

# Feature-Based Attention Increases the Selectivity of Population Responses in Primate Visual Cortex

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## Summary

**Background:** Attending to the spatial location or to non-spatial features of visual stimuli can modulate neuronal responses in primate visual cortex. The modulation by spatial attention changes the gain of sensory neurons and strengthens the representation of attended locations without changing neuronal selectivities such as directionality, i.e., the ratio of responses to preferred and anti-preferred directions of motion. Whether feature-based attention acts in a similar manner is unknown.

**Results:** To clarify this issue, we recorded the responses of 135 direction-selective neurons in the middle temporal area (MT) of two macaques to an unattended moving random dot pattern (the distractor) positioned inside a neuron's receptive field while the animals attended to a second moving pattern positioned in the opposite hemifield. Responses to different directions of the distractor were modulated by the same factor (approximately 12%) as long as the attended direction remained unchanged. On the other hand, systematically changing the attended direction from a neuron's preferred to its anti-preferred direction caused a systematic change of the attentional modulation from an enhancement to a suppression, increasing directionality by about 20%.

**Conclusions:** The results show that (1) feature-based attention exerts a multiplicative modulation upon neuronal responses and that the strength of this modulation depends on the similarity between the attended feature and the cell's preferred feature, in line with the feature-similarity gain model, and (2) at the level of the neuronal population, feature-based attention increases the selectivity for attended features by increasing the responses of neurons preferring this feature value while decreasing responses of neurons tuned to the opposite feature value.

## Introduction

Directing attention to a particular location in the visual field modulates neuronal responses in primate visual cortex [1–3]. Although the magnitude of this space-

based attentional effect changes with stimulus contrast [4–5], it is a multiplicative modulation that preserves the shape of a neuron's tuning curve [2–3]. Recently, we have demonstrated a non-spatial, feature-based attentional modulation of neuronal responses in direction-selective cells of the macaque cortical middle temporal (MT) area [2]. The magnitude of neuronal responses to an unattended stimulus (the distractor) located inside the cells' receptive field (RF) and moving in the cells' preferred direction was dependent on the direction of an attended stimulus (the target) even though the target stimulus was located outside the RF. When attention was directed toward a target moving in the preferred direction, responses were higher than when it was directed to the anti-preferred direction. This finding led to the proposal of a feature-similarity gain model in which attention changes responses in a multiplicative fashion, with the sign and strength of the modulation reflecting the similarity between the attended stimulus feature and the neuron's preferred feature [2]. (We use the term "feature" to denote a particular value of a stimulus dimension. For example, two motion directions represent two different features).

Although this model provides a good description of the known properties of feature-based attentional modulation of single-cell responses, two of its main predictions remain untested. The first one is that the feature-based modulation of responses is multiplicative, i.e., the response of a given neuron to different features (e.g., different motion directions in the RF) should be multiplied by the same factor when attention switches between two features (e.g., two different target directions). The second is that the magnitude of the attentional modulation is a function of the similarity between the attended feature and a cell's preferred feature, i.e., when an individual attends to a particular feature, the amount of response modulation across individual neurons should vary depending on the similarity between the attended feature and the cell's preferred feature. On the other hand, response modulation should depend neither on the properties of the stimulus to which the cell is responding nor on the similarity between this stimulus and the current target (feature-matching hypothesis).

Our previous data cannot rule out a feature-matching process, which receives support from a recording study by Motter in macaque cortical area V4 [6]. He reported that responses of color- and orientation-selective neurons to a stimulus feature increased when this feature matched the attended stimulus feature. This effect does not follow the predictions of the feature-similarity gain hypothesis because the critical factor determining the attentional modulation in Motter's experiments is the match between the attended feature and the feature of the stimulus to which the cell is responding, independently of the similarity between the attended and the cell's preferred feature. It should be noted, though, that a "non-match suppression" has to be postulated as part of the feature-matching hypothesis to provide an

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explanation for the suppression of responses observed if the animal attends to an anti-preferred stimulus inside the receptive field [2].

Here we report that attention scales responses to different stimulus features (directions) by the same factor as long as the attended stimulus feature remains unchanged. This modulation is independent of the relationship between the stimulus feature to which the cell is responding and the attended feature (feature-matching); rather, it is determined by the similarity between target direction and the cell's preferred direction (feature-similarity). Secondly, when the attended feature (e.g., the target's direction) is varied, the response modulation changes smoothly from a response increase when attention is directed to the neuron's preferred feature toward a response decrease when attention is directed to the neuron's anti-preferred feature. These results are in agreement with the feature-similarity gain model predictions and suggest that a multiplicative attentional modulation at the level of individual neurons—differentially tuned for the attended stimulus feature—can result in nonmultiplicative changes in the activity profiles of neuronal populations. The overall effect of these changes is an improvement in the selectivity of the population for attended features, which creates an enhanced signal-to-noise ratio for attended features that has not been seen with the traditional designs for determining response modulation by spatial attention.

