Neuron, Vol. 15, 843–856, October, 1995, Copyright © 1995 by Cell Press

Improvement in Visual Sensitivity by Changes in Local Context: Parallel Studies in Human Observers and in V1 of Alert Monkeys

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Summary

To explore the role of primary visual cortex in contour integration, we measured the contextual sensitivity of human contrast thresholds and of superficial layer complex cells in monkey V1. An observer's contrast detection was 40% improved by a second suprathreshold bar; the effect was decreased as the two bars were separated along their axis of orientation, were displaced from colinearity, and had their relative orientation changed. Recordings from V1 showed that 42% of complex cells demonstrated facilitation for a second bar outside their classical receptive fields with a similar dependency on relative location and orientation. Both effects were eliminated by an orthogonal line between the two iso-oriented lines. Multiple randomly placed and oriented lines in the receptive field surround often caused a reduction in a cell's response to an optimally oriented stimulus, but this inhibition could be eliminated by changing the orientation of a few of these elements to colinearity with the centrally located target.

Introduction

A feature common to many aspects of visual processing is that the perception of an object's attributes is dependent on the context within which the object is observed. For visual spatial integration, the visual system uses context to distinguish objects in complicated environments consisting of different textures, surfaces, and occlusions. The integration of an object's component contours into a unified percept makes the object cohere and causes it to emerge from its surroundings.

The processes involved in spatial integration have been examined in a number of psychophysical studies. It has been established by the Gestalt psychologists that certain characteristics of visual images, including continuity and contiguity, give certain contours the ability to stand out from their environment. The attribute of good continuation of a contour is based on the relative position and orientation of the line segments of which it is composed (Wertheimer, 1938; Grossberg and Mingolla, 1985; Ullman, 1990; Field et al., 1993). When successive line elements are positioned close together and have similar orientations, the series shows increased saliency and tends to pop out of its background, but if either the separation or the difference in orientation between the elements is increased, the contour becomes difficult to distinguish from its surroundings. Spatial integration, therefore, depends on both orientation and spatial position. Other psychophysical experiments have shown that the detection of an individual feature can be enhanced by additional, simultaneously presented stimuli (Dresp, 1993; Polat and Sagi, 1993, 1994).

The present study is an attempt to find cellular correlates of binding, saliency, and segmentation. To address the neuronal mechanisms underlying contour saliency, we used comparable stimuli in psychophysical and physiological experiments. The psychophysical studies were performed with human subjects, and physiological experiments with a similar stimulus configuration were conducted on alert, fixating monkeys in order to compare the two parts of the study under equivalent conditions.

A number of factors suggest that the substrate for spatial integration can be found at early levels of visual processing. Studies of striate cortex using physiological, anatomical, and optical recording techniques have shown interactions between widely separated positions in visual space and the coactivation of multiple cortical columns tuned to the same orientation (Ts'o et al., 1986; Ts'o and Gilbert, 1988; Gilbert and Wiesel, 1989; Das and Gilbert, 1995). The substrate for these lateral interactions in cortex is found in the long-range horizontal connections formed by cortical pyramidal cells, which enable their targets to integrate information from dispersed parts of the visual field well beyond the boundaries of the classical receptive field (RF; for review, see Gilbert, 1992). The interactions seen in primary visual cortex are reminiscent of the rules governing contour saliency and suggest that the physiological basis of the perceptual phenomena might be found in contextual influences from outside the classical RF.

Results

Psychophysics

The influence of context on the visibility of a target was analyzed in terms of the threshold level of contrast required for detection of the target (Figure 1). When a short line segment, or target, was flanked by an additional, colinear line, the target could be reliably detected at much lower contrasts than when it was presented alone. An optimally placed flank could result in a reduction in detection threshold of as much as 40%.

We determined the spatial constraints for this enhancement by varying the spatial position of the flank. When the flank was placed at different positions along its orientation axis, the facilitation was maximal when the two bars were in close proximity and declined as the bars were further

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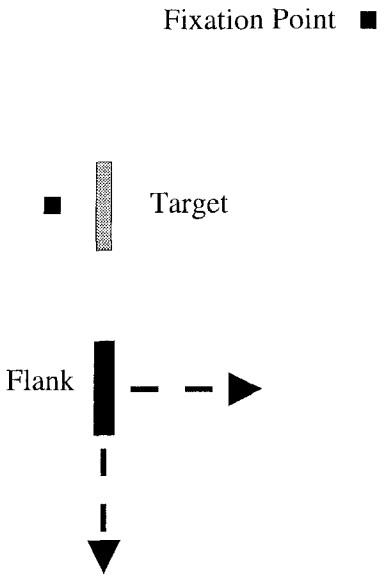

Figure 1. Schematic Representation of the Psychophysical Stimulus

The fixation point and the position cue always remained on the screen, while the target and flank were turned on and off. During each trial, the two bars could appear in one of four randomly chosen configurations: target shown alone, flank shown alone, both bars presented simultaneously, or an empty condition where neither was displayed. The target always appeared in an identical location, but the position of the flank was varied between trials, allowing us to examine the spatial characteristics of the contextual interaction.

separated along the axis of colinearity (Figure 2). Little or no change in sensitivity was seen after the bars were separated past a critical distance, which depended on the retinal eccentricity and varied between observers.

When the flanking line was displaced in directions orthogonal to the orientation axis by as little as 10′ of arc, the enhancement declined considerably (Figure 3). The decline occurred several times more rapidly than with equivalent displacements along the axis of colinearity. When the bars were offset further, a reduction in sensitivity was seen; i.e., it became more difficult to detect the target than when it was presented alone.

To test the orientation dependency of the enhancement effect, we examined detection thresholds when the target and flank differed in orientation. The orientation of the flank was adjusted by tilting it while fixing the position of the end of the flanking line that was closest to the target line. In this manner, the orientation of the flank could be changed while preserving its continuity with the target at the adjacent end. The reduction in detection threshold was maximal when the two bars had the same orientation and declined as the difference in orientation between target and flanking line was increased (Figure 4).

These experiments showed that the threshold reduction effect was dependent on colinearity and proximity between the target and flank. Introducing a lateral offset or a large difference in orientation caused a decline in the effect.

Reduction in detection thresholds due to adjacent light stimuli is a well-established phenomenon (Westheimer, 1965, 1967) known as sensitization. In its usual form, it is a manifestation of spatial opponency or center/surround organization of the retina. Since our experiments are intended to highlight cortical interaction, it is important to verify that the findings reported here cannot be ascribed to retinal sensitization. This was accomplished by placing the test stimulus in one eye and the flank in the other, i.e., by dichoptic viewing. No threshold reduction would be expected to occur if the interaction were at the retinal or thalamic level. In fact, we found full interocular transfer (98%) in one observer and a partial transfer (65%) in another. We can therefore conclude that our psychophysical results were indeed due to facilitatory cortical interactions.

If the interactions between colinear lines reflected the process of binding of line segments belonging to a common contour (e.g., "good continuation"), the influence of the flanking line might be disrupted by introducing a feature that destroyed the continuity between the lines. When

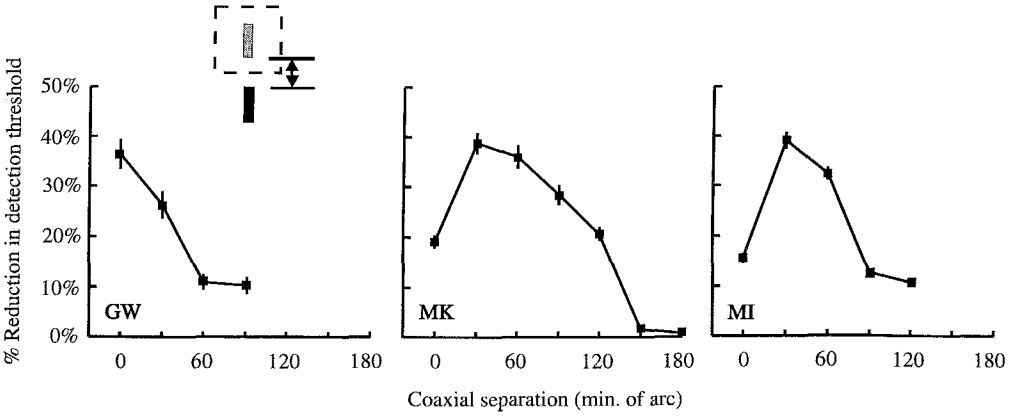

Figure 2. Psychophysical Data on the Dependency of the Facilitatory Interaction on the Distance between the Target and Flank along Their Axis of Colinearity

Data points represent the percentage reduction in detection threshold of the target in the presence of the flank as compared with the target presented alone. Bars, one standard error of this value. The largest facilitatory influences occurred when the flank was close to the target, with the effect declining as the bars were further separated.

