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RESEARCH ARTICLE

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Neuronal responses from beyond the classic receptive field in V1 of alert monkeys

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Abstract Responses of primary visual cortex (V1) neurons to stimuli inside the classic receptive field (CRF) can be modulated by stimuli outside the CRF. We recently reported that responses of most V1 neurons to a line in the CRF center are inhibited by large surround-stimuli and that this modulation is stimulus selective. Here we report that a significant proportion of V1 neurons in alert monkeys respond directly to stimuli outside the CRF with very long latency and much reduced selectivity. When surround stimuli are presented alone, three response patterns can be distinguished in 153 single- or multiunits tested: (1) 31.4% have no significant response; (2) 50.3% show excitatory responses that are significantly higher than spontaneous activity. The average latency of these responses is about 145 ms, 2–3 times longer than center responses; (3) 18.3% show suppressed spontaneous activity after stimulus onset. The direct surround responses are found to be only weakly selective for the orientation of contextual lines, and not selective for other contextual patterns tested. While the outburst of responses to stimuli within the CRF is not affected by reducing stimulus duration from 500 ms to 50 ms, late excitatory surround responses are virtually eliminated. We propose that the late excitatory surround responses to extra-CRF stimulation alone are the reflection of feedback from higher cortical areas and may contribute to reduced contextual inhibition of cells in V1. This could play a role in figure-ground segregation.

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Introduction

The classic receptive field (CRF) or, simply, the receptive field (RF), is usually plotted by flashing and moving a small patch of light in the visual field. When this stimulus is presented outside the CRF, no overt neuronal response is observed (Hubel and Wiesel 1962). It has been known for a long time that, in the primary visual cortex, stimulation of the regions outside the CRF alone cannot activate the cells directly, but can only modify the cell responses evoked by stimuli inside the CRF (Blakemore and Tobin 1972; Maffei and Fiorentini 1976; Nelson and Frost 1978; Allman et al. 1985; Knierim and Van Essen 1992; DeAngelis et al. 1994; Li and Li 1994; Gilbert et al. 1996;Sengpiel et al. 1997; Lamme et al. 1998a, 1998b; Bringuier et al. 1999; Nothdurft et al. 1999). In recent years, however, there have been some reports demonstrating that the regions outside the CRF are not completely silent. Some cells respond directly to luminance modulation of regions outside the CRF (Rossi et al. 1996; Rossi and Paradiso 1999), and some cells have been found to respond directly to the onset of textured patterns outside the CRF (Rossi et al. 1998).

We have studied recently the influence of contextual stimuli on responses of neurons in V1 of alert monkeys (Li et al. 2000). We observed that responses of most V1 neurons to a line in the RF center are suppressed by various contextual stimuli. Two distinct phases of contextual inhibition were observed after stimulus onset: a fast strong inhibitory phase in the initial cell responses is followed by a late disinhibitory or facilitatory phase. We proposed that the former could result from the long-range horizontal connections within V1, while the latter might originate from the feedback connections from higher cortical areas. In addition to the inhibitory modulation effect, we also noticed that some V1 cells respond directly to the contextual stimuli presented well outside

the CRF even if no stimulus is presented within the CRF. As little is known so far about the direct responses from beyond the CRF, we investigate in the present study the properties of these neuronal responses in V1 of alert monkeys activated by stimulation of regions outside the CRF. Our data show that the direct excitatory surround responses revealed in this study could have the same neural basis as the late disinhibitory or facilitatory phase of contextual modulation observed in our previous study.

Some of our observations have been reported elsewhere (Wehrhahn et al. 1999).

Materials and methods

Details of animal preparation, visual stimulation, and data collection were described in an earlier paper (Li et al. 2000) and are therefore described in an abbreviated form here. Three male juvenile rhesus monkeys (*Macaca mulatta*) were used as subjects. The animals, seated in a primate chair in a dark room with head fixed, looked into a pellicle mirror (National Photocolor, ST-SQ-NP40), which allowed 40% transmission/reflection of the amount of light. The images from two CRT displays were superimposed through the pellicle mirror. The viewing distance was 60 cm. Under computer control, grating patches and luminance squares with all parameters adjustable could be generated by an image synthesizer (Innisfree, Picasso) on one CRT (Tektronix 608, green phosphor) at a frame rate of 200 Hz. Fixation spot and stimuli made of line segments could be displayed on the other CRT (HP1345A, P31 phosphor), which was refreshed at 100 Hz.

The activity of single units or multiunits in V1 was recorded with tungsten-in-glass microelectrodes of 1–3 M impedance. Eye position signals were recorded by a custom-made, computerized search-coil system (Bechert and Koenig 1996) at a sampling rate of 600 Hz. A square fixation window was used, the size of which ranged from 0.4°×0.4° to 1.0°×1.0°, but was 0.5°×0.5° for most recordings.

