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Contour Saliency in Primary Visual Cortex

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Summary

Contour integration is an important intermediate stage of object recognition, in which line segments belonging to an object boundary are perceptually linked and segmented from complex backgrounds. Contextual influences observed in primary visual cortex (V1) suggest the involvement of V1 in contour integration. Here, we provide direct evidence that, in monkeys performing a contour detection task, there was a close correlation between the responses of V1 neurons and the perceptual saliency of contours. Receiver operating characteristic analysis showed that single neuronal responses encode the presence or absence of a contour as reliably as the animal's behavioral responses. We also show that the same visual contours elicited significantly weaker neuronal responses when they were not detected in the detection task, or when they were unattended. Our results demonstrate that contextual interactions in V1 play a pivotal role in contour integration and saliency.

Introduction

To recognize an object in visual scenes, contour elements that belong together must be correctly linked and segregated from other contours, a process known as contour integration. Contour integration follows the Gestalt law of "good continuation" (Wertheimer, 1923), by which discrete contour elements positioned and oriented along a smooth path are readily grouped together (such as the straight contour shown in Figure 1C), forming a continuous visual contour that is globally salient and "pops out" from its background (Field et al., 1993). However, depending on the spatial configuration of contour and background elements, the perceptual saliency of contours can be different (compare the three contours shown in Figure 1; see also Field et al., 1993; Li and Gilbert, 2002).

Evidence from physiological (Bauer and Heinze, 2002; Kapadia et al., 1995; Kourtzi et al., 2003, 2005; Polat et al., 1998), psychophysical (Adini et al., 1997; Dresp, 1993; Field et al., 1993; Kapadia et al., 1995; Li and Gilbert, 2002; Polat and Sagi, 1994b), and anatomical (Gilbert and Wiesel, 1979, 1983, 1989; Rockland et al., 1982; Schmidt et al., 1997; Stettler et al., 2002) studies, as well as computational approaches (Ernst et al., 2004; Li, 1998; Ullman, 1992; VanRullen et al., 2001; Yen and Finkel, 1998), suggests that contour integration, a form of intermediate-level vision, can be mediated by primary visual cortex (V1), the first stage in visual cortical processing. Support for the involvement of V1 in contour integration comes from parallel psychophysical measurements in human subjects (Kapadia et al., 1995; Li and Gilbert, 2002; Polat and Sagi, 1994a) and quantification of neuronal response properties (Kapadia et al., 1995) and circuits (Stettler et al., 2002) within V1. These experiments show that, though contour integration can extend across large areas of visual space, this global integration capability is based on a cascade of interactions of more limited spatial extent, and that the visuotopic extent of these interactions is comparable to that of the intrinsic horizontal interactions in V1.

Although the substrate for contour integration has been suggested to lie in V1 on the basis of the earlier studies, no direct correlation has yet been established between V1 responses and perceptual saliency of contours. In the current study, by taking advantage of the graded nature of contour saliency (Li and Gilbert, 2002), we examined in behaving monkeys the relationship between the responses of V1 neurons and the performance of the animals on detection of contours of various saliencies.

Results

Two monkeys (MA and MB) were trained in a contour detection task, in which straight contours of various saliencies were made of a series of collinear line segments embedded in the center of an array of randomly oriented and positioned line segments (Figure 1).

Contour Saliency and Neuronal Responses in V1

Within a trial in the contour detection task (Figure 2A), a contour pattern was presented randomly either at the receptive field (RF) location of the recorded cell or in the opposite hemifield. Simultaneously, a similar noise pattern without any embedded contour was displayed in the hemifield opposite to the contour pattern. After stimulus exposure, the animal reported which of the two patterns contained the embedded contour by making a saccadic eye movement to either of two dot targets displayed at the end of the trial. Responses of single orientation-selective neurons in V1 were recorded together with the animal's behavioral responses. The orientation of the contour in the contour pattern was adjusted to the preferred orientation of the recorded cell and so was the central line segment in the noise pattern.

Data collected from a typical recording session in MB are shown in Figures 2B1–2B4. We examined the animal's behavioral response as a function of two independent variables in two sets of experiments. In one set of experiments, contour saliency was increased by increasing the number of collinear lines (Figure 2B1). In the other set of experiments, contour saliency was decreased by increasing the spacing between collinear lines (Figure 2B2; see Figure 1 for a demonstration of the saliency change). The change of contour saliency was reflected in the change of the animal's performance on contour detection, which was around 50% (the chance level) for the least salient contours and was

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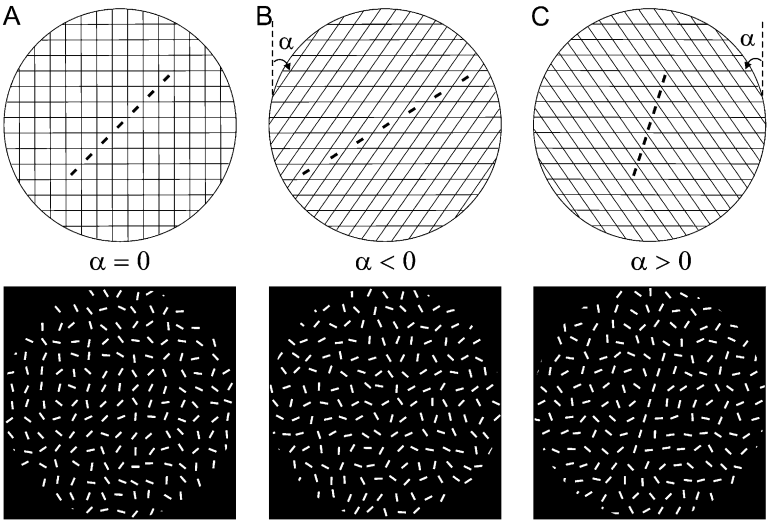

Figure 1. Design of Visual Contours

(A) A circular area of 5.2° in diameter was divided into 0.4° squares (top panel). Each square contained a randomly oriented line segment of 0.2° by 0.05° (bottom panel), whose position was slightly jittered within the small compartment. The orientation and position jitter of each line was re-randomized in each trial. By aligning some adjacent line segments along a diagonal of the grids in a collinear, evenly spaced arrangement, a straight contour was generated in the center of stimulus pattern.

(B and C) To vary the spacing between collinear elements comprising the contour while keeping the density of line segments in the full stimulus pattern unchanged, a skew angle "α" was introduced to the grids. A clockwise skew ([B], $\alpha < 0$) increased the spacing between contour elements, while a counterclockwise skew ([C], $\alpha > 0$) decreased the spacing. Contour saliency was altered by changing either the number of collinear lines forming the contour or the spacing between them. The "average spacing" was defined as the width or height of an individual square or diamond compartment, which was fixed at 0.4°. The "(relative) collinear spacing," which was defined as the center-to-center distance between two adjacent contour elements, was calculated relative to the average spacing. Therefore, a relative collinear spacing of 1.0 represents an absolute spacing of 0.4°.

close to 100% for the most salient contours. These observations are consistent with our previous study on human subjects (Li and Gilbert, 2002). The animal's behavioral performance, calculated as "proportion correct," was our psychophysical measure of perceptual saliency of contours in the current study. To explore the relationship between performance on contour detection and V1 responses, we recorded from neurons in the superficial layers of V1 during the same trials when the animal was performing the discrimination task (Figures 2B3 and 2B4). Changes in the perceptual saliency of contours were closely correlated with the responses of the recorded cells. When contours were rendered more salient by increasing the number of collinear lines, the neuronal responses were increased monotonically (Figure 2B3). Conversely, when contour saliency was reduced by increasing the spacing between collinear lines, the neuronal responses were correspondingly reduced (Figure 2B4).

