Attention Modulates Contextual Influences in the Primary Visual Cortex of Alert Monkeys

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Summary

The response properties of cells in the primary visual cortex (V1) were measured while the animals directed their attention either to the position of the neuron's receptive field (RF), to a position away from the RF (focal attention), or to four locations in the visual field (distributed attention). Over the population, varying attentional state had no significant effect on the response to an isolated stimulus within the RF but had a large influence on the facilitatory effects of contextual lines. We propose that the attentional modulation of contextual effects represents a gating of long range horizontal connections within area V1 by feedback connections to V1 and that this gating provides a mechanism for shaping responses under attention to stimulus configuration.

Introduction

The attentional modulation of contextual influences seen in psychophysical experiments (Ito et al., 1998) can be interpreted as operating selectively on the interaction between the receptive field and its surround. The contextual modulation of cells' responses has been shown to endow them with a sensitivity to the global context within which features are embedded. The influences grouped under the rubric of the "nonclassical receptive field" have been implicated in a number of roles in intermediate level vision, from contour integration (Kapadia et al., 1995) to perceptual fill-in, surface segmentation, and orientation contrast (Blakemore and Tobin, 1972; Maffei and Fiorentini, 1976; Nelson and Frost, 1978; Allman et al., 1985; Nothdurft and Li, 1985; Tanaka et al., 1986; Orban et al., 1987; Gilbert and Wiesel, 1990; Knierim and Van Essen, 1992; Li and Li, 1994; Lamme, 1995; Sillito et al., 1995; Rossi et al., 1996; Zipser et al., 1996; Kastner et al., 1997; Levitt and Lund, 1997).

The contextual influence that is the focus of this study is the interaction between nearby collinear line segments, which has been proposed to play a role in contour saliency (Wertheimer, 1938; Ullman, 1990; Field et al., 1993; Kapadia et al., 1995). The cortical interactions underlying contour saliency may be found within primary visual cortex (V1). In V1, long range horizontal connections run between columns of similar orientation preference and between cells with widely separated receptive fields, therefore having characteristics consonant with

the properties of salient contours. These interactions are manifest at the cellular level in the facilitation by lines lying outside of the classical receptive field when presented simultaneously with a collinear line segment lying inside the receptive field center (Kapadia et al., 1995).

Attention may be directed either toward a location in space or toward particular objects or stimulus configurations. Object-oriented attention is related to perceptual learning, in that improvement in the discriminability of visual stimulus attributes is intimately related to the configuration within which the discriminated feature is presented. The specificity for visual field location of perceptual learning seen in psychophysical studies suggests involvement of early stages in visual cortical processing. The further specificity for stimulus configuration suggests a possible interaction between top-down influences and these early levels (Shiu and Pashler, 1992; Treisman et al., 1992; Ahissar and Hochstein, 1993; Fahle and Morgan, 1996; Crist et al., 1997; Ito et al., 1998).

Visuospatial attention has been shown to affect the response properties of cells at many cortical stages along the visual pathway. A growing body of physiological evidence shows that visuospatial attention changes neuronal activities at various levels of cortical visual pathways both in humans and monkeys, including areas in the dorsal and ventral streams of visual processing (for review see Desimone and Duncan, 1995; Hillyard et al., 1995; Maunsell, 1995). There has been some dispute concerning the existence of attentional modulation as far back in the visual pathway as the primary visual cortex (Wurtz and Mohler, 1976; Haenny and Schiller, 1988; Motter, 1993; Luck et al., 1997a; Vidyasagar, 1998). The fact that the effects of context are reflected in the activity of cells in primary visual cortex (Kapadia et al., 1995), however, suggests that the change in contextual influences with attentional state might be manifest there as well (Ito et al., 1998). In this study, we concentrated on attentional modulation in the superficial layers of primary visual cortex.

Since the effects of visuospatial attention are subject to learning, the relative influences of focal and distributed attention may vary from subject to subject. In studies involving awake monkeys trained to do a discrimination task, the physiology inevitably reflects a measure of perceptual learning. We make use of this individual variation to help establish the correlation between attentional effects observed in psychophysical experiments and the response properties of cells in primary visual cortex.

Results

In an earlier psychophysical study (Ito et al., 1998), we reported that brightness discrimination thresholds and facilitation by collinear flanking lines are modified by visuospatial attention and that the attentional effects are dependent on perceptual learning, both in human subjects and monkeys. The object of these experiments

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was to explore the effects of visuospatial attention on the contextual modulation of responses in primary visual cortex and to compare these effects with attentional modulation of classical response properties. The animals were trained and their performance was studied as described in the previous paper (Ito et al., 1998). They were trained to operate under two attentional states: either "distributed attention," in which they were cued to attend to all of four stimuli, or "focal attention," in which they were cued to a single stimulus among the four (Figure 1). With respect to the receptive fields of individual cells, one could distinguish between locations of focal attention: one in which the animal attended to the receptive field location and one in which the animal attended to positions away from the receptive field. The cue was always delivered well in advance ($\sim$1 s) of the stimulus presentation and was not part of the stimulus itself.

The task engaging the animal's attention, and the probe for measuring the effect of attention, was a comparison of the brightness of a reference line presented near the fixation point with one of four target lines presented at the 45/135/225/315° meridia, each at an eccentricity of 3.5°. During the recording sessions, one test line was placed within the RF location and the others were placed symmetrically around the fixation point, as shown in Figure 2. This target line was presented at varying contrasts bracketing that of the reference line, the other three being kept at the same contrast as the reference. We refer to this array as the "stimulus configuration." The subject had to judge whether the target line was brighter or dimmer than the reference line. In order to measure contextual effects, a set of flanking lines was added to the basic four line pattern, as shown in Figures 1A and 2A. The identical configuration was used for all attentional conditions. In the focal attention trials, the monkey was cued to which of the four peripheral lines was the target line during that exposure; in the distributed attention trials, any of the four could be the target. Trials for the different attentional conditions were randomly interleaved. Each trial contained a random number of stimulus presentations, varying from one to six; in the last trial, the stimulus array contained the target with the changed brightness, which served as the basis for the subject's response. Since the animal did not know a priori which was to be the last until the saccade targets were presented, he had to perform the discrimination task on all of the stimuli in the series.

After the monkeys were well trained to perform the brightness discrimination task, we studied neuronal responses of superficial layer complex cells in area V1. For every cell, before examining the effects of attention, a series of baseline experiments were performed under fixation trials (without cueing the animal to attend to the periphery) to measure the standard properties of receptive field position, size, and orientation. Then we studied neuronal responses while the monkeys performed the brightness discrimination task, in which target lines were presented in four positions (in subsequent experiments on the second monkey, targets were presented in six positions). One line segment (the target line) was presented within the receptive field at the cell's optimum orientation. The other lines were located symmetrically around the fixation point, as shown in Figure
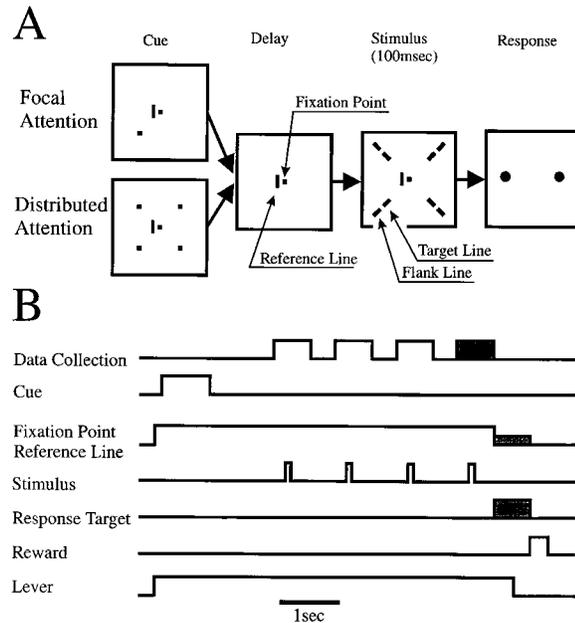