Mapping of the CRF

Mapping procedures have been described in an earlier paper (Li et al. 2000). Briefly, once neuronal activity was isolated, an orientation tuning curve was measured using a patch of drifting square-wave gratings. Optimal orientation of the cell was determined from the peak of the tuning curve. Subsequently, by listening to the speaker, the spatial frequency and movement speed of gratings were adjusted to optimal values of the cell. A small grating patch was positioned at different locations along the axes parallel and orthogonal to the optimal orientation of the cell, with all grating parameters set to the optimal values for maximum activation of neuronal responses (see Fig. 1A; for details, see Li and Li 1994). The four boundaries of the CRF were determined from the data points on those response profiles where the cell responses did not differ significantly from the spontaneous activity. The CRF *length* was defined as the CRF dimension along the optimal orientation, and the *width* as that orthogonal to the optimal orientation. The term *CRF size* was used to refer to the longer dimension of width and length. The RF center was also determined and all subsequent stimuli were centered on the RF.

In RF mapping we used a small patch of optimal gratings rather than flashing lines (bars) that were used in all later experiments. The reason is as follows: in addition to orientation, most V1 cells are also well tuned to other stimulus parameters such as spatial frequency, movement direction, movement speed, stimulus width, and length. Using a grating patch as a mapping tool allowed us to adjust easily all these parameters to approximate the optimal values of the cell to ensure maximum activation of neuronal responses. Moreover, on the fringes of the CRF where the responsiveness of the cell is very weak, a grating patch with optimal parameters is more effective than a single line to activate the cell due to spatial summation. As a result, grating patches are more efficient in defining the CRF than flashing lines. As already reported on the basis of recordings carried out in area 17 of anesthetized cats, using grating patches in RF mapping yields a larger estimate for RF spatial extent than flashing bars (Li and Li 1994; see also for details of comparison of different CRF mapping approaches).

Stimuli

The basic stimuli were either a center test line at optimal orientation inside the RF, or surround contextual patterns of various configurations outside the RF, or the sum of both (see insets in Figs. 2, 3, 4, 5, 6, 7, 8). After the monkeys had held their fixation within the fixation window for 500 ms, stimuli were presented for 500 ms. The length of the center test line was about the same as the CRF length. In most experiments, for cells (71% of the cells tested) whose CRF sizes were less than 1°, the contextual stimuli were confined to a 4.9°×4.9° area around the RF and composed of 7×7 elements, each 0.7° long. A blank square window of 2°×2° was used in the stimulus center so that all the contextual patterns were well outside the CRF. For cells (29% of the cells tested) whose CRF sizes were bigger than 1°, bigger contextual patterns up to 7.0°×7.0° composed of 10×10 elements were used, and the size of the center blank window was increased accordingly to ensure its size was at least twice the size of the CRF. Note that, to prevent the surround patterns from stimulating the CRF due to eye movement, the fixation window used in recordings was always smaller than the blank space between the CRF borders and the texture patterns. The fixation error amounted to one-half the size of the fixation window on each side of the CRF for the animals (see Fig. 1C). All trials with a larger fixation error were discarded. The mean luminance of all contextual stimuli was about 1.5 cd/m^2. In one experiment (Fig. 6), a homogeneous, bright (1.5 cd/m^2) surround was used instead of textured patterns. For each stimulus condition, a total of 5–20 trials were tested and, for each experiment, different stimulus conditions were presented in pseudorandom sequence.

Data analysis

A peristimulus time histogram (PSTH) was first constructed for each trial using a bin width of 10 ms. Then the PSTH was smoothed by doing a simple adjacent-averaging of three bins. That is, the number of spikes in each bin is the average of this bin and the two bins before and after it. A time period of 500 ms before stimulus onset was used for spontaneous activity calculation. The PSTHs of all trials under the same stimulus condition were then averaged and a *t*-test was performed between the mean responses in each bin after stimulus onset and the mean spontaneous responses before stimulus onset. All the bins with responses significantly different (P<0.05) from the spontaneous activity were marked.

The latencies of both center and surround responses were determined as follows: For the time period of 0–300 ms after stimulus onset, we looked for the first occurrence of three successive bins that gave significantly different responses from the spontaneous level. The time corresponding to the end of the first bin of these three successive bins was taken as the response latency. The resolution of this analysis is 10 ms and is good enough for our present study.