In both MA and MB, the effects of parametrically changing the contour settings on the animal's behavioral responses and on the neuronal responses were qualitatively similar in all recording sessions and in all recorded cells (Figures 2C1–2C4). Thus, the behavioral data from each experiment were averaged across all recording sessions for the same animal (Figures 2C1 and 2C2). To determine the mean response of all neurons, we calculated, for individual cells, the ratio between the mean responses to the contour patterns and to the noise patterns. This ratio is referred to as the "relative (neuronal) response" throughout the text. A relative response greater than 1.0 indicates facilitation of neuronal responses induced by the contours. The relative responses were averaged across all recorded cells in the same animal for the same test conditions (Figures 2C3 and 2C4). Very similar to the single example shown in Figures 2B1–2B4, for both animals systematic changes in contour parameters resulted in parallel changes in the animal's behavioral performance and the neuronal responses (compare Figure 2C1 with Figure 2C3 and Figure 2C2 with Figure 2C4). In addition, for the most salient contours (detection performance close to 100%) neuronal responses were facilitated on average by more than a factor of two relative to the responses to the noise patterns. Note that the same visual contours seemed to be more salient on average to subject MB, whose overall performance was better than MA's (Figures 2C1 and 2C2). Correspondingly, the facilitation of neuronal responses by the same visual contours was stronger on average in MB than in MA (Figures 2C3 and 2C4).

Note that the facilitatory effect induced by the embedded contours extended well beyond the classically defined RF. The RF lengths of all recorded cells were in the range of 0.2° and 1.3° with a mean of 0.6°, while nine collinear lines, the largest number of collinear lines tested in our experiments, extended 3.4° in visual space. Even at this contour length the collinear interactions had not reached a plateau, suggesting that the facilitatory interaction could extend over larger distances (Figures 2B3 and 2C3; the vertical lines indicate the sizes of classical RF). While for cells with bigger RFs integration of contour elements could start within the classical RF, our data indicate that the boundary of the classical RF was not a property that was relevant to contour integration, since there was no correlation between the RF size and the facilitation strength (Figure S3 in the Supplemental Data available with this article online). Moreover, for all recorded cells, without exception, neuronal responses to very salient contours were enhanced relative to the noise pattern. This suggests that contour integration is a generic feature of orientation-selective neurons in superficial layers of V1.

The data shown in Figure 2 imply a close correlation between neuronal responses and contour saliency. Note that saliency is a perceptual phenomenon that is not solely determined by stimulus configurations. Even for the same contour patterns the perceptual saliency

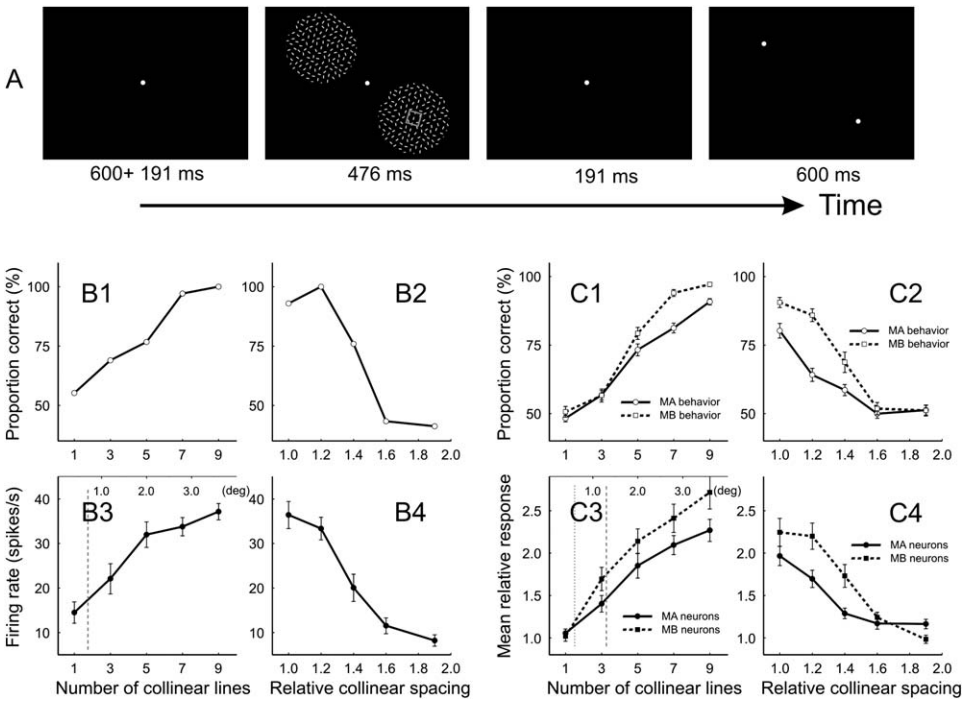

Figure 2. Behavioral and Neuronal Responses in the Contour Detection Task

(A) Stimulus and behavior paradigm. A trial consisted of four consecutive intervals: fixation, stimulus exposure (the small gray square denotes the RF), continuing fixation, and choice (see Experimental Procedures for details).

(B1–B4) Data from subject MB in a typical recording session. (B1) The animal's performance on contour detection as a function of the number of collinear lines. When the number was 1, the two stimulus patterns were identical noise patterns, and the "contour pattern" was randomly assigned to either of them. The relative collinear spacing (for definition see Figure 1 legend) was fixed at 1.0 in this experiment. (B2) The animal's performance as a function of the relative collinear spacing. The contours consisted of seven collinear lines in this experiment. (B3 and B4) The mean responses of a V1 cell to the contour patterns recorded in the session shown in (B1) and (B2), respectively. This V1 cell had a RF of 0.55° by 0.70° in width and length, and orientation tuning width of 47° (see Experimental Procedures for definitions). The upper abscissa in (B3) indicates the corresponding contour length in degrees of visual angle, and the RF length of this cell is indicated by the dashed vertical line.

