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Interacting Roles of Attention and Visual Salience in V4

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Summary

Attention increases the contrast gain of V4 neurons, causing them to respond to an attended stimulus as though its contrast had increased. When multiple stimuli appear within a neuron's receptive field (RF), the neuron responds primarily to the attended stimulus. This suggests that cortical cells may be "hard wired" to respond preferentially to the highest-contrast stimulus in their RF, and neural systems for attention capitalize on this mechanism by dynamically increasing the effective contrast of the stimulus that is task relevant. To test this, we varied the relative contrast of two stimuli within the recorded neurons' RFs, while the monkeys attended away to another location. Increasing the physical contrast of one stimulus caused V4 neurons to respond preferentially to that stimulus and reduced their responses to competing stimuli. When attention was directed to the lower-contrast stimulus, it partially overcame the influence of a competing, higher-contrast stimulus.

Introduction

Physiological studies in area V4 have found evidence for competitive interactions between stimuli. Neural mechanisms for attention can bias these competitive interactions toward one stimulus or another, so that behaviorally relevant stimuli are processed in the cortex while irrelevant stimuli are filtered out (Moran and Desimone, 1985; Luck et al., 1997; Reynolds et al., 1999). When an effective, or "good," sensory stimulus for a V4 neuron (i.e., a stimulus that drives the cell well when presented alone) is paired with an ineffective, or "poor," one within the same receptive field (RF), the poor stimulus typically suppresses the response to the good stimulus. The magnitude of this suppression increases with the selectivity of the neuron, such that a very poor stimulus is typically more suppressive than a stimulus that gives an intermediate response. When attention is directed to the good stimulus, this suppression from the poor stimulus is diminished. Conversely, when attention is directed to the poor stimulus, its suppressive effect is magnified.

One way to account for this is that selective attention depends on hard-wired competitive circuits in extrastriate visual cortex, which can be biased by attentional feedback. According to this "biased competition" model (Desimone and Duncan, 1995; Reynolds et al., 1999), when attention is directed to a stimulus, this increases its effective strength or efficacy in driving visual cells that contain the stimulus within their RFs. Signals from both attended and unattended stimuli in the visual field propagate through successive stages of cortical processing until they reach a cortical site where RFs are large enough to encompass the competing stimuli within a single RF. Here, the magnified signals from the attended stimulus suppress the signals from unattended ones and dominate neuronal responses. As a result, neuronal responses in higher cortical areas reflect the attended stimulus, and unattended stimuli are effectively filtered out of the visual stream.

Evidence for a bias in favor of attended stimuli has been found in several extrastriate areas, in studies that have found either an increase in response to a single attended stimulus in the RF (Bushnell et al., 1981; Mountcastle et al., 1987; Spitzer et al., 1988; Treue and Maunsell, 1996; Connor et al., 1996, 1997; McAdams and Maunsell, 1999; Treue and Martínez-Trujillo, 1999; Reynolds et al., 2000), an increase in baseline firing rate for cells whose RF contains the attended stimulus (Luck et al., 1997), or an increase in effective contrast for an attended stimulus (Reynolds et al., 2000; Martínez-Trujillo and Treue, 2002). Reynolds et al. (2000) found that the effect of attention is to cause a leftward shift in the neuronal contrast response function. When attention is directed to a stimulus, V4 neurons respond as though the physical contrast of the stimulus had increased, an effect that has also been observed in area MT (Martínez-Trujillo and Treue, 2002).

We reasoned that if this increase in the effective stimulus strength is what biases the competition between stimuli in the same RF, we should be able to bias the same competitive mechanisms by directly manipulating stimulus strength in the absence of attention. We tested this by measuring the responses of V4 neurons to two stimuli, presented together or one at a time at locations within the RF, while varying their relative luminance contrast. Both stimuli were unattended. Consistent with the prediction of the biased competition model, we found that V4 neurons were driven preferentially by the higher-contrast stimulus. Furthermore, we found that when attention was directed to either of the two stimuli, attention and relative contrast were additive in their effect on competition. Thus, the attended stimulus was effective in dominating the cell's response, even if the physical contrast of the stimulus was low. These results reveal a simple mechanism by which attention can pull a less salient stimulus out from among more salient distracters.

Results

We recorded the responses of 80 V4 neurons in two monkeys (38 neurons in one monkey, 42 in the other)

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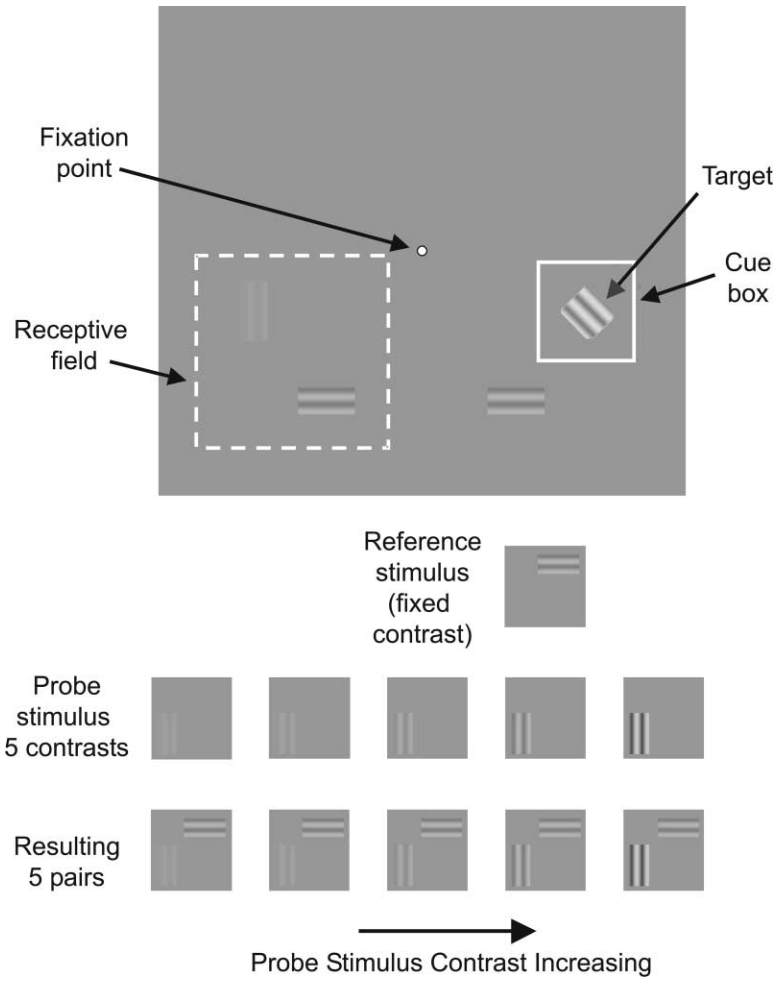