The cells were categorized into three classes based on the *t*-test described above under the surround-stimulation condition. If no three successive bins were found significantly different from spontaneous activity during the whole 300 ms period after stimulus onset, the cell was classified into no-response category, which is named *silent class* in this study. If at least three successive bins were found significantly higher or lower than spontaneous responses, the cell was put into excitatory-response class (named *excitatory*

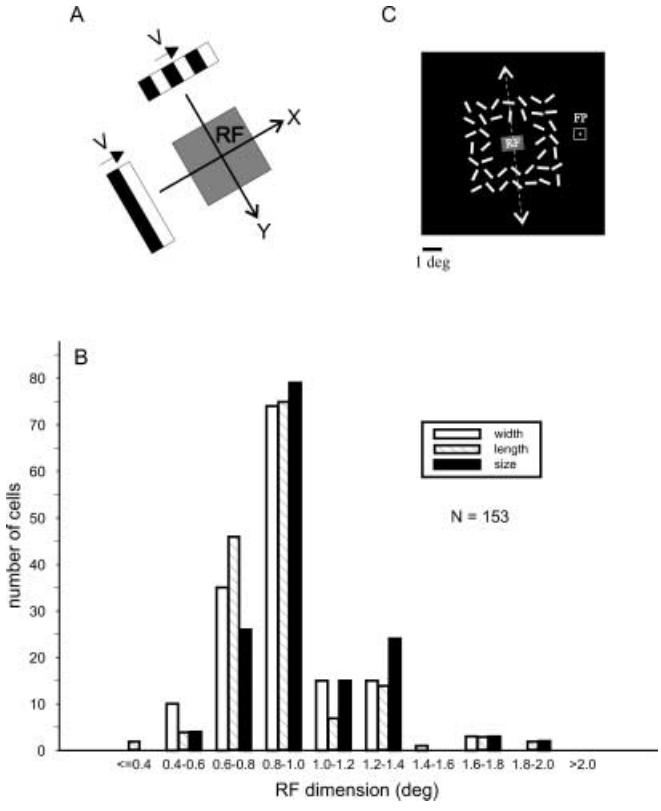

Fig. 1 **A** The stimuli used for receptive field (*RF*) mapping in this study. The classic receptive field (*CRF*) was mapped as minimal responsive rectangular area (*gray rectangle*) by positioning a small patch of drifting square-wave gratings at different locations along the two axes parallel (*y*-axis) and orthogonal (*x*-axis) to the optimal orientation of the cell. All grating parameters (orientation, spatial frequency, movement direction, movement speed, and patch size) were set to the optimal values of the cell for maximum activation of neuronal responses. The four boundaries of the CRF were determined from the data points on those response profiles where the cell responses were not significantly different from the spontaneous activity. **B** The distribution of CRF width, length, and size of all recording sites. The CRF size of a recording site is defined as the bigger dimension of width and length of the CRF. **C** The parameters used in the recording of the sample cell shown in Fig. 2A. The width of the fixation window (the *square* around the fixation point *FP*) was 0.5°×0.5°. Only trials during which the eye position was maintained within the window were included in the data analysis

class) or inhibitory-response class (named *inhibitory class*) according to the sign of activity in the first occurrence of these bins.

The response latencies and cell classification quantitatively determined using the analysis mentioned above were found to closely match the results determined manually in a previous version of this paper, where the latency of neuronal responses to a stimulus was determined in the following way (similar to Celebrini et al. 1993): the neuronal activity was displayed on a computer monitor in the form of a raster plot, as well as a PSTH. A cursor was generated by the computer on top of the raster plot and PSTH. Then the cursor was moved manually using a keyboard along the time axis to the beginning of cell responses (see Fig. 2A, for example). The cursor position in milliseconds was displayed on the monitor.

All clinical and experimental procedures used in this study were approved by local authorities and were in full compliance with applicable European Community guidelines (EUVD 86/609/EEC). They were also in accordance with the National Institutes of Health guidelines and the policy of the American Physiological Society.

Results

A total of 153 recording sites in V1 of three monkeys were analyzed. Most recordings were from multiunits (clusters of two to four cells). Throughout the text, the term *recording site* is used to encompass single units as well as multiunits, and the term *receptive field* (RF) represents the RF of single unit or the aggregate RF of multiunits. Figure 1B shows the distribution of CRF length, width, and size of all the cells tested. All RFs have sizes (refer to Materials and methods for the definition of CRF size) between 0.4° and 2.0° (0.95°±0.26°, mean ± SD) and eccentricities between 0.9° and 4.2° (2.7°±0.6°, mean ± SD). The aggregate CRF sizes reported by Lamme et al. (1999) from multiunit recordings on awake macaque monkeys ranged from 0.18° to 1.4° (mean 0.52°) at eccentricities between 1.3° and 5.35°. Similarly, the mean CRF sizes reported by Ito and Gilbert (1999) were 0.69°at eccentricities between 1.9° and 5.3°. The CRF sizes measured in our present study at smaller eccentricities are even bigger than the sizes reported in the literature measured at larger eccentricities. The most likely reason is that we used a different approach in defining the extent of the CRF. A small grating patch (Fig. 1A) was used in our study, with all parameters set to the optimal values of the cell, while moving or flashing bars were used in most previous studies reported in the literature (Knierim and Van Essen 1992; Kapadia et al. 1995; Zipser et al. 1996; Ito and Gilbert 1999; Lamme et al. 1999).