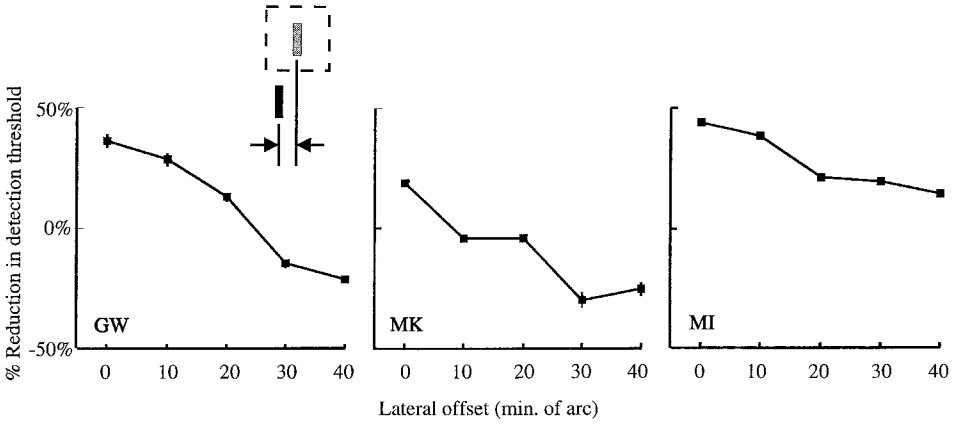

Figure 3. Psychophysical Data on the Dependency of the Facilitatory Interaction on the Distance between the Target and Flank along an Axis Orthogonal to Their Orientation

Maximal threshold reductions occurred when the target and flank were colinear and declined as the flank was moved away from alignment. The decline occurred over much shorter distances than that seen with displacements along the axis of colinearity. As the bars were further separated, an inhibitory interaction was observed: it became more difficult to see the target in the presence of the flank than when the target was presented alone. For these subjects, the separation of the two bars along the orientation axis was 0′ (M. K. and G. W.) and 30′ (M. I.).

the flanking line was replaced by a T-shaped stimulus, the threshold reduction was significantly reduced (Figure 5).

Physiology

Facilitation with a Single Flank

The physiological experiments were designed to examine whether we could find the neuronal counterpart of our psychophysical results in primary visual cortex. We found indeed that the response properties of certain cells were modified by contextual stimuli in a pattern similar to the reductions in detection threshold. In these experiments, we examined the responses of neurons to an optimally oriented bar located within the RF while an additional bar was presented in the RF surround (Figure 6). The flanking bar was positioned outside the classical RF, such that when it was presented in isolation, it did not elevate the firing of the cell above spontaneous activity. Despite this, an optimally positioned flank often increased the response to the bar inside the RF (Figure 7). A single long bar did not show a similar enhancement.

Statistically significant facilitatory interactions were observed in a least one stimulus configuration in 42% (123 out of 291) of the single units or multiunit clusters of 2–3 cells that were studied ($p < .05$, Kolmogorov–Smirnov test). The recordings included 126 single units and 165 multiunit recordings consisting of 2–3 units. Facilitation was observed in 48% (60) of the single units and 38% (63) of the multiunit recordings. The median change in response for these cells at peak facilitation was 230%, with values ranging from 136% to 1800%. Single and multiunit recordings comprised approximately equal fractions of the total pool and showed similar results. No significant change was observed in 32% (92), and 26% (76) showed an inhibition (with a median decrease of 55%). Of the cells

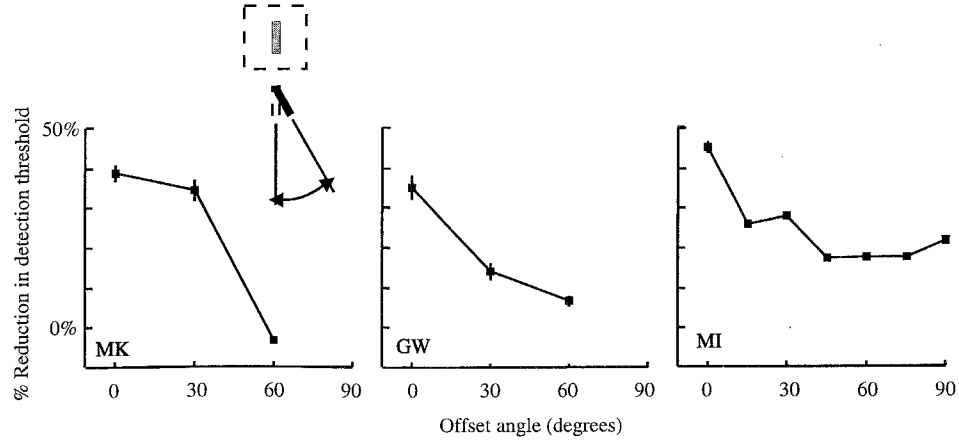

Figure 4. Psychophysical Data on the Dependency of the Facilitatory Interaction on the Relative Orientation of the Flank and Target

The orientation of the flank was changed by moving the bottom of the bar, preserving continuity between the bottom of the target and the top of the flank. Strongest facilitatory influences were found when the two bars had the same orientation. The effect declined as the flanking bar was tilted relative to the target. In these experiments, the separation of the two bars along the orientation axis was 0′ (G. W.) and 30′ (M. K. and M. I.).

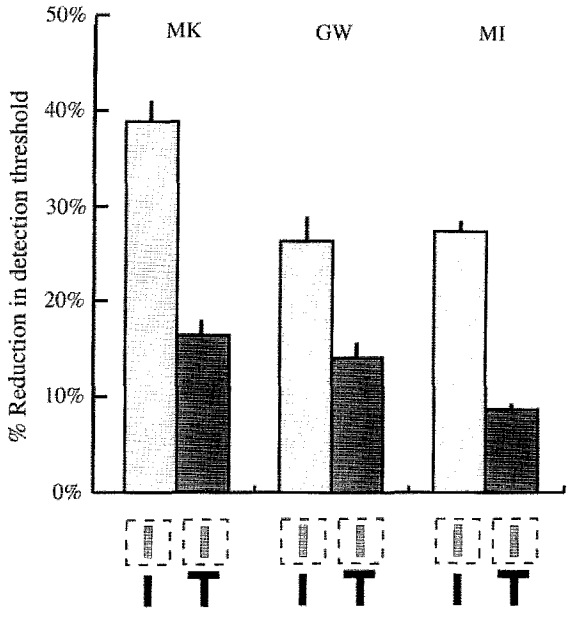

Figure 5. Psychophysical Data on the Dependency of the Facilitatory Interaction on Stimulus Continuity

When the flank was replaced by a T-shaped stimulus, the continuity between the two bars was destroyed, and the threshold lowering effect of the flank was reduced. Threshold reductions are shown for three observers.

included within the facilitatory group, 35 showed both facilitatory interactions with one stimulus configuration and inhibitory interactions with another.

This paper focuses on those cells that exhibited facilitatory interactions. Our methods were likely to underestimate the number of these cells for two reasons. First, the geometric relationship between the target and flanking bars that produced a facilitatory interaction varied between cells (see below). Since all stimulus configurations were not tested on all cells, some cells were likely to show facilitation under conditions that were not tested. Second, the criterion of statistical significance places an additional constraint on which cells are defined as facilitatory. In practice, over the 5–10 trials performed at each stimulus configuration, statistically significant interactions were observable only in cells whose response increased by a third or more.

The dependence of these interactions on the spatial position of the flank was studied systematically using arrays of stimulus locations similar to those used in the psychophysical experiments. Over the population studied, the dependency on stimulus configuration followed a pattern similar to that seen in the psychophysical results.

To characterize the response properties of cells within the time limits imposed by the stability of the recording and the motivation of the animal to perform the behavioral task, each set of tests was performed in relation to a common flank location and orientation. A flank position was chosen with the same orientation as the target and was located sufficiently outside the RF to elicit no response from the cell when the animal's fixation was controlled. Each set of stimuli examined the response of the cell by changing one of three parameters of the flanking bar: its separation from the target along a colinear axis, its distance from the target along an orthogonal axis, or its orientation. Because of the constraints of the experiment, it was not feasible to study the cells at all permutations of the stimulus parameters. If, for example, a peak facilitatory response was observed when the flank was tilted by 30° relative to the target, examination of the subsequent stimulus parameters was still done with a flank orientation that matched that of the target.