Figure 1. Stimuli and Task

Monkeys fixated a small spot at the center of the display. Stimuli appeared at up to four positions: two inside the RF (dashed box, upper panel) and two at mirror-symmetric positions across the vertical meridian. At the beginning of a block of trials, a cue box (solid square in upper panel) appeared, which indicated where the monkey was to attend throughout that block of trials. The cue box was removed after a few instruction trials, and the monkey continued to perform the task at that location without the cue. The task was to detect a diamond-shaped target stimulus that appeared at the cued location after a variable length sequence of nontarget stimuli, while ignoring distracter targets that occasionally appeared at the other three locations. The three rows of panels show the combinations of nontarget stimuli that appeared within the RF: (1) a reference stimulus, which appeared at a fixed contrast (single panel in first row), (2) a single probe stimulus, which varied in contrast (second row), or (3) a fixed-contrast reference stimulus and a variable-contrast probe stimulus (third row).

as we varied the relative contrast of two stimuli within the RF (see Experimental Procedures and Figure 1), presented either alone or as a pair. One stimulus (the "reference stimulus") had a fixed, high level of contrast (typically, 40%) and was chosen to be of the preferred orientation and spatial frequency of the neuron. The other stimulus (the "probe") was presented at five different levels of contrast (typically 5%, 10%, 20%, 40%, and 80%, though these values were sometimes adjusted if they did not span a sufficient portion of the neuron's contrast response function for a single stimulus inside the receptive field) and was chosen to be of a nonpreferred orientation and spatial frequency. Occasionally, we recorded simultaneously from two neurons with different orientation and/or spatial frequency selectivity. In these cases, we chose the probe and reference stimuli according to the response preferences of one of the neurons. As a result, occasionally neurons were recorded for which the probe stimulus elicited a stronger response than the reference. In separate behavioral conditions, monkeys either attended to the probe in the RF (attend-RF condition) or else attended to a stimulus in the opposite hemifield, ignoring the stimuli in the RF (attend-away condition).

In the attend-away condition, we measured the response to the reference stimulus alone in the RF and compared this to the response when reference and probe appeared together in the RF. The addition of the probe stimulus caused a significant change in response to the reference stimulus for 56 of 80 neurons (70%) tested, according to an ANOVA computed on the response to the pair of stimuli as a function of the probe contrast level (see Experimental Procedures). Fifty of the fifty-six neurons responded selectively to the reference and probe stimulus when they were presented alone at equal contrast, i.e., gave significantly different responses to the reference stimulus versus the probe stimulus, according to a t test ($p < 0.05$), and all further analyses were restricted to these 50 neurons. None of the stimuli tested elicited inhibitory responses, compared to baseline.

As found in a previous study (Reynolds et al., 1999), when the reference and probe stimulus had equal contrast, adding a poor probe to a preferred reference stimulus suppressed the response to the reference stimulus. We tested the model prediction that the poor stimulus should become increasingly suppressive as it increased in contrast, even when attention was engaged elsewhere, far from the neuron's RF. Figure 2 illustrates the effect of varying the probe stimulus contrast on the response to the pair of stimuli for one highly selective neuron. The probe stimulus for this cell (left column)

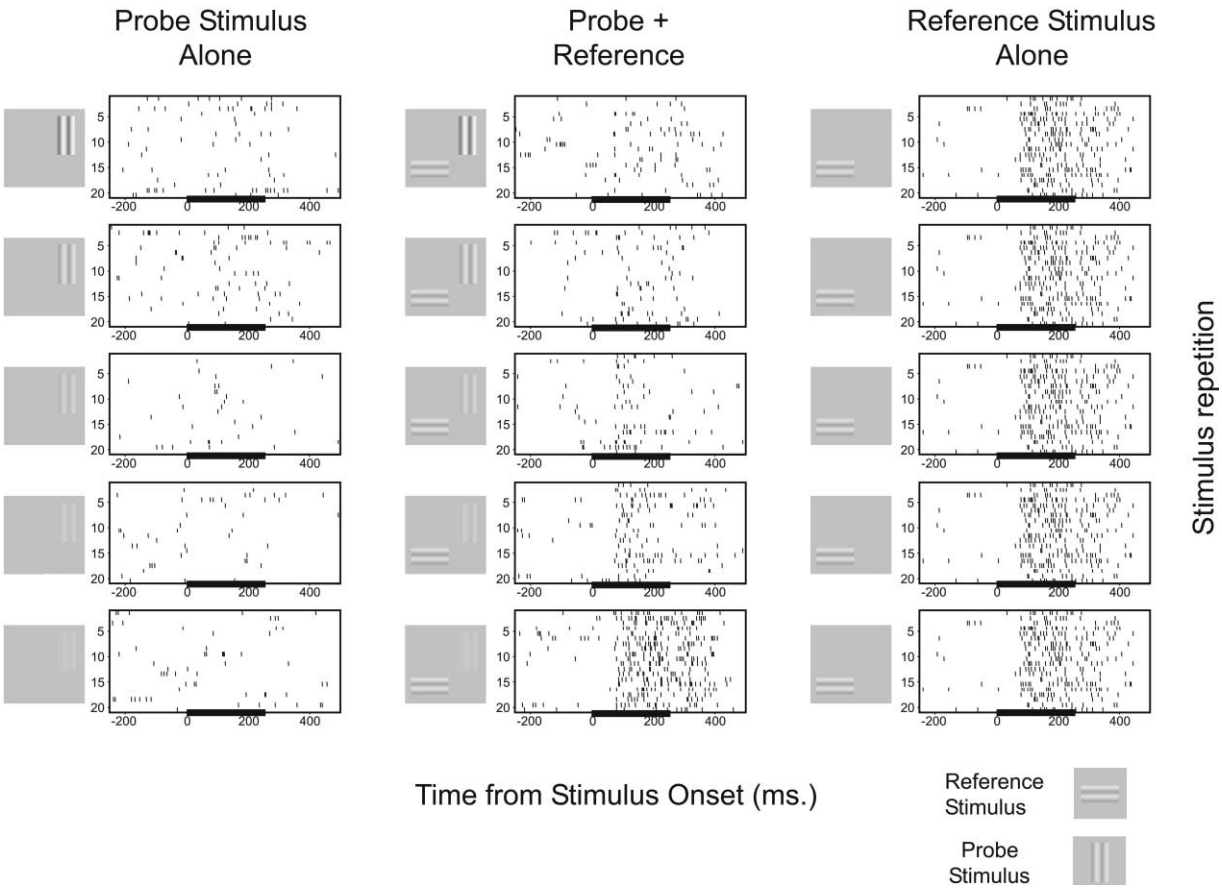

Figure 2. Example Neuron

Raster plots showing spikes from a single V4 neuron, with each row corresponding to a single presentation of the stimulus that is illustrated in the panel to the left of the raster plot. Stimulus duration (250 ms) is indicated by a thick bar at the bottom of each rastergram. The first column of raster plots shows responses to a (nonpreferred) probe stimulus presented alone at five contrasts arranged from lowest contrast on bottom up to highest contrast on top. The middle column of raster plots shows the responses of the same neuron, when the probe was presented together with a high-contrast reference stimulus (the horizontal grating). The third column shows the response to the reference stimulus when it was presented alone. Panels are repeated to aid in comparison. As the probe stimulus contrast increased, this resulted in a small increase of response to the probe alone. When the probe was paired with the reference stimulus, it had little impact on the neuronal response at low contrast, but as contrast increased, it became increasingly suppressive.

elicited a very small excitatory response when presented alone, even at the highest contrast tested, whereas the reference stimulus (which was held at constant 40% contrast) was of the cell's preferred orientation and spatial frequency and elicited a robust response (right column). As shown in the middle column, the response to the pair of stimuli varied according to the contrast of the probe. When the contrast of the probe was low (bottom row), the response to the pair was indistinguishable from the response to the preferred stimulus alone. That is, the low-contrast probe stimulus had little or no effect on the response elicited by the higher-contrast reference stimulus. However, as the contrast of the probe stimulus increased, it became steadily more suppressive, until at the highest contrast, it virtually eliminated the response elicited by the reference stimulus. Thus, consistent with the model prediction, a high-contrast probe dominated the cell's response to the pair of stimuli, with attention directed away from the RF.