Examples of cells showing direct responses to stimuli outside the CRF

Two examples of recording sites showing direct excitatory responses to stimuli placed outside the CRF are shown in Fig. 2A, B. Figure 2A depicts a well-isolated single unit, and Fig. 2B shows multiunits. For comparison, the PSTHs of neuronal responses to both center (Fig. 2B, inset 1) and surround (inset 2) stimuli are drawn in the same plot. The smooth gray curves result from adjacent averaging of three bins. Time zero represents stimulus onset; the bin width is 10 ms. In Fig. 2A, raster plots of cell responses based on the two stimulus conditions are also shown.

It can be seen that, for these two recording sites, the latencies (indicated by open arrows in Fig. 2) of responses to a line at optimal orientation inside the CRF are between 40 and 50 ms. The latencies (indicated by filled arrows) of responses to an array of randomly oriented lines outside the CRF, however, are between 140 and 190 ms, more than 3 times longer than the latency of center responses.

For some recording sites, instead of giving direct excitatory responses to surround stimulus, their spontaneous activity is significantly suppressed after the onset of the surround stimulus. One example of such a recording site is shown in Fig. 2C. The initial suppression of spontaneous responses is usually followed by a rebound of activity back to spontaneous level. For the recording

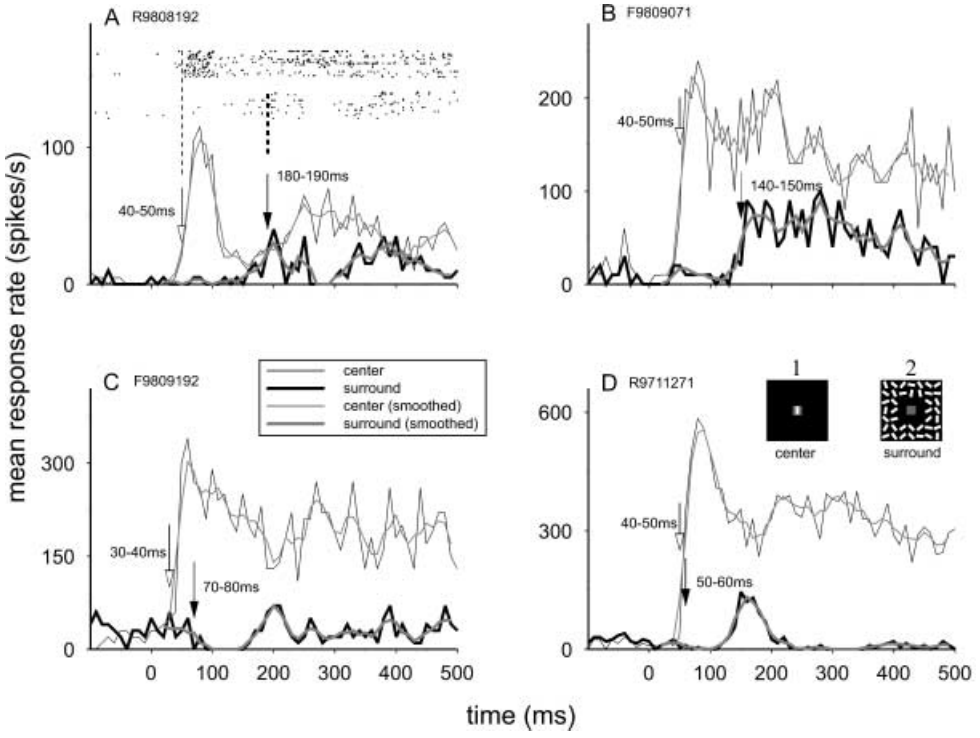

Fig. 2A–D Four examples of recording sites showing direct responses to stimuli placed outside the classic receptive field (CRF). Two stimulus conditions, *insets 1 and 2* in **D**, are compared here. For center stimulation (*inset 1*), a bright line of the same length as the CRF (*small gray square in the inset*) was centered on the CRF at the optimal orientation of the cell. For surround stimulation (*inset 2*), an array of randomly oriented bright lines were evenly distributed outside the CRF (refer to Materials and methods for details of stimulus configurations). A bin width of 10 ms was used to construct the peristimulus-time histograms (PSTHs). Time zero indicates stimulus onset. *Arrows* indicate the response outset. The *numbers beside the arrows* are response latencies (for data analysis, see Materials and methods). The CRF sizes of the cells shown in **A–D** are 1.2°×0.8°, 1.7°×2.0°, 1.2°×0.7°, and 1.2°×1.0°, respectively. **A, B** Examples of recording sites showing excitatory surround responses. **A** is a well-isolated single unit, and **B** shows multiunits. In **A** raster plots are also shown for responses under two conditions. **C, D** Examples of recording sites showing inhibitory surround responses, the spontaneous activity was suppressed after stimulus onset. The example of recording site in **D** showed an excitatory afterdischarge following the suppression period

site shown in Fig. 2D, the rebound of activity is significantly higher than the spontaneous level. This afterdischarge occurs at a time phase comparable with the late excitatory surround responses shown in Fig. 2A, B.