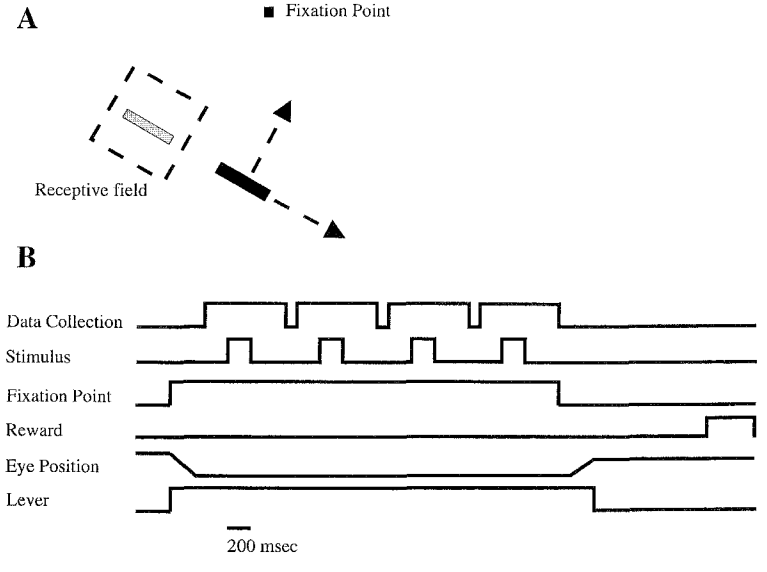

Figure 6. Stimuli Used in Physiological Experiments

(A) Diagrammatic depiction of physiological stimuli. The dotted square represents the RF of a V1 cortical neuron. The test line was presented at low contrast within the RF of the cell as determined by hand mapping, while the flank, which was presented at high contrast, was always outside this region. Each stimulus presentation consisted of a randomly chosen configuration of either bar displayed alone or the two bars presented simultaneously. When both bars were shown together, the flank could appear in one of several predetermined spatial positions or orientations.

(B) Temporal representation of a single trial in the physiological experiments. The trial began with the onset of the fixation point. After the monkey achieved fixation, there was a delay of 300 ms followed by 3–5 cycles of stimulus presentation. Each of these cycles consisted of a 200 ms delay, a 200 ms presentation of the test line and/or flank, and a second delay of 300 ms. The animal was rewarded if fixation was held throughout the trial. The next trial began 3 s after completion of the reward. For monkey #2, the sequence was self-initiated.

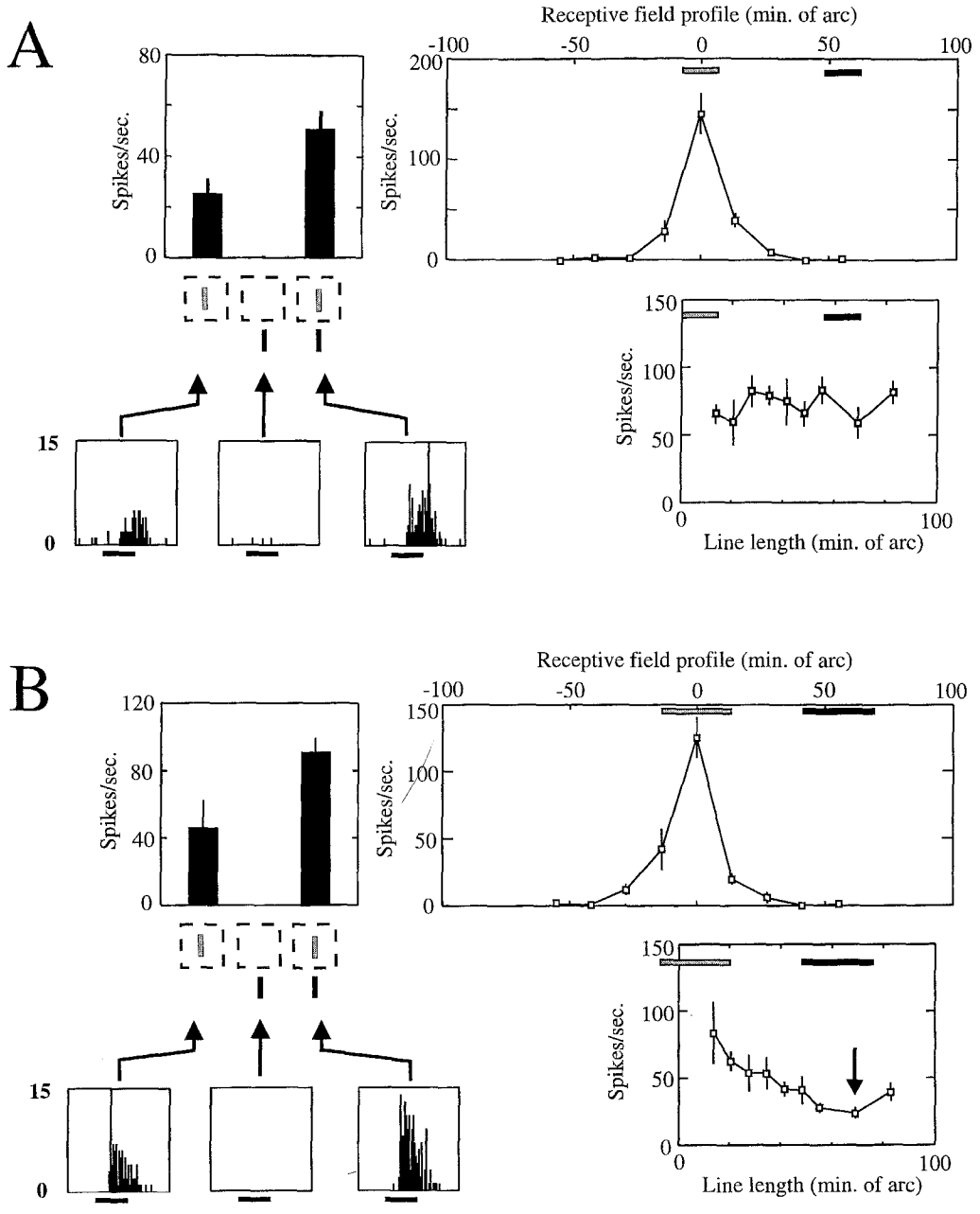

Figure 7. Comparison of Contextual Effects Generated by Stimuli Lying outside the Classical RF with Conventional Measures of RF Dimension

The largest measurable extent of the classical RF was determined by placing a high contrast test bar at different positions along the orientation axis of the RF (receptive field profile) and by using stimuli of increasing length (a length–tuning curve, with Line Length represented along the abscissa). Both provided equivalent measures of RF length. The effect of contextual stimuli was determined by comparing a cell's response to a low contrast line placed within the RF (left response histograms in [A] and [B] and first bar in bar graph), its response to a high contrast line placed outside the RF (middle response histogram and middle bar in bar graph), which was indistinguishable from spontaneous levels of activity, and its response to the two lines displayed together (right response histogram and right bar in bar graph), which was often two or more times the response to the line placed within the RF alone. The fact that the flanking line lay outside the classical RF was confirmed by the fact that it lay in the silent region of the RF profile (the open bar lying above the profile graph indicates the size and position of the line within the RF, and the black bar indicates the size and position of the flanking bar used in the contextual experiment shown at left) and in the level portion of the length–response curves. The differences in contrast between the stimuli used to obtain the RF profile and those used to measure facilitation account for the differences in firing level to the same size stimuli in the different plots.

(A) Example of a non-end-inhibited cell. The flanking line used as a contextual stimulus (black line) lay more than one line length outside the classical RF. The line length–response curve is placed under the RF profile curve such that the test positions and lengths along the abscissae correspond to equivalent positions relative to the cell's RF. In the length tuning curve, the line length is increased such that the stimulus increases its extent on one side of the RF.

(B) Example of an end-inhibited cell. Despite the existence of a flanking inhibitory region along the orientation axis, as seen by the decrease in response with increasing bar length, a flanking line (black line) can double the response of the cell to the line placed within the RF (open line).