Neurons like the one in Figure 2, which strongly preferred the reference stimulus compared to the probe, are of particular interest for the following reason. According to the model, increasing the contrast of the probe stimulus should result in an *increase* in the response to the probe when it is presented alone, while at the same time causing a *reduced* response to the pair of stimuli in the RF. That is, for such a cell, increasing the contrast of a poor stimulus will make it more excitatory when it is presented alone, but will make it more suppressive when it is presented together with a preferred stimulus. This counterintuitive reduction in response to the pair occurs because the increased contrast of the probe magnifies its suppressive effects on the response to the preferred reference stimulus.

Thus, the model draws a fundamental distinction between the two reasons why a stimulus might elicit a poor response from a neuron: either because tuning of the neuron does not match the features of the stimulus or because the stimulus is low in intensity. The greater the mismatch between the neuron's feature tuning and the stimulus (e.g., a green stimulus for a cell that strongly prefers red), the *more effective* the stimulus will be in

suppressing the neuron's response to a simultaneously presented preferred stimulus. In contrast, the lower the intensity of a poor probe stimulus (e.g., almost invisible, in the extreme case), the *less effective* it will be in suppressing the response to a fixed-contrast preferred stimulus. For example, a cell that prefers red may respond poorly to both a green stimulus and a very dim near-red, or orange, stimulus, but the green stimulus is more likely to have a greater suppressive effect on the response to a simultaneously presented red stimulus. Thus, the best predictors of suppression by a given probe stimulus should be the selectivity of the cell against that stimulus and its level of contrast.

We therefore divided the 50 neurons in our sample into three groups, according to selectivity. The majority of cells showed a response preference for the reference stimulus, because we attempted to select probe stimuli that elicited a smaller response than an equal contrast reference stimulus. We divided these cells into two groups: the half of the cells showing the most stimulus selectivity (the greatest response difference between the reference and probe stimulus at equal contrast) and the half showing the least stimulus selectivity. For both groups, we expected the addition of the probe stimulus to have a *suppressive* effect on the response to the pair, but with the largest and clearest suppressive effects in the most selective group. We further expected that for these cells, increasing the contrast of the probe would magnify their suppressive effect. We also separated out a third, small group of cells, for which the response to the probe stimulus was significantly *larger* than the response to the reference stimulus when presented at equal contrast. As indicated in the Experimental Procedures, we did not specifically set out to study cells with a probe stimulus that was a more preferred stimulus than the reference stimulus, but they happened to be included in the recorded population and the results from these cells did provide a test for one aspect of the model. For these cells, we expected the addition of the probe stimulus to have an *enhancing* effect on the response to the pair. We will describe the results from this latter group of cells first.

As expected, the 11 neurons that responded significantly better to the probe stimulus than to the reference stimulus tended to increase their response when the preferred probe was added to the reference stimulus within the RF. With attention directed away from the RF, 7 of the 11 neurons showed significant increases in response when the probe was added to the (equal contrast) reference stimulus (unpaired t test, $p < 0.05$), with only one neuron showing a significant effect in the opposite direction. All 11 neurons elicited significantly stronger responses when the probe was added to the RF and the animal attended to the probe stimulus (unpaired t test, $p < 0.05$).

Turning next to the two groups of cells that responded significantly less to the probe stimulus than to the reference, we found that suppression by the poor probe stimulus increased with selectivity, i.e., the greater the response difference between the reference and probe, the more suppressive was the probe. As described above, this is consistent with the model and with the results of earlier experiments (Reynolds et al., 1999). Considering the less selective group first, these cells were, on average, only modestly suppressed by the addition of the poor probe. With attention directed away from the RF, for these 20 cells the addition of the poor probe reduced the mean response to the reference stimulus by 7% over the period from 70 to 400 ms after stimulus onset (reference alone, 39.3 spikes/s; probe alone, 27.1 spikes/s; reference plus probe, 36.5 spikes/s), which was significant for 7 of the 20 cells (unpaired t test, $p < 0.05$). As predicted, the addition of the poor probe had a much clearer suppressive influence among the remaining, most selective group of neurons ($n = 19$). For these cells, with attention directed away from the RF, the addition of the poor probe reduced the mean response to the reference stimulus by 31.3% (reference alone, 29.5 spikes/s; probe alone, 8.8 spikes/s; reference plus probe, 20.2 spikes/s). This effect was highly significant overall (paired t test, $p = 0.0007$) and was also significant for 18 of the 19 neurons tested individually (unpaired t test, $p < 0.05$). As predicted, the magnitude of suppression increased with the contrast of the probe in this group of selective cells. This is illustrated in the population histograms shown in the upper row of panels of Figure 3, which shows average responses for the 19 cells, when attention was directed away from the RF. Panels are arranged according to the contrast of the probe, with contrast increasing from left to right. The response to the reference stimulus (solid gray line) is repeated across all five panels, for comparison. The mean response to the probe stimulus presented alone (dark dotted line) increased with contrast, from 4.0 spikes/s at the lowest contrast tested to 10.1 spikes/s at the highest contrast tested. At the lowest contrast tested (far left panel), the probe had no measurable influence on firing rate, i.e., the mean response to the pair of stimuli (29.4 spikes/s) was not significantly different from the mean response to the reference stimulus presented alone (29.5 spikes/s) according to a paired t test ($p = 0.81$). However, as the contrast of the probe increased, the response to the pair decreased. As noted above, when the contrast of the probe was increased so that it equaled the contrast of the reference stimulus (fourth panel from left, highlighted), this caused a 31.3% reduction in response.

As the contrast of the probe was increased even further (far right panel), the probe was even more suppressive. The average response to the pair during the first 100 ms of the response (70–170 ms after stimulus onset) was 25.3 spikes/s, a reduction of 17 spikes/s from the reference stimulus response of 42.3 spikes/s, which was highly significant ($p = 0.0001$), according to a paired t test. Interestingly, the later phase of the response was not strongly suppressed by the probe. The response to the pair during the period from 170 to 400 ms after stimulus onset was 19.8 spikes/s, only slightly reduced from the response to the reference stimulus (24.0 spikes/s), a difference that was not significant, according to a paired t test ($p = 0.1$).

