

Attentional Modulation Strength in Cortical Area MT Depends on Stimulus Contrast

Julio C. Martínez-Trujillo¹ and Stefan Treue^{2,3}

¹Center for Vision Research
York University
Toronto Ontario M3J 1P3
Canada

²German Primate Center
Cognitive Neuroscience Laboratory
Kellnerweg 4
37077 Goettingen
Germany

Summary

The attentional modulation of sensory information processing in the visual system is the result of top-down influences, which can cause a multiplicative modulation of the firing rate of sensory neurons in extrastriate visual cortex, an effect reminiscent of the bottom-up effect of changes in stimulus contrast. This similarity could simply reflect the multiplicity of both effects. But, here we show that in direction-selective neurons in monkey visual cortical area MT, stimulus and attentional effects share a nonlinearity. These neurons show higher response gain for both contrast and attentional changes for intermediate contrast stimuli and smaller gain for low- and high-contrast stimuli. This finding suggests a close relationship between the neural encoding of stimulus contrast and the modulating effect of the behavioral relevance of stimuli.

Introduction

Voluntary visual attention exerts a top-down influence on the processing of sensory stimuli in visual cortex that is modulated by a stimulus' behavioral relevance. We have previously demonstrated such attentional influences for direction-selective cells in extrastriate visual area MT in the macaque monkey (Treue and Maunsell, 1996, 1999; Treue and Martínez-Trujillo, 1999). Using a paradigm where attention was either directed toward a stimulus inside the receptive field of a given neuron or to a similar stimulus outside the receptive field, we showed multiplicative changes in the responses to all directions of stimulus motion by the same factor, without changes in a cell's tuning width (i.e., its selectivity). Similar multiplicative response modulations by attention have also been observed in the temporal pathway (McAdams and Maunsell, 1999). This effect of spatial attention is complemented by modulations based on the attended feature (i.e., in the absence of shifts of the spatial locus of attention) that are far reaching, extending into the opposite visual hemifield (Treue and Martínez-Trujillo, 1999; McAdams and Maunsell, 2000). We have proposed that these attentional effects are best accounted for by a response gain change of neurons whose magnitude reflects the similarity between the attended stimu-

lus properties (position, direction, etc.) and the sensory preferences (receptive field location, preferred direction, etc.) of the neuron (feature similarity gain model of attention; Treue and Martínez-Trujillo, 1999). While we view the modulation as acting on neurons rather than on the representation of individual stimuli, the functional effect of such attentional multiplication will be an increase in the saliency of the attended stimulus and a corresponding weakening of the neuronal representation of distractors.

Interestingly, multiplicative response changes are not only obtained by manipulating the behavioral relevance of stimuli. In the visual system, a nonattentional, multiplicative effect can be achieved by changing the contrast of a visual stimulus (Tolhurst, 1973; Dean, 1981; Albrecht and Hamilton, 1982; Sclar and Freeman, 1982; Treue and Martínez-Trujillo, 1999). This similarity between the effects of a bottom-up, sensory mechanism and a top-down, cognitive mechanism could simply reflect the similarity of two multiplicative mechanisms, or it could indicate that the two processes use common neural hardware. In the latter case, attentional modulation might not be independent of the sensory conditions, as the two signals would be combined and possibly become indistinguishable.