Figure 1. Presentation of Attentional Cues and Visual Stimuli

(A) Stimuli and sequence of presentations with a standard stimulus pattern. Lines were bright against a dark background. Each trial was initiated when the monkey pulled a lever. The subject fixated the central spot (fixation point) and had to judge whether the target line was brighter or dimmer than a reference line adjacent to the fixation point. The luminance of the target line was selected from seven levels including that of the reference line. In the focal attention trials, the monkey was cued to which of the four peripheral lines was the target line during that exposure; in the distributed attention trials, any of the four could be the target. The identical stimulus pattern was presented in the two sets of trials. To examine the contextual effect, there was a set of flanking lines in addition to a basic pattern. The animals were trained to ignore the flanking line in performing the visual discrimination task, and trials with and without flanking lines were randomly interleaved. During the response period, two response targets were presented. The animal reported his judgement by making a saccade to either response targets. The left target was brighter than the other target and was used to indicate a judgment that the target line was brighter than the reference.

(B) Diagram illustrates the sequence of events in a trial. The fixation spot and reference line were presented first, allowing the monkey to stabilize fixation before the cue spots were presented. The cues indicated to which of four sites the monkey had to attend during focal attention trials or signaled all four stimulus positions for distributed attention trials. In each trial, several stimuli were presented after one cue presentation. The number of presentations was randomly varied from one to six. For physiological recordings, we modified this task: for all but the last stimulus presentation, the luminance of all four test lines were similar to that of the reference line. In the last stimulus presentation of the discrimination trials, data collection was canceled, and brightness of the target line was changed. In the fixation trials, the reference line was not shown, and the fixation point was dimmed after the last stimulus presentation instead of presenting the response targets. Animals were rewarded when they released the lever immediately after the fixation spot dimmed.

2A. A second line segment, presented alone and outside the receptive field, elicited no response. When the two stimuli were presented together, however, the cell's response was often increased substantially, by as much as a factor of 3.

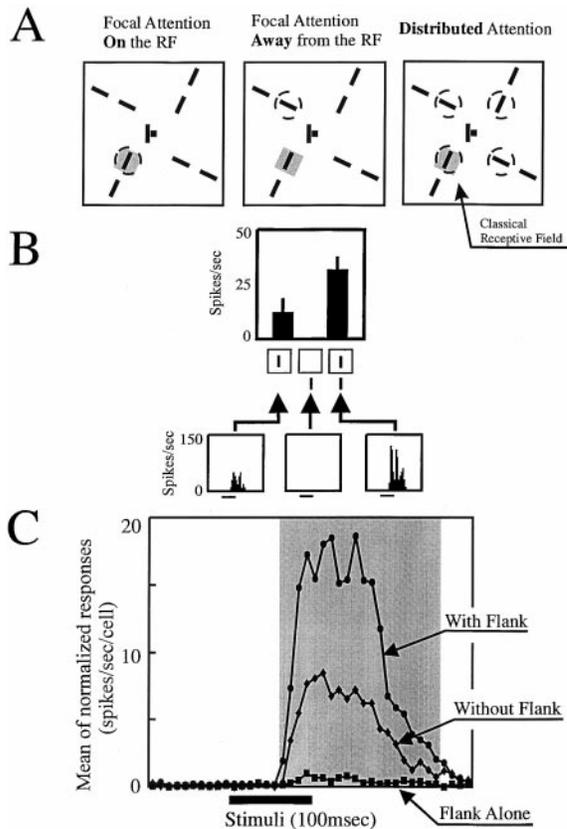An example of the kind of contextual facilitation seen

Figure 2. Contextual Facilitation in Neuronal Responses in the Primary Visual Cortex

(A) Contextual facilitation was examined under three attentional states. Gray squares indicate the classical receptive field (RF) of the cell. Dotted circles indicate attended locations. One of four test lines was presented within the classical receptive field of the cell, and the other lines were presented symmetrically around the fixation point.

(B) Typical results in one unit recording. The size of the contextual influence was measured by comparing a cell's response to a test line presented within the classical receptive field (left response histogram and first bar in bar graph), its response to a flanking line placed outside the receptive field (middle response histogram and middle bar in bar graph) and its response to the two lines presented together (right response histogram and right bar in bar graph). The fact that the flanking line lay outside the receptive field was confirmed by the fact that the response was indistinguishable from spontaneous levels of activity.

(C) Averaged response histograms among all cells that showed significant contextual facilitation in any attentional condition (86 cells). The response to contextual stimuli at the relative angle and attentional state showing the highest facilitation was selected for each cell. Before averaging, the response was normalized so that the area (total spike number during the recording period) under the without-flank response would equal 1.0. The facilitation extended throughout the entire time course of the cells' responses. Response to contextual stimuli at the relative angle and attentional state showing the highest facilitation was selected for each cell. Bin size is 10 ms width. The black underlining indicates stimulus presentation time. Significant facilitation ($p < 0.05$, t test) was observed during the period indicated by the gray bar.

in this study is shown in Figure 2. For each cell, the receptive field size was measured by the minimum response field technique, and because of variability in eye fixation, this would represent an overestimate. Even

though the contextual line by itself produced no response, it increased the response to the target line over 2.5-fold (Figure 2B). The time course of the facilitation followed that of the responses themselves. Over a population of 86 cells showing facilitation in any attentional condition, the increased response induced by a contextual line began at the outset of the response and was maintained during the entire time course of the response (Figure 2C; the gray bar indicates period during which statistically significant facilitation was observed).

Statistically significant facilitation ($p < 0.05$, Kolmogorov-Smirnov test) was observed in 86 cells (37%) out of 230 cells included in this study. Single and multiunit recordings comprise approximately equal fractions of the total pool and showed similar results. No significant change was observed in 75 cells (33%) and inhibition in 69 cells (30%). Of the cells included within the facilitatory group, 34 cells showed both facilitation with one stimulus configuration and inhibition with another. We also studied contextual influences before monkey UM received training in the brightness discrimination task. When the monkey performed the fixation task, 24 cells out of 81 cells (30%) showed significant facilitation. This is comparable to the effects seen after training and to the previous study, in which dim test lines were presented in fixation trials (123 cells out of 291 cells, 42%; Kapadia et al., 1995).

Figure 3 shows an example of the effects of attention on contextual modulation. The receptive field profile was measured by placing a single 0.45° bar at various positions along the orientation axis of the cell (Figure 3A), which in the example shown gives a measure of receptive field length of 0.91° (known as the minimum response field). The target (within the receptive field) stimulus used was 0.45° long. The contextual stimulus, also 0.45° long, was placed 0.91° from the first bar (center to center spacing), 0.23° from the edge of the receptive field (at its closest point). The separation between the target and contextual bars ensured that the latter was well outside the boundary of the classical receptive field. The target line was placed in the center of the receptive field, where the response was highest.