(C1–C4) Population analysis. (C1) Proportion correct in contour detection, averaged across all recording sessions for MA (n = 30) and MB (n = 24) respectively, as a function of the number of collinear lines. (C2) Proportion correct for MA (n = 25) and MB (n = 20) as a function of the relative collinear spacing. (C3) The mean relative responses of all the recorded cells (n = 30 for MA; n = 24 for MB) as a function of the number of collinear lines. The "relative response" is defined as the ratio between the mean neuronal responses to the contour patterns and to the noise patterns. The mean and maximum RF lengths of the recorded cells are indicated by the dotted and dashed vertical lines. (C4) The mean relative neuronal responses (n = 25 for MA; n = 20 for MB) as a function of the relative collinear spacing. Error bars in all figures represent ±SEM.

can be different for different subjects (Figures 2C1 and 2C2; see also Li and Gilbert, 2002). Contour saliency can also be profoundly affected by practicing the detection task (Kovács et al., 1999; Li and Gilbert, 2002) and can vary across experimental sessions depending on other factors, such as the observer's cognitive state. On the other hand, contours that are embedded in the same noise context but that have different configurations can be equally salient in perception. For example, a contour made up of five collinear lines can be as salient as seven collinear lines spaced further apart. Considering the combination of properties that contribute to contour saliency, a more appropriate analysis of the correlation between neuronal responses and contour saliency is to directly compare the neuronal responses with the behavioral performance (Figure 3). To this end, we performed correlation analysis on the raw data obtained from individual recording sessions, where saliency was adjusted by changing the number of contour elements (Figure 3A1) or by changing the spacing between them (Figure 3B1). Each data point in the figure corresponds to a given contour configuration in a given recording session in which a pair of mean neuronal and behavioral responses was collected. Due to the response variability across and within sessions, the data points are scattered. Nevertheless, a strong and highly significant correlation is evident between neuronal responses and the animal's performance, as indicated by the large correlation coefficients (the r values in the figure). Note that, in Figures 3A1 and 3B1, the relative neuronal response was plotted as a function of the animal's performance on contour detection, which is a psychophysical measure of contour saliency. In this case, the results obtained from changing the number of collinear lines (Figure 3A1) or changing the collinear spacing (Figure 3B1) could be related to a common measure, allowing us to pool the data from the two experiments (Figure 3C1). Moreover, the difference in the mean relative neuronal responses between MA and MB, which is substantial in Figures 2C3 and 2C4, is negligible when the neuronal response is measured as a function of contour saliency rather than as a function of the stimulus parameters themselves (see the two nearly superimposed clouds of data points and regression lines in Figures 3A1,

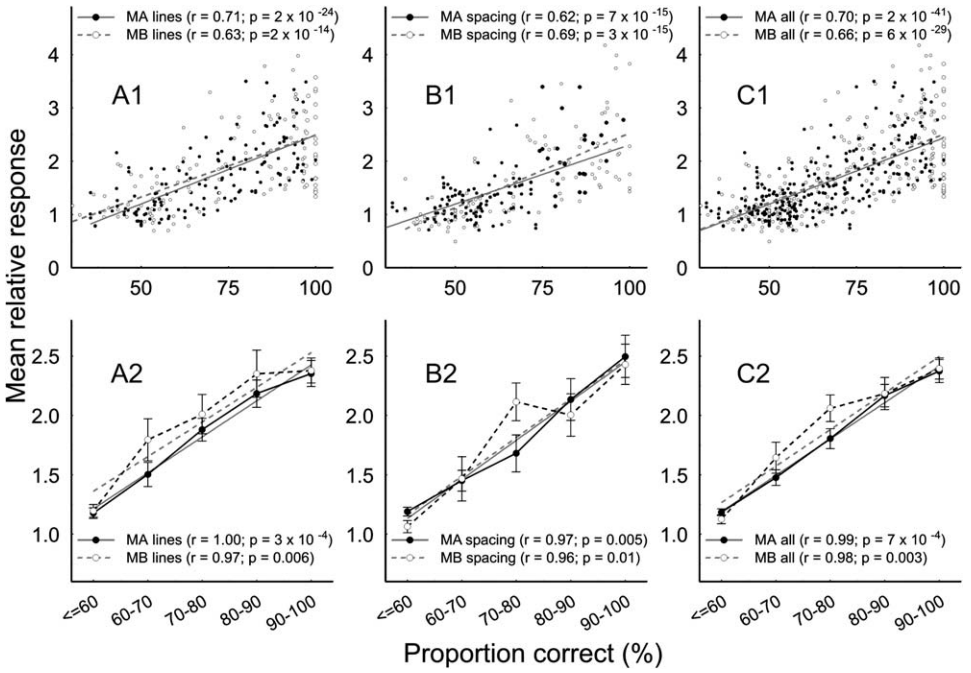

Figure 3. Correlation between Neuronal Responses and Contour Saliency

(A1, B1, and C1) The mean relative neuronal response obtained on a session by session basis for each animal is plotted against the animal's behavioral performance on contour detection, which is a psychophysical measure of contour saliency. Data are shown for the experiment of changing the number of collinear lines (A1), and for the experiment of changing the spacing between the contour elements (B1), and for both experiments pooled together (C1). The straight lines are from linear regression. The r value indicates the correlation coefficient, and the p value gives the probability under the null hypothesis that the observed correlation was due to random variation of responses.

(A2, B2, and C2) The same data shown in (A1), (B1), and (C1) were binned and averaged according to the specified levels of performance. Error bars represent ±SEM.

3B1, and 3C1). All these data demonstrated a close correlation between perceptual saliency of contours and neuronal responses in V1. To further demonstrate this close relationship, for the same data shown in Figures 3A1, 3B1, and 3C1, respectively, we grouped the data points by dividing the animal's performance into five bins (Figures 3A2, 3B2, and 3C2). The data points falling within the same performance level were pooled and averaged to generate a single data point representing the averaged neuronal response and averaged performance. The binned and averaged data showed closer correlation than the raw data.

Psychophysical evidence has shown that contour integration involves complex interactions between contextual stimuli (Field et al., 1993; Li and Gilbert, 2002). In this regard, contour integration is a stimulus-driven, bottom-up process. To further explore the process of contour integration in V1 in the absence of top-down control, we compared neuronal responses to the same contour patterns for the same cells when the animal performed a task unrelated to contour detection: MA did a three-line bisection discrimination task presented in the visual field opposite to the RF (Figure 4A1; see Experimental Procedures), and MB did a simple fixation task (Figure 4A2). In these conditions neuronal responses were mainly driven by the stimuli, and any potential top-down components were largely removed. We plotted the mean relative population response to the contour patterns for correct trials in the contour detection task as a function of contour saliency and compared these responses to trials when the animals performed a task unrelated to contour detection (Figure 4B). In this figure contour saliency was determined as the animal's performance in the detection task and was binned as indicated in the figure. The same saliency values were assigned to the corresponding contour patterns used in the unattended condition in order to compare neuronal responses between contour-attended and contour-unattended conditions. Data from both animals in both experiments were pooled, since the neuronal responses were very similar in the detection task when binned according to contour saliency (refer to Figure 3).

As shown in Figure 4B, neuronal responses to the same contour patterns in the unattended trials were significantly lower than those in correct trials in contour detection task. Moreover, the difference was neither additive (inset B1) nor multiplicative (inset B2). At an intermediate level of contour saliency (corresponding to 70%–80% correct) the absolute (inset B1) or relative (inset B2) difference between attended and unattended conditions increased by about a factor of two relative to the lowest ($\leq$60% correct) or highest (90%–100% correct) level of saliency. These differences were statistically significant as determined by bootstrapping (for details see Figure 4 legend and Experimental Procedures). Although attention greatly boosted neuronal responses, there was still a clear correlation between responses and saliency in the unattended condition, indicating an important role of stimulus-driven, bottom-up processes in contour integration.