Here, we investigated the interaction between sensory response changes caused by modulating stimulus contrast and attentional response changes caused by shifting spatial attention between stimuli. The relationship between stimulus contrast and a cell's response is represented by the sigmoidal shape of the typical contrast response function (CRF). This nonlinear relationship, which can be expressed by the sigmoid function shown in Figure 1 (Albrecht and Hamilton, 1982; Sclar et al., 1990), allows us to distinguish two possible interactions between sensory and attentional signals. If attentional and contrast modulations of cells' responses in area MT are independent, the strength of attentional modulation of a given cell should only reflect the attentional state and not depend on the stimulus contrast. This would cause a multiplication of the CRF by attention ("response gain model," Figure 1A) in a way similar to the multiplicative attentional modulation demonstrated for direction (Treue and Martínez-Trujillo, 1999) or orientation (McAdams and Maunsell, 1999) tuning functions. If, on the other hand, attentional modulation and sensory signals are combined, the effect of attention might be indistinguishable from a change in stimulus contrast. In this case, the CRF would be shifted horizontally by attention, and the largest response changes would occur along the central, steep part of the CRF ("contrast gain model," Figure 1B). Such an effect can be achieved by changing the C50 value and has been reported in V4 neurons (Reynolds et al., 2000).

The most straightforward way to distinguish between these two possibilities experimentally is to present a single stimulus inside the receptive field of the neuron under study and compare the attentional modulation as a function of stimulus contrast when directing attention to the stimulus and when ignoring it. Such a design has

³Correspondence: treue@gwdg.de

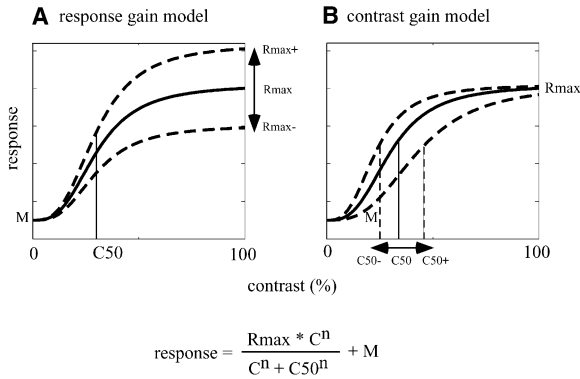


Figure 1. Hypothetical Relationships between Attention and Contrast

The two graphs show hypothetical contrast response functions (CRF) obtained by varying either R_{max} (A) or $C50$ (B) in the equation shown at the bottom (see Experimental Procedures for details). In (A), the attentional modulation of the cells' response predicted by the response gain model (changes in the parameter R_{max}) is shown. In (B), the attentional modulation of apparent stimulus contrast predicted by the contrast gain model (changes in the parameter $C50$) is shown. The two-headed arrows indicate the axis along which the modulation occurs.

several shortcomings, though. It is difficult to know if the animal is indeed ignoring a single stimulus when instructed. Attention, therefore, needs to be directed to a second stimulus presented outside the receptive field. By positioning it equidistant from the fixation point and moving it in the same direction, complete symmetry is achieved, equating the attentional task, the attended feature (direction of motion), and the task difficulty (eccentricity). One confounding factor remains, however. Changing the luminance of the attended stimulus (target) will create changes in task difficulty that might lead to changes in attentional effect (Spitzer et al., 1988). We therefore exploited the finding that unattended stimuli (distractors) are also affected in their efficacy by attention (Moran and Desimone, 1985; Treue and Martínez-Trujillo, 1999) and introduced an additional stimulus into the receptive field that was always presented at full luminance and was the one the animal was instructed to attend to. For symmetry, a similar paired stimulus arrangement was used outside the receptive field (see Experimental Procedures and Figure 2 for details). Each pair consisted of two moving random dot patterns (RDP), the potential target moving in the cells' null direction ("null" pattern), and the distractor moving in the preferred direction ("preferred" pattern).

Results

We recorded the cells' responses to various luminance/contrast levels of the distractor patterns (moving in the preferred direction) in two attentional conditions: when the stimulus outside the receptive field was the target (attending outside) and when the stimulus inside the receptive field was the target (attending inside).

Figure 3 shows the results for two neurons. In both graphs, the average responses (ordinate) are plotted as a function of the preferred pattern's contrast (abscissa).