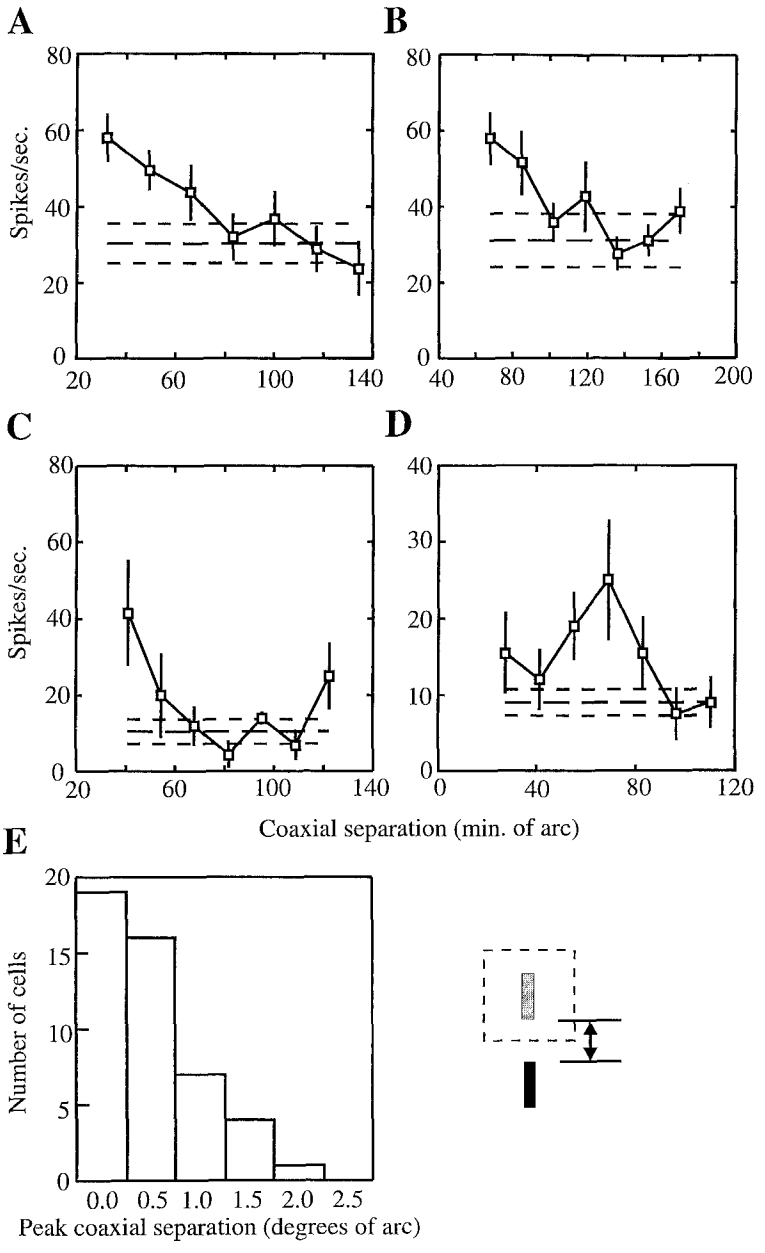

Figure 8. Physiological Data Showing Facilitatory Interactions in the Response of a V1 Cortical Neuron and Its Dependency on Coaxial Separation

(A) An example of a typical facilitatory interaction that declined with increasing separation. The central dashed line represents the cell's response to the line presented within the RF alone. The two dashed lines above and below represent one standard error of this value. The plotted points represent the response of the cell to the two lines shown simultaneously when they were separated along their axis of colinearity. In the presence of the flanking line, the response of the cell increased to twice the firing rate of that when the line was presented within the RF alone. The enhancement decreased as the flank was displaced along its orientation axis. This cell, and all cells shown subsequently, had no significant visual response to the flanking line presented alone.

(B and C) Other examples of facilitatory cells, which increased their responses when the flanking line was present to two (B) and four times (C) their response to the line presented within the RF alone.

(D) An example of a cell that showed a peak facilitatory interaction when the two lines were separated by 68′ of arc.

(E) Peak facilitatory interactions over the population of cells. A coaxial offset of 0.0 represents the position of the flank closest to the target for each cell studied, with other values representing displacements away from this point. The greatest number of cells showed peak interactions when the target and flank were closest together; a smaller number of cells showed peak interactions at larger separations between the bars.

Coaxial Separation

Figure 8 shows the response of several facilitatory cells when the flanking line was displaced along the colinear axis away from the stimulus line within the RF. When presented alone in the surround of the RF, the flanking line elicited no response, but the response was enhanced when the two bars were shown simultaneously.

The geometric relationship between the line within the RF and the flanking line that produced the greatest facilitation differed from cell to cell. For most cells, the enhancement was greatest when the lines were closest together (Figures 8A–8C). For the cell in Figure 8C, at the position of greatest facilitation, the response to the two bars was four times that of the response to the single line presented alone within the RF. A smaller number of cells in our sample showed the strongest facilitation when the lines had a greater displacement from one another along the colinear axis. In Figure 8D, for example, the maximal facilitation was seen with a separation between the two bars of 68′. Other cells showed primarily inhibitory interactions, most of which were maximal when the two lines were adjacent. The population histogram in Figure 8E shows, for the facilitatory cells having a clear peak response, that the greatest proportion exhibited peak facilitation when the pair of lines were close together, and the proportion showing facilitation at greater line separation progressively decreases as the separation increases. We examined the effect of coaxial separation in 56 of the cells showing facilitation. Of these, 84% (47) showed a clear dependency on the amount of separation and are included in the population

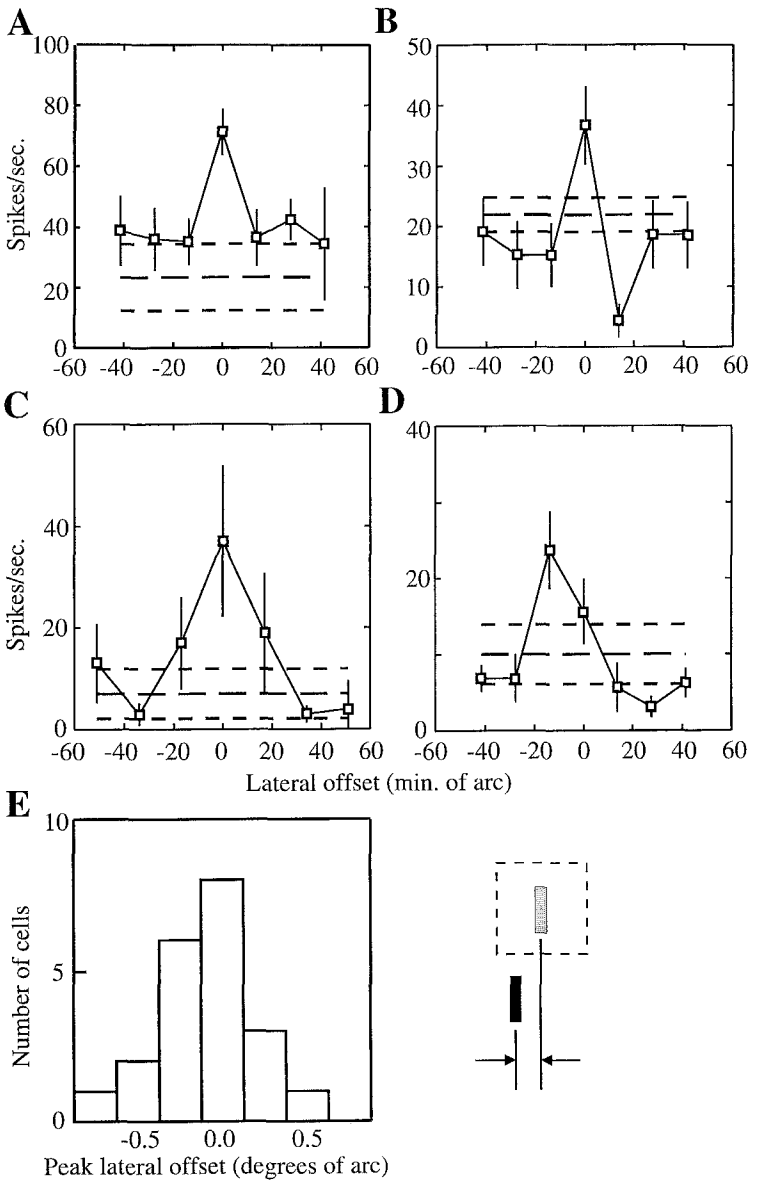

Figure 9. The Dependence of Physiological Enhancement on the Lateral Offset between the Target and Flank

(A) An example of a cell showing maximal enhancement when the bars were colinear. In this case the enhancement was about 3-fold and was sharply tuned. A lateral offset of as little as 16′ of arc caused the enhancement to decline to insignificant levels. The cell showed a typically strong dependence on colinearity.

(B) A cell showing peak enhancement when the bars were colinear and strong inhibition when the flank was displaced to either side. The inhibition was asymmetric and was stronger when the flank was displaced to the right.

(C) A cell showing a similar response pattern to the cell in (A) but more broadly tuned.