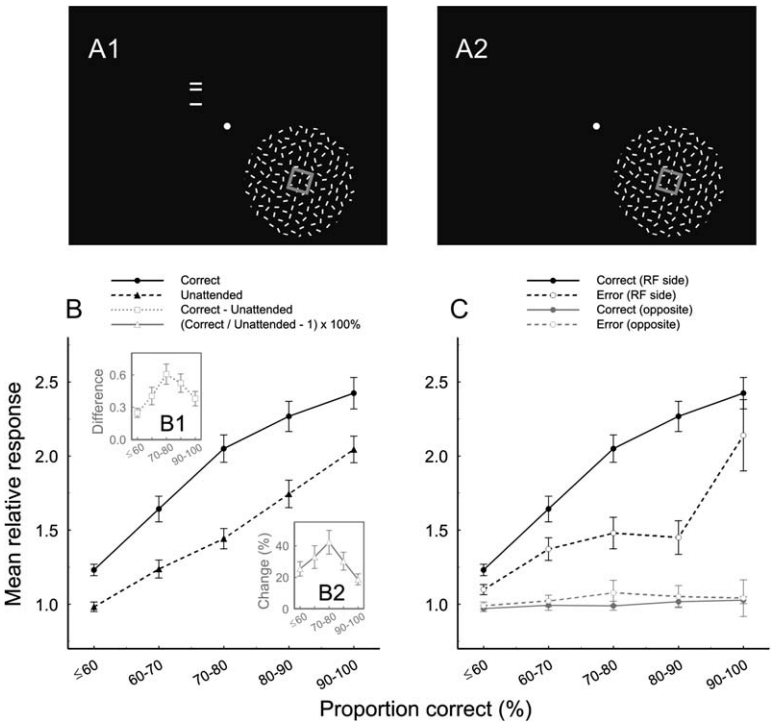

Figure 4. Contour Integration in the Absence of Top-Down Influences, and in Correct versus Error Trials

(A1 and A2) Stimulus paradigm. During V1 recordings, MA did not do the contour detection task at the RF location (denoted by the small gray square) but instead performed a three-line bisection discrimination task in the opposite hemifield (A1). MB performed a fixation task (A2).

(B) The mean relative responses of the neuronal population, for correct trials in the detection task and for the trials in the unattended condition, are plotted against contour saliency, which was measured as the animal's performance in the detection task but was also assigned to the same stimulus patterns used in the unattended condition. Data from both animals in both experiments were pooled and bootstrapped to calculate the mean responses and SEM. The differences between the two curves were highly significant (correct versus unattended; $p < 10^{-5}$ for all data points, determined by bootstrapping). Inset (B1) shows the difference in mean relative responses between correct trials and unattended trials. The middle data point (corresponding to 70%–80% correct) is significantly different from the leftmost data point (≤60% correct; $p < 10^{-4}$ determined by bootstrapping) and the rightmost data point (90%–100% correct; $p < 0.02$). Inset (B2) shows the percentage change of neuronal responses in correct trials relative to the unattended trials. The middle data point is significantly different from the leftmost data point ($p < 0.02$) and the rightmost data point ($p < 10^{-3}$).

(C) Comparisons of the mean relative responses of the neuronal population between correct and error trials for the condition when the contour patterns were displayed on the RF side and the noise patterns on the opposite hemifield (dark curves), and for the condition when the positions of the contour and noise patterns were switched with the noise patterns on the RF (gray curves). Error bars in all figures represent ±SEM obtained by bootstrapping.

In some trials of the contour detection task, the animals failed to detect the embedded contours. Comparing correct and error trials when the contour patterns were displayed on the RF side showed a significant difference in firing rates (Figure 4C; correct [RF side] versus error [RF side]). In contrast, if the noise was presented at the RF location and the contour pattern was on the opposite side, no significant difference was observed between correct and error trials (Figure 4C, correct [opposite] versus error [opposite]). Thus, withdrawal of attention has a much greater effect on the responses to embedded contours than on the responses induced by the noise pattern.

Analysis of Relation between Behavioral and Neuronal Responses

The relation between V1 responses and contour saliency allowed us to perform additional analysis to determine the degree to which V1 responses were predictive of contour saliency. Receiver operating characteristic (ROC) analysis (Parker and Newsome, 1998; Tolhurst et al., 1983) was employed to calculate the probability that an ideal observer can correctly discriminate the contour pattern from the noise pattern using only a single neuronal spike count. By calculating this probability as a function of the stimulus parameters, (the number of collinear lines or the spacing between them), we obtained a neurometric curve, which indicates how well the contour and the noise pattern could be differentiated at different contour settings simply based on a single spike count. Comparing this neurometric curve with a psychometric curve (the animal's performance on contour detection as a function of the stimulus parameters) gives an indication of how useful a single neuronal response could be for making a behavioral decision.

The neurometric curves (averaged across all cells) and the psychometric curves (averaged over the corresponding recording sessions) in the contour detection task were largely in agreement (Figure 5). Therefore, given the optimal strategy (which is implied by "ideal observer"), a single spike count would be generally predictive of the animal's performance in the contour detection task. Detailed examination of Figure 5 reveals two noticeable discrepancies between neurometric and psychometric curves. One discrepancy is that the actual behavioral performance in the most salient condition is somewhat better than predicted from single neuronal responses using ROC analysis (for example, the rightmost data points in Figures 5A1 and 5B1). A situation similar to this has been explained by more cells sampling the visual space outside the RF of the recorded single unit (Parker and Newsome, 1998). Thus, this is not unexpected in view of the fact that there are many additional neurons with RFs lying along the contour that can contribute to the perceptual salience of the contour. The other discrepancy is that in Figure 5B1 but not in Figure 5A1 the neurometric curve is significantly elevated above the psychometric curve at the data point

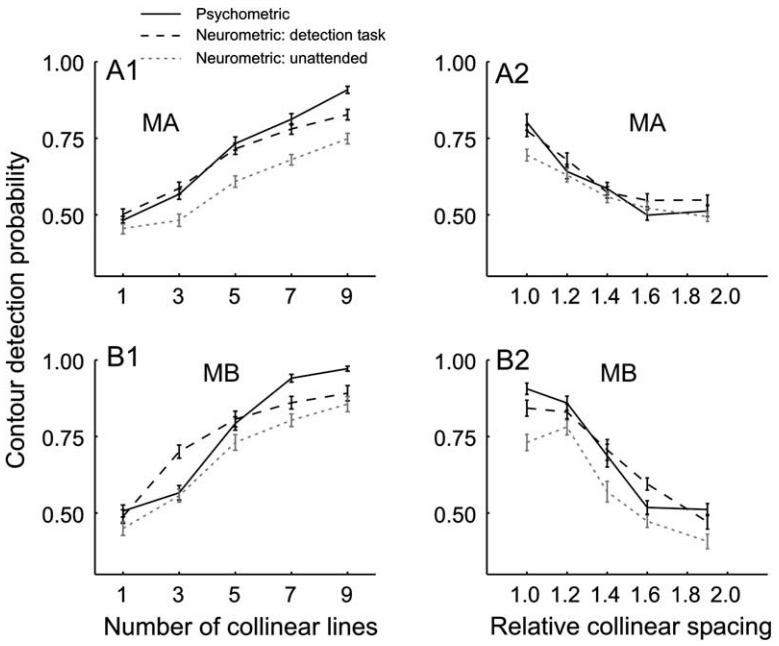

Figure 5. ROC Analysis

The animal's performance on contour detection (psychometric curve) and the neurometric curve (see Experimental Procedures) are compared. Data from MA and MB are shown in the top (A1 and A2) and bottom (B1 and B2) panels, respectively. The left and right panels show the results from two different experiments, changing the number of collinear lines (A1 and B1) and changing the collinear spacing (A2 and B2). Neurometric curves are shown for both the contour detection task condition and the contour-unattended condition. The neurometric curve was averaged across all cells, and the psychometric curve was averaged over the corresponding recording sessions. Error bars represent ±SEM.

corresponding to three collinear lines. This may be explained by a bias by one of the subjects (MB) toward selecting the RF side when presented with low-saliency contours. Note that the neurometric curves from the contour detection task are elevated above those from contour-unattended conditions and are closer to the psychometric curves. This indicates that neuronal responses in the contour detection task were better predictive of the animal's behavioral performance than those in unattended conditions.