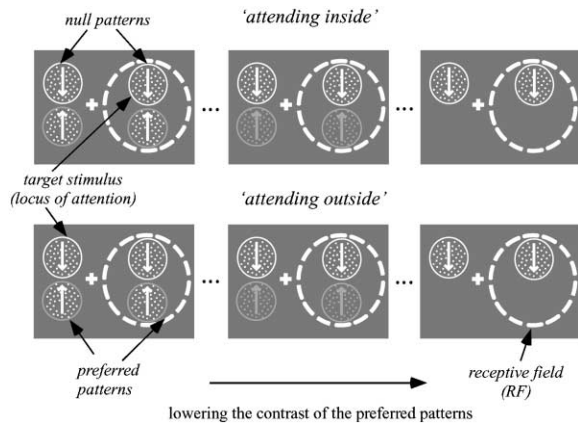


Figure 2. Experimental Design for a Cell Preferring Upward Motion

Two pairs of RDPs appeared on the screen, one positioned inside and the other outside the cells' receptive fields (dashed circle). Each pair consisted of one preferred and one null pattern. In an attending inside condition (top row), the monkeys were attending to the null pattern inside the receptive field. In an attending outside condition (bottom row), the animals were attending to the null pattern located outside the receptive field. From left to right, the panels illustrate decreasing luminance values of the preferred patterns, leading to a decrease in responses.

The squares represent the attending outside, and the circles, the attending inside conditions. The two data sets (attending inside and attending outside) were fitted with a sigmoid function (see Figure 1 and Experimental Procedures). The four parameters (R_{max} , $C50$, n , and M) of the two CRFs for each example unit are shown in the inserts. In both cases, attending inside the receptive field strongly increased $C50$ with only a negligible change in R_{max} . This result is in agreement with the predictions of the contrast gain model (Figure 1A), i.e., attentional effects are not a simple multiplication of a cell's response but vary nonlinearly with stimulus contrast. One possible explanation that has been suggested for a similar nonlinearity found in V4 neurons (Reynolds et al., 2000) is that when the cell reaches its maximal

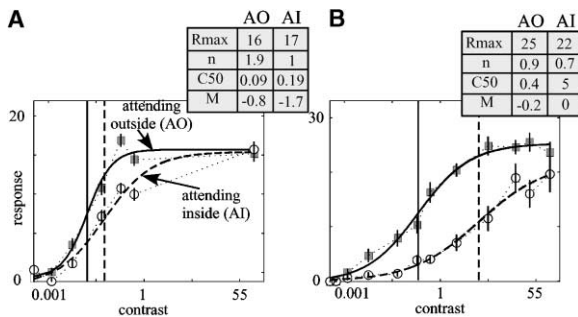


Figure 3. Example Results

The graphs show the average responses above baseline (ordinate) to different contrast levels (abscissa) of two different MT units in the attending outside (AO, squares) and attending inside (AI, circles) conditions. The solid line represents the fit through the data points for the attending outside, and the dashed line, the attending inside conditions. The vertical lines indicate the $C50$ value for each curve, and the tables show the values of the four parameters (R_{max} , $C50$, n , and M) of the CRFs. The error bars indicate the standard errors.