The attentional modulation of this cell's response is shown in Figure 3B. The three attentional regimes were randomly interleaved from trial to trial. The strongest contextual facilitation was seen under focal attention on to the receptive field position, with a 3-fold increase in the cell's response. This facilitation disappeared under distributed attention and under focal attention away from the receptive field position. To check for possible artifacts due to differences in eye position under the different attentional conditions, we recorded eye position during these trials. For each stimulus presentation, we calculated eye positions relative to the mean eye position under distributed attention. As shown in Figure 3C, the distribution of eye position in the three attentional states overlapped completely, with no significant difference in mean eye position (averaging less than 0.08°) in the three attentional states. Taking the data for one day's recordings and grouping the trials into sets corresponding to the different attentional foci, it was clear that there was no significant bias in fixation position according to the site to which attention was directed
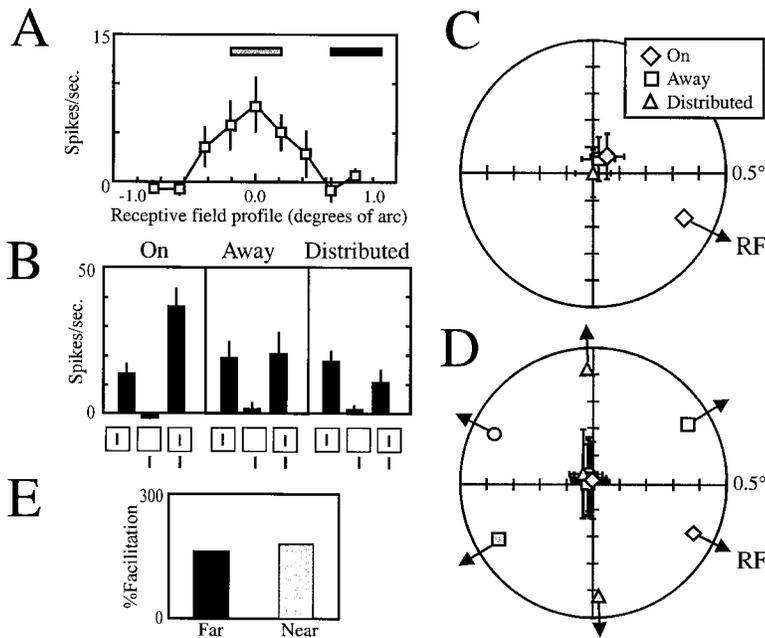
A

B

C

D

E

Figure 3. Measurement of Receptive Field Size, Facilitation, and Eye Position

(A) Measurement of receptive field profile and stimulus placement. A 0.45° length bar was placed at intervals along the orientation axis of the cell's receptive field. In this example, a single bar was placed at half bar length intervals, and significant responses (p > 0.05, Kolmogorov-Smirnov test) were obtained at five locations. This provided a measure of receptive field length of 0.9° (double the bar length) by the minimum response field technique. The target stimulus, 0.45° long, was centered over the position of highest response, and a second stimulus of equal size was placed 0.9° away from the first, with a separation of 0.23° from the edge of the receptive field (at its closest point) to ensure that it would not activate the cell by itself.

(B) Attentional modulation of responses of cell in (A). Contextual facilitation was maximal when the monkey attended to the receptive field position (focal on) and disappeared when the animal distributed his attention to all four sites or attended to positions away from the receptive field. Note that the target-alone response was the same for focal attention on and focal attention away, even though the contextual modulation was very different.

(C) There was no predictive eye drift toward the cued location while we collected the responses shown in (B). The mean eye position under distributed attention is represented as the center of the graph, and the eye positions measured under the other conditions are shown relative to this point. For each attentional state, the averaged position and standard deviation are indicated. The outer circle represents a distance 0.5° from the center. The arrow indicates the direction toward the receptive field (RF) of this cell.

(D) Eye positions measured in the entire day's session, during which we recorded from the cell shown in this Figure. We divided data into six groups for each cued location. Description was same as in (C). Arrow and mark indicate corresponding direction toward cued location. Since the receptive field position was different for each cell, directions toward the receptive field are rotated to the same direction (arrow RF), and the other cued locations are shown relative to the RF direction.

(E) The data shown in (B) (focal on) was divided into two groups, one half taken from trials where the eye fixations were closer to the receptive field of the cell (near) and the other half from trials where the eye was farther from the receptive field (far). Though the eye position in these two groups differed by 0.11°, there was no difference in the degree of facilitation.

(Figure 3D). For the focal attention conditions, the mean (+ standard deviation) size of the bias toward the cued direction was −0.002° + 0.094° (n = 428), as compared with 0.000° + 0.70° under distributed attention (n = 211), which represents no significant difference (t test, t = 0.534, p > 0.05).

In order to evaluate the potential effect of shifts in eye position on our results, we grouped the trials into two sets, one half including the fixation positions closest to the focus of attention, the other half including the positions farthest away. The mean eye positions in these two sets differ by 0.11°, yet, as shown in Figure 3E, the facilitation in these two sets was quite similar. Given that the differences in eye position under different attentional states were less than this, it is unlikely that shifts in eye position could account for the observed effect of attention on facilitation.

Two monkeys, SA and UM, were used in this study. Since the attentional effects observed in the companion psychophysical study were dependent on learning (Ito et al., 1998), it was important to measure the animals' performance at different times during the study. As described in the earlier paper (Ito et al., 1998), the animals' performance was described by a psychometric curve that showed relationships between luminance level of the target line and the frequency of reporting a brighter target. We evaluated two parameters: (1) the threshold of brightness discrimination, which was represented by the inverse of the slope of the psychometric curves for the without-flank trials, and (2) facilitation, which was measured by the leftward shift in the psychometric curve, at the 50% point, from the without-flank to the with-flank trials. In addition to making psychometric curves early in the animals' training (once they understood the task but before extensive training had occurred), we measured the animals' performance several weeks later at the beginning of the physiological part of the study and after the recordings were completed (Figure 4).

In monkey SA, the first data of facilitation was obtained at the eighth week after we began to get reliable behavioral data. Thus, it might be expected from our work with humans that the difference in the magnitude of facilitation between distributed and focal attention had already narrowed at this time. Recordings began at the 32nd week after overtraining. In monkey UM, the first graph was obtained at the first week. Recordings started earlier than with SA, commencing at 6 weeks. Given the earlier stage in training at which recordings had begun for monkey UM, it is likely that the trend of perceptual learning would have continued even after the end of the recording period. As reported in the previous
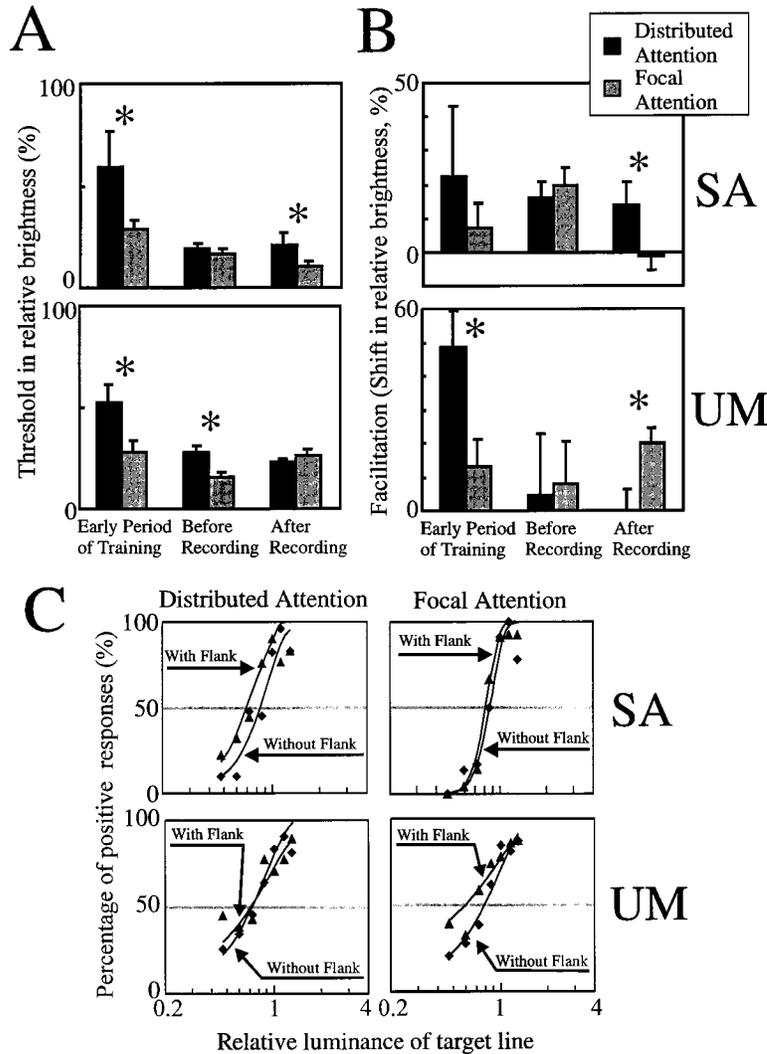
Figure 4. Behavioral Performance of Animal Subjects