## Results

Our experiments were aimed at (1) determining whether feature-based attention has a multiplicative effect on neuronal responses in area MT of macaques, (2) determining whether the feature-based attentional modulation of responses in area MT depends on the similarity between the attended feature and the neuron's preferred feature (feature-similarity gain model), and (3) determining whether the feature-based attentional modulation in area MT improves the selectivity of the population response to the attended stimulus features.

### Feature-Similarity Gain versus Feature-Matching and Multiplicative Effects of Attention

We recorded the responses of 135 direction-selective neurons in area MT of two macaque monkeys to a random dot pattern (RDP) moving in the cells' preferred or anti-preferred direction inside the RF (the distractor) while attention was directed to a second RDP positioned outside the cells' RF, in the opposite hemifield. This attended RDP (the target) could move either in the same (attend-same) or opposite (attend-opposite) direction to the distractor. This design allowed us to determine whether responses to a given direction of motion inside the RF were increased when an individual attended to the *same* direction outside the RF (as predicted by the feature-matching hypothesis) or if responses were increased whenever the individual attended to the *preferred* direction outside the RF (as predicted by the feature-similarity gain hypothesis) (see Figure 1A). Additionally, the design allowed us to determine whether feature-based attention has a multiplicative effect. Multi-

plicative modulation would scale responses to both the preferred and the anti-preferred direction inside the RF by the same factor when attention switched between two directions outside the RF.

Figure 2 plots the results for one MT neuron. Panels A and B show spike density functions (SDF) for the responses to the distractor pattern located inside the RF moving in the preferred (A) and anti-preferred (B) directions in the attend-same (gray SDFs) and the attend-opposite (black SDFs) conditions. Whereas in panel 2A the stronger responses in the attend-same condition (gray SDF) could reflect either feature-matching effects (i.e., the matching directions of the two patterns) or feature-similarity effects (i.e., the allocation of attention to the neuron's preferred direction), in panel 2B the higher responses in the attend-opposite condition (black SDF) can only be accounted for by the feature-similarity model. Note that this cell shows an excitatory response even to the anti-preferred direction during the attend-fixation condition (the dashed lines in Figures 2A and 2B indicate the cell's background activity, i.e., the response in the absence of a stimulus inside the receptive field and the gray arrow along the ordinate indicates the average attend-fixation response to the anti-preferred direction).

Figures 2C and 2D plot the average firing rates from panels A and B, with lines connecting data points from preferred (open circles) and anti-preferred (filled squares) motion inside the RF, respectively. Panel 2C plots the data according to the relationship between the distractor and target directions (i.e., attend-same versus attend-opposite) and thus according to the feature-matching hypothesis. Panel 2D is arranged according to the attended direction (i.e., attend-preferred versus attend-anti-preferred) and thus according to the predictions of the feature-similarity account. In each panel the corresponding hypothesis would predict higher responses in the left data point of each pair. Instead, in panel 2C the modulation ratios (see Experimental Procedures) between the attend-same and attend-opposite conditions (displayed on the right ordinate) were unequal (1.32 for the preferred (open circle) and 0.73 for the anti-preferred direction (filled square)). This result is incompatible with the feature-matching predictions (dashed line). On the other hand, the data shown in Figure 2D match the predictions of the feature-similarity hypothesis. Responses to both directions were higher when individuals attended to the preferred rather than to the anti-preferred direction. Furthermore, the attentional modulation ratios between the attend-preferred and attend-anti-preferred conditions (right ordinate) for both the preferred (open circle) and anti-preferred (filled square) directions were very similar (1.32 and 1.36, respectively; points are plotted along the right ordinate). This example suggests that when attention switches from the anti-preferred to the preferred target direction, responses to the two different directions of the distractor (preferred and anti-preferred) were enhanced by the same factor (multiplicative modulation).