(D) A cell showing a peak enhancement at a 14′ of arc lateral separation between the bars.

(E) Peak facilitatory interactions over the population of cells. The largest number of cells showed peak enhancements when the target and flank were colinear; a smaller number of cells showed peaks as the lateral separation between the bars was increased.

histogram of Figure 8E. The remaining cells had curves that were too broadly tuned relative to their variability in firing to select a separation value of maximal facilitation.

Lateral Separation

The facilitatory interaction also declined as the bars were separated along an axis orthogonal to their orientations. For many of the cells studied, the facilitatory interaction was strongest when the bars were colinear and was reduced as the flank was displaced from colinearity (Figures 9A–9C). The drop off occurred over shorter distances than displacements along the axis of colinearity. Some cells showed peak facilitatory interactions at various lateral displacements between the bars (Figure 9D). The distribution of this effect over the population of cells studied, like the responses of individual cells, was sharply tuned (Figure 9E). For the individual examples shown, the greatest facilitation was seen when the lines were colinear; likewise, over the population studied, the greatest proportion of cells showing facilitation did so when the lines were aligned. Of the cells showing facilitation, 33 were examined for the effect of lateral separation, and of these, 64% (21) were included in the population analysis. Of the remaining cells, 6 showed a peak on either side of alignment.

Offset Angle

As with the psychophysical results, the physiological enhancement was dependent on the relative orientation of the two lines. Figures 10A and 10B show examples of the facilitatory interaction that peaked when the two lines had the same orientation. As the orientation difference between the two lines was increased, the facilitation declined until the neuron fired at the same rate as when the line within the RF was presented alone. A smaller number of cells showed peak interactions when there was an orientation difference between the lines. Figure 10C shows the

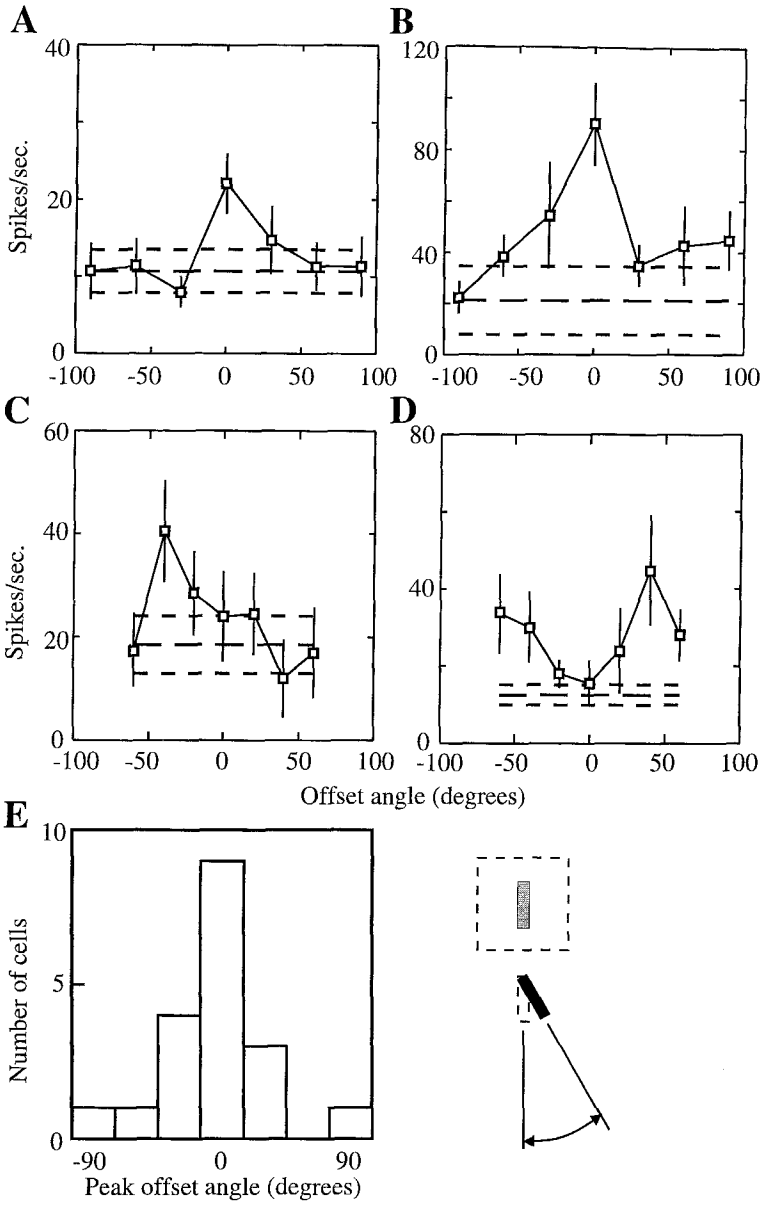

Figure 10. The Dependence of Physiological Enhancement on the Angular Difference between the Target and Flank

(A) An example of a cell showing maximal enhancement when the bars had the same orientation. The effect declined asymmetrically as an orientation contrast was introduced.

(B) A cell showing peak enhancement when the bars were parallel but with a broader tuning than the previous cell.

(C) A cell showing peak enhancement with a 40° orientation difference between the bars.

(D) A cell showing a minimum in facilitation at 0° offset angle. In a small proportion of the cells studied, there was no significant facilitation when the bars were of the same orientation, but an enhancement was seen as the flank was tilted to either side.

(E) Peak facilitatory interactions over the population of cells. The greatest number of cells showed peak interactions when the target and flank had the same orientation; progressively fewer cells showed peaks with increasing relative tilt of the two lines.

response of a cell that was maximally facilitated when the flank was tilted 40° from the orientation of the target. A small subset of cells showed double facilitation, with a minimum facilitation near 0°, as exemplified by the cell shown in Figure 10D, and these were excluded from the population histogram. Over the population of cells, there was a range in the offset angle of peak facilitatory interaction (Figure 10E). The greatest number of cells showed peak interactions when the test and flanking bars were parallel. A smaller number of cells showed peak facilitatory interactions when the two bars had different orientations. Of cells showing facilitation, 35 were tested for angular dependency, and of these, 56% (19) showed a peak allowing inclusion in the population histogram.

We examined the dependency of the facilitation effect on the continuity between the two lines in a few cells. The simple, single, straight-line flank was replaced with a T-shaped stimulus similar to that used in the psychophysical experiments. Two examples of this phenomenon are shown in Figure 11, where facilitatory interaction with the simple flanking line is seen to be eliminated when the crossbar of the T was introduced. This loss of facilitation was observed in 5 out of 10 cells showing facilitation that were studied for this effect. The remaining cells showed no significant reduction in facilitation.

Facilitation in Complex Environments

Up to this point, we have restricted the stimuli to a line or a pair of lines. To explore the relationship of these facilitatory effects to the phenomenon of contour saliency, we devised a more complex stimulus pattern. Ordinarily, owing to the extensive inhibitory regions surrounding RFs (Hubel and Wiesel, 1962; Bishop et al., 1973; Gilbert, 1977; Ferster, 1981; Das and Gilbert, 1995), the presence of multiple contours and surfaces that are normally present in natural

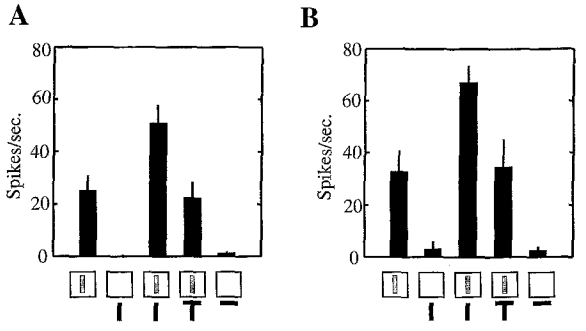

Figure 11. The Dependence of Physiological Enhancement on Continuity between the Target and Flank

In both cells, the enhancement declined significantly when the continuity between the bars was broken by replacing the flanking bar with a T-shaped stimulus.

scenes would be expected to greatly inhibit the response of cells, even where there is an appropriately oriented line segment within their centers. How is this inhibition affected when there are lines of the appropriate orientation lying outside the RF?

Figure 12 compares the effects of placing an iso-oriented flanking line outside the RF with the effect in the presence of a large number of randomly oriented and placed lines outside the RF. In itself, the pseudorandom background stimulus had a significant suppressive effect on the response of the cell to an optimally oriented line presented inside the RF. However, when the orientations of a few elements in the background were changed so that they became colinear with the target, this surround inhibition was eliminated. Of the 60 cells studied with similar stimuli, 21 were significantly inhibited by a pseudorandom surround, and of these, 9 showed a significant increase in firing, compared with the response to the target line in a random surround, when some of the surround elements were aligned with the one within the RF. Some of those that were not inhibited by the random surround nevertheless showed facilitation with iso-oriented flanking lines.