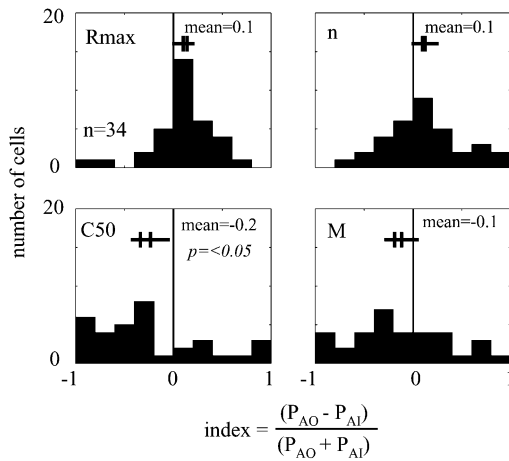


Figure 4. Changes in CRF Parameters as a Function of Attentional Condition

The histograms show the distribution of the indices $(P_{AO} - P_{AI}) / (P_{AO} + P_{AI})$, where P_{AO} and P_{AI} are the correspondent curve parameters values for each condition. The name of the parameter is indicated in each graph, as well as the mean index value (which is equivalent to the geometric mean of the simple ratios), and the probability value associated to the null hypothesis that the mean of the distribution is not different from zero. Index values below zero represent smaller values in the attending outside condition. The mean index value for the C50 (-0.2) corresponds to a ~50% increase in C50 in the attending inside relative to the attending outside conditions.

firing rate, a further increase in response by attention cannot be achieved. This argument is not applicable to the results reported here because in our experiments, the effect of attention is a suppression of the response. Furthermore, it should be noted that the cells are capable of much higher firing rates if responses are not reduced by the presence of a null-direction pattern in the receptive field. For the unit in Figure 3A, the response to the preferred direction RDP alone was ~55 spikes/s, more than twice the maximal firing rate for the two-pattern configuration (~15 spikes/s). For the cell shown in Figure 3B, the response to the preferred direction was about 40 spikes/s, while its maximal response to the two-pattern configuration was about 25 spikes/s.

We applied the analysis demonstrated in Figure 3 to 34 of our sample of 63 MT units. The other 29 units were excluded because their C50 values in at least one of the attentional conditions was higher than the maximum contrast used during the experiments (this could cause an improper estimation of the CRF-parameters). For the 34 included cells, there was no significant difference between the observed and the fitted maximal firing rates. In all 34 analyzed cells, the goodness of fit of the model determined by the correlation coefficient between the data and the predicted values was larger than 0.8.

To quantify the differences between the CRF parameters in the two conditions, a modulation index MI = $(P_{AO} - P_{AI}) / (P_{AO} + P_{AI})$ was computed with P_{AO} and P_{AI} referring to the parameters of the attending outside and attending inside conditions, respectively. Figure 4 shows the distribution of the indices. The distribution is significantly shifted from zero (only for C50), indicating a significant increase in this parameter ($p = 0.03$, paired

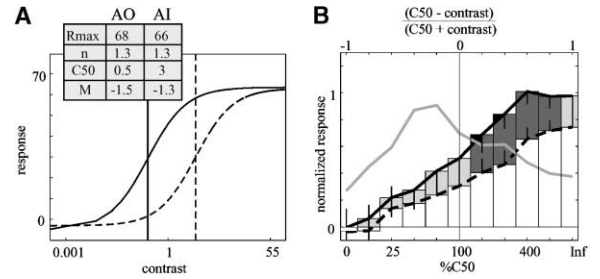


Figure 5. Contrast Sensitivity Versus Attentional Modulation

(A) Contrast response functions obtained from the average fit parameters in the attending outside (AO, solid line) and the attending inside (AI, dashed line) conditions (see table at the bottom). The abscissa represents stimulus contrast, and the ordinate, the response. The vertical lines represent the C50 values.

(B) Average normalized responses after aligning the contrast response functions in all units to their respective C50 values (see Results) in the attending outside condition. The upper abscissa represents the values of the index $(C50 - \text{contrast}) / (C50 + \text{contrast})$, and the lower abscissa, the same values converted to percentage of the C50 units. The ordinate represents the normalized response. The error bars represent the standard errors. The shaded area indicates the magnitude of the absolute differences in response for each bin, and the gray solid line represents the values of the attention index (response attending inside - response attending outside) / (response attending inside + response attending outside). Dark gray shaded areas represent differences that reached statistical significance. The shift of those dark bars away from the center reflects poor statistical power for the left bars because of a small sample size, but note that the last bin does not contain significant differences despite the largest number of contributing data points.

t test) in the attending inside condition. Thus, spatial attention causes a change in the C50 value of MT units without significantly changing the other parameters of the CRF.