The same analysis was performed for all recorded neurons. Attentional modulation ratios between the different attentional conditions for both stimulus conditions, i.e., with the preferred and anti-preferred direc-

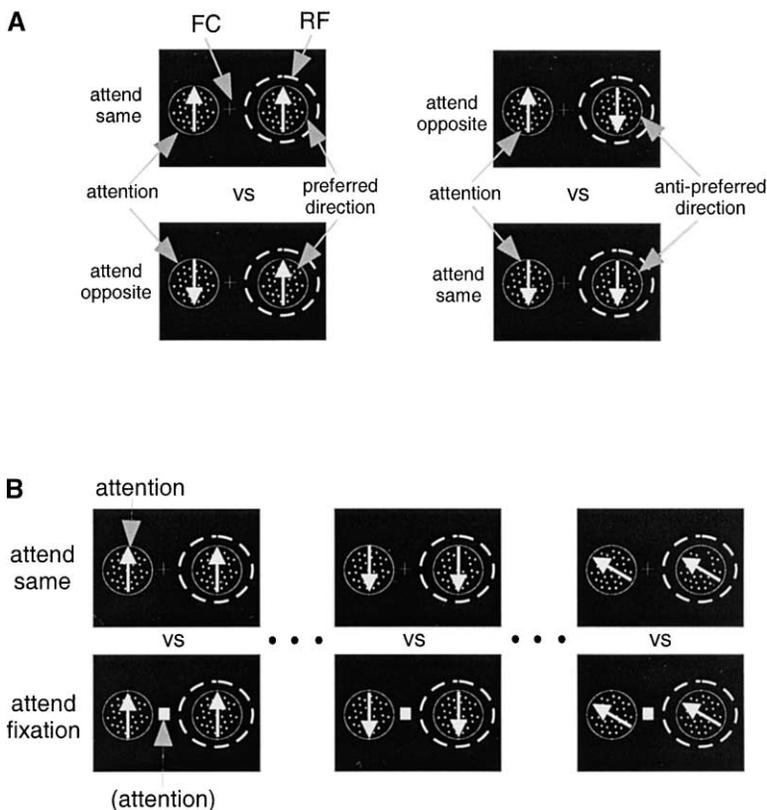


Figure 1. Experimental Design

(A) Experiment 1: the panels in the two columns represent the two attentional conditions (attend-same and attend-opposite) for the two motion directions (preferred and anti-preferred) of the RDP shown inside the RF. The arrows indicate the directions of the dots. RF: receptive field, FC: fixation cross. (B) Experiment 2: the top panels represent the conditions in which the monkey attended to the same motion direction presented inside the RF (attend-same). The bottom panels represent the condition in which the animals ignored both stimuli and attended to a color square on the fixation point (attend-fixation). The allocation of attention and the different comparisons are indicated. The black dots indicate that similar conditions existed for directions in between.

tions inside the RF, were calculated and then averaged across units so that average modulation ratios were obtained for the entire sample. Figure 3A shows the ratios, which exhibit the same pattern as the example cell in Figure 2. Both attentional hypotheses predict the ratio computed at the left of the panel to be more than 1 (open circle,  $p < 0.05$ , paired t test; average response ratio: 1.12). The pattern of the two ratios on the right is consistent only with the feature-similarity hypothesis; it indicates an enhancement only for attention to the preferred direction (open square,  $p < 0.05$ , paired t test; average response ratio: 1.13), not for attention to the same direction (filled square,  $p < 0.05$  paired t test; average response ratio: 0.87).

Moreover, the modulation ratios between the attend-preferred and the attend-anti-preferred conditions for both the preferred and the anti-preferred directions were not different from each other (1.12 versus 1.13, respectively;  $p = 0.7$ , paired t test). This represents a similar multiplicative modulation of responses to both distractor directions when attention switches between anti-preferred and preferred target directions.

The modulation ratios plotted in Figure 3A are averages across cells, including those (such as the example in Figure 2) that show an enhanced response even to the anti-preferred-direction as well as those that are suppressed by the appearance of the anti-preferred-direction. It is conceivable that, rather than modulating a cortical neuron's overall response (which can only be positive), attentional modulation influences those response components (inhibitory or excitatory) that cause the cell's response to change from its baseline firing

rate. If this is the case, the feature-matching hypothesis might be able to account for the reduced response when two anti-preferred-stimuli were present in our experiments by suggesting that this reflects an increased inhibition. Note that the modulation observed in the example cell in Figure 2 cannot be accounted for in this way because that cell shows an enhanced response even to the anti-preferred direction presented during the attend-fixation condition (gray arrow on the ordinate of all the panels in Figure 2). Nevertheless, the population data in Figure 3A might reflect the contribution of the proportion of cells that were suppressed by the anti-preferred direction in the receptive field in our sample.