The contextual facilitation of two monkeys during training and during recording period. (A) The threshold and (B) the size of facilitation (+ one standard error) is shown for monkey SA (upper row) and monkey UM (lower row). Performance was measured at a point early in training, before recording, and after recording. Perceptual learning reduced contextual facilitation under distributed attention. After the recording, monkey SA showed greater contextual facilitation under distributed attention, and monkey UM showed more facilitation under focal attention. Asterisks indicate where the facilitation was significantly different between the two attentional states, distributed attention (black bars) and focal attention (gray bars).

(C) Psychometric curves taken at the end of the recording period for without-flank (squares) and with-flank (triangles) conditions, under distributed and focal attention, for SA and UM. The abscissa is normalized by the brightness of the reference line.

paper, the difference in the contextual effects observed under distributed and focal attention was greatly reduced by the time recordings began, but the two animals ended with very different behavioral effects. Monkey SA showed greater contextual facilitation under distributed attention, and monkey UM showed more facilitation under focal attention (Figure 4). It is important to keep this difference in mind when viewing the physiological results.

The response properties of representative cells from the two animals are shown in Figure 5. The strengths of the contextual effects were highly dependent on the attentional state of the animal. One cell (cell 1 in Figure 5) showed a three-fold facilitation (184% increase in response) to the contextual stimulus under distributed attention, but this facilitation disappeared entirely (and, in fact, the contextual stimulus became somewhat inhibitory) with focal attention to the receptive field. There was also a substantially reduced facilitation when the animal attended to a location away from that of the receptive field. Another example of this is shown in cell 2, with a 164% facilitation under distributed attention, which was absent under focal attention. While many

cells showed attentionally modulated contextual influences, some showed a greater facilitation under focal attention than under distributed attention (cell 3, 128% facilitation under focal attention). Monkey UM had many more cells showing contextual facilitation under focal attention on the receptive field position than under distributed attention. The example shown in Figure 5 (cell 4) showed a 126% facilitation with focal attention onto the receptive field position, which was greatly reduced with focal attention toward other positions and reduced even further under distributed attention. The remaining examples shown for UM (cell 5 and cell 6 in Figure 5) showed similar tendencies. Cell 6 reversed the sign of the contextual influences from facilitation (360%) under focal attention to inhibition (70%, though not statistically significant) under distributed attention.

In order to evaluate modulation of facilitation by attention, we calculated the modulation index in 86 cells showing contextual facilitation. As shown in Figure 6, the modulation index over the population had a mean of 0.34 ± 0.02 (n = 86). To see how the index would be distributed for an equivalent amount of variation from trial to trial, without any systematic change according
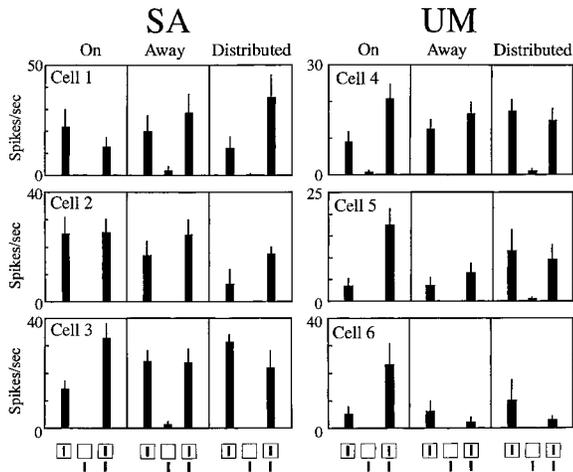
Figure 5. Influence of Attention on Responses of Individual Cells in V1

Attentional state influenced the contextual facilitation in the superficial layers of area V1. Examples of three cells from monkey SA (left column) and three cells from monkey UM (right column). For each cell, the three boxes show the mean firing rates and their standard errors under focal attention on the RF (left box), under focal attention away from the RF (middle box), and under distributed attention (right box). In each box, three responses were shown as in Figure 2.

to attentional state, we made a Monte Carlo simulation of the data. In this simulation, the responses of each cell were pooled and then randomly assigned to one of the three attentional states (e.g., shuffling the data). This yielded an average modulation index of 0.21 ± 0.02. The experimental data and shuffled data were significantly different, at a probability of <0.01 (t test, t = 5.76). Therefore, one can conclude that there was significant attentional modulation of the contextual effects, well beyond that expected from the variability in cell responses. When we performed a similar Monte Carlo analysis of the attentional modulation of the target-alone responses, there was no significant difference relative to the shuffled control.
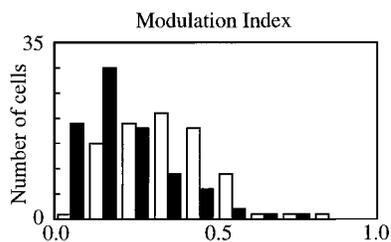

Figure 6. Modulation Index and Attention—Monte Carlo Simulation

Modulation index among three attentional states (see Experimental Procedures for formula). In most cells, contextual modulation was gated by attention (0 indicates no difference between the three attentional states). Gray bars indicate the range of modulation for the cell population studied, with an average modulation of 0.34 ± 0.02 (n = 86). To determine the expected modulation from response variability alone, we performed a Monte Carlo simulation with target alone and target with contextual line trials randomly assigned to one of the three attentional states (black bars). The average facilitation in the simulation was 0.21 ± 0.02 and differed significantly from the experimental data (p < 0.01, t test, t = 5.76).
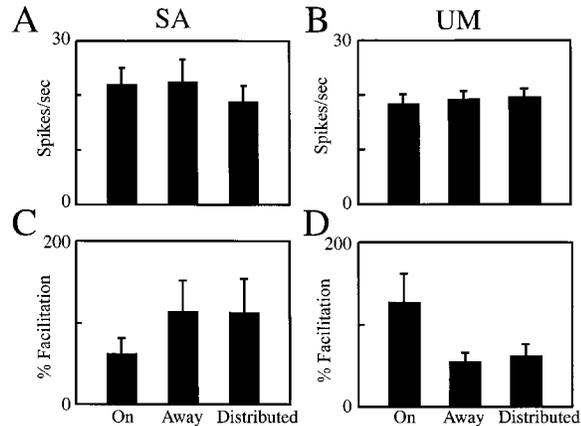