The effects of attending to the probe stimulus are shown at the bottom of Figure 3, which shows population response histograms from the same neurons under identical stimulus conditions, when attention was directed to the poor probe stimulus. Eighteen out of nineteen neurons were significantly suppressed by the addition of the attended probe when it was equal in contrast

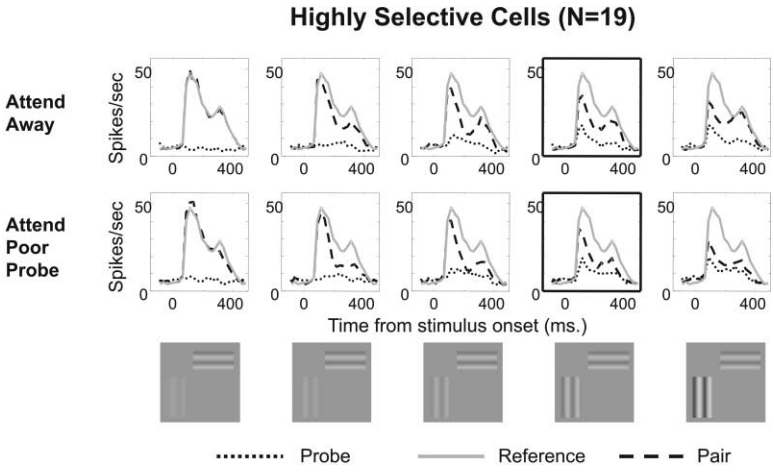

Figure 3. Average Responses for the Most Selective Neurons

Each panel shows the average response of the 19 most highly selective neurons. Panels are arranged according to the contrast of the probe stimulus, increasing from left to right. The upper row of panels shows responses when the monkey attended away from the RF. The lower row of panels shows the responses of the same 19 neurons, under identical stimulus conditions, but when attention was directed to the probe stimulus in the RF. Each panel shows the average response to the probe (dotted line), reference stimulus (solid line), and pair (dashed line), with time zero corresponding to the onset of the stimulus (stimulus duration, 250 ms). The two highlighted panels (second from right) indicate responses when probe and reference stimulus were of equal contrast.

to the reference stimulus. With the lowest-contrast probe stimulus, there was no suppressive effect of the probe without attention, and attending to the probe caused only a slight reduction in response. As the probe was increased in contrast, its suppressive effect without attention increased, and attending to it magnified this suppressive effect. At intermediate contrast levels of the probe, the additional suppressive effect of attention appeared strongest following the initial transient onset response to the reference stimulus. For the highest-contrast probe, attending to it caused it to exert almost complete control over the response to the pair. With attention to the highest contrast probe, the mean response to the pair (16.6 spikes/s) was slightly higher than the mean response to the probe alone (12.0 spikes/s), but this was not statistically significant, according to a paired t test ($p = 0.20$). Thus, when attention and higher contrast both favored the probe stimulus, neurons were driven by the probe with little or no influence of the higher firing rate reference stimulus.

In order to examine the effects of attention across neurons, we computed an attentional modulation index (AMI) in which the size of the attention effect was scaled by the size of the sensory response. For each neuron, the mean firing rate above baseline over the period from 70 to 400 ms after stimulus onset was computed both when attention was directed to the poor probe stimulus in the RF (attend RF condition) and in the attend-away condition. The AMI was then computed as the difference between these two responses, divided by their sum: AMI = (pair response, attention to the probe − pair response with attention away) / (pair response, attention to the probe + pair response with attention away). The AMI can range between −1.0 (which would occur if attention to the probe stimulus in the RF completely suppressed the response to the pair) and +1.0 (which would occur if the cell only responded when attention was directed to the probe stimulus in the RF). A value of 0 would indicate that attention had no effect on the response to the pair.

As illustrated in Figure 4, attention to the probe stimulus consistently caused the pair response to move toward the probe response. For the subset of cells that strongly preferred the reference stimulus, attention to the *poor* probe caused a significant *reduction* in pair response, at all five levels of contrast, according to a one-tailed t test ($p < 0.05$). For the subset of cells that mildly preferred the reference stimulus, attention caused no significant change at any contrast. For the sample of cells that preferred the probe stimulus, attention to the probe caused an increase in pair response at all contrasts, which was significant in four out of five contrasts ($p = 0.055$ at the highest contrast tested), despite the small sample size ($n = 11$).

The AMI values can be transformed into a percent change measurement, in which the difference between attended and ignored responses is scaled by the size of the ignored response by the following formula: percent change = 100 × 2AMI / (1 − AMI). Applying this formula to the mean AMI values, averaged across contrasts, we derived the mean change in response with attention to the probe. For the most selective subset, attention to the poor probe reduced the response to the pair by 26.2%. For the cells that weakly preferred the reference stimulus, attention reduced the pair response, nonsignificantly, by 0.8%. For the subset of cells that preferred the probe stimulus, attention to the probe increased the response to the pair by 29.1%.

In order to provide a measure of the magnitude of the attention effect in terms of equivalent units of contrast, we computed a complementary index, the Pair-Probe Similarity Index (PPSI), and compared how it changed with both contrast and attention. The PPSI is defined as: 1 − the absolute value of (pair response − probe response), divided by the largest response observed in any experimental condition. Thus, the PPSI ranges from 0, which would occur when the pair and probe responses are the largest and smallest responses observed for the neuron, and 1, which would occur if the pair and probe responses were identical.

Increasing the contrast of the probe stimulus caused the pair response to move toward the response elicited by the probe presented alone, as illustrated in Figures 2 and 3, and also caused an increase in response to the probe alone. As a result of these changes, the responses to the pair and probe alone converged as probe contrast increased, resulting in an increase in the PPSI. This is illustrated in Figure 5A, which shows the distribution of

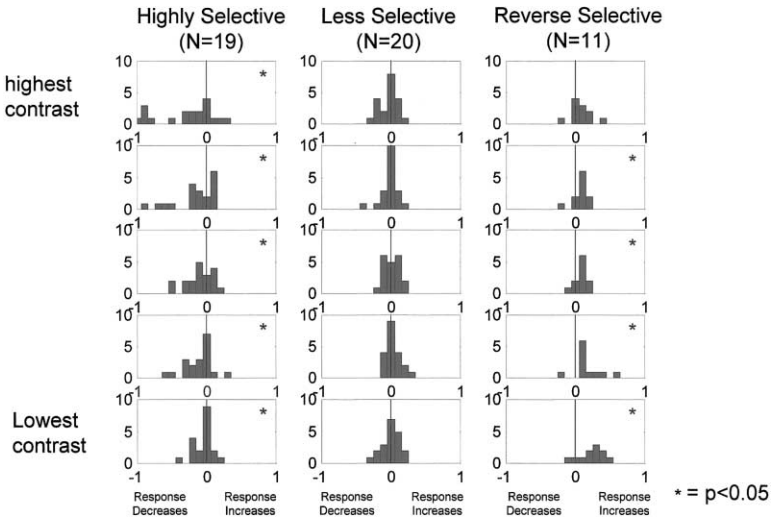

Figure 4. Changes in Response to the Pair when Attention Was Directed to the Probe Stimulus, across Contrasts