We therefore repeated the analysis shown in Figures 2C and 3A in a subset of 13 of our neurons whose sensory responses to the anti-preferred direction inside their RFs (gray arrow in the ordinate of Figure 3B) were higher than their baseline responses (dashed line in Figure 3B), i.e., by removing the suppressed cells. The average responses in the attend-same (circles) and attend-opposite (squares) conditions are illustrated in panel 3B. The responses for each neuron were normalized to the response to the preferred direction in the attend-same condition and then averaged across neurons. Matching the result depicted in Figure 2C, responses to the anti-preferred direction were lower in the "attend-same" condition relative to the "attend-opposite" condition (filled square), whereas responses to the preferred direction showed the reversed pattern (open circle). In agreement with the predictions of the feature-similarity gain model, the respective ratios, plotted in Figure 3C, were essentially the same as those for the complete data set (Figure

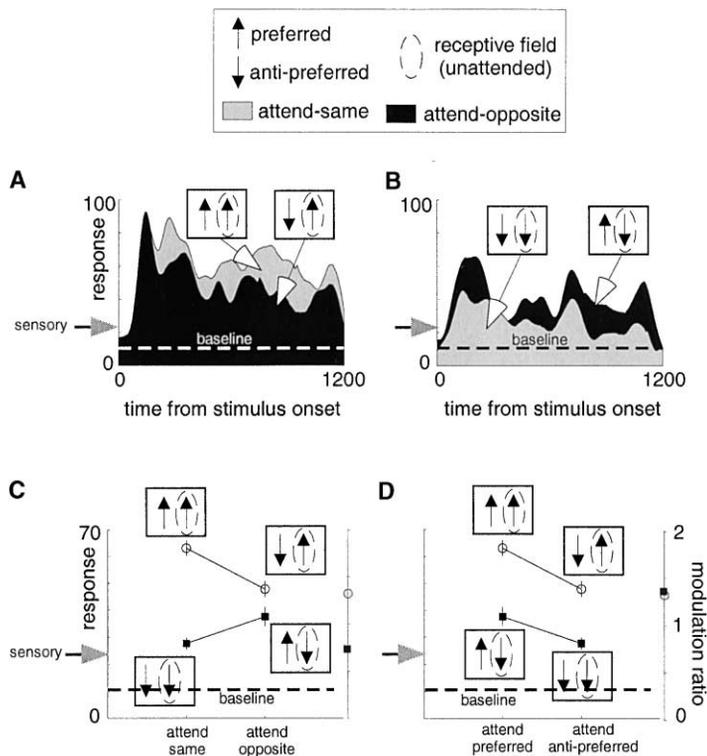


Figure 2. Experiment 1. Example Neuron (A and B) Spike density functions (SDF, obtained by convolving of each spike with a Gauss function [sigma: 30 ms]) for the responses to the preferred (A) and anti-preferred (B) directions of one MT neuron. The abscissa represents time from stimulus onset, and the ordinate represents the response. The gray area represents the attend-same condition, and the black area represents the attend-opposite condition. The symbols indicate the stimulus configuration for each condition. The gray arrow on the ordinate indicates the average “sensory” response of the neuron (determined from the attend-fixation condition) to the anti-preferred direction, and the dashed line represents the baseline response (i.e., the response without a stimulus inside the RF). (C) Average responses of the same neuron to the preferred (open circles) and anti-preferred (filled squares) directions in the attend-same and attend-opposite conditions. The abscissa represents the magnitude of neuronal responses, and the ordinate on the right displays the values of the modulation ratio between the responses in the two attentional conditions for the preferred (open circle) and anti-preferred (filled square) directions in the receptive field, respectively. The feature-matching hypothesis would predict

both solid lines to show a downward slope from left to right. The symbols are the same as in (A) and (B). (D) The same data as in (C), but note that the conditions are grouped such that the feature-similarity gain hypothesis would predict both solid lines to show a downward slope from left to right. The two points plotted on the secondary ordinate of panels (C) and (D) indicate the ratios between the responses of the data connected by solid lines (this analysis is repeated in Figure 3 for the populations of cells). The similarity of the two ratios in panel (D), but not (C), support the feature-similarity hypothesis.

3A). Even though the attentional modulation with the anti-preferred direction inside the RF failed to reach statistical significance ( $p = 0.2$ , Wilcoxon test) because of the low firing rates and the small sample size, the highly significant difference between the two ratios computed according to the feature-matching hypothesis (empty circle and filled square,  $p < 0.001$ , Wilcoxon test) and the similarity of the feature-similarity ratios (empty circle and empty square,  $p = 0.5$ , Wilcoxon test) mirror the behavior of the complete data set and match the predictions of the feature-similarity hypothesis.

### Determining the Gain of Feature-Similarity Effects in Individual Neurons

The previous experiment demonstrated that responses of MT neurons tended to be higher when the monkey attended to motion in a cell’s preferred direction versus the anti-preferred direction. We have previously suggested that this modulation is a combination of an enhancement of sensory responses when attention is directed to the cells’ preferred direction and a suppression of sensory responses when attention is directed to the cells’ anti-preferred direction [2]. The feature-similarity gain model generalizes this finding across directions and predicts that, for a given neuron, the strength of the attentional modulation is a monotonic function of the angle between the attended direction and the cell’s preferred direction.