Figure 7. Effect of Attention over the Recorded Population on Test Alone Responses and on Contextual Facilitation
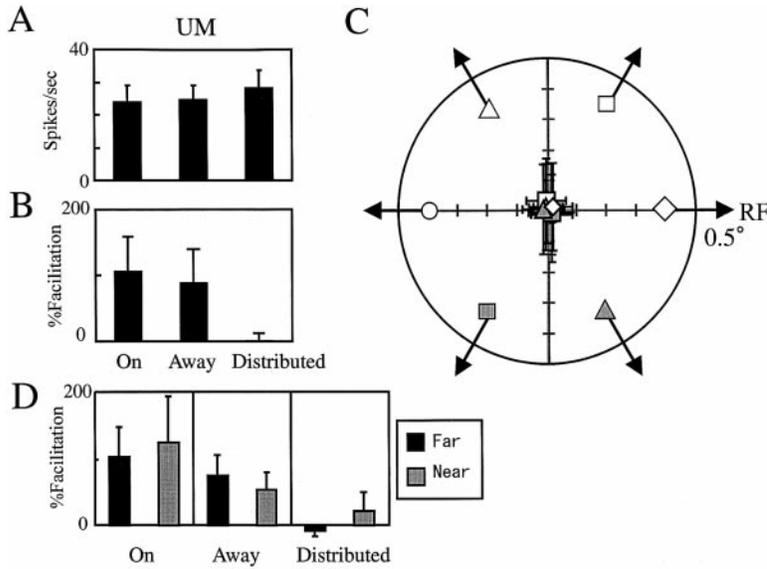
Averaged amplitude (and standard error) of the contextual facilitation of all cells, which showed contextual facilitation under any condition. Averaging was done in each monkey: SA ([A and C], 25 cells) and UM ([B and D], 61 cells).

(A and B) Mean response to the test line alone under the three attentional states.

(C and D) Mean percentage facilitation by a flanking bar (amount of facilitation, normalized by the response to the test line alone, 0 indicating no facilitation, and 100% indicating a doubling of the response to that seen when the bar within the receptive field was presented alone). For monkey SA, the facilitation was larger under distributed attention than under focal attention. For monkey UM, on the other hand, the facilitation was much larger under focal attention.

The response over the full population of cells that showed facilitation under any attentional condition, is shown in Figure 7. The sample includes 25 cells showing facilitation for SA (out of a total of 86 cells, or 29%) and 61 cells for UM (out of a total of 144 cells, or 42%). The figure shows both the effect of attention on the firing rate of the cell to the stimulus presented within the receptive field alone and on the facilitation of response to a flanking line. For SA, there was a small difference in response to a single line with focal attention onto the position of the receptive field, as compared with distributed attention (−15%). The facilitation for the flanking line was influenced much more by attention, with an overall 107% increase under distributed attention, which was reduced to a 61% increase under focal attention (t = 1.72, p < 0.05, paired t test). The results on facilitation for monkey UM were the reverse. Again there was no significant difference in the response to the target line alone under the three attentional states. There was a substantial difference, however, in the contextual effects. Facilitation under focal attention to the receptive field position was 126%, which was substantially reduced under distributed attention (62%, t = 1.83, p < 0.05, paired t test) and even less with attention to positions away from the receptive field (54%).

To test further the possible contribution of deviation in eye position to these results, eye position was continuously recorded during all physiological data collection for 32 cells under three attentional states in the second monkey. These experiments were done with a six-position stimulus set. Of the 32 cells, 14 showed significant

Figure 8. Effect of the Attentional Cue on Eye Position over a Sample Population

Eye position was consistent among the three attentional states. In monkey UM, eye position during stimulus presentation was measured in 14 cells showing significant facilitation under any of the three states.

(A) Mean response to the test line alone and (B) mean percentage facilitation. The facilitation was larger under focal attention than under distributed attention.

(C) Averaged eye position under focal attention measured during recordings of this population. The data were divided into six groups according to the cued location. The graph organization is similar to that shown in Figure 3D. Since the receptive field position was different for each cell, direction toward receptive field was normalized to the right horizontal direction, and eye positions are indicated relative to that measured under distributed attention.

(D) For each cell, data was divided into two groups, as done for the example shown in Figure 3E. The averaged position differed by approximately 0.1°, yet even this degree of eye deviation, larger than the difference observed under the three attentional states, yielded the same amount of facilitation.

facilitation, and the results from these are shown in Figure 8. During this last period of recording, psychophysical measures of contextual facilitation showed substantial facilitation under focal attention, and no significant contextual effects under distributed attention. Consistent with the entire data set, there was no difference in the response to the target line alone under the three attentional conditions (Figure 8A). The contextual facilitation, on the other hand, showed a marked dependence on attentional state, with the largest effects under focal attention to the receptive field position, none under distributed attention, and small facilitation with focal attention to positions away from the receptive field (Figure 8B). The eye positions averaged during the measurements of all 14 units, divided between the six loci of focal attention and the condition of distributed attention, are shown in Figure 8C. Since the receptive field position was different for each cell, the coordinates were rotated to make the receptive field positions coincide on the right horizontal direction. There was no significant difference in eye position for these different states, and no drift of eye position toward the cued locations. The mean + standard deviation in eye position under focal attention was $0.011° + 0.097°$ (n = 392) and under distributed attention was $0.000° + 0.064°$ (n = 196), representing no significant difference (t test, t = 1.327, p > 0.05).

As in the example in Figure 3, we evaluated the effect of eye position on the facilitation, dividing the data set into trials when the eyes were positioned closer to and farther from the cue. The difference in eye position, again roughly 0.1°, was insufficient to alter the basic finding, maintaining the same amount of facilitation under each of the three attentional states. We therefore concluded that no significant predictive eye movements occurred and that the modulation of facilitation was due to differences in attentional state.

In addition to the population showing facilitation, a number of cells showed only inhibition to the contextual stimulus, but this inhibition showed no modulation according to the state of attention (Figure 9). Over this population (38 cells for SA and 65 cells for UM), the average amount of inhibition was approximately 25%, with no significant difference in either animal among focal attention toward the receptive field position, focal attention away from the receptive field, or distributed attention to all four sites.