Each panel shows the distribution of the Attentional Modulation Index, an index that can range from −1 to 1. Values below 0 correspond to cells for which attending to the probe stimulus reduced the response, while values above 0 correspond to cells for which attending to the probe increased the response. Panels are arranged by rows according to the contrast of the probe stimulus, with the highest-contrast probe appearing at the top of figure, and the lowest-contrast probe appearing at the bottom. Panels are arranged into three columns, each of which corresponds to a subset of neurons, arranged according to their relative preferences for the probe and reference stimuli. The column on the left shows results for cells that responded very poorly to the probe stimulus. For these cells, the AMI was significantly shifted to the left at all contrasts, indicating that attention to the poor probe caused a reduction in the response to the pair. The middle column shows results for cells that mildly preferred the reference stimulus. For these cells, attention to the probe caused no clear change in response to the pair. The column on the right shows results for cells that preferred the probe stimulus. For these cells, attending to the probe caused a significant increase in response to the pair at four contrasts and a marginally significant increase ($p = 0.055$) at the highest probe contrast.

changes in the PPSI when probe contrast was doubled, with attention away from the RF (across all contrast values). The distribution is shifted significantly to the right, according to a one-tailed t test ($p < 0.001$), indicating that increasing the contrast of the probe caused the probe and pair responses to converge, as expected.

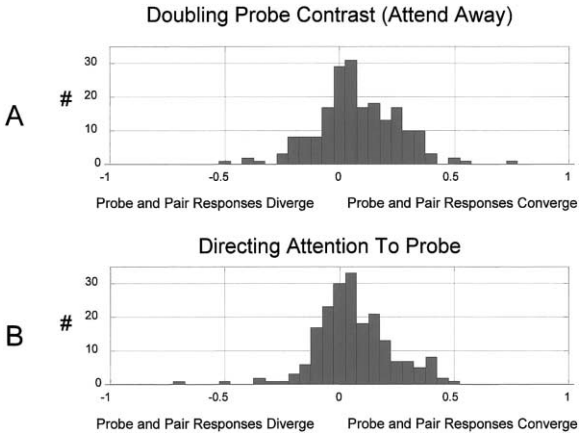

Figure 5. Increases in Similarity of Responses to Probe and Pair, with Increases in Probe Contrast and Attention to Probe

A Probe-Pair Similarity Index (PPSI) was computed for each cell at each level of probe contrast with and without attention to the probe. This index, which can range in value from 0 to 1, provides a measure that indicates how similar were the responses to the probe and pair.

(A) This panel shows the distribution of *changes* in the PPSI when contrast was doubled across all contrasts tested, with attention directed away from the RF. The distribution is shifted to the right, indicating that doubling the probe contrast typically caused the pair and probe responses to become more similar.

(B) This panel shows the distribution of changes in the PPSI (across all contrasts tested) when attention was directed to the probe stimulus and contrast was held constant. The distribution is also shifted to the right, indicating that directing attention to the probe caused the pair and probe responses to converge. The magnitude of the shift with attention to the probe is smaller than the magnitude of the shift with a doubling of contrast, indicating that the effect of attention was smaller than the effect of doubling contrast.

To quantify the effect of attention in units of luminance contrast, we measured changes in the PPSI when probe contrast was held constant and attention was directed to the probe. The distribution of changes in the PPSI with attention to the probe is illustrated in Figure 5B. Attention caused a highly significant increase in PPSI, indicating that attending to the probe, like increasing probe contrast, caused the pair and probe responses to converge. The magnitude of the shift with attention to the probe (median, 0.043; mean, 0.064) was smaller than the shift resulting from doubling contrast (median, 0.064; mean, 0.079), consistent with earlier studies that have estimated the strength of attention in units of contrast, and found that attention is equivalent to increasing contrast by less than a factor of two. The median effect of attention is 0.67 times the effect of doubling contrast (0.67 $\log_2$units, which is equivalent to increasing contrast by 59%), and the mean effect of attention is 0.81 times the effect of doubling contrast (0.81 $\log_2$units, which is equivalent to increasing contrast by 75%). These estimates are similar to those of earlier studies that have quantified the value of attention in units of luminance contrast in V4 (Reynolds et al., 2000) and MT (Martínez-Trujillo and Treue, 2002), which have found that changes in neuronal response rates with attention are equivalent to increasing luminance contrast by 50%–79%.

The results presented so far indicate that when two stimuli appear together within the RF, the higher-contrast, but nonpreferred, probe stimulus suppresses the response to the lower-contrast but preferred stimulus. If the suppression is trigged by inputs to the cell that are driven by the probe stimulus, then the timing of suppression should be dependent on the timing of the response to the probe stimulus alone at each of the different contrasts. To examine this, we compared the time course of the response elicited by the poor probe and by the pair, averaged across the 39 neurons that responded

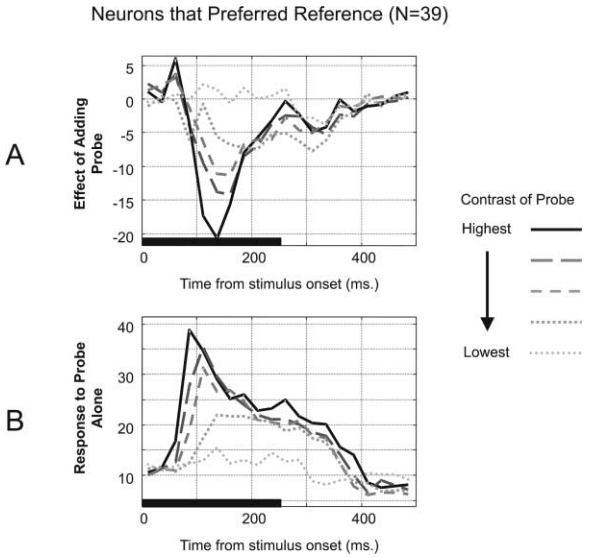

Figure 6. Suppression by Poor Probe, and Probe Response

(A) Response elicited by the pair of stimuli minus the response elicited by the reference stimulus alone, averaged across the population of 39 neurons that preferred the reference stimulus to the probe, at equal contrast. Negative values indicate that the addition of the probe suppressed firing rate, relative to when the reference stimulus appeared alone.

(B) Average response to the probe stimulus alone. Line type indicates contrast of the probe stimulus in both panels. The suppressive effect of the probe and the response to the probe, presented alone, both increase with contrast. Both response latency and the time course of suppression are delayed at low contrast, with suppression lagging behind the time of the response to the probe stimulus presented alone. These averages are computed from responses recorded when the monkey attended to the variable contrast stimulus. A similar pattern was observed when attention was directed away from the RF, though the magnitude of suppression was smaller.

selectively to the preferred reference and poor probe stimulus. The results are illustrated in Figure 6. The response to the probe alone (Figure 6B) decreased in both latency and time-to-peak as the contrast of the probe was increased. Likewise, the suppressive effect of the probe appeared to occur earlier in time as probe contrast increased, although the peak suppressive effects appeared to occur later than the peak excitatory response to the probe alone. This delay in the peak suppressive effect is consistent with the idea that input from the probe stimulus triggers suppressive competitive interactions, but that competition takes time to resolve.