To test this prediction, we measured the responses

of the same 135 MT units to twelve different motion directions in the attend-same condition of the previous experiment, i.e., when attention was directed to the target outside the RF and the distractor moved in the same direction as the target. These responses were compared to a neutral condition in which the animals responded to a luminance change in a small color square centered on the fixation point (attend-fixation; see Figure 1B and Experimental Procedures).

Figure 4A shows the responses of one MT cell preferring upward motion. The modulation between the two conditions changed monotonically from an enhancement of the neutral (‘attend-fixation’) response when individuals attended to directions close to the preferred one (light-gray shaded area) to a suppression when they attended to directions close to the anti-preferred one (dark-gray shaded area). The direction index (ratio of responses to the preferred direction versus responses to the anti-preferred direction) increased from 5.3 in the neutral condition to 12.5 in the attend-same condition, representing a very large increase in selectivity by feature-based attention.

Figure 4B shows the response modulation ratios as a function of the absolute angular distance between the attended direction and the preferred direction. A linear fit through the data with a significant negative slope ( $p < 0.05$ , t test) and a linear correlation coefficient of  $-0.95$  show a monotonic inverse relationship between the angular distance and the response modulation, i.e., the

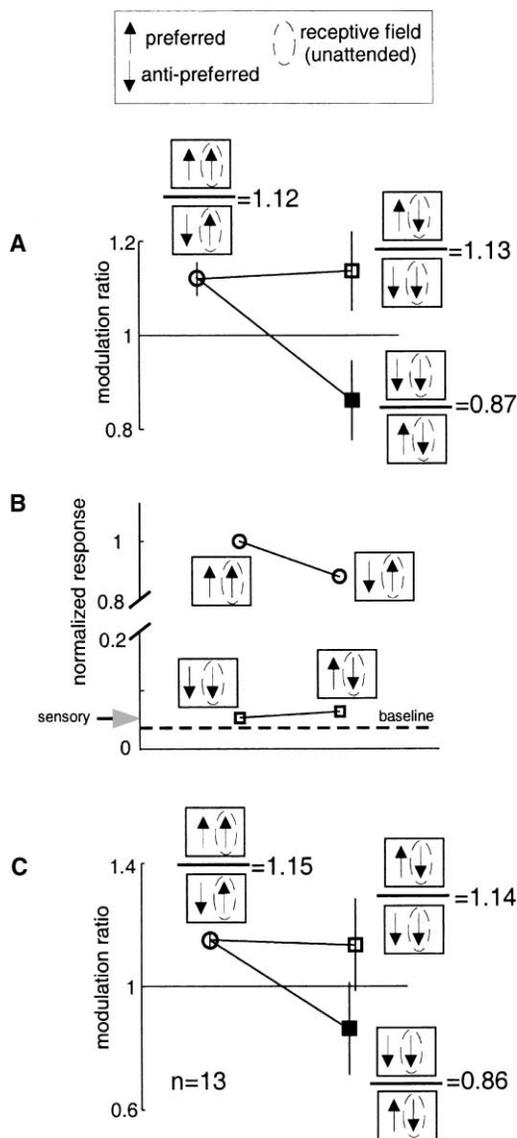


Figure 3. Experiment 1. Population Data

(A) Average modulation ratios between the different conditions for the responses to the preferred and anti-preferred directions for the sample of 135 MT neurons. The circle represents the ratio for the responses to the preferred, the squares for the responses to the anti-preferred direction. The abscissa represents the attentional condition and the ordinate the modulation ratios. The error bars represent the 95% confidence intervals for the mean. The symbols are the same as in Figure 2. The ratios attend-same/attend-opposite corresponding to the responses to the preferred (open circle) and anti-preferred (filled square) are significantly different from each other ( $p < 0.001$ , Wilcoxon test). The ratios attend-preferred/attend-anti-preferred for the responses to the preferred (open circle) and anti-preferred (open square) directions do not differ significantly ( $p > 0.9$ , Wilcoxon test).

(B) Average normalized responses to the anti-preferred and preferred direction across the population of neurons, with sensory (attend-fixation) responses to the anti-preferred direction (gray arrow on the ordinate) being higher than the baseline response (dashed line), plotted as in Figure 2C.

(C) Average modulation for the data in (B) plotted as in (A). See text for details.