Figure 5A shows the two CRFs that were computed using the average parameters (see table insert) from the sample. As an additional test of whether the data follow the predictions of the contrast gain model, we compared the differences between the normalized population responses across the 34 cells in the two attentional conditions for different levels of stimulus contrast. The response modulation should have been stronger for intermediate contrast levels (steep part of the CRF) and weaker for contrast levels close to zero or to saturation (lowest and highest parts of the CRF, see Figure 1). The contrast sensitivity (C50) varied between MT neurons, placing the steep portions of their CRFs at different absolute contrast values. We therefore placed the data points along a normalized abscissa using the equation $(C50 - \text{contrast}) / (C50 + \text{contrast})$. The effect of this procedure is to align the C50 values in all units (the slope of their CRF) to the zero point (upper abscissa, Figure 5B). The normalized contrast values can also be converted into a percentage of the C50 value (lower abscissa, Figure 5B). In such a plot, the contrast gain model would create the largest differences in response between the two conditions at intermediate contrast values. To test this hypothesis, the normalized responses for each condition were binned and averaged across units (Figure 5B). As predicted by the contrast gain model, the ratio between the normalized responses in the two conditions (solid gray line in Figure 5B) peaks

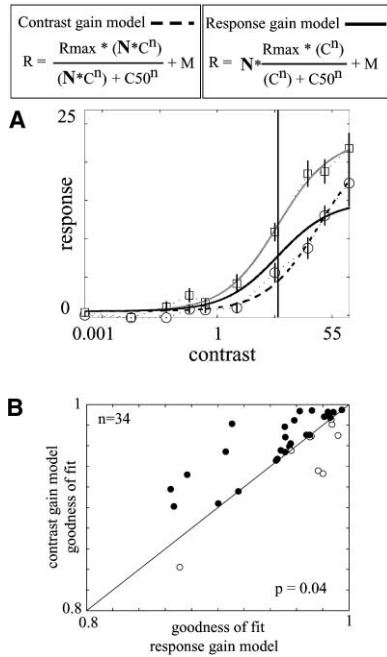


Figure 6. Comparing the Goodness of Fit of the Two Models

(A) Responses of one neuron in the two attentional conditions (ordinate) as a function of stimulus contrast (abscissa). The squares represent the responses in the attending outside condition, and the gray, solid line represents the best fit to them provided by the equation shown in Figure 1. The circles represent the responses in the attending inside condition. The black, dashed line represents the best fit to these data provided by contrast gain function, and the dark, solid line represents the best fit provided by the response gain function. The error bars represent the standard errors.

(B) Scatter plot of the goodness of fit provided by the response gain model (abscissa) versus the goodness of fit provided by the contrast gain model (ordinate). The black circles represent the units that were better fit by the contrast gain model (25 of 34), while the empty circles represent those better fitted by the response gain model.

in the middle portion of the graph and drops off toward the high- and low-contrast values.

An additional way to corroborate this result is by directly comparing the goodness of fit of the contrast gain and the response gain models to the data. For this purpose, we used the parameters of the CRF fitted through the attending outside condition data for each of the 34 units used in the previous analysis. We then introduced a single free parameter (N) to either multiply contrast (contrast gain model, equation 1 in Figure 6) or to multiply the overall response (response gain model, equation 2 in Figure 6). We fitted the data from the attending inside condition with the two models and determined the goodness of fit of each model by computing a correlation coefficient between the data and the values predicted by the model.

Figure 6A shows one cell example. The solid black line and squares represent the predicted values and data points corresponding to the attending outside condition. The circles represent the data from the attending inside condition, the black dashed line the values predicted by the best fit provided by the contrast gain model, and the solid black line those predicted by the “response gain model.” Clearly, the contrast gain model

provides a better fit to the data. The scatter plot in Figure 6B displays the goodness of fit values for the response gain model (abscissa) and the contrast gain model (ordinate) for the 34 units tested. The data points falling above the diagonal line (black circles) represent the cases that were better fitted by the contrast gain model (25 out of 34), and the ones falling below (empty circles) represent the cases in which the response gain model provided a better fit (9 out of 34). This shift was significant, i.e., the contrast gain model provides a better fit ($p < 0.05$, paired t test).