Except for the absolute magnitude of the firing rates, we did not observe any significant difference between single cells and multiunits in the phenomena that we looked into, so all the data were pooled in the population analysis.

Classification of cells by responses to stimuli outside the CRF

By analyzing the responses of individual recording sites to stimuli outside the CRF, three classes of cells can be distinguished (for details of data analysis, see Materials and methods):

1. For 48 recording sites (31.4%), no significant change of activity is observed before and after the presentation of the surround stimulus.
2. For 77 recording sites (50.3%), including the two examples shown in Fig. 2A, B, excitatory responses significantly higher than spontaneous level are activated by the surround stimulus.
3. For 28 recording sites (18.3%), spontaneous activity is suppressed when the surround stimulus is presented alone (for an example, see Fig. 2C); and, for 6 of these sites, a rebound of activity significantly higher than spontaneous level is observed after the initial suppression period (see Fig. 2D for an example).

For convenience, the three classes of units are named *silent class*, *excitatory class*, and *inhibitory class*, respectively, in this paper. The silent class of cells is similar to the typical cells reported in the literature cited previously: They are not directly responsive to stimuli presented outside their CRFs, but the contextual stimuli suppress their responses to the center stimuli.

Similar to the examples of recording sites in Fig. 2, the direct surround responses of most recording sites feature long latencies. Figure 3 compares the latencies of center and surround responses for the excitatory and inhibitory classes of cells.

Figure 3A is the population distribution of latencies of center responses to an optimally oriented line in the CRF center. The mean latency for all the recording sites is 47±9 ms (SD), which is comparable with the latencies reported in other V1 studies (Vogels and Orban 1990; Knierim and Van Essen 1992; Maunsell

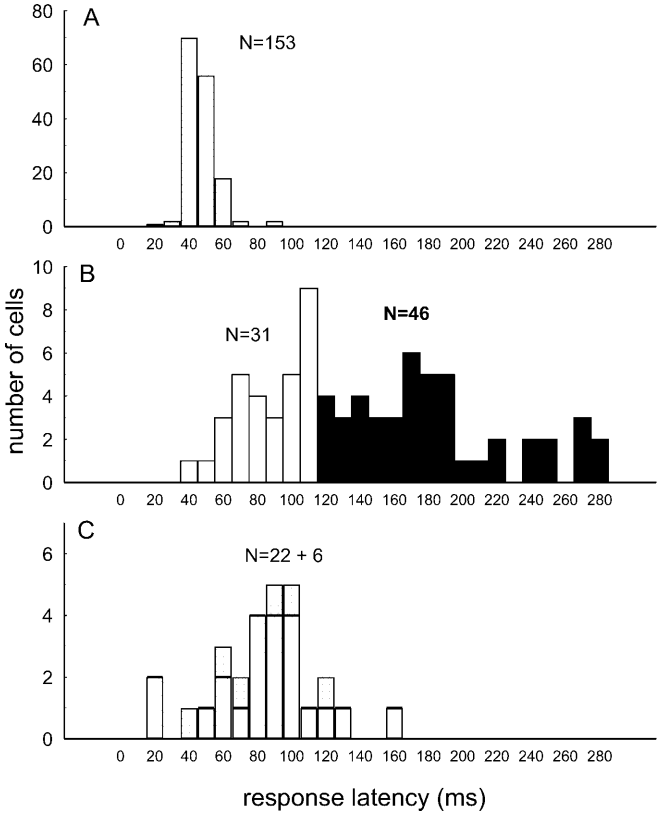

Fig. 3A–C Population analysis of center and surround response latencies. **A** Distribution of center response latencies of all recording sites (*N*=153). **B** Distribution of surround response latencies of recording sites showing direct excitatory surround responses (excitatory class). Two subgroups are arbitrarily divided using 110 ms as the delimiter. For 31 recordings sites, the latencies are shorter than 110 ms, and for 46 recording sites, the latencies are longer than 110 ms. **C** Distribution of surround response latencies of recording sites showing inhibitory surround responses (inhibitory class). For 6 recording sites, an excitatory afterdischarge followed the initial inhibitory period

