" long-range connectivity (Bosking et al. 1997; Smolyanskaya et al. 2013) to produce the spread of attentional enhancement across visual space that is the hallmark of feature attention (McAdams and Maunsell 2000; Treue and Martinez-Trujillo 1999). Similarly, dense, nonspecific local connectivity within retinotopic maps may be the necessary anatomical correlate of spatial attention (Maunsell and Treue 2006). Thus the nature of cortical maps and the rules of local and long-range connectivity within these maps may set the limits by which top-down projections can influence the neuronal activity responsible for attentional improvements in perception. It remains unknown whether the capacity of feature attention to affect behavior, or alter neuronal firing rates, is limited to features that are represented in an organized fashion in cortex.

Feature Attention Effects Are Not Necessarily Task Related

Our results demonstrate that the responses of sensory neurons can be modulated by attention to features that are unrelated to the behavioral task. The monkeys in the present study performed a speed change detection task on stimuli whose direction of motion and binocular disparity changed from trial to trial. The binocular disparity of the stimulus was clearly irrelevant for the task, yet feature attention effects for binocular disparity were still observed. This is consistent with previous studies in which feature attention effects were observed for direction of motion regardless of whether the animals performed a direction change or a speed change detection task (Martinez-Trujillo and Treue 2004; Treue and Martinez-Trujillo 1999) and with the finding that similar amounts of feature-attention modulation for direction of motion were observed in MT when animals switched between a color change and a

direction change detection task (Katzner et al. 2009) However, other studies have found explicitly task-related feature attention effects on either the firing rates or correlation structure of sensory neurons (Cohen and Maunsell 2011; Cohen and Newsome 2008; Mirabella et al. 2007) or effects specifically related to visual search (Bichot et al. 2005; Zhou and Desimone 2011). Additionally, visual search tasks have led to observations that better support the FM model rather than the FSG model (Zhou and Desimone 2011). These results suggest that distinct task demands such as those required by a visual search task compared with those required by a discrimination or detection task (which requires sustained covert attention) may require distinct mechanisms for creating feature attention effects in cortex (Martinez-Trujillo 2011). Further work will be required to more fully characterize the ways in which feature attention interacts with task demands.

Feature Attention Depends on Tuning Strength

A relationship between the magnitude of feature attention effects and tuning strength for binocular disparity was found (see Fig. 5C). The formulation of the FSG model was based on observations about the relationship between an attended stimulus and a neuron's tuning curve: attention to a feature that matches the preferred stimulus produces a gain increase, whereas attention to a null feature produces a gain decrease. This two-way modulation has the net effect of sharpening the tuning of a given neuronal population for the feature of an attended stimulus, thus possibly accounting for improvements in sensory discrimination produced by attention (Martinez-Trujillo and Treue 2004; Maunsell and Treue 2006). Such an effect on the selectivity of neuronal populations would be further enhanced if the attentional gain changes were greatest for the neurons with the strongest tuning, and this is precisely the relationship that we have demonstrated.

Such a relationship is reminiscent of the well-established association between neurometric reliability and choice probability that has been found in numerous behavioral tasks (Britten et al. 1996; Celebrini and Newsome 1994; Cook and Maunsell 2002; Law and Gold 2008; Price and Born 2010; Purushothaman and Bradley 2005; Shadlen et al. 1996; Uka and DeAngelis 2004). This means that the neurons that most reliably represent a behaviorally relevant stimulus are the same neurons whose activity best predicts behavioral performance on judgments about that stimulus. Such a relationship can be accounted for by a reinforcement learning model (Law and Gold 2009), which produces shared connectivity between the most sensitive neurons. It is possible that these shared connections are also related to the mechanism underlying feature attention (Nienborg and Cumming 2010).

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

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