Information theory was also used to calculate the mutual information between the stimuli and neuronal responses, which tells us how much the uncertainty whether the contour or the noise pattern was displayed over the RF location was reduced by knowing the spike count of one cell during one trial. Results from mutual information analysis, either directly based on the spike count of neurons (Figure S4), or as a control based on the probabilities from ROC analysis (Figure S5), were in close agreement with the ROC analysis.

Figure-Ground Effects

An isolated visual contour without any context is always conspicuous, but within a complex environment perceptual saliency of the contour depends on the global context within which the contour appears (Li and Gilbert, 2002). For the figure-ground segregation involved in the presence of a complex background, one might expect that even without top-down control the background itself influences the characteristics of neuronal responses and is critical for the aforementioned facilitatory effects in V1 to take place. To measure center-surround interactions in the absence of top-down influences, particularly as they pertain to the influence of a complex background on contour integration, we recorded neuronal responses when the animals performed a three-line bisection task in the opposite hemifield (MA; Figure 6A1) or a simple fixation task (MB; Figure 6A2). The collinear lines were presented at the RF location, either with the surrounding background of randomly positioned and oriented lines (Figures 4A1 and 4A2), or in isolation with the background removed (Figures 6A1 and 6A2). By comparing the contour-unattended conditions with and without the complex context, we observed that the background itself produced very strong inhibition of neuronal responses, up to a 60% reduction in firing rates when the number of collinear lines was small (Figure 6B) or when the spacing between collinear lines was large (Figure 6C). Moreover, the effect of increasing the number of collinear lines forming the contour was strikingly different with and without the presence of the complex environment (Figure 6B). Without the background, at the contrast used (Michelson contrast 50%), a small proportion of cells showed facilitation by three collinear lines compared with a single line in the RF. Adding more collinear lines tended to inhibit neuronal responses as the contour was increased in length. In contrast, in the presence of the complex background, neuronal responses increased monotonically with increasing contour length for nearly all recorded cells. This finding highlights the complexity of contextual effects in V1: the contextual interaction between collinear lines could be either inhibitory or facilitatory, depending on the greater stimulus context.

Time Course of Saliency Effects

By examining the neuronal responses over time after stimulus onset (peristimulus time histogram [PSTH]), we observed that the neural signal for contour saliency was delayed relative to the outset of neuronal responses. The amplitude of the initial peak of the PSTHs recorded during the detection task was independent of the number of collinear lines within the contours (Figures 7A1 and 7B1). The significant facilitation with increasing number of collinear lines was seen after the initial response peak and was maintained for the remaining time course of the response. The onset of facilitation was somewhat different for the two animals, beginning

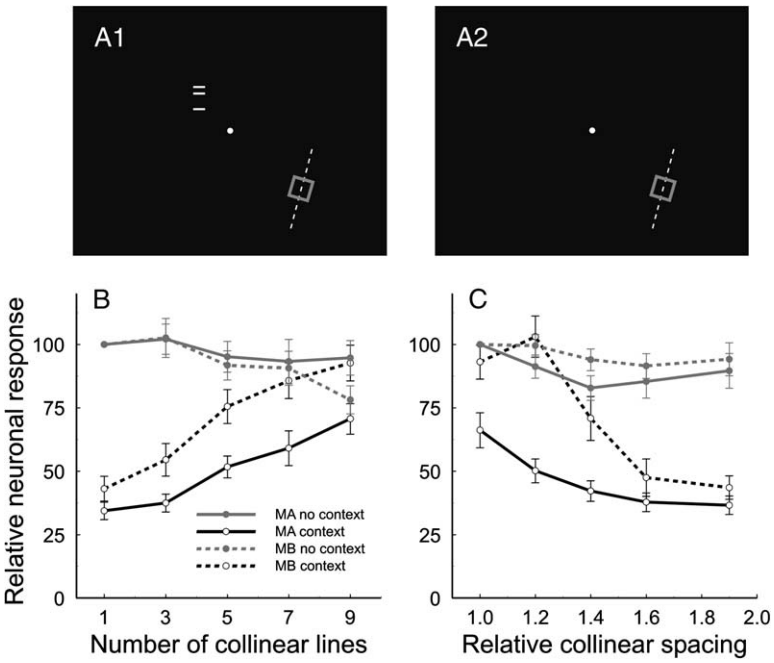

Figure 6. Figure-Ground Interactions

(A1 and A2) Stimulus paradigm. MA performed a three-line bisection discrimination task (A1) and MB a fixation task (A2), while the collinear lines alone were presented at the RF location (denoted by the small gray square). (B) Mean responses of neurons (n = 30 for MA; n = 24 for MB) as a function of the number of collinear lines. In this particular figure, a relative response of 100 represents the mean response of a neuron to a single line element in the RF. Data from the conditions with (dark curves) and without (gray curves) the complex background are compared for each subject. Error bars represent ±SEM. (C) Mean responses of neurons (n = 25 for MA; n = 20 for MB) as a function of the relative collinear spacing. In this figure, a relative response of 100 represents the mean response of a neuron to the contour alone with seven collinear lines and a relative collinear spacing of 1.0.

150–160 ms after stimulus onset for MA and 90–100 ms for MB (see Experimental Procedures for statistical significance analyses). The response latencies (response outset after stimulus display) of neurons in MA and MB were 60 ms and 50 ms, respectively. Thus, V1 neurons in MB not only had a 10 ms shorter response latency and stronger collinear facilitation effect, but also a 60 ms smaller latency for the onset of facilitation. Analysis of PSTHs under different experimental conditions also showed that the late response components associated with contour saliency in the detection task were stronger than those seen in the unattended condition, while the initial burst peak of neuronal responses was little affected by attentional state (no statistically significant difference for the first 150 ms of neuronal responses for MA and the first 100 ms for MB). On the other hand, the inhibitory influence of the complex background, as compared with the no-background condition, started in the initial phase of neuronal responses and rapidly reached a maximum within the period of the initial burst (Figures 7A2 and 7B2; statistically significant inhibition could arise as early as the very beginning of the neuronal responses).

Discussion

Neural Basis of Contour Integration

The Gestalt law of "good continuation" that governs contour integration may have its neural substrate in V1. Earlier supporting evidence is that pyramidal cells in V1 with nonoverlapping RFs but similar orientation selectivity are wired together via intrinsic horizontal connections (Bosking et al., 1997; Gilbert and Wiesel, 1979, 1983, 1989; Rockland et al., 1982; Schmidt et al., 1997; Stettler et al., 2002) and that responses of orientation-selective neurons in V1 to an oriented visual stimulus in the RF can be facilitated by collinear context placed outside the RF (Ito and Gilbert, 1999; Kapadia et al., 1995; Polat et al., 1998). Previous studies from our laboratory (Ito and Gilbert, 1999; Kapadia et al., 1995) showed lateral interactions between collinear line segments with respect to brightness induction rather than to contour saliency per se. Other studies have investigated the neural correlates of perceptual pop-out in V1 based on orientation contrast (Knierim and Van Essen, 1992; Nothdurft et al., 1999), texture difference (Lamme, 1995), or more complex attributes (Lee et al., 2002), which base saliency on discontinuities rather than continuity.