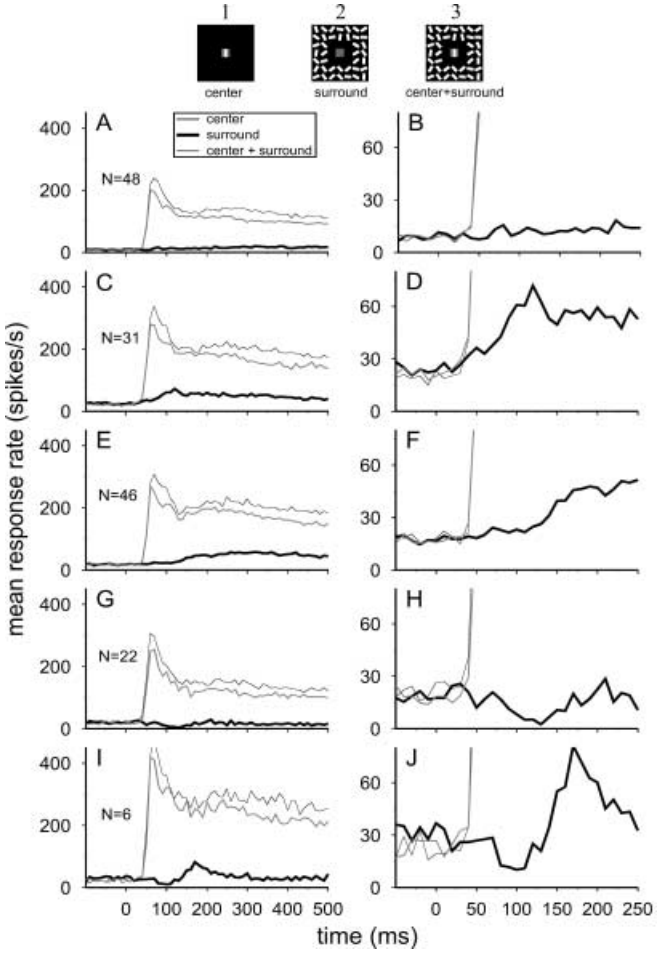

Fig. 4A–J Population responses (PSTHs averaged for all the recording sites) under three different conditions (see *insets 1–3*) for three classes of cells and their subgroups. The *left panel* shows the population PSTHs, and the same data are re-plotted in the *right panel* using rescaled axes to show the details of the initial responses. Time zero indicates stimulus onset. A bin width of 10 ms was used to construct the histograms. The *1st row* (**A, B**) shows the silent class of cells that did not respond to surround stimulus onset. The *2nd and 3rd rows* (**C–F**) show the two arbitrarily-divided subgroups of excitatory class, whose surround response latencies are shorter than 110 ms (**C, D**) and longer than 110 ms (**E, F**), respectively. The *bottom two rows* (**G–J**) show the two subgroups of cells in inhibitory class. One subgroup (**I, J**) showed an excitatory afterdischarge above the spontaneous activity level following the initial inhibitory period, while the other subgroup did not show such an afterdischarge (**G, H**). The responses only returned to noise level. Stimulus configurations are the same as described in Fig. 2, except that a new condition was added in which both center and surround stimuli were presented simultaneously (*inset 3*). Note that for all three classes of cells and their subgroups, the surround stimuli outside the CRF inhibit the cell responses to a line in the CRF center (compare *thin dark curves* with *black curves*)

and Gibson 1992; Celebrini et al. 1993; Lamme et al. 1999).

For the excitatory class of cells, the surround response latencies are much more broadly distributed than center responses, with a mean of 145±61 ms (SD; Fig. 3B). As can be seen for the majority of these cells, the surround response latencies are at least twice as long as center responses. Only a very small proportion of cells have surround response latencies overlapped with center responses (less than 60 ms). In order to see whether the properties of cells with short and long latencies differ, we arbitrarily divided the excitatory class of cells into two subgroups using 110 ms latency as the delimiter. The data from these two subgroups are presented separately in all subsequent analyses.

For the inhibitory class of cells, including six cells with an excitatory afterdischarge, the latencies of inhibitory responses are also longer than center responses and broadly distributed, with a mean of 84±31 ms (SD; Fig. 3C).

For a better demonstration of the direct surround responses of different classes of cells and their subgroups, we averaged the PSTHs of all the cells in each class and subgroup, and the results are shown in Fig. 4. The left panel shows the population PSTHs of three classes of cells and their subgroups under three stimulus conditions (insets 1–3 at the top of Fig. 4), and the same data are

replotted in the right panel using rescaled axes to show the details of the initial responses. Time zero indicates stimulus onset. Figure 4A, B shows the silent class that does not respond to surround stimulus onset. Figure 4C–F shows the two arbitrarily divided subgroups of the excitatory class, whose surround response latencies are shorter than 110 ms (Fig. 4C, D) and longer than 110 ms (Fig. 4E, F), respectively. Figure 4G–J shows the two subgroups of cells in the inhibitory class. One subgroup (Fig. 4I, J) shows an excitatory afterdischarge above the spontaneous activity level following the initial inhibitory period, while the other subgroup does not show such an afterdischarge (Fig. 4G, H). We emphasize that the responses return to the spontaneous activity level.