To estimate the lag between the response to the probe presented alone and the suppressive effect of the probe, we performed a correlation analysis (see Experimental Procedures). Briefly, for the 39 neurons that preferred the reference stimulus, we computed the crosscorrelation coefficient between (1) the average response to the probe and (2) the average suppression caused when the probe was added to the reference stimulus. The correlation coefficient was computed as a function of the relative temporal lag between the response and the suppression caused by the probe. This yielded a curve whose negative peak corresponded to the temporal offset that best matched the time course of the probe response with the time course of suppression.

The results are illustrated in Figure 7 for both the attend-away (left) and attend-RF (right) conditions. The dark line corresponds to the highest-contrast poor stimulus, with each lower contrast level being represented by a curve with a slightly shallower negative peak. With the exception of the lowest contrast stimulus, which did not elicit a response, the negative peaks are offset by between −17 and −27 ms (mean offset 23 ms ± SEM 1.3 ms), indicating that suppression consistently lagged behind the probe response. These lags do not appear to be systematically related to the level of contrast, and they are similar in both attention states.

Discussion

Summary

These results support the proposal that when multiple stimuli occupy the RF, both bottom-up differences in stimulus strength and attention-induced changes in *effective* stimulus strength influence automatic competitive mechanisms in area V4. These automatic competitive mechanisms were evidenced by suppression caused by a poor stimulus when it was added to a preferred stimulus in the RF, even when attention was directed away from the RF. Suppression was greatest for neurons that showed the greatest response difference between the good and poor stimulus, measured at equal contrast. For these neurons, increasing the contrast of the poor stimulus or directing attention to the poor stimulus led to greater suppression. When attention and higher contrast both favored the poor stimulus, it exerted almost complete control over the neuronal response, effectively eliminating the influence of the preferred stimulus. The fact that the poor stimulus, which elicited a weak response, dominated the response to the pair of stimuli indicates that it is not simply the stimulus that elicits the higher firing rate that controls the cell's response to the pair. When attention was directed to the lower-contrast poor stimulus, this enabled the poor stimulus to exert greater control over the neuronal response, despite the presence of the higher-contrast preferred stimulus. These data suggest a simple mechanism by which attention selects out behaviorally relevant stimuli, even in the presence of very intense distracter stimuli.

Features and Intensity

These results point to a fundamental distinction between the neural circuitry underlying the processing of stimulus features, such as orientation, and the processing of stimulus intensity, such as luminance contrast. In this and previous studies that have varied stimulus features such as orientation, color, direction of motion, and spatial frequency (Recanzone et al., 1997; Reynolds et al., 1999), it has been found that when a poor stimulus is added to a preferred stimulus in the RF, the resulting suppression is typically greater for a poor stimulus that elicits a very weak response than for a poor stimulus that elicits an intermediate response when presented alone. That is, as the response to the poor stimulus alone *decreased* because it did not contain the cell's preferred features, the suppressive effect of the poor stimulus *increased*. In the present experiment, when we held features constant and increased the intensity of

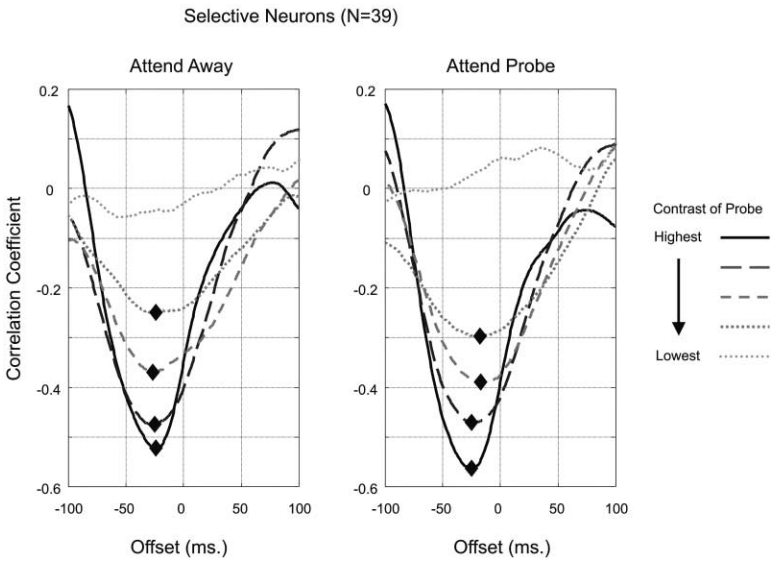

Figure 7. Comparison of the Time Courses of Suppression and Probe Stimulus Response

Each panel shows a plot of the crosscorrelation coefficient between the response to the poor probe stimulus and the suppression caused when the probe was added to the reference stimulus, as a function of their temporal offset. See text for more details of analysis. Responses are averaged from the 39 neurons that responded selectively to the poor probe and preferred reference stimulus. The contrast of the probe is indicated by line type, as indicated in the key on the right. The negative peak of each curve (indicated by the dot) corresponds to the temporal offset at which the probe response and suppression were most strongly anticorrelated with one another. The left panel shows this measure when the monkey was attending away from the RF. The right panel shows the corresponding measure when the monkey attended to the poor probe stimulus in the RF. For all cases except the lowest contrast tested (which did not result in clear response or suppression), the best offset falls between −17 and −27 ms (mean 23 ms), indicating that suppression by the poor probe lagged behind the time at which the probe would elicit a response, if it were presented alone.

the poor stimulus, the response to the poor stimulus presented alone *increased*, and the suppressive effect of the poor stimulus also *increased*. These opposite effects of stimulus features and stimulus contrast are both in agreement with the biased competition model, in which stimulus features and stimulus intensity play separate roles in determining the neuronal response. According to the model, as one alters the features of the added probe stimulus to make it a poorer one for the cell, this causes its contribution to the total mix of excitation and inhibition to be more inhibitory, reducing the response to the pair. As the poor stimulus increases in contrast, this biases competition in favor of the population of neurons that respond to the poor stimulus, resulting in a decrease in response among neurons that respond to nearby competing stimuli.

Response Gain versus Contrast Gain

It has recently been proposed that attention operates by increasing neuronal firing rates by a gain factor. Consistent with this proposal, several studies have found that when attention is directed to a single stimulus in the RF, this causes responses to stimuli of different orientations, colors, and directions of motion to grow in proportion to one another (McAdams and Maunsell, 1999; Treue and Martínez-Trujillo, 1999). The biased competition model proposes instead that attention magnifies the effective salience of stimuli, and that this has three effects on neuronal responses. First, attention causes a leftward shift in the contrast response function, causing subthreshold stimuli to elicit a response when they are attended (Reynolds et al., 2000; see also Martínez-Trujillo and Treue, 2002, who have found related changes in contrast gain with attention in area MT). This prediction is inconsistent with models in which increased attention simply multiplies firing rates, because there is no firing rate gain factor that can be applied to cause a subthreshold stimulus to elicit a response. Second, according to the biased competition model, the change in effective contrast with increased attention increases firing rates for all individual stimuli, resulting in a gain change in the tuning curve for individual stimuli (Reynolds et al., 2000). Finally, and most critically, when two stimuli appear together in the RF, the attention-dependent increase in salience is predicted to bias responses toward the higher-contrast stimulus. This results in a reduction in response when attention is directed to the poor stimulus in the pair (Reynolds et al., 1999), a result which is not predicted by models that simply posit an increase in the firing rate gain for the attended stimulus in the pair. The biased competition model also predicts that increasing the luminance contrast of a poor stimulus will cause the neuronal response to a good stimulus in the RF to be driven downward, even in the absence of attention to either stimulus in the RF. The results of the present experiment are consistent with this prediction.