Somewhat more direct evidence that V1 cells can mediate contour integration comes from studies using elongated contours displayed in complex environments, where neuronal responses were enhanced by visual contours (Bauer and Heinze, 2002; Kapadia et al., 1995; Roelfsema et al., 1998, 2004). These studies did not allow examination of the relationship between perceptual saliency and neuronal responses. Despite the implications from previous studies on the role of V1 in contour integration, the strongest evidence is to establish a direct correlation between neuronal responses and the perception of the animal in which and at the time the recordings are made, as done in the current study.

The nature of the neural code for contour saliency has been a matter of some debate. As suggested by some studies, contour saliency could be derived from an increase of neuronal responses through facilitatory horizontal interactions (Bauer and Heinze, 2002; Kapadia et al., 1995, 1999; Li, 1998; Polat and Bonneh, 2000; Roelfsema et al., 1998, 2004). Other studies suggest that temporal encoding could also be involved in representation of contour saliency (Gray et al., 1989; Li, 1998; Singer, 1999; Yen and Finkel, 1998). However, recordings in monkeys trained in a contour-tracking task indicate that response synchrony is not related to contour perception (Roelfsema et al., 2004). Our current study clearly showed that the mean firing rate is at least one form of the neural code for contour saliency.

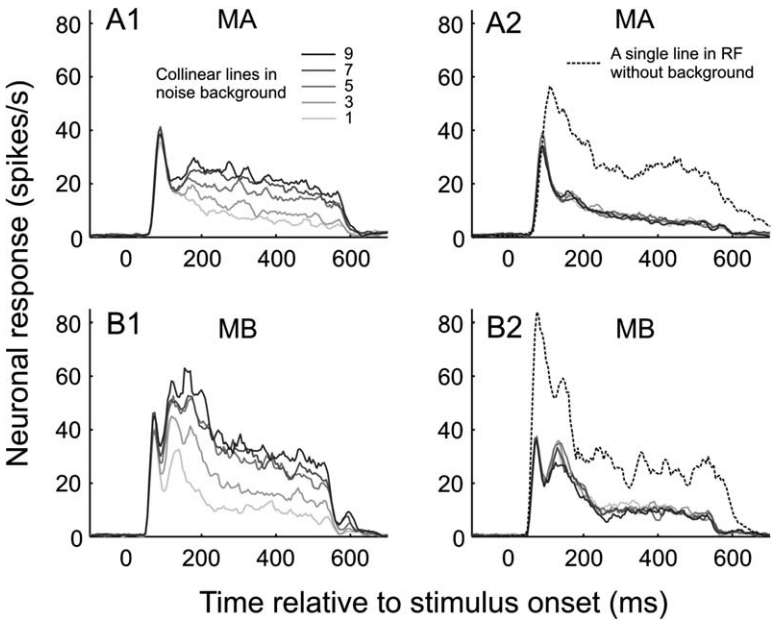

Figure 7. Time Course of Neuronal Responses

Peristimulus time histograms (PSTHs) were constructed by binning neuronal spikes at 5 ms resolution over time and averaged for all trials in all recorded cells in each animal. The PSTHs were smoothed using a rectangular window of 20 ms (boxcar filter). Time 0 indicates stimulus onset. (A1 and B1) PSTHs, for MA and MB, respectively, from neuronal responses in the detection task to contours made up of 1, 3, 5, 7, and 9 collinear lines embedded in the complex background, showing the delayed response components associated with contour saliency. (A2 and B2) The five continuous PSTH curves at the bottom, which are nearly superimposed, were constructed from neuronal responses to the noise patterns when the contour patterns corresponding to the five conditions described in (A1) and (B1) were displayed in the opposite hemifield. Thus, the stimuli in these instances were composed of a single optimally oriented line in the RF surrounded by the complex background of random lines. The single dotted curve shows the PSTH from the condition of a single line in the RF alone without any context when MA did the bisection task in the opposite hemifield and MB did the fixation task. By comparing the solid curves with the dotted one we see that the inhibition induced by the complex background arises very early in the neurons' responses.

The contrast detection threshold for an oriented target is decreased by the presence of collinear flankers (Dresp, 1993; Kapadia et al., 1995; Polat and Sagi, 1993), and this enhancement increases with the number of collinear elements (Adini et al., 1997; Bonneh and Sagi, 1998). This perceptual phenomenon has its neural correlate in V1. The interaction between collinear line segments in V1 tends to be facilitatory at low contrast but inhibitory at high contrast (Kapadia et al., 1999, 2000; Polat et al., 1998). Our results are in accord with and extend these earlier findings. At the contrast level used in the current study (50%), and in the absence of the complex background, a small proportion of neurons showed facilitation by a pair of flanking collinear lines, and adding additional collinear lines invariably led to a decline in response. However, by presenting a complex background around the contour, nearly all cells' responses increased monotonically with an increasing number of collinear lines. Our results support the notion that embedding a target in a complex environment leads to a shift toward a dominance of facilitation in collinear interactions, equivalent to the effect of a reduction in contrast (Kapadia et al., 1999; Polat and Bonneh, 2000). The complex interactions among the contour elements and the global contextual elements shown in the current study are also consistent with our previous psychophysical observation that contour saliency depends on not only the geometry of contour elements but also on the surrounding context (Li and Gilbert, 2002). In integrating the contour elements and generating the saliency map, there is a cascade of nonlinear interactions among stimulus elements across visual field areas much larger than the RF in V1. Therefore the ultimate output from a V1 neuron with its RF lying on the contour path conveys information not only about the contour segment within its RF but also the global structure of visual stimuli extending over much larger areas of visual space.

Delayed Saliency Effects

Our data showed that neuronal responses to a line were greatly suppressed when the line was placed in a complex environment and even tended to be suppressed when the line was flanked by a stack of collinear lines. These observations are consistent with the evidence for inhibitory modulation from outside the classical RF (Bair et al., 2003; Bishop et al., 1973; Hubel and Wiesel, 1965; Knierim and Van Essen, 1992; Li et al., 2000; Nothdurft et al., 1999; Walker et al., 2000). Moreover, this contextual inhibitory effect started in the initial phase of neuronal responses and reached a maximum very quickly, as reported previously (Bair et al., 2003; Knierim and Van Essen, 1992; Li et al., 2000; Nothdurft et al., 1999). Though much of the earlier work emphasizes inhibitory contextual influences, the current study reinforces that the sign of these influences depends strongly on the position of the stimuli (e.g., collinear) and on the greater context (contours embedded in a complex background). Collinear inhibition can be reversed to a powerful facilitation in the presence of the fast and strong inhibition induced by the complex background, in contrast to that seen without the background. Under these circumstances, the collinear facilitation associated with contour saliency developed much later than the background induced inhibition. This is reminiscent of earlier findings of delayed components in V1 responses related to higher-order, contextually dependent properties (Bauer and Heinze, 2002; Kinoshita and Komatsu, 2001; Lamme, 1995; Lee et al., 2002; Li et al., 2000, 2001;