A prediction directly derived from this result is that for a given high-contrast unattended stimulus, the attentional suppression of MT cells’ responses to it will be stronger for the less-sensitive cells (cells with a higher C50). The most-sensitive neurons (low C50) should be less suppressed by attention because they have already reached the maximal response for that stimulus. Such an effect might account for some of the different amounts of attentional modulation observed within and between studies each using stimuli of different and non-variable contrast. To evaluate this possibility, we determined the correlation between the C50 values and the attentional suppression at maximal contrast for the 34 units included in the previous analysis. While there was the predicted negative correlation between the C50 and the attentional suppression at maximum contrast (i.e., the more sensitive cells tended to show less attentional modulation at a given high contrast), this trend was not significant for our data set.

Discussion

This study demonstrates that the magnitude of response modulation by attention depends on stimulus contrast of unattended stimuli inside the receptive field. Responses of direction-selective MT neurons were more strongly affected by attention when a distractor presented in their receptive field had intermediate, rather than low or high, contrast. This finding would not be expected if the multiplicative effect of attentional modulation acted directly on the firing rate of the neurons we recorded from (response gain model, see Figure 1A). Rather, it can be accounted for by an attentional influence that acts differentially on the gain of the various inputs converging on a given MT cell or even already on the firing rates of the neurons providing the input to MT (contrast gain model, see Figure 1B). V1 provides a major direct sensory input to MT. Since attentional modulation in V1 seems to be weaker than in later areas of the visual cortex, the attentional effects observed in MT might result from the modulation of input gain. The effect of this influence is similar to a change in the contrast of the stimulus and raises the interesting issue of whether and how the two can be disentangled perceptually. In this context, it should be noted that it has been suggested that the CRF in MT neurons cannot be explained solely on the basis of the CRFs of the afferents to MT (Majaj et al., 2000, Soc. Neurosci. Abstr.)

Our study provides further support for the proposal that attention does not only enhance the influence of an attended stimulus onto a cell’s response but, similarly, also reduces the influence of unattended stimuli.

This likely explains the weaker attentional modulations observed in studies that present just one stimulus inside the receptive field compared to studies that switch attention between two stimuli inside the receptive field and, therefore, combine the attentional enhancement of the attended stimulus with the attentional suppression of the unattended stimulus in a push-pull fashion. The attentional suppression of unattended stimuli allows the visual system to achieve a response modulation, even in the presence of high-contrast target stimuli, that brings the subpopulation of input neurons encoding them close to saturation. An attentional enhancement of only the attended stimulus' representation would prevent attentional effects under such conditions. But, by reducing the response in those subpopulations encoding the distractors, the visual system is able to achieve an enhanced saliency even for high-contrast targets. Interestingly, this suggests that behaviorally, only the perceptual strength of the unattended stimuli should be affected.

Our findings in the dorsal pathway of the visual cortex complements a recent study in area V4 in the temporal pathway (Reynolds et al., 2000). In those experiments, attentional enhancement was determined as a function of the contrast of a single stimulus inside the receptive field when it was the target or the distractor, respectively. In this experimental design, task difficulty covaries with stimulus contrast. Since task difficulty per se can modulate responses (Spitzer et al., 1988), the authors used short stimulus presentation times and interleaved trials with different contrast levels in an effort to minimize this confounding factor. As predicted from the contrast gain model response, modulation was stronger for intermediate contrasts. This supports the hypothesis of similar attentional mechanisms operating in the areas along the two pathways of primate visual cortex.