Comparing the PSTHs based on the three stimulus conditions of center only, surround only, as well as the simultaneous presence of both center and surround stimuli in Fig. 4, we see that for all three classes of cells including their subgroups, no matter whether the regions outside the CRF are silent, excitatory, or inhibitory by themselves, an array of random lines outside the CRF always suppresses the responses to a line in the RF center (compare thin dark curves with gray ones in Fig. 4), and the inhibition starts almost from the beginning of cell responses. This agrees well with the commonly reported effects of contextual modulation in V1: for most neurons in the primary visual cortex of cats and monkeys, large patches of stimuli presented outside the CRF inhibit the cell responses evoked by stimuli inside the CRF (Blakemore and Tobin 1972; Knierim and Van Essen 1992; DeAngelis et al. 1994; Li and Li 1994; Sengpiel et al. 1997; Nothdurft et al. 1999; Li et al. 2000)

No significant difference is found between these three classes of cells with respect to the mean RF eccentricity, the mean RF size, and the bandwidth of orientation tuning (one-way ANOVA, $P>0.05$). During recordings the depth of each recording site was taken as the depth relative to the first-shown neuronal activity. While all classes of cells were encountered in all recording depths (0–1,850 μm), cells in the silent class (Fig. 4A, B) tend to appear in superficial layers where spontaneous activity is also low, and cells in the excitatory (Fig. 4C–F) and inhibitory (Fig. 4G–J) classes tend to appear in deeper layers where spontaneous activity is higher. This difference is not significant when analyzed by one-way ANOVA ($P>0.05$).

Direct surround responses are less orientation selective

Most V1 neurons are selective for the orientation of stimuli inside the CRF (Hubel and Wiesel 1962, 1968), and contextual modulation of cell responses by stimuli outside the CRF is also orientation-selective (Blakemore and Tobin 1972; Maffei and Fiorentini 1976; Nelson and Frost 1978; Knierim and Van Essen 1992; Li and Li 1994; Gilbert et al. 1996; Nothdurft et al. 1999; Li et al. 2000). Are the direct responses activated by stimulation of regions outside the CRF alone also selective for the orientation of contextual lines?

For 52 recording sites showing excitatory surround responses and 16 recording sites showing inhibitory surround responses, we tested the effects of orientation of center and surround lines of stimuli on cells' responses. The results are presented in Fig. 5 (stimuli are shown schematically as insets 1–6 at the top). The orientation 0° represents the optimal orientation of the cells. Figure 5A–D shows the two subgroups of cells in the excitatory class whose latencies of surround responses are shorter (Fig. 5A, B) or longer (Fig. 5C, D) than 110 ms, respectively. Figure 5E, F shows the inhibitory class of cells. The plots in the left column show the PSTHs averaged for all recording sites in each group of cells. Time zero indicates stimulus onset. The plots in the right column show the mean cell responses averaged for all the recording sites in each corresponding group of cells. The mean center responses are calculated for the time period of 40 to 340 ms after stimulus onset. The mean surround responses are calculated for the time period indicated by the gray horizontal arrows on the corresponding PSTHs in the left column (40–340 ms in Fig. 5A; 110–410 ms in Fig. 5C; 40–160 ms in Fig. 5E). The baseline or spontaneous activity is determined based on a time period of 500 ms before stimulus onset. We see that, for an array of lines covering the CRF (insets 1–3), the cell responses markedly depend on the orientation of the stimulus lines for all groups of cells. When the lines are aligned with the optimal orientation of the cells (inset 1), the cells produce the strongest response. The responses are significantly lower for randomly oriented lines (inset 2), and are even lower when the lines are orthogonal to the optimal orientation (inset 3). For stimulus lines outside the CRF (insets 4–6), however, the responses of neurons are not nearly as selective for the orientation of lines. For a clear comparison with the center responses, we scaled the mean surround responses in such a way that the center and surround responses for the 0° condition have the same amplitude. We see that, in the surround stimulus condition, optimally oriented lines and randomly oriented lines drive the cell responses almost equally for all groups of cells. Moreover, the mean responses activated by lines orthogonal to the optimal orientation are only slightly less than that activated by optimally oriented lines.

One-way ANOVA shows that, in the center stimulation condition, orientation of center lines significantly affects neuronal responses ($P=0.002$ for the excitatory subgroup of cells shown in Fig. 5A, B; $P=0.0003$ for the subgroup in Fig. 5C, D; $P=0.00009$ for the inhibitory class of cells in Fig. 5E, F). In the surround stimulation condition, however, orientation of surround lines is not a significant factor in neuronal responses ($P=0.74$, 0.57, 0.66, respectively).

Direct surround responses are not selective for the stimulus patterns

Our recent study (Li et al. 2000) showed that inhibition of cell responses to a line in the RF center by contextual stimuli depends on the type of composing elements of