Salience and Visual Search

Lesion studies have found that area V4 plays an important role in selecting low-salience stimuli out from arrays of high-salience distracters (Schiller and Lee, 1991; Schiller, 1993; DeWeerd et al., 1999). With lesions in area V4, monkeys have great difficulty discriminating a low-salience stimulus when it is presented together with high-salience distracters, despite only modest impairments in identifying the same low-salience stimulus when it appears alone. The present results offer a possible explanation for these findings, namely that V4 selects low-contrast targets from among nearby high-contrast distracters by boosting the effective salience of the attended stimulus so that it can have greater influence over neuronal responses. In the absence of V4, the visual system evidently is unable to bias competition in favor of the discriminandum, making it difficult for the monkey to determine its orientation when it is presented with high-contrast distracters.

In a related study, Braun (1994) found that when human subjects were asked to search for a salient target

among less salient distracters, all at an extrafoveal location, their performance was only moderately impaired by requiring them to perform an attention-demanding task at the fovea. Subjects then performed the same search task, but with a low-contrast target among high-contrast distracters. After equating performance by increasing stimulus presentation times in this second task, Braun measured the effect of adding the foveal task. Performance with a low-contrast target was devastated when attention was directed away from the search array by the foveal task.

In the present experiment, in the absence of attention, neuronal responses were determined preferentially by the higher-contrast stimulus in a pair of stimuli. Thus, in a search task in which the target is more salient than the distracters, attention should not be needed to bias competition among stimuli in favor of the target. In such a task, the bottom-up bias of stimulus salience would already shift control to the target, rendering attention unnecessary. However, in a search task in which the target is less salient than the distracters, attention is needed to shift control of visual processing to the target. Therefore, if attention were directed away from such a search task, the high-contrast distracters would drive V4 neurons, and any target, if present, would be filtered out of visual processing, reducing performance.

Timing of Suppression

The latency of the suppressive effect caused by adding a poor stimulus to a preferred stimulus in the RF was longer than the latency of response to the poor stimulus presented alone, even when the poor stimulus was attended. High-contrast stimuli have shorter neuronal response latencies than do low-contrast stimuli. Therefore, the initial neuronal response to a pair of stimuli was determined by the higher-contrast stimulus of the pair, even if that stimulus was ignored. The effect of attention was to magnify the suppressive influence of the poor stimulus later in the response to the pair, which began approximately 23 ms after the poor stimulus would have excited the neuron had it appeared alone.

By the late phase of the response to the pair, the attended poor stimulus exerted substantial control over the neuronal response, even when it was presented at one half the contrast of the preferred stimulus. This may provide a partial explanation for the results of psychophysical studies showing that salient targets are particularly effective at "capturing attention," especially when they appear suddenly (Theeuwes, 1994; Irwin et al., 2000; but see Yantis and Hillstrom, 1994).

This delay is similar to delays that have been reported for center-surround interactions in primary visual cortex (Knierim and van Essen, 1992; Nothdurft et al., 1999). Allman et al. (1985) found that responses to sustained motion in the classical receptive field of MT neurons are suppressed by the addition of a motion stimulus in RF surround and estimated that the onset of this suppression was delayed by approximately 40 ms relative to the onset latency for the RF stimulus.

The Possibility that Distracters Attracted Attention

Many behavioral studies have reported evidence that endogenously cued attention can be drawn away by the appearance of a salient distracter, although this may be minimized with a high task load at the attended location (Rees et al., 1997). We cannot exclude the possibility that some degree of attention may have been allocated to the unattended location in the present study. To the extent that the high-contrast reference did draw some attention away from the endogenously cued low-contrast probe stimulus, this would have resulted in a reduction in its ability to control the neuronal response, causing us to underestimate the strength of the attentional effect. Our estimate therefore represents a lower bound on the true size of the attention effect.

However, several considerations lead us to conclude the distracters were not very effective at drawing attention away from the cued location. First, distracters appeared in both sides of fixation, thereby neutralizing any tendency to draw attention to one or the other side of fixation. Second, the task we used was difficult, with a high attentional load. The animal rarely responded with false alarms to stimuli at the unattended location and rarely missed a target except when it was very low contrast.

The strongest evidence that attention was not inadvertently misdirected to the uncued high-contrast distracter is based on the timing of the attention effect. Suppose the high-contrast uncued reference stimulus had attracted the monkey's attention. Then, even though the monkey was instructed to attend to the low-contrast probe, reallocation of attention following the appearance of the high-contrast reference stimulus in the RF would eliminate the effect of this instruction, with a delay reflecting the time necessary to reallocate attention. In fact, we find the opposite pattern of results. Attention had little or no influence on firing rates at the very beginning of the response to the pair, only emerging later in the response when, according to the above explanation, it should have disappeared. Therefore, it is unlikely that the monkey inadvertently attended to the uncued high-contrast reference stimulus in the receptive field.

Related Models

The biased competition model is related to other models that assume the existence of shunting inhibition. Such models have been used to account for changes in sensitivity to luminance (Sperling and Sondhi, 1968). They have also been used to explain a number of effects of contrast on responses in primary visual cortex, including contrast normalization and contrast-independent feature tuning (Grossberg, 1973; Albrecht and Geisler, 1991; Heeger, 1992), reduced onset latencies with increasing contrast, and contrast-dependent crossorientation inhibition (Carandini et al., 1997). Models that do not assume shunting inhibition have also been proposed to explain some of these effects (e.g., Kayser et al., 2001).

All of these models are, of course, only rough approximations to the true underlying neuronal circuitry. However, the ability of such simple models to account for such a broad variety of response properties is encouraging. That they can account for contrast normalization in primary visual cortex and also explain a variety of data on attentional modulation in area V4 suggests that that extrastriate cortex has coopted circuits that may initially have developed to maintain neuronal selectivity across

a wide range of visual input intensities. Consistent with this, Britten and Heuer (1999) have used a similar normalization model to account for their finding that when two excitatory stimuli appear together within the RF of an MT neuron, the response to the pair is less than the sum of the responses to the two individual stimuli.

Experimental Procedures

Subjects and Surgical Techniques

Two adult male rhesus monkeys were cared for according to NIH guidelines. Many of the details of the surgical techniques have been described previously (Reynolds et al., 1999). Briefly, monkeys were surgically implanted with a head post, a scleral eye coil, and a recording chamber. Surgery was conducted under aseptic conditions with isoflurane anesthesia. Preoperative magnetic resonance imaging (MRI) was used to identify the stereotaxic coordinates of V4 on the prelunate gyrus, which was then covered by a recording chamber.