Roelfsema et al., 1998; Rossi et al., 2001; Super et al., 2001; Zipser et al., 1996), where complex center-surround interactions or top-down influences are involved. The source for these delayed components is a matter of debate. Some have speculated that delayed facilitatory response components are due to feedback (Lamme, 1995; Lee et al., 2002; Li et al., 2001; Zipser et al., 1996), and others have argued that feedback is associated with early, inhibitory influences on neuronal responses (Bair et al., 2003). Alternatively, it is equally possible that, in the presence of a complex stimulus context, considerable delays could arise from an iteration of cascading processes within V1 (Bauer and Heinze, 2002). In this view, recurrent interactions between V1 neurons via horizontal connections could require a period of time to reach a stable state, with horizontal propagation of activity in V1 being rather slow (Bringuier et al., 1999). Further support of figure-ground interactions arising within V1 comes from their persistence after inactivation of V2 (Hupe et al., 2001a) and the relative rapidity of feedback effects from higher cortical areas to V1 (Hupe et al., 2001b).

In our study, the delayed responses occurred both when the animal was performing the contour detection task, as well as when the animal did an unrelated task. While the delay in a component of neuronal responses could be explained in terms of the time required for directing attention to the stimulus, as is seen in extrastriate cortical areas (for review see Treue, 2001), the fact that one still sees the delayed facilitation in the absence of attention suggests the involvement of the complex lateral interactions described above. But the conclusion that we can draw from the current study is that information about contour saliency is represented in V1. The connectivity underlying this interaction remains to be determined, but it is tempting to speculate that it involves an interaction between feedback connections from higher-order visual areas to V1 and long-range horizontal connections intrinsic to V1. One may ask which components of the computation are contributed by V1. In this regard, it is worth considering the properties of contour integration in terms of its spatial extent and orientation dependence, which are consistent with the circuits and functional architecture of V1 (Gilbert and Wiesel, 1989; Li and Gilbert, 2002; Stettler et al., 2002). It has been suggested, however, that contour integration operates at multiple spatial scales, each of which engages different cortical areas, including V1 (Kourtzi et al., 2003).

Bottom-Up, Top-Down, and Perceptual Learning

In the current study we showed that information about contour saliency was encoded by V1 neurons even if the stimulus was not the focus of attention. This observation is in agreement with other studies, in which collinear facilitation (Kapadia et al., 1995) and contour-associated enhancement (Bauer and Heinze, 2002) of neuronal responses in V1 is observed in a simple fixation task. Collinear facilitation is seen even in the primary visual cortex of anesthetized animals (Polat et al., 1998), although the degree of facilitation and the proportion of neurons showing facilitation are reduced in the anesthetized state. These results suggest that contour integration contains a bottom-up process driven by the configuration of visual stimuli.

In addition to this bottom-up contribution to contour integration, our data showed profound differences in neuronal responses when animals performed the contour detection task as compared with the contour-unattended condition. With our current experimental design we were unable to identify what forms of top-down influences were responsible for these differences. The range of possibilities includes spatial attention, object-based attention, the perceptual task of contour detection per se, or a combination of them. A clear answer to this question requires further investigation. But in any event, our data revealed striking top-down modulation in V1 with amplitude comparable to that reported in higher visual areas (see review Maunsell and Cook, 2002). While earlier studies have suggested that V1 only shows minimal attentional effects, with a hierarchy of attentional modulation along the visual pathway, the effects presented here emphasize the importance of stimulus geometry and behavioral context in eliciting the strongest top-down effects. To see the attentional effects that are appropriate to any given cortical area, it is of key importance to explore them in the context of the specific integrative functions of that area. To wit, based on our finding that V1 is intimately involved in linking contour elements within a complex background for the purpose of contour integration and saliency, the strongest top-down influences in V1 are seen with a stimulus context that adheres to the rules of contour saliency (Field et al., 1993; Sigman et al., 2001; Wertheimer, 1923) and a behavioral context involving either attending to or detecting contours.

In the current study, the most significant top-down modulation was seen for contours of intermediate saliency rather than high saliency. This may be due to the difficulty in drawing attention away from a highly salient stimulus even in the unattended condition. As a result, the difference in neuronal responses is smaller between attended and unattended conditions for the most salient contours. On the other hand, one may need an effective stimulus to deploy spatial attention, so that when no detectable contour is embedded in the complex background, the top-down modulatory effect is lessened due to a decrease in attentional resources dedicated to the target. The strongest top-down influences are consequently observed for contours of intermediate saliency.

Given the findings that performance on contour detection can be changed by experience (Kovács et al., 1999; Li and Gilbert, 2002), it is likely that different observers may have different contour integration capability. In the current study subject MB's performance in contour detection was better than MA's for the same contour patterns. Interestingly, V1 neurons in MB also exhibited, on average, stronger collinear facilitation by the same visual contours as well as a shorter latency for the effect to develop. This suggests an experience-dependent difference in V1 responses between the two subjects, as supported by the findings that past experience with some pop-out targets enhances perceptual detection (Lee et al., 2002; Sigman et al., 2001; Wang et al., 1994) as well as neuronal responses (Lee et al., 2002) and fMRI signals (Kourtzi et al., 2005; Sigman et al., 2005) in V1. Moreover, our earlier studies have also shown that perceptual learning can result in

profound long-term changes in response properties of V1 cells (Crist et al., 2001; Li et al., 2004). The difference in facilitation and contour detection between the two experimental animals likely reflects different stages of perceptual learning in the contour detection task, but interestingly, despite their difference in performance, the two subjects were very similar in the relationship between behavioral performance and neuronal responses (Figure 3). Thus, the learning is unlikely to involve a change in the significance attributed to a given level of firing in V1 by a higher stage, but rather an alteration in the level of facilitation generated by a given stimulus. This could be achieved by a change in the interaction between top-down influences and lateral interactions within V1, as well as by a change in the lateral interactions themselves. The representation of learned information in lower visual cortical areas in other perceptual learning paradigms has also been shown to involve top-down influences, leading to global alterations in the representation of learned shapes across the visual pathway (Sigman et al., 2005).

In summary, our current study highlights the role of V1 in contour integration and the neural code for contour saliency. Taken together with our earlier studies (Crist et al., 2001; Li et al., 2004), our findings suggest that V1 acts as an adaptive processor whose processing is profoundly influenced by context, top-down control and training. Our findings have a broader implication for the general mechanisms underlying early cortical processing of visual information in a natural environment, where visual stimuli are rarely isolated but rather embedded in a rich context, and viewing is usually driven by behavioral goals and shaped by past experiences.

Experimental Procedures

Stimulus and Behavior Protocols

Stimuli were generated by a visual stimulus generator (VSG2/5, Cambridge Research Systems) on a monitor (NANAO FlexScan F2-21) at a resolution of 1024 by 769 pixels and a refresh rate of 105 Hz. The viewing distance was 145 cm. The stimuli consisted of an array of randomly oriented white (19.5 cd/m^2) line segments displayed on a gray (6.5 cd/m^2) background. The positions of line segments were defined by geometric rules that allowed precise control of stimulus parameters (Figure 1; for more details see Li and Gilbert, 2002).