Discussion

Our results suggest that the substrate for contour integration and saliency is present in primary visual cortex. The effect of a flanking line on the threshold contrast level for perception of a target line is paralleled by the contextual sensitivity of superficial layer complex cells in V1. Both effects are seen as a marked facilitation that is maximal when the pair of lines are aligned, in close proximity, and of the same orientation. While not all cells show optimal facilitation for colinear, iso-oriented lines, over the population of cells studied, there is good agreement with the psychophysical observations. However, the minority of cells, those showing a preference for flanking lines that are tilted relative to the RF orientation, might have an additional use in the perception of curvature.

The Role of Context on the Perception of Local Features

The importance of contextual interactions in the perception of the visual attributes of local features has been shown in a wide variety of experiments. The contextually dependent attributes include position (Badcock and Westheimer, 1985; Burbeck and Hadden, 1993; Kapadia et al., 1994), depth (Westheimer, 1986), orientation (Gibson and Radner, 1937; Westheimer et al., 1976), and motion (Westheimer and Wehrhahn, 1994). The influence of context on perceived brightness has also been well documented in the perception of surface brightness, although many of these effects are inhibitory and are explainable by local contrast (Shapley and Reid, 1985).

The facilitatory perceptual effects shown in this study have in part been previously reported using other stimuli, such as Gabor patches (Polat and Sagi, 1993, 1994) or iso-oriented lines (Dresp, 1993). Our own results differ from those of earlier studies in the geometric layout of the stimuli, which may account for quantitative differences in the position and orientation dependency of the facilitatory effect. By using comparable stimuli in psychophysical and electrophysiological experiments, a quantitatively similar dependency on position and orientation emerges. Furthermore, our findings on the detectability of line segments are comparable to earlier experiments on contour saliency effects (Wertheimer, 1938; Grossberg and Mingolla, 1985; Ullman, 1990; Field et al., 1993), suggesting that they invoke the same mechanisms. The contextual effects may also play a role in fill-in of contours (e.g., illusory contours; Kanizsa, 1979).

Comparison of Psychophysical and Physiological Results

In comparing the psychophysical and physiological parts of the study, it is important to note that both effects operated over roughly the same scale. Psychophysical experiments were performed with the target 4° away from the fovea, and although the location of RFs in the physiological experiments varied, they were centered at approximately the same distance from the fovea. In the psychophysical measurements, and over the population of cells studied, the facilitation was reduced to negligible levels when the target and flank were separated by about 2° along the colinear axis, when they were separated by 30′–45′ along an orthogonal axis, or when their orientations differed by 60° or more.

A number of RF properties, in addition to the "nonclassical" RF effects emphasized here, might play a role in the perceptual effects discussed above. One would expect, for example, that many RFs would overlap with both target and flank, such that more traditional length-summation effects would account for some of the heightened response of cells. The importance of classical RF properties would, however, play less of a role as the separation between the lines increases. A minority of cells show inhibition, rather than excitation, to lines placed in the region flanking the RF, a property known as end inhibition. While facilitation seemed to outweigh inhibition in terms of the

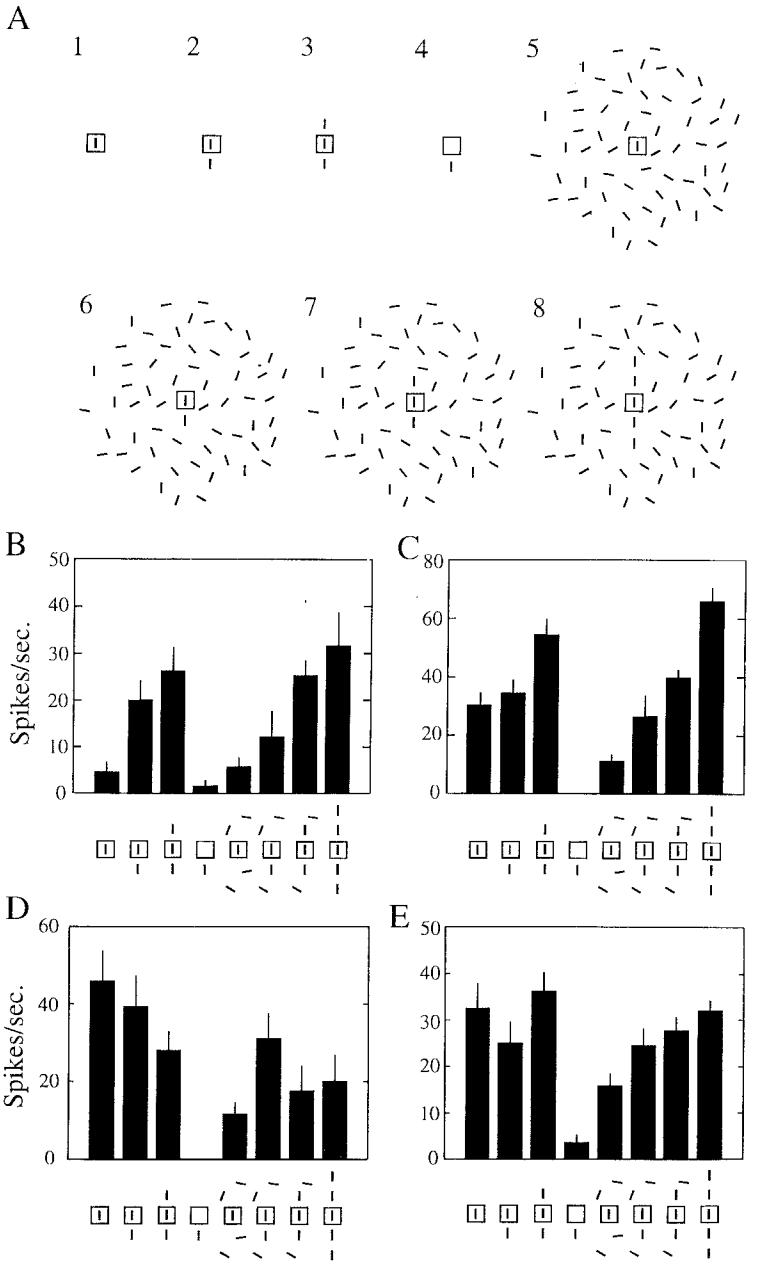

Figure 12. Physiological Data Using a Complex Background Stimulus

(A) Depictions of the stimuli used in this set of experiments. In addition to normal target/flank combinations, four new stimuli were introduced in which the target was placed within a background of pseudorandomly oriented line segments.

(B–E) The response patterns of 4 cells to the various stimuli. Each data bar represents the response to the corresponding stimulus depicted in (A), as labeled. When placed within the noisy background, the response of cells to the target often declined substantially (C–E). As surround elements were rotated to become colinear with the target, however, much of this inhibition was eliminated and, in some instances, increased beyond the response to the central bar stimulus.

numbers of cells involved, two additional considerations apply to minimize further the importance of inhibition in this stimulus situation. First, at threshold levels, where cells are barely spiking above spontaneous levels, the effect of inhibition would be minimal, whereas facilitation could induce a large change in firing. Second, the gap between the two lines may leave out the strongest part of the inhibition. At the cellular level, joining the target and flank into a continuous line eliminated the facilitatory effect. This might account for the observation in the psychophysical experiments that, for some subjects, there is less facilitation when the lines are closest than when they are a bit displaced from each other. It seems that the processes revealed by our experiments are most effective for contours made up of line segments with gaps between them, and it is not clear what role they would play in contour integration along continuous lines. The latter might be dealt with in other ways, perhaps by cells with larger classical RFs in higher order cortical areas as opposed to interactions arising from outside the classical RF in area V1.

Beyond the several points of equivalence between the psychophysical and physiological results outlined above, one should also be clear about the differences in the stimulus conditions. Although similar contrast levels were used in the two experiments, the stimuli were at threshold levels for the psychophysical experiments but were at suprathreshold levels for cell responses. We do not know whether this represents a difference in contrast sensitivity between man and monkey, or if threshold level responses in V1 simply do not reach conscious awareness. Also, the

stimuli in the psychophysical experiments were attended to and discriminated, while those in the physiological experiments were unattended. While passive stimulation demonstrates that contour interactions can result from bottom-up processes, it will be worthwhile in the future to explore the role of attention in modulating these interactions.