In our previous work on facilitation for lines placed along the orientation axis, the largest number of cells showing facilitation had the strongest effects for contextual lines with the same orientation as the line within
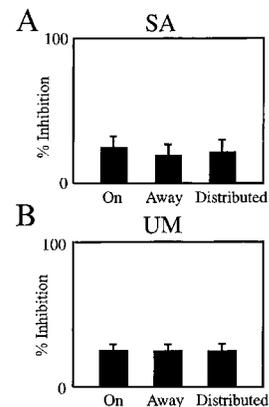

Figure 9. Effect of Attention on Contextual Inhibition

Averaged amplitude (and standard error) of the inhibitory effect of all cells, which showed contextual inhibition under any conditions. Averaging was done in each monkey: SA ([A], 38 cells) and UM ([B], 65 cells). There was no difference between the different attentional states.
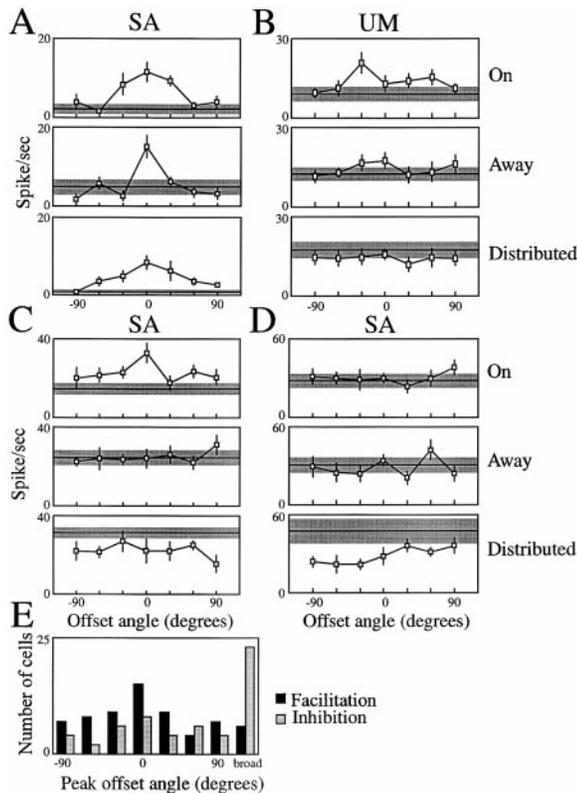
Figure 10. Effect of Attention on Orientation Tuning of Contextual Effects

Orientation specificity of contextual facilitation. Contextual facilitation was dependent on relative angle between the target line and the flank line.

(A–D) Examples of four cells showing facilitation (A, B, and C) and inhibition (C and D). Tuning to relative angle of the bars inside and outside the receptive field was shown under each of the three attentional states: focal attention on the RF (top), focal attention away from the RF (middle), and under distributed attention (bottom). Each point shows response (and one standard error) when both test line and flank line were presented together. Horizontal line and gray area indicate response (and one standard error) to the test line alone. Offset angle was changed from −90° to 90°. Some cells showed contextual facilitation under all three attentional states (for example, cell A). However, most cells showed contextual facilitation only under one state. In some cells, facilitation and inhibition were observed under different attentional states. In general, facilitation was specific to a particular offset angle. The effect was almost eliminated by changing the relative angle by 30°. Although some cells showed similar orientation specificity for inhibition, many cells showed broad tuning of inhibition (for example, cells C and D).

(E) Distribution of peak offset angle for the facilitation (black bars) and for the inhibition (white bars).

the receptive field. There was, however, a considerable variability in this behavior, with some cells having maximal facilitation over a range of relative angles. This was true for the cells included in this study as well, and we asked whether visuospatial attention had any systematic effect on the orientation tuning of the facilitatory effects. The orientation tuning of facilitatory effects at the three attentional states is shown for several cells in Figure 10. In Figure 10A, the optimum angle was 0°, and though the amount of facilitation was different under the different attentional conditions, it peaked at the same

relative angle. In Figure 10C, the change from focal attention on the receptive field position to distributed attention represented a removal of facilitation seen at 0° and an unmasking of a broadly tuned inhibition. We never observed a shift in the peak of facilitation, but instead a modulation of the facilitation at the same relative angle as well as changes in the overall level of inhibition across all relative angles. Over the entire sample as shown in Figure 10E, the facilitation was the most pronounced and affected the greatest number of cells at a relative angle of 0°. Inhibition, on the other hand, peaked over a wide range of relative orientations, and many cells individually showed a broadly tuned inhibition.

Discussion

The principal finding of this study is that one can not only see the effects of visuospatial attention in primary visual cortex, but that these effects are particularly exerted on the contextual facilitatory influences from outside the classical receptive field. While there was a small amount of modulation according to the state of attention in the response to the target stimuli alone in the absence of the contextual stimuli, this modulation did not reach a level of significance when averaged over the sample population. In addition, for the population of cells where inhibitory influences for collinear stimuli predominated, there was no effect of attention. The collinear facilitation did, on the other hand, show considerable modulation according to whether the monkey focused his attention on to the receptive field location, to a site away from the receptive field, or distributed his attention to all target locations. For many cells, a pronounced facilitation seen under one state of attention could be completely abolished under another state of attention.

Due to the variability in training effects at the time of the recording, the two monkeys showed differences in the attentional state in which the greatest facilitation was observed. Monkey SA showed the largest effects under distributed attention, and monkey UM showed the greatest effects with focal attention onto the target. The attentional state showing the greatest facilitation at the cellular level correlated well with the animals' behavior: facilitation in area V1 was largest for monkey SA under distributed attention and for monkey UM under focal attention. The learning observed under distributed attention effectively turned it into "multifocal" attention (Ito et al., 1998). Since a measure of training had already occurred when recordings began, more pronounced attentional modulation of contextual effects may exist at the cellular level for naïve subjects. The existence of perceptual learning as a factor in the performance on the attention task leads to differences between individuals on the behavioral performance, particularly with respect to facilitation, and on the associated physiology. The fact that the animals were overtrained on the task leads to the different effects of attention on facilitation than that observed before recording and to differences relative to that reported in our earlier psychophysical study (Ito et al., 1998). The fact that one animal received more training than the other might account for the differences in their relative performance on the focal versus

distributed attention tasks. Whatever accounts for the differences in performance between the two animals, it is important that the consistent difference in facilitation between focal and distributed attention seen at the end indicates that both animals used different strategies for the two conditions, reflecting a difference in attentional state. This difference is then reflected in the attentional modulation of contextual facilitation of cell responses in V1.

The relatively small effect of attention on the response to the target alone as compared with the much larger effect on contextual modulation might account for the variability in earlier reports on the presence or absence of attentional effects in area V1. Previous studies reported either little or no effect of attention in area V1 (Haenny and Schiller, 1988; Motter, 1993; Luck et al., 1997a). Some studies that show a lack of attentional modulation averaged over a population of cells in V1 used stimuli equivalent to our target-alone stimulus, even if individual cells appeared to show substantial attentional modulation (Haenny and Schiller, 1988). Our Monte Carlo analysis of the data indicates that the target-alone attentional modulation can be accounted for by random variation in responses, while the attentional modulation of contextual facilitation is clearly associated with the attentional state, and not due to random changes in excitability. Several studies showed that focal attention modulated spontaneous firing rate as well as response to visual stimuli (Colby et al., 1996; Luck et al., 1997a). As shown in Figure 2, this effect was not observable in this study because of low spontaneous activity in the superficial layers of the primary visual cortex. The degree of modulation may depend on the number of stimuli, or distractors, presented in the visual field (Motter, 1993; Vidyasagar, 1998). The difference between the earlier work and the current study arises from the nature of the visual stimuli and their positions relative to the receptive field boundary. Our results emphasize the importance of the specific juxtaposition of stimuli with respect to the receptive field boundary and the interaction between stimuli lying inside and outside the receptive field as critical factors in obtaining the maximal attentional effects.