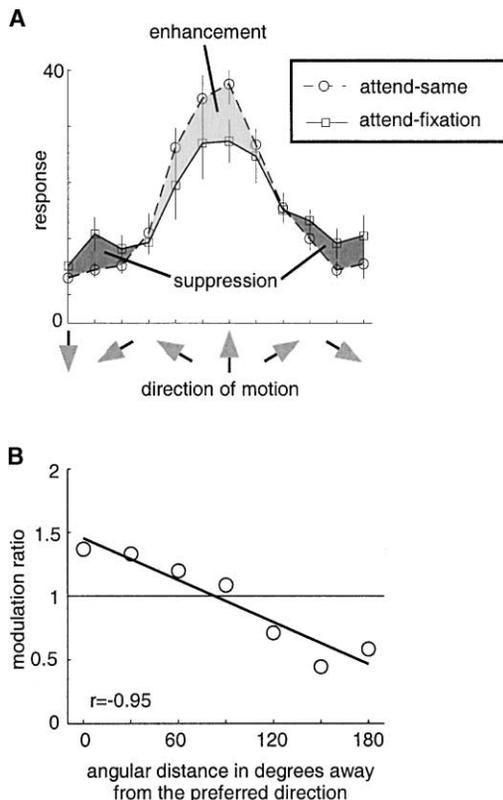


Figure 4. Experiment 2. Example Neuron

(A) The average firing rate of an MT neuron (ordinate) in the attend-same (open circles and dashed line) and attend-fixation (open squares and solid line) conditions was plotted as a function of the direction of the pattern inside the RF (abscissa). The error bars represent standard errors. The light-gray shaded area between the two curves represents the region of response enhancement, and the dark-gray shaded area represents the area of response inhibition. (B) Modulation ratios between the responses in the two conditions shown in (A) (open circles). The abscissa represents the angular distance between the direction of the RDPs and the cells' preferred direction, and the ordinate represents the modulation ratio. Note that the 12 directions tested were collapsed into seven data points because directions that were angled clockwise and counterclockwise by the same angular distance from the preferred direction have been pooled and averaged. The line represents the best linear model fitted to the data (intercept:  $1.45 \pm 0.18$ , slope:  $-0.0054 \pm 0.0016$ ). The linear correlation coefficient ( $r = -0.95$ ) is indicated.

attentional modulation of the neutral responses is a monotonic function of the similarity between the attended direction and the cell's preferred direction.

The same analysis was repeated for every neuron. For each of the seven angular difference values, we averaged the modulation ratios across neurons to obtain an average ratio for every direction. Figure 5 shows that, just like for the individual cell in Figure 4B, the slope of the linear fit through the data points is significantly lower than zero ( $p < 0.05$ , t test). The correlation coefficient ( $-0.93$ ) indicates a highly significant negative correlation between the response modulation and the angular distance. The maximum response increase occurred at  $0^\circ$  (significant mean increase of 7% for attention to the preferred direction,  $p < 0.05$ , paired t test), no modulation occurred around  $90^\circ$ , and the maximum decrease

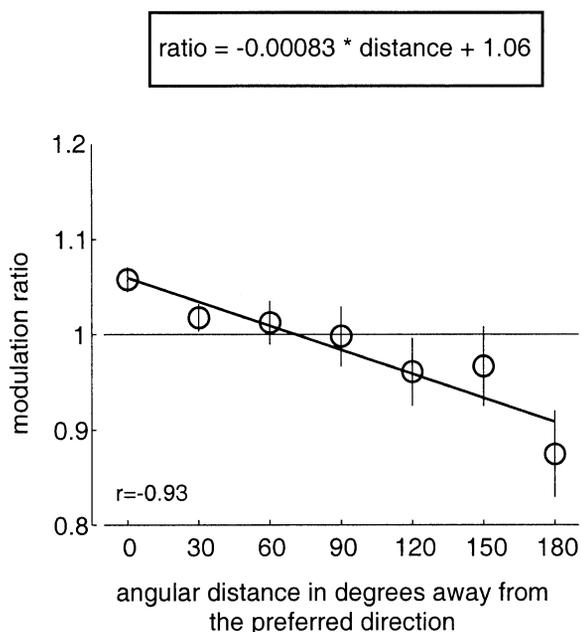


Figure 5. Experiment 2. Population Data

Average modulation ratios (circles) for the sample of 135 neurons were plotted in the same way as in Figure 4B. The error bars represent standard errors. The line represents the linear model best fitted to the data (intercept:  $1.06 \pm 0.03$ , slope:  $-0.00083 \pm 0.0002$ ;  $r = -0.93$ ).

occurred at 180 degrees (significant mean decrease of 12% for attention to the anti-preferred direction,  $p < 0.05$ , paired t test). The absolute magnitudes of the response increase when individuals attended to the preferred direction and the response decrease when they attended to the anti-preferred direction were not different from each other ( $p = 0.8$ , paired t test). This combination of attentional enhancement and suppression increased the direction index and therefore the selectivity for attended features across the population of cells by 20% (median).