Cortical Substrate of Facilitatory Effects

There are several aspects of the facilitation we see in V1 that indicate the phenomenon is cortical in origin and is not due to stray light or to interactions at antecedent levels. While surround effects have been observed in retina (the "McIlwain effect"; McIlwain, 1964) and in the lateral geniculate nucleus (e.g., the "shift effect" in Fischer et al., 1978), the orientation dependency of the effect seen here suggests that it involves interactions between cortical cells with oriented receptive fields. In addition, we see interocular transfer, where presenting the target stimulus to one eye affects the appearance of the flanking stimulus in the other eye. Finally, the effect is reduced when we place a crossbar at the RF end of the flanking bar, reinforcing the importance of orientation on the effect.

Facilitatory influences from outside the classical RF are a well-established phenomenon (Maffei and Fiorentini, 1976; Allman et al., 1985; Nelson and Frost, 1985; Gilbert and Wiesel, 1990; Knierim and Van Essen, 1992). Some of the work on this subject focused on the cellular mechanisms by which animals distinguish foreground from background movement (Allman et al., 1985; Tanaka, 1986; Orban et al., 1987). Many of the studies referred to above have tended to use stimuli in the region surrounding the RF that were distributed in space (i.e., including multiple lines or gratings), making it difficult to compare the influences coming from specific spatial locations. Some studies have shown facilitatory interactions from orthogonally oriented lines outside the RF and have been used to account for the perception of borders defined by textural differences (Knierim and Van Essen, 1992; Lamme, 1995), but these might be explained by the presence of iso-oriented inhibitory regions whose influence is eliminated by the presence of orthogonally oriented line segments in the RF surround. The current study emphasizes the importance of the precise relative positioning of lines within and outside the RF in determining the kind of influence that one sees. The sign and strength of the surround influences depend on the geometry of the contours passing through the RF, and this dependency at the cellular level may account for the principles governing contour saliency.

Although the overall population of cells in our study shows a very similar behavior to the psychophysical observations, it is intriguing that some cells do not have peak facilitation for iso-oriented, aligned, and adjacent lines but give maximal response with a defined offset angle. Some of these cells even show minimum facilitation for parallel lines (see Figure 10D), reminiscent of the "tuned inhibitory" class of cells showing disparity tuning (Poggio and Fischer, 1977). They potentially would allow discrimination of curvature and the linkage of contours comprised of differently oriented segments.

We postulate that the anatomical basis for the phenomena presented here is the plexus of long-range horizontal connections found in primary visual cortex (Gilbert and Wiesel, 1979, 1983, 1989; Rockland and Lund, 1982, 1983; Martin and Whitteridge, 1984). These connections allow integration of information over much longer distances than the extent of individual RFs and may serve as relays for contextual information from surrounding parts of the visual field. It has been shown that the horizontal connections formed by superficial layer pyramidal cells contact both inhibitory and excitatory neurons (McGuire et al., 1991) and that the horizontally evoked synaptic potential can include both excitatory and inhibitory components (Hirsch and Gilbert, 1991). The balance between excitation and inhibition in these might account for the spatial dependency of these effects.

The specificity of these connections enhances the likelihood that they play a role in the particular contextual effects demonstrated here. Horizontal projections tend to connect cells with similar orientation preferences (Ts'o et al., 1986; Gilbert and Wiesel, 1989; Malach et al., 1993; Das and Gilbert, 1995) and, even more specifically, cells whose RFs are topographically aligned along an axis of colinearity (D. Fitzpatrick, unpublished data). The relative ratios in which horizontal connections follow these rules of connectivity resemble the orientation dependency of the psychophysical and physiological effects (Ts'o et al., 1986). Further evidence for the role of horizontal connections comes from the extent of their projections. The cortical scale of the contextual interactions can be inferred from the monkey physiological experiments. At the eccentricity at which the experiments were done, the 2° of visual arc over which information must be integrated to produce the described facilitatory effects corresponds to roughly 5 mm of cortical surface (Hubel and Wiesel, 1974; Dow et al., 1981). This distance is well within the measured spread of horizontal connections. Nevertheless, feedback from higher-order cortical areas with larger RFs cannot be ruled out as a contributing mechanism.

Role of Facilitatory Effects in Contour Integration

It is tempting to link the psychophysical and physiological effects of a flanking line to the integration of the line elements of a contour and to the saliency of the contour in a noisy background. Experiments done with two lines in isolation and with contours in complex environments show similar dependencies on the relative positions and orientations of the component line segments. The observations on the facilitatory effects on cell responses of iso-oriented, colinear lines presented in an environment of randomly placed and oriented lines suggest that facilitatory influences from outside the classical RF may be more important under such circumstances, because some cells showed either no facilitation or an inhibition to a flanking line with an otherwise blank background, but showed substantial facilitation to a flanking line when the background was filled with other stimuli. In fact, one might expect that,

owing to the inhibitory regions surrounding the RF, a cell would not respond very well in natural visual environments, which is consonant with our finding of the profound inhibitory effect of multiple randomly placed and oriented lines outside the RF. The results presented here, however, suggest further that, with the appropriate configuration of contours surrounding the RF, the cell is lifted from a rather profound level of inhibition, and its excitatory inputs are unmasked, allowing it to respond to the stimulus. The push–pull nature of the surround effects brings up the firing level of cells whose RFs coincide with salient stimuli and suppresses the firing of cells whose RFs overlap with noise or confounding contours.

Experimental Procedures

Psychophysics

Psychophysical experiments on human observers were designed to measure detection of line stimuli in isolation and in the presence of flanking lines. Stimuli were presented on a CRT monitor (Barco CCID7351) refreshed at a rate of 60 Hz. At an observation distance of 114 cm, the visible area of the display subtended 14° × 18.5° and was composed of 640 × 480 pixels. Stimulus presentation was controlled by a Sergeant Pepper #9 graphics board and a PC-compatible 486 computer. No error feedback was provided. Observation was binocular with normal pupils and free head.

The target consisted of a white vertical line, 30′ × 5′, against a uniform background of 10.4 cd/m^2 luminance (Figure 1). A 7.5′ square on which the subject was asked to maintain fixation was shown 4° away from the location of the target. An additional square of the same size was positioned 30′ of arc to the left of the target and served as a position cue to direct the observer's attention. The fixation point and position cue always remained on the screen even when the other stimuli did not.

The psychophysical experiments presented here investigated the effects of a second bar, or flank, on the detection threshold of the target. The location and orientation of the flank relative to the target was systematically varied between experiments. To compensate for differences in detection thresholds between daily sessions, experimental trials consisting of the target and flank shown simultaneously were interspersed with control trials consisting of the target shown in isolation. The flanking bar, when present, was shown at high contrast (84 cd/m^2), while the target could appear at one of seven different contrasts near the limits of detection of human observers. After each presentation, the observer had to indicate whether or not a target was visible by pressing the appropriate key on a keyboard. The percentage of "yes" responses was computed separately for experimental and control trials at each of the seven target contrasts and was used to calculate a detection threshold (see below).

Each trial consisted of a 1500 ms cycle. The target and/or the flank was presented for 200 ms and followed by a 1300 ms interstimulus interval during which a response was recorded. As an auditory cue alerting the observer, there was a short audible beep at the onset of the visual stimulus.

To compensate for guessing, at least 10% of all trials were null conditions in which no target was present. For control trials, this corresponded to an empty screen aside from the fixation point and positional cue, while in experimental trials, the flanking bar was present as well. Positive responses in the null condition were accumulated separately for the experimental and control trials, and a separate false-positive rate was calculated for each. This false-positive rate, fp, was used to adjust the percentage of positive responses, p, in each of the seven contrast conditions according to the formula:

$$p' = (p - fp)/(1 - fp),$$

to yield p′, the true positive rate.

The seven target contrasts and their adjusted proportion of positive responses were then fitted to a psychometric curve by the method of probits. The detection threshold was determined from the curve as the contrast at which the observer could successfully detect the target 75% of the times it was presented, after adjusting for guessing.

All data points presented here are based on a total of at least 600 trials each for experimental and control conditions, plus additional null trials. The trials were distributed over a minimum of 2 days. Although our observers, which included three of the authors, were well practiced in the task, absolute thresholds showed considerable variation between them. The values reported here, however, refer to changes in the detection threshold caused by the flank. We report throughout the difference in detection between experimental and control conditions divided by the detection threshold in the control condition, i.e., the change in detection threshold between the two conditions. The standard error of this value is calculated by propagation of errors in the same formula.