Two adult male monkeys (*Macaca mulatta*, referred to as MA and MB) were trained in a contour detection task. A two-alternative forced choice (2AFC) task was used to measure the animal's ability to detect contours of various saliencies (Figure 2A). A stimulus pattern containing an embedded contour (contour pattern) and a similar pattern without any embedded contour (noise pattern) were displayed simultaneously at two locations symmetrical around the fixation point. During V1 recordings the RF center of the recorded cell was one of these two locations. The probability that a given pattern was display at a given location was 50%. The task was to report which of these two patterns contained a contour. Note that the noise pattern was derived from the contour pattern simply by randomizing the orientations and position jitters of the collinear lines forming the contour, leaving the central line segment in the pattern and all background noise elements unchanged. Therefore, the very central line segment and all the noisy contextual lines in the contour pattern were identical to those in the noise pattern. The central line segment in both contour and noise pattern was set at the optimal orientation of the recorded cell and was centered in the RF for the stimulus pattern presented at the RF location. Different stimulus conditions in an experiment were randomized, and different experiments were arranged in different blocks. Each stimulus condition was repeated five to ten times in a block of trials, and typically two to four blocks of trials were repeated for the same experiment. At trial outset a 0.08° fixation point (FP) was displayed in the screen center. Eye positions were sampled at 30 Hz by an infrared tracking system (K. Matsuda et al., 2000, Soc. Neurosci., abstract). Within 600 ms after FP presentation the animal was required to fixate within an invisible circular window of 0.5° in radius around the FP. After the animal maintained fixation for 191 ms, the contour pattern and noise pattern were presented for 476 ms. Another 191 ms later, the FP was extinguished and two 0.15° saccade targets were presented for 600 ms at the locations where the two stimulus patterns were centered (Figure 2A). The animal indicated the hemifield in which the contour pattern was presented by executing a saccadic eye movement to either target.

One animal (MA) was used in our previous study and had been trained to perform a three-line bisection discrimination task (Li et al., 2004). In the experiments examining neuronal responses in the absence of potential top-down influences, MA performed the bisection task while exposed to the contour patterns at the RF location (Figures 4A1 and 6A1). The task stimulus was three parallel lines displayed in the hemifield opposite to the RF. In different trials the positions of two flanking lines were fixed while the middle line was displaced up or down to varying extents from the center. The monkey reported to which of the two flankers the middle line was closer by making a saccade to either of two targets (for more details see Li et al., 2004). Since training the bisection task is time consuming, in the other animal (MB), a fixation task was performed in the unattended condition (Figures 4A2 and 6A2), which had the desired effect of directing the animal's attention away from the contour display. The animals were cued to the to-be-performed task by a few leading trials in which only the task-relevant stimuli were presented and all irrelevant stimuli were omitted. Only if the animal made a few correct responses to the task did the actually experimental trials start. Moreover, the first few experimental trials were used as practice trials, and only if the animal made correct choices in the practice trials did data collection begin.

Animal Preparation and Electrophysiological Recordings

Details were described elsewhere (Li et al., 2004). Orientation-selective cells in V1 superficial layers were recorded by a spike sorting and acquisition system (Plexon Inc.) with platinum-iridium or tungsten microelectrodes (impedance 0.5–2 MΩ at 1 KHz). RF eccentricities ranged between 2.5° and 4.5°, RF lengths between 0.2° and 1.3° (0.64° ± 0.28°; mean ± SD), RF width between 0.3° and 1.2° (0.66° ± 0.21°). The RF length or width was determined using an optimally oriented bar, 0.25° by 0.1° in size, presented 0.25° apart along or orthogonal to the orientation axis across the RF. The mean neuronal responses corresponding to different bar positions were fitted with a Gaussian function. The RF center was defined as the position corresponding to Gaussian peak, and the RF length or width was defined by the interval containing the central 95% of the area under the Gaussian (2 × 1.96 SD) with the length or width, respectively, of the mapping bar subtracted. The orientation tuning curve was quantitatively determined by using a bar, 0.5°–0.8° long and 0.1° wide, placed in the RF center at varying orientations, and the optimal orientation and tuning width were measured in a similar way by Gaussian fitting except that orientation tuning width was defined as the full width at half height (2 × 1.17 SD). The orientation tuning widths measured in this way for recorded neurons were between 33° and 94° (54° ± 16°, mean ± SD). Neurons that were not responsive to single bars or did not show a clear orientation tuning preference were skipped. All procedures were conducted in compliance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and under approval of the Institutional Animal Care and Use Committee at Rockefeller University.

Data Analysis

Two measures were taken to ensure that our results were not contaminated by eye movements. First, we discarded all those trials in which the animal's eye position changed more than 0.3° in either the vertical or horizontal direction during the trial. All data analyses were based on the remaining trials (about 70% left), though the results were similar to those from the full set of trials. Second, we

provide Supplemental Data to demonstrate that our eye tracking system has sufficient resolution to track biased movements smaller than 0.05° (3 arcmin) and that no such movements occurred in any condition during the recordings (see Figures S1 and S2).

Following the neuronal response latencies (about 60 ms for MA and 50 ms for MB after stimulus onset), a 400 ms window was used for calculating the mean firing rates of a cell. Mean responses averaged across all recorded cells were used to examine the change of neuronal responses associated with different stimuli or behaviors. To calculate the mean response across all recorded cells, the mean neuronal responses from individual neurons were normalized to the responses to the noise patterns. The spike counts within the same 400 ms window were used to calculate the neurometric curve with ROC analysis (Parker and Newsome, 1998; Tolhurst et al., 1983). In brief, the ROC curve for a given stimulus condition was calculated by plotting the hit rate (the percentage of spike counts larger than a given decision threshold when the stimulus was presented to the RF) against the false alarm rate (the percentage of spikes larger than the same threshold when the noise pattern was shown) while varying the decision threshold from the smallest to the largest spike count. The area under the ROC curve corresponds to the probability that an ideal observer can correctly identify whether the contour or noise pattern was presented for the given stimulus condition and thus gives a data point on the neurometric curve.

To determine the time point at which the mean firing rate started to deviate between contour and noise pattern, and the onset time of contextual suppression, the mean response of each cell was determined in successive windows of 10 ms width. These values were compared between the corresponding conditions with a paired nonparametric statistical test (Wilcoxon signed rank test), since they were significantly different from a Gaussian distribution (assessed with Lilliefors test). The onset time was defined as the first of three successive intervals significant at the 5% level.

To calculate meaningful error bars and statistical significance for the non-Gaussian distributed data pooled across animals and conditions (Figure 4), the cell population was resampled by bootstrapping method (Effron and Tibshirani, 1993) (this technique allows significance tests without assuming distribution shapes or equal variance of the data sets being compared), and then the spike counts for each stimulus from a single unit were resampled as well (10^5 resampling iterations were used in both cases). This resampling method accounts for both the variability due to the limited number of trials per stimulus display and that due to the difference between individual cells, and thus allows rigorous statistical inference about the population of cells from which the recorded cells were selected (i.e., orientation-selective cells in the superficial layers of V1).

Supplemental Data

The Supplemental Data include Supplemental Experimental Procedures, Supplemental References, and five supplemental figures and can be found with this article online at http://www.neuron.org/cgi/content/full/50/6/951/DC1/.

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