We have previously provided evidence that the contextual influences seen in primary visual cortex arise, at least in part, from long range horizontal connections that are intrinsic to V1 (Gilbert and Wiesel, 1979, 1983, 1989, 1990; Kapadia et al., 1995). In this study, there are several additional points to add to the contextual effects. Earlier, we had shown brightness induction for a detection task at threshold levels of brightness. Here, we used suprathreshold stimuli, with a brightness discrimination task relative to a reference line. Recent studies suggest that the occurrence of facilitation depends on the contrast of the target stimulus (Polat et al., 1998). We see as high a proportion of cells showing facilitation as in our earlier work (Kapadia et al., 1995), but here there is the additional overlay of peripheral attention as well as the presence of additional stimuli in the visual field, both of which may shift the balance toward facilitation, despite the use of higher contrast stimuli. A number of factors, including contrast and foreground/background relationships, contribute to changes in receptive field size and surround interactions (M. Kapadia et al., 1998, Soc. Neurosci., abstract). In the initial study, we correlated human psychophysics with monkey physiology; in the current study, we have both the psychophysics and the physiology in the same animal. Finally, we have presented results concerning the time course of the contextual effect. The fact that the contextual effect arises at the same time as the response itself supports the idea that it arises via a feedforward mechanism like the horizontal connections as opposed to feedback connections from higher order cortical areas. Other contextual effects, such as facilitation from texture boundaries located well outside the receptive field, have been shown to arise late in the response, leading to an interpretation that they are mediated by feedback connections (Lamme, 1995; Zipser et al., 1996). Whether timing alone is a good indicator of the source of facilitation remains to be seen.

The modulation of contextual influences by attention suggests a gating of the horizontal connections by feedback connections from higher order cortical areas, which can account for the more profound influence of attention on contextual modulation. The reason why we favor this model of the attentional effects is that the target-alone responses were not significantly modulated by changing the focus of attention. Thus, it is unlikely that cells with receptive fields within which the contextual lines were located were changing their responses to these lines. Rather, it appears that attention influences the interaction between cells having widely separated receptive fields and, hence, produces a specific effect on contextual influences. (One should not confuse the immediacy of the attentional effects, however, with the considerations of the source of contextual effects, since the attentional state of the animal is preset by the cue before the stimulus is presented.) The contextual facilitation tended to be the same for focal attention away from the receptive field and for distributed attention. This suggests that the attentional modulation of lateral interactions is specific for cells with receptive fields at or near the focus of attention. Since the contextual effects in V1 may play a role in contour integration, the modulation of these effects by top down influences provides a mechanism by which internal representations of stimulus configuration can be tested against inputs reflecting physical reality.

While our results emphasize the facilitatory effects of attention, work in other visual cortical areas have shown either an inhibitory influence or a bias toward one of two competing stimuli. This modulation is generally observed when both attended stimuli and distractors were presented within a cell's receptive field. When subjects attend to an object's location, there is an inhibition at the sites surrounding the attended area or a filtering between target and distractors (Moran and Desimone, 1985; Chelazzi et al., 1993; Treue and Maunsell, 1996; Luck et al., 1997a, 1997b). This type of modulation was reported in extrastriate areas, but not in area V1. On the other hand, a facilitatory attentional modulation, enhancement at the target site, was observed when subjects' attention was directed toward a stimulus attribute that is being discriminated (Haenny et al., 1988; Haenny and Schiller, 1988; Spitzer et al., 1988; Motter, 1993). The

latter is perhaps more consonant with our experimental paradigm, where the animals were required to discriminate the brightness of a line at the same time as attending to one or more stimulus locations. This resulted in a specific modulatory effect on contextual facilitation but not inhibition.

The results presented here provide additional support for the idea that the response properties of cells at all stages in cortical processing are dynamic. They point further to the idea that the sources of receptive field mutability, context, attention, and learning are all highly interdependent and that it is difficult to consider the role of any one of these influences isolated from the others. The emerging picture is that response characteristics are modulated or gated by a nested and interactive set of internal influences and that the responses of cells, even in the primary visual cortex, are not exclusively a reflection of the immediate physical environment.

Experimental Procedures

Two Rhesus monkeys (Macaca mulatta, male, adult, weighing 4.4 kg and 4.8 kg) were trained to perform a brightness discrimination task and were used for unit recordings. All procedures followed "NIH guide for the care and use of laboratory animals" (U.S. Department of Health and Human Services, 1985).

Training and Preparation

Details of the training procedures for monkeys were described previously (Ito et al., 1998). Animals were initially trained to perform a fixation task, in which they detected the dimming of a fixation point and released a lever within a short interval after the dimming occurred. Animals were then trained to do the brightness discrimination task by modifying the original fixation task gradually. We used a dimming detection task as the fixation task. This task required more precise fixation than that allowed by the fixation window. We gave the fixation task during training and recording to reinforce the monkeys' fixation. Both monkeys were trained to release a lever even when fixation point disappeared in discrimination trials.

Training started with one test line. After they learned to discriminate the brightness of the test line, the number of distractors was increased one by one, and the range of brightness levels of the test line was gradually narrowed. Finally, a flanking line was added, and they were trained to ignore its presence during the task. The first monkey (SA) was used for unit recordings after it was overtrained to perform the brightness discrimination task. Initial training continued for 31 weeks after we began to obtain psychometric curves. The first reliable data for contextual effect was obtained at the eighth week. After the monkey was trained with the standard four-position stimulus array for 13 weeks, it was then trained with the eight-position stimulus array for 17 weeks, as described previously (Ito et al., 1998). At the 31st week, we again presented the standard four-position stimuli and the monkey's performance was comparable to that seen before we presented the eight-position stimuli. Training procedures were also given in a part of the recording procedures, which continued until the 54th week.

The second monkey (UM) was used to obtain control data after fixation training (e.g., fixation trials without attention to the periphery) but before training on the attention task. UM was subsequently trained to perform the brightness discrimination task, after which we continued the recordings. Contextual influences were measured from the first week after we began to obtain psychometric curves. Recordings were initiated at a relatively early stage of the training (the sixth week).

Electrophysiological Recording

In general, the physiological methods and the recording apparatus were the same as described in the previous paper (Kapadia et al., 1995). A fiberglass recording chamber with an inner diameter of 16 mm was implanted, and trephination was done inside the chamber after completion of training of the fixation task. All surgical procedures were performed under deep pentobarbital sodium anesthesia and under aseptic conditions. The chamber was positioned to allow access to the primary visual cortex. Penetrations were made through the dura matter using glass-coated platinum iridium microelectrodes (Wolbarsht et al., 1960) with typical impedance between 1.0 and 3.0 M ohm at 1 kHz. Electrodes were driven using a stepping motor microdrive (Narishige PC-5N). Successive penetrations were usually positioned 0.5 mm apart without repeating previous recording sites. The recording chamber was filled with silicone oil (DS Fluid, 200 C_s) during the recording session to prevent the dural surface from drying. At the end of each recording session, the electrode and microdrive were removed, and the chamber was disinfected with 0.05% chlorhexidine diacetate (Nolvasan) before being sealed. Topical antibiotics (Maxitrol, 2–3 drops) were added twice a week. The dura was periodically stripped under anesthesia to facilitate electrode penetration.

Daily recording sessions typically lasted 2–3 hr. During each session, we recorded the activity of either single isolated units or of clusters of two to three units. After neural activity was isolated, we obtained a crude receptive field map by using a hand-held stimulator and by listening to discharges on an audio monitor while the animal was performing the fixation task. Recording sites were on the opercular surface of the striate cortex in one hemisphere of each monkey. The eccentricity of receptive fields ranged from 1.9° to 5.3°. The mean receptive field size was 0.69°. The anterior boundary of the primary visual cortex was estimated by measurements of the lunate sulcus at the time of chamber implantation and was further determined by movement of receptive field positions as one approached and crossed the V1/V2 border. The electrode was usually kept near the position at which it first encountered spike activity, and all recording sites were restricted to the superficial 600 μm of cortex. Characteristics such as high spontaneous activity and brisk on/off responses were taken to indicate that the electrode had entered layer 4 (von der Heydt and Peterhans, 1989; Snodderly and Gur, 1995). Using this strategy, we restricted recordings to the superficial cortical layers. We avoided recording tracks, in which cells were color-selective, were not orientation-selective, and showed high spontaneous activity, indicative of penetrations in the CO-blob regions. In experiments examining the orientation dependence of contextual interactions, we selected cells in which the bandwidth for orientation was less than 90°.