## Discussion

The activity of MT neurons is modulated by the attended direction of motion [2, 7]. Here, we demonstrated that this modulation is multiplicative and, as predicted by the feature-similarity gain hypothesis, for a given MT neuron the sign and amplitude of this feature-based attentional modulation of responses is a monotonic function of the relationship between the attended motion direction and a cell's preferred direction rather than reflecting the relationship between attention and the stimulus features to which a cell is currently responding.

The data show that the response of a given neuron was increased if the attended feature was close to the tuning curve's center (i.e., for directions close to the preferred direction), decreased if the attended feature was close to the cell's anti-preferred feature (i.e., for directions close to the anti-preferred direction), and unmodulated if attention was allocated to an intermediate feature. This behavior represents a tuning of attentional

modulation across the range of neuronal preferences. Therefore, the firing rate of a neuron is the result of the interaction of sensory responses (determined by the location of the features of the stimulus that activates the neuron along the sensory tuning curve of the cell) with a multiplicative attentional modulation (determined by the location of the *attended* feature along the sensory tuning curve of the cell). Note that the latter is a factor that is independent of the actual stimulus that drives the cell.

In a typical design for the investigation of spatial attention, attention is switched between two identical stimuli, one inside and the other outside the RF. The comparison of responses in these two conditions reveals a multiplicative modulation across the whole tuning curve [2–3]. The feature-similarity gain model interprets this constant modulatory factor as an expression of the identical feature-similarity between any corresponding points of the two tuning curves. This design and analysis is of little help when one asks what the population response to a stimulus outside the spatial focus of attention is. The current study demonstrates that because the sign and amplitude of attentional modulation are functions of the relationship between the attended feature and a cell's preferred feature, the response modulation caused by the allocation of attention to a particular feature will vary across the population of neurons differing in their preferred feature within the attended dimension. Figure 4A can be interpreted as the population response across a set of neurons sharing the same receptive field but differing in their preferred direction [8]. Because of the enhancement of neurons preferring the attended feature and the suppression of neurons preferring the non-attended direction, the signal-to-noise ratio (or the population direction index) is enhanced for all stimuli across the visual field sharing the attended feature. This should support improved detection and discrimination for these stimuli even outside the spatial focus of attention whenever performance is limited by signal-to-noise ratios. Such changes in the shape of population tuning functions are remarkably similar to predictions of the shape of population tuning curves from Lee et al.'s attention studies modeling psychophysical data (see Figure 6 of [9]), even though we did not observe the sharpening of the tuning of individual neurons postulated by Lee et al. It should be emphasized that despite this nonmultiplicative change across the population tuning curve, attentional modulation is still multiplicative, but the factor is different for neurons preferring different directions of motion.

We found no indication for the workings of attention being in line with a feature-matching hypothesis in which the attentional modulation depends on the match between the attended feature and the feature of the stimulus to which the cell is responding [6]. Note the similarity between the feature-matching hypothesis and the predictions of the Gestalt law of common fate that would lead to grouping effects between stimuli moving in the same direction [10–14], possibly allowing the transfer of attentional modulation to unattended locations.

One possible explanation for the differences between our results and those reported by Motter [6] is that Motter's study used a paradigm in which the animal might

have allocated attention to all possible targets, including stimuli that matched the cued feature inside the RF. If so, a multiplicative space-based increase in response to every potential target independent of the cells' selectivity for the selected feature would be expected [2–3]. This effect would very likely interact additively with a possible feature-similarity gain effect such as the one described here [2, 15].

## Conclusions

In summary, our results are well accounted for by the feature-similarity gain hypothesis prediction that attention will enhance the population response to attended stimulus features across the visual field in the neurons most tuned to these features while decreasing the population response in units preferring opposite features. This will selectively enhance the representations of environmental aspects that are similar to those to which the organism is currently attending. These results impose important constraints on models of attentional selection and contribute to our understanding of the physiological basis of attentional mechanisms in the brain.

## Experimental Procedures

We recorded the responses of 135 direction-selective cells in area MT of two male macaque monkeys to a moving random-dot pattern (RDP) while the animals performed an attentional task. After initial training, a head post, a scleral search coil [16] to monitor eye position [17], and a recording chamber were implanted in each animal. A custom computer program running on an Apple Macintosh PowerPC controlled the stimulus presentations, monitored eye position and behavioral responses during the experiments, and recorded the behavioral and neuronal data. The experiments reported in this study were conducted according to local and national rules and regulations and were approved by the Regierungspraesidium Tuebingen.