All visual neurons show a monotonic dependency of firing rate as a function of stimulus contrast. Thus, an influence of attention of the neural mechanisms underlying contrast encoding provides a way to influence stimulus saliency across visual cortical areas. The shared nonlinearity between the contrast response function and the magnitude of attentional modulation indicates a tight link between attentional mechanisms and the mechanisms responsible for contrast encoding. This tight link does not seem to exist for the encoding mechanisms of other stimulus properties. For example, MT neurons are also monotonically modulated by the coherence in random dot patterns (Britten and Newsome, 1998). Because this modulation is a linear function of coherence (Britten et al., 1993), the nonlinear attentional effects we observed are not functionally equivalent to a change in stimulus coherence. Thus, the mechanism responsible for the encoding of motion coherence (or any other stimulus property that is encoded in a quasi-linear way) does not seem to be directly modulated by attention.

Combining the results of the present study with our previous report of multiplicative modulation of direction tuning curves by attention demonstrates that attention cannot be thought of as a mechanism that is best understood as creating changes in neural responses. The same intermediate response of a given MT neuron will, at best, be modulated only moderately by attention if it is caused by a high-contrast pattern moving off the

neuron's preferred direction, but it will be modulated more strongly if the response was caused by a low-contrast stimulus moving in a direction closer to the preferred direction.

In summary, our results should provide powerful constraints for mechanistic models of attentional modulation and for the location where attentional modulation can be inserted into existing models of sensory information processing in the visual cortex. The data also suggest that behaviorally, attention should interact with stimulus saliency while leaving other perceived stimulus properties relatively unchanged.

Experimental Procedures

We recorded the responses of direction-selective cells in area MT of two macaque monkeys to moving random dot patterns (RDPs) in two attentional conditions. A head post and a scleral search coil (Judge et al., 1980) were used to monitor eye position (Robinson, 1963). A custom computer program running on an Apple Macintosh PowerPC controlled the stimulus presentations, monitored eye position and behavioral responses of the animal, and recorded the behavioral and neuronal data.

Cells were determined to be from MT by their physiological characteristics (strength of direction selectivity, receptive field position, and receptive field size) as well as by the position of the electrode in the cortex. We tested only cells showing at least a 4-fold response modulation between preferred and null direction during an initial evaluation with RDPs moving at the preferred speed.

Behavioral Task

The monkeys were trained to attend to a moving RDP (the target) in the presence of other moving RDPs (distractors) while maintaining fixation on a stationary fixation cross. Every trial began with the appearance of the fixation cross. 300 ms after foveating it, a stationary RDP (the cue) appeared at a given position on the screen, indicating the location of the target. After the animal pressed a touch bar, the cue disappeared. 1000 ms later, two RDPs appeared inside the receptive field of the recorded cell, one moving in the cells' preferred direction (preferred pattern) and the other moving in the null direction (null pattern). At the same time, an identical pair of RDPs appeared far outside the receptive field, generally in the other hemifield. The monkey had to respond to a small direction change in the target by releasing the touch bar within a response time window (more than 200 ms and less than 650 ms after the change). The other RDPs could also change direction or speed but never simultaneously with the target. Correctly performed trials were only those where the monkey responded within the response-time window to the target change. A trial was terminated as soon as the monkey released the touch bar, moved his gaze out of the fixation window, or 650 ms after the target change. We recorded the cells' responses in two attentional conditions: (1) when the monkeys were attending to the null pattern located outside (attending outside), and (2) when the monkeys were attending to the null pattern located inside the receptive field (attending inside). Trials differed in the luminance of the dots making up the two preferred patterns.

Stimuli

Stimuli were RDPs of small white dots (density: five dots per degree²) plotted within a stationary virtual aperture on a computer monitor. Dots moved coherently at the preferred speed of the neurons and were replotted to the opposite side when they crossed the border of the aperture. The monitor refresh rate was 75 Hz, and the viewing distance was 57 cm.