Stimuli and Data Collection

The recordings followed a sequence of receptive field mapping under fixation trials and exploration of response properties under three attentional conditions, focal toward the receptive field, focal away from the receptive field, and distributed. Care was taken to map classical receptive field properties in order to optimize stimulus conditions during the attentional protocol. The cells' receptive field size and position were mapped during fixation trials, when the animal did not attend to any stimuli in the periphery. The receptive field response profiles were measured by placing a short line segment (0.2°–0.45°) at a series of positions along and orthogonal to the orientation axis of the cell, and their orientation specificity determined by placing a line at the center of the receptive field and measuring responses at 20° steps.

To study the effects of attention on these cells, the cells were recorded under one of the three attentional regimes. The experimental sequence started with a fixation spot, to which the animal had to saccade, and an adjacent reference line. Next, a cue frame was presented, where in addition to the fixation spot and reference, either one or four cue spots were presented, requiring the animal to attend to one (focal attention) or to all stimulus locations simultaneously (distributed attention). Under focal attention, the animal could be cued either to a position corresponding to that of the receptive field under study (focal on) or to positions away from the receptive field (focal away). The cue spots were then turned off, and a series of stimulus frames were shown, each for 100 ms. The number of stimuli was randomly varied from one to six. In the last stimulus, one of the four test lines was a target line whose brightness had to be judged as dimmer or brighter than the reference, and the animal was required to saccade to one of two saccade targets

(one direction indicating stimulus brighter than reference, the other direction indicating stimulus dimmer than reference). During recording sessions the recording protocol was randomly alternated with the training protocol, so that the animal would not bias its attention toward the RF position.

These different attentional protocols were randomly interleaved during measurements. The stimulus presentation began 1 s after the initial cue and lasted for 100 ms. Stimulus arrays were presented at 0.9 s intervals after the initial cue. During data collection, all four lines were presented at the standard luminance. At the final presentation in the series, data collection was halted and the target line was presented at a luminance that varied in seven steps from −60% to 80% relative to the luminance of the reference line. The brightness levels were selected to balance the responses around the 50% response ratio and were adjusted appropriately for the target alone and target with flank conditions. The animal had to report whether the target line appeared brighter or dimmer than the reference during the following 0.6 s by making a saccade to either of two response targets, which were presented immediately after the last stimulus presentation. Correct responses were rewarded with a drop of juice. For the fixation trials, no reference line was presented. After the last stimulus presentation, the fixation point dimmed and the monkey had to release a lever within 0.6 s.

To anticipate the fact that we would be recording from cells with different orientation preferences, the animals were trained to do the task with lines of different orientation, with four sets of stimuli placed symmetrically about the fixation point. We then adjusted the array appropriately for each unit, with an optimally oriented line within the receptive field, a collinear flanking line placed more peripherally, and four sets of target and flanking lines symmetrically placed in each of four quadrants. This approach was used in the recording as well as in the training procedure.

Data collection followed a random block design. A standard set of stimuli consisted of nine stimuli for each attentional state: test line alone, flank line alone, and test and flank lines with seven different relative angles (from −90° to 90°). Data were collected for 5–15 trials for each stimulus. During each cycle of stimulus presentation, the stimulus was off for 200 ms, on for 100 ms, and off for 700 ms. Spikes occurring within the initial 200 ms of each cycle were used to calculate the background firing rate of the cell. The magnitude of response was represented by the mean firing rate during stimulus presentation minus the mean firing rate of background activity. The time window of the measured response was 200 ms wide with a latency adjusted according to the response latency of each cell. This corresponded to the average response duration of the cells (see Figure 2). Responses to 5–15 trials of the different stimulus conditions were compared using the Kolmogorov-Smirnov test ($p < 0.05$). In a set of stimuli, we changed the offset angle of the flanking line in a range between −90° and 90°. For each cell, we chose the orientation showing the largest contextual effect, whether it was facilitation or inhibition, for further analysis.

Eye Positions

Eye movements were monitored using a scleral search coil system (CNC engineering) and used for controlling animals' behavior during training and recording by on line procedures. In the second monkey, we also sampled eye position at 100 Hz during stimulus presentation and data collection, enabling us to analyze the relationship between eye position and trial by trial responses. In addition to the direct monitoring of eye position, we had several controls under the protocols observed in the physiological recordings. First, the animal had to maintain fixation within a prescribed window, where shifts in eye position greater than 0.5° aborted the trial. Second, we intermingled some of the fixation task during training and recording to reinforce the monkeys' fixation. Since animals had to detect dimming of fixation point, this task required more precise fixation than that allowed by the fixation window. Third, the fixation spot was presented first, to which the animal had to saccade before the attentional cues were presented. Eye position was stable after initial fixation, and we observed no drift in eye position after the cues were presented. Eye position was continuously monitored during every trial and was consistent from trial to trial. Fourth, the stimulus was presented in the center of the receptive field, which was determined by detailed

mapping during fixation trials (without attentional cues). Any consistent shift away from the fixation position during cued trials would result in a significant decrease in the cell's response. The fact that, over the population, there was no significant difference in the target-alone responses under the different attentional states represents an internal control on eye position.

On days when the monkeys were not engaged in recording sessions, they participated in training sessions as described previously (Ito et al., 1998). The standard stimulus pattern consisted of a central fixation spot, a vertical reference line and four similar lines, set radially along the 45° and 135° meridians, and at 3.5° eccentricity. All lines had similar size of either 18′ × 4′ or 27′ × 4′. The standard luminance of all test lines and flanking lines was 37.7 cd/m2 seen against the uniform screen background luminance of 17.7 cd/m2. During recording sessions, one of the test lines was presented within a cell's receptive field at its optimal orientation. The other lines were placed symmetrically about the fixation point. The size and luminance of all lines were the same as those of the reference line. For 32 cells recorded in the second monkey, lines were presented in six symmetrical positions instead of four. Tests for contextual influences were performed by comparing the responses of the cell to an optimally oriented bar located inside the receptive field with the response to the same bar when each test line was accompanied by a 27′ × 4′ flanking line, of the same orientation and situated 0.7° further out from the fixation point along its axis of orientation (Figure 1B).

Data Analysis

The magnitude of facilitation and the magnitude of inhibition were calculated with the following formula:

$$\% \text{ Facilitation} = \left(\frac{\text{Response to the test line accompanied by the flank line}}{\text{Response to the test line alone}} - 1 \right) \times 100$$

$$\% \text{ Inhibition} = \left(1 - \frac{\text{Response to the test line accompanied by the flank line}}{\text{Response to the test line alone}} \right) \times 100$$

The modulation of facilitation among three attentional states was calculated with the following formula:

Modulation index = (maximum facilitation ratio among the three attentional states − minimum facilitation ratio among the three attentional sites)/(facilitation ratio with attention on + facilitation with attention away + facilitation with distributed attention)

Here, the facilitation ratio is the response to target and contextual line divided by the response to the target line alone. A modulation index value of 0 would indicate that facilitation did not vary between the three attentional states.

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