The psychophysical experiments examining the effects of interocular transfer required a separate apparatus in which a different stimulus could be presented separately to each eye. Two vector scopes (Hewlett-Packard 1345A) were positioned with a system of semisilvered mirror and polaroid filters so that each eye would see only one scope. Unlike the other psychophysical experiments, a head rest was used for increased stability, and experiments were done in the fovea instead of the periphery. A full set of binocular experiments performed in the fovea on one observer showed only quantitative differences to data in the periphery (data not shown). The scopes subtended 2.3° × 2.8° at a viewing distance of 200 cm and were refreshed at a rate of 66.7 Hz. Changes in brightness were produced by varying the number of times a line was drawn within each 15 ms refresh cycle.

The target and flank were 30′ × 1′ horizontal bars and could be presented in either eye independently as needed. A small dot was presented binocularly above the target to serve as a positional cue and to stabilize fusion. In experiments where we tested for interocular transfer of the threshold reduction effect, the target and flank were presented separately in each eye. The values that we report reflect the reduction in detection threshold observed for this stimulus when compared with a control in which both bars were presented in the same eye.

Physiology

The physiological portions of the study involved recordings in awake, behaving primates. Two adult, male Rhesus macaques (Macaca mulatta) weighing 9 and 4.3 kg were used in the experiments. After several weeks of fixation training, we implanted a fiberglass recording chamber over a portion of the striate cortex and recorded unit and multiunit activity. The animal's fluid intake was restricted during the training and recording periods with liquid rewards. All surgical procedures were performed under pentobarbital sodium anesthesia under aseptic conditions. The animals were allowed to recuperate for several days after each procedure. All procedures follow NIH guidelines on the care and use of laboratory animals.

Training and Preparation

During each training session, the monkey's head was restrained using a surgically implanted steel post. At the start of each trial, a small target appeared on the screen, and the animal was rewarded for holding fixation on the target for a variable amount of time. Training continued for several weeks until the animal could reliably hold fixation within a 0.3° radius around the target for 2–3 s. Eye movements were monitored using an infrared oculometer (monkey #1, Bouis, Germany; Bach et al., 1983) or a scleral search coil system (monkey #2, CNC Engineering; Judge et al., 1980).

Monkey #2 was trained to perform a detection task, allowing self-initiation of each trial. A target appeared on the screen after the animal pulled a lever attached to the primate chair. The animal had to hold the lever in position until the target dimmed. Release of the lever within a short interval after the dimming resulted in a juice reward. The animal was trained until it could reliably release the lever within 400 ms of the dimming. The animal was rewarded for correctly performing the dimming task. Fixation was maintained within 0.1°, generally, as monitored with the eye coil system. The monkey performed the task correctly in ~80% of trials during recording sessions. Only these were used for analysis of cell responses. The greater accuracy of fixation ensured that the flanking-bar stimulus lay consistently outside the RF.

Moreover, by interspersing flank-only control trials between the test trials, we could ensure that errant eye movements did not give specious results with the flanking bar overlapping the classical RF.

Electrophysiological Recording

Physiological recordings were made in three hemispheres. A fiberglass recording chamber with an inner diameter of 16 mm was implanted after completion of fixation training. The chamber was positioned to allow access to a large portion of striate cortex. Penetrations were made through the dura mater using glass-coated platinum iridium microelectrodes (Wolbarsht et al., 1960) with typical impedances between 1.0 and 3.0 MΩ at 1 kHz. Electrodes were driven using a stepping motor microdrive (Narishige PC-5N). Successive penetrations were usually positioned 0.5–1.0 mm apart without repeating previous recording sites. This pattern allowed us to use each recording chamber for up to 7 months. The recording chamber was filled with silicone oil (DS Fluid, 200cs) during the recording session to prevent the dura surface from drying and to prevent pulsations. 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.

Data acquisition and behavior control were performed using separate PC-compatible 486 computers. The electrode signal was amplified and filtered (Model 1800, AM Systems) and passed into a time–amplitude window discriminator (Bak DDIS-1) to distinguish spikes. The output from the discriminator was, in turn, passed into a computer that stored individual spike times and sorted according to the stimulus condition. Patterns of neural activity and response histograms were visible on-line, but statistical analysis was performed after the recording session was completed. The amplified electrode signal was also surveyed through an audio monitor.

A third 486 computer controlled stimulus presentation on a CRT monitor (NEC Multisync 5D) through a Sergeant Pepper #9 graphics board using proprietary software (STIM). The monitor was 24 × 36 cm; it was placed at a viewing distance of 112 cm (monkey #1) or 138 cm (monkey #2) and refreshed at 60 Hz. Resolution was 640 × 480 pixels. Observation was always binocular.

Daily recording sessions typically lasted 2–4 hr. During each session, we recorded the activity of either single, isolated units or of clusters of several units. After neural activity was isolated, we obtained a crude RF map by using a hand-held stimulator and by listening to discharges on an audio monitor while the animal was performing the fixation task. Most recording sites were on the opercular surface of the striate cortex, although in the second hemisphere of monkey #1, several penetrations were made into the roof of the calcarine fissure. The eccentricity of RFs ranged from 1.5° to 5.5° on the operculum and from 9.2° to 12.4° on the roof of the calcarine fissure. In this study, all recordings were made within area V1. The anterior boundary of striate cortex was estimated by measurements of the lunate sulcus at the time of chamber implantation and was further determined by the movement of RF 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 500 μm of cortex. This ensured that all of our recording sites would be restricted to the superficial cortical layers, although we did not analyze them histologically. In the experiments that examined the dependency of the interaction on the orientation of the flank, the cell pool was restricted to those cells that were orientation selective. Cells whose orientation tuning curves demonstrated a half-bandwidth ≥90° were excluded from this part of the analysis. In the figures, the single unit recordings were the examples shown in Figures 7A and 7B; 8A, 8B, and 8D; 9D; 10A and 10B; 11A and 11B; and 12B–12E. The multiple unit recordings were those shown in Figures 8C; 9A–9C; and 10C and 10D. Of 291 cells studied, 100 were in monkey #1 (two hemispheres) and 191 were in monkey #2 (one hemisphere).

Data Collection

After mapping the RF and estimating its optimal orientation, we began quantitative data collection. The stimuli used in the experiments were similar to those used in the psychophysical studies (see Figure 6). Each trial began with the onset of the fixation point. After the monkey had begun to hold fixation, stationary stimuli were flashed on the screen while recording spike activity. Stimulus presentation began 300 ms after the monkey had moved its eyes into the fixation window and ran through several presentation cycles. During each cycle, the stimulus was off for 200 ms, on for 200 ms, and off for another 400 ms. Each trial consisted of 2–6 of these cycles, at which point the fixation spot dimmed, with the stimulus configuration varying randomly between presentations among a predefined set. If fixation was broken during the trial, the stimulus presentation was aborted.

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 rate of background activity. The time window of the response was adjusted to each cell within the range of 50–250 ms after stimulus onset, depending on the latency and length of response. In some cells, longer durations were used to include offset responses. Responses to 5–10 trials of the different stimulus conditions were compared using the Kolmogorov–Smirnov test ($p < .05$).

Tests for Contextual Interactions

Tests for contextual influences were performed by comparing the response of the cell to an optimally oriented bar located inside the RF with the response to the same bar when an additional bar was simultaneously presented outside the RF borders (see Figure 6). The second bar, or flank, was positioned such that, alone, it either elicited no response or caused a suppression in the background firing rate of the cell (see Figure 7).

Stimuli were presented against a background of 17 cd/m^2 luminance. The flanking bar was presented at high contrast (62%). Though the stimulus within the RF was normally presented at low contrast (10%–22%), a higher contrast stimulus was used for those cells for which a low contrast stimulus was not adequate to induce consistent responses.

The experiments followed a random block design, with one condition each where the target or flank was shown alone and seven conditions in which they were presented simultaneously, varying only in the location or orientation of the flank. The position of the flank in the condition in which it was shown alone corresponded to its position when it was closest to the RF center. Data collection continued until each stimulus was presented between 5 and 15 times.

In one set of experiments, we examined the effects of presenting the target–flank combination within a complex background. The bars were of equal size and luminosity as the flank and were presented at a pseudorandom orientation and position over a radius of 4.5° around the RF.

Acknowledgments

We thank Kaare Christian for development of the visual stimulator, behavior control, and data acquisition programs. Ella Leers and Kathleen McGowan provided expert technical assistance. We would also like to thank the many people who helped us develop the awake-monkey electrophysiology preparation, including Richard Andersen, Nikos Logothetis, Pietro Mazzoni, John Maunsell, and Steven Kane. The work was supported by National Institutes of Health grants EY07968 (C. D. G.) and EY00220 (G. W.) and by a Charles H. Revson fellowship (M. I.).

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Received June 13, 1995; revised July 27, 1995.

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