Recording Technique

Extracellular recordings were made using tungsten microelectrodes (impedance 0.5–2 M Ω , Microprobe, Inc. and FHC, Inc.). Transdural penetrations were made using guide tubes through a chamber, which was implanted in a stereotaxic surgery on top of a craniotomy of the parietal bone, providing access to MT along a vertical

approach. Single units were isolated using a window discriminator (Bak Electronics Corp.).

Data Analysis

We measured the neuronal responses during fixation and stimulus presentation. Cells were included in the analysis only if at least eight or more correctly performed trials in the two attentional conditions and data for at least five different contrast levels were available. Mean firing rates were obtained by averaging the responses in every trial over 1000 ms of stimulus presentation time starting 200 ms after target onset and then subtracting the baseline response (response when the animal was fixating and no stimulus was shown inside the receptive field). The contrast causing half of the saturation response (C50) was determined by fitting a sigmoidal function (hyperbolic ratio function; $\text{response} = [\text{Rmax} \times \text{C}^n / (\text{C}^n + \text{C50}^n) + \text{M}]$) through the responses (C) at different contrast levels where Rmax represents the differences between the response at the lowest contrast (M) and the response at saturation, and n is the exponent determining the slope of the function (see Figure 1). This function has been previously used to fit CRFs for neurons in the visual cortex of cats and monkeys (Albrecht and Hamilton, 1982; Sclar et al., 1990). The goodness of fit was computed by determining a correlation coefficient between the data and the predicted values. In all cases, the correlation coefficient was higher than 0.85.

To compute the differences between the parameters of the curves in the two attentional conditions, the index $(P_{AO} - P_{AI}) / (P_{AO} + P_{AI})$ was used, where P_{AO} and P_{AI} are the curve parameters in the attending outside and attending inside conditions, respectively.

Eye Position

The animals were required to maintain fixation within a circular fixation window of 0.7° radius throughout each trial. Due to the different locations of the attended stimulus in the different experiments, the monkey might have directed its gaze to different positions inside of the fixation window, and it is conceivable that differences in response could be due to corresponding changes of the relative stimulus location inside the cells' receptive field. A displacement (0.03°) in average eye position toward the attended stimulus was measurable (see Treue and Maunsell, 1999 for a more detailed description of this analysis). This value is very small and cannot account for the differences in responses between attentional conditions.

Psychophysical Performance

On average, the animals broke fixation in 21% of the trials. In 88% of the remaining trials the animals performed correctly, and in 12%, they responded outside the reaction-time window. There were no significant differences in performance between the two attentional conditions.

Luminance Values and Measurements

The dots in the RDPs were too small to determine their luminance directly. We therefore estimated their luminance by measuring circular, homogeneously shaded patches with a diameter of about 10° , using a Minolta photometer. Combining preferred and anti-preferred stimuli in MT receptive fields causes intermediate responses (Treue et al., 2000). Therefore, the field responses we observed were only about half of those reached when a preferred pattern is presented alone inside the receptive field. This might allow neurons to show increases in responses up to slightly higher contrasts.

In 23 of the cells, we used a black background with a luminance below our photometer's sensitivity ($\sim 0.01 \text{ cd/m}^2$) and in the other 40, a background with a luminance of 0.1 cd/m^2 . The luminance values used with a given neuron were chosen according to the sensitivity of that cell. As a contrast measurement, we used the standard deviation of the mean luminance of the stimulus: $\text{contrast} = \sum [p(i) \times (L(i) - L_m)^2]$ where $p(i)$ is the proportion of pixels with luminance $L(i)$, and L_m is the mean luminance of the stimulus. L_m was calculated using the formula $L_m = \sum [p(i) \times L(i)]$. This metric has been shown to provide a better estimate of contrast in RDPs than the Michelson formula (Moulden et al., 1990; Kukkonen et al., 1993).

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