## Stimuli

We used RDPs of small bright dots (density = 5 dots per degree<sup>2</sup>) plotted within a stationary circular virtual aperture on a computer monitor (viewing distance = 57 cm). The diameter of the aperture varied from about 1° to 12° depending on the size of each neuron's receptive field. The luminance of the dots was 55 cd/m<sup>2</sup>. Movement of the dots was created by displacement of each dot by the appropriate amount at the monitor refresh rate of 75 Hz. In every trial we presented two RDPs of equal size; one was positioned inside the recorded cell's classical receptive field (RF), and the other was positioned outside, in the opposite hemifield (see behavioral task). Both stimuli were positioned at the same distance from the central fixation point. The separation between the two stimuli varied from about 10° to about 25°, depending on the eccentricity of the recorded neuron's RF. The size of the stimuli was chosen so that the stimulus did not exceed the boundaries of the classical RF.

## Recordings

Extracellular recordings from the left hemisphere were made with tungsten microelectrodes (impedance 0.5–2 mΩ, Microprobe and FHC). Single units were isolated with a window discriminator (Bak Electronics). The unit was classified as MT based on its RF size, eccentricity, direction-selectivity, and position within the recorded area. We recorded only from those units showing clear direction-selectivity during initial mapping.

## Behavioral Task

The monkeys were trained to attend to a moving RDP (the target) in the presence of another moving RDP (the distractor) while maintaining fixation on a stationary fixation cross (Figure 1A). Every trial began with the appearance of the fixation cross. A stationary RDP (target) appeared at one position on the screen 300 ms after fixation,

and the trial continued if the monkey touched a lever. Then, 200–400 ms after the monkey touched this lever, another RDP (the distractor) appeared at a different position, and both RDPs began to move. The animals obtained a liquid reward (drop of water or juice) if they released the lever in response to a direction or a speed change in the target within a response time window (250–700 ms after the change). The direction or speed change occurred randomly from 260 to 2300 ms after target onset. The distractor could also change speed or direction during the trial, but with a temporal separation of at least 600 ms from the target change. Trials in which the monkey broke fixation or responded outside the reaction time window were considered to be errors and were aborted without reward.

In the first experiment, the animals were instructed to direct their attention to a moving RDP located outside the cells' RF (the target) while we recorded the responses to a second RDP (the distractor) located inside the RF. In one of two attentional conditions, the target moved in the same direction as the distractor (attend-same); in the other condition it moved in the opposite direction (attend-opposite). In every unit, we recorded the responses to the preferred and anti-preferred directions of motion of the distractor in the two attentional conditions (Figure 1A). For a given neuron, we defined as the preferred direction the one out of 12 different directions (sampled every 30 degrees) causing the strongest response in a condition when both RDPs were ignored and the animals detected a luminance change of a small square centered on the fixation point (attend-fixation condition). The anti-preferred direction was the direction of motion 180° away from the preferred direction.

The second experiment combines the attend-same condition of the first experiment with the attend-fixation condition (Figure 1B). We recorded the responses to 12 different motion directions (sampled every 30 degrees) of the pattern located inside the cells RF in both conditions.

The different conditions from both experiments (attend-same trials, attend-opposite trials, and attend-fixation trials) were randomly interleaved within a block of trials.

## Data Analysis

We measured the neuronal responses in the different conditions. Cells were included in the analysis only if at least four correctly performed trials per condition were available. A total of 135 neurons (83 from one animal and 52 from a second animal) were included in the analysis. We determined response rates by averaging the frequency of action potentials over 1000 ms of stimulus presentation starting 200 ms after target motion onset. We excluded from the analysis trials in which a direction change occurred earlier than the end of this analysis period in the target or the distractor, i.e., all data included were from before any change occurred in the display.

We quantified the modulation of responses between the different attentional conditions, e.g., attend-same (AS) versus attend-opposite (AO), by computing an attentional modulation index:  $AMI = [\text{response AS} - \text{response AO}] / [\text{response AS} + \text{response AO}]$  [18]. We determined mean attentional modulations across cells by averaging the AMIs. For an easier visualization of the results, these mean indices were plotted as the equivalent ratio of response rates. A ratio higher than 1 indicates that the response was larger in the AS relative to the AO condition, a ratio lower than 1 indicates the opposite, and a ratio equal to 1 indicates that responses were unchanged between the two conditions.

## Psychophysical Performance

We adjusted the magnitude of the direction or speed change so that the animals performed correctly between 75% and 95% of the trials that were not aborted by fixation breaks. In the first experiment, animals A and B broke fixation in 15% and 7%, respectively, of the attentional trials and performed correctly in 75% and 83%, respectively, of the remaining trials. Performance in the attend-fixation condition was above 95% and was homogeneous across the different stimulus configurations (different motion directions). We did not find differences in performance within the same condition across different stimulus configurations (directions of motion).

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