Confirmation of Recording Sites

At the beginning of the study, several penetrations were made in each chamber to ensure that the electrode was in the appropriate part of V4 based on RF size, topographic organization, and feature preferences at each site. All implants were nonferromagnetic, and after our experimental data were collected, we verified the locations of our recording sites using additional MRI scans with a marker electrode in the cortex, as described previously (Reynolds et al., 1999).

Task

Monkeys fixated a small ($0.1^\circ \times 0.1^\circ$) spot at the center of a computer screen throughout each trial. Fixation was measured using a scleral eye coil, and trials were terminated if eye position deviated from fixation by 0.6° or more. On each trial, sequences of stimuli appeared synchronously either at one or at two locations inside the RF, and at one or two mirror symmetric positions across the vertical meridian from the RF (see Figure 1).

The task was to detect the appearance of a diamond-shaped target stimulus appearing at the end of the sequence at one of the locations. The location where the target would appear was indicated by a white cue box that appeared during instruction trials at the beginning of a block of trials. Distracter targets, or "foils," occasionally appeared at the noncued locations, and the monkey had to ignore these and continue to await the cued target in order to earn reward.

The monkey received a juice reward if it released the bar within 200–500 ms after target onset. If the monkey released the bar outside of this 300 ms time window, or failed to release the bar when the cued target appeared, the computer screen went blank, and after a brief delay, a new sequence began.

The number of stimuli appearing on a given trial was selected at random from a uniform distribution of 1–6 elements, with the final element including a target stimulus at the cued location. Monkeys could not know in advance when a target would appear. Therefore, they had to attend to the cued location throughout the trial in order to detect the target, release the bar, and earn reward. The period of time between successive stimulus onsets (Stimulus Onset Asynchrony, SOA) varied across a uniform distribution from 650 to 800 ms. While SOAs varied randomly for each stimulus, onset times were matched across locations, so stimuli appeared synchronously.

When attention was cued to a stimulus in one hemifield, foils could appear at any of the other stimulus locations where nontarget stimuli appeared during the trial. When a distracter appeared, it took the place of one of the nontarget stimuli that would otherwise have appeared in the stimulus sequence. When the distractor appeared, its onset and offset were identical to the nontarget stimuli appearing elsewhere on the monitor. Distracters only appeared prior to the appearance of the target. Our analyses exclude stimulus presentations in which a distracter was present anywhere in the visual field.

Once the monkey was responding reliably to targets appearing at the cued location and was ignoring distracter targets at the uncued locations, the cue was removed and the monkey had to continue to perform the task in the absence of the cue. Occasionally, monkeys responded to several distracter targets in a row, indicating that they had misunderstood or forgotten the location of the cue. When this occurred, we immediately terminated the block of trials and recued the monkey to attend to the correct location.

Across trials in which the monkeys did not break fixation, they almost always detected and responded to high-contrast targets. At lower contrast, performance declined. The percentage of trials on which the monkeys correctly detected the target, arranged from highest-contrast to lowest-contrast target, were 95%, 97%, 79%, 79%, and 44%. This decline was almost entirely due to an increase in the failure to detect the low-contrast target. The percentage of trials on which the monkeys missed the target were 4%, 2%, 20%, 21%, and 55%. Monkeys incorrectly responded to distracter targets (i.e., made false alarms) on 1% or fewer of all trials regardless of target contrast.

Stimuli

All stimuli were 250 ms in duration. Nontarget stimuli were rectangular patches of sinusoidal luminance grating, typically about 0.4° wide by about 1.5°–2° in length, at one of four orientations (vertical, 45°, horizontal, or 135°), with spatial frequencies of 0.5, 1, 2, 4, or 8 cycles/degree. For each neuron, we attempted to identify a pair of nontarget stimuli in this set to which the neuron responded selectively. One of these two stimuli, which would remain at fixed contrast throughout the experiment, we designated as the "reference stimulus." The other stimulus, whose contrast was variable, we designated as the "probe stimulus." Typically, the reference stimulus was of the preferred orientation and spatial frequency for the neuron, and the probe was of a nonpreferred orientation and spatial frequency. However, we occasionally recorded simultaneously from pairs of neurons with different stimulus selectivity, and we selected the reference and probe stimuli according to the selectivity of one of the two neurons. As a result, for some neurons the probe stimulus was of a more preferred orientation and/or spatial frequency than the reference stimulus. Targets and distracters were square patches of grating that were typically 1.5° in length and width rotated to be 45° from the orientation of the probe stimulus, and of the same spatial frequency as the probe.

During the attention task, the luminance contrast of each successive probe and of the target stimulus were chosen at random from a set of five possible contrasts, after linearizing the color lookup table with a photometer. Typically, contrasts were 5%, 10%, 20%, 40%, and 80%, where % contrast = (maximum luminance − minimum luminance) / (maximum luminance + minimum luminance). The contrast of the reference stimulus remained fixed throughout a recording session and was equal to the second highest contrast of the probe stimulus (typically 40%). Because the target contrast was selected randomly on each trial, the monkeys did not know the contrast of the target until the end of the trial. Thus, attention effects for nontarget stimuli cannot reflect variation in effort with target contrast.

Analysis of Neuronal Responses

Responses were analyzed only for correctly performed trials, excluding instruction trials. All data analysis was restricted to nontarget stimuli because neuronal responses to target stimuli were typically interrupted by the behavioral response or the delivery of reward, which only occurred (on correct trials) after the appearance of the target. In addition, the larger number of nontarget stimuli provided a more reliable measure of response strength.

Firing rates were averaged over the period from 70 to 400 ms following stimulus onset. This time window was selected because it encompassed the entire response for most neurons. We also analyzed data using a window of 30–300 ms, and this did not substantially alter our results. Selectivity was defined as the response to the probe stimulus minus the response to the reference stimulus at equal contrast, divided by the strongest response to probe, reference, or pair, in either attention condition.

To identify neurons whose responses changed significantly when the probe was added, we performed a one-way ANOVA of the firing rate elicited by the pair, as a function of probe stimulus contrast

level (from 0 = absent to 5 = highest contrast tested). To compare the timing of the excitatory response to the (poor) probe alone with the timing of suppression caused by adding the (poor) probe to the (preferred) reference stimulus, we performed the following correlation analysis. At each level of contrast, we computed the average firing rate elicited by the probe stimulus, at 1 ms resolution. We then computed the average difference in response between the reference stimulus and the pair (i.e., the change in firing rate caused by the addition of the probe), also at 1 ms resolution. We then shifted these two vectors relative to one another across a range of ±100 ms in steps of 1 ms. For each step, we calculated the crosscorrelation coefficient between the overlapping parts of the shifted vectors. This resulted in a curve whose negative peak corresponded to the temporal offset at which the time course of the response to the probe best matched the time course of its suppressive effect (see Figure 7). The peak was negative because the probe presented alone caused a positive response, while the suppressive effect of adding the probe to the reference stimulus was a decrease in response. To reliably estimate the peak of this curve, we smoothed it with a Gaussian kernel of 25 ms standard deviation and computed the negative peak of the resulting smoothed curve.

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