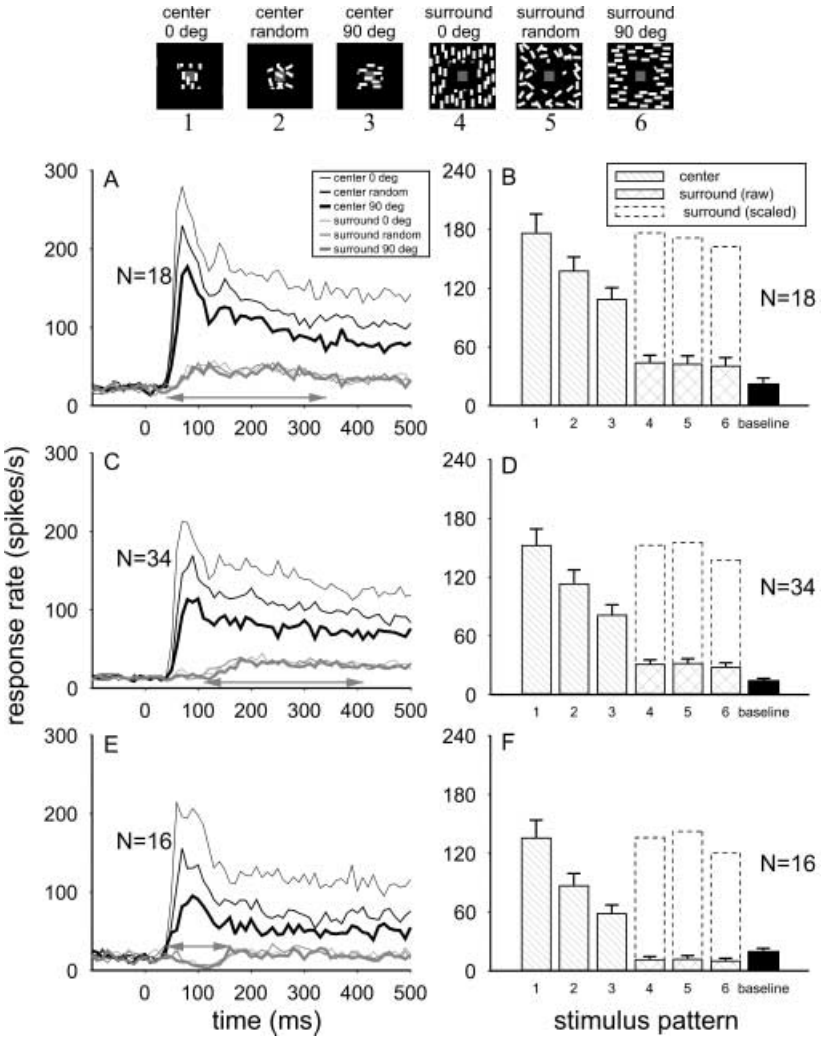

Fig. 5A–F Effects of orientation of center and surround stimuli on responses of those V1 neurons showing direct surround responses. Stimulus configurations are shown schematically at the *top* (*insets 1–6*). The *small gray squares* in the center of stimuli denote the CRF. A full stimulus pattern was composed of 7×7 (can be up to 10×10 depending on the CRF size) bright lines, 0.7° long each. The position of each line was randomized from trial to trial within a 4.9°×4.9° (can be up to 7.0°×7.0° depending on CRF size) dark area centered on the CRF. For center stimuli (*insets 1–3*), a blank window was put in the surround so that only the center 2°×2° area of the full stimulus was exposed. For surround stimuli (*insets 4–6*), a blank window of minimum size at least twice the size of CRF was put in the center so that only the surround area of the full stimulus was exposed. The orientation 0° represents the optimal orientation of the cell. The *top and middle rows* show the two subgroups of cells in excitatory class whose latencies of surround responses are shorter (**A, B**) or longer (**C, D**) than 110 ms, respectively. The *bottom row* (**E, F**) shows the inhibitory class of cells. The plots in the *left column* show the PSTHs averaged for all recording sites in each group of cells. Time zero indicates stimulus onset. The plots in the *right column* show the mean cell responses averaged for all the recording sites in each corresponding group of cells. The mean center responses (*right-hatched bars*) were calculated for the time period of 40–340 ms after stimulus onset. The mean surround responses (*cross-hatched bars*) were calculated for the time period indicated by the *gray horizontal arrows* on the corresponding PSTHs in the *left column* (40–340 ms in **A**; 110–410 ms in **C**; 40–160 ms in **E**). The baseline or spontaneous activity (*black bar*) was determined based on a time period of 500 ms before stimulus onset. *Error bars* represent 1 SEM. For a clear comparison with the center responses, the surround responses (conditions *4–6*) were scaled (*empty bars*) in such a way that the center and surround responses under 0° condition had the same amplitude

contextual stimuli. An array of straight lines tends to give the strongest suppression of neuronal responses compared with contextual stimuli made of semicircles, circles, or dots. For 60 recording sites in the excitatory class (20 recording sites with a latency shorter than 110 ms, 40 recording sites no shorter than 110 ms) and 22 recording sites in the inhibitory class, we tested the effect of these surround stimuli on cell responses. The results are shown in Fig. 6 (stimuli are shown at the top of the figure, insets 1–5). The surround stimuli (insets 2–5) consisted of random dots, circles, semicircles, and straight lines, respectively. The total length of stimulus elements was kept constant, and so was the mean luminance in the surround. Even though the composing elements of the surround are rather different, all surround stimuli activate the cell responses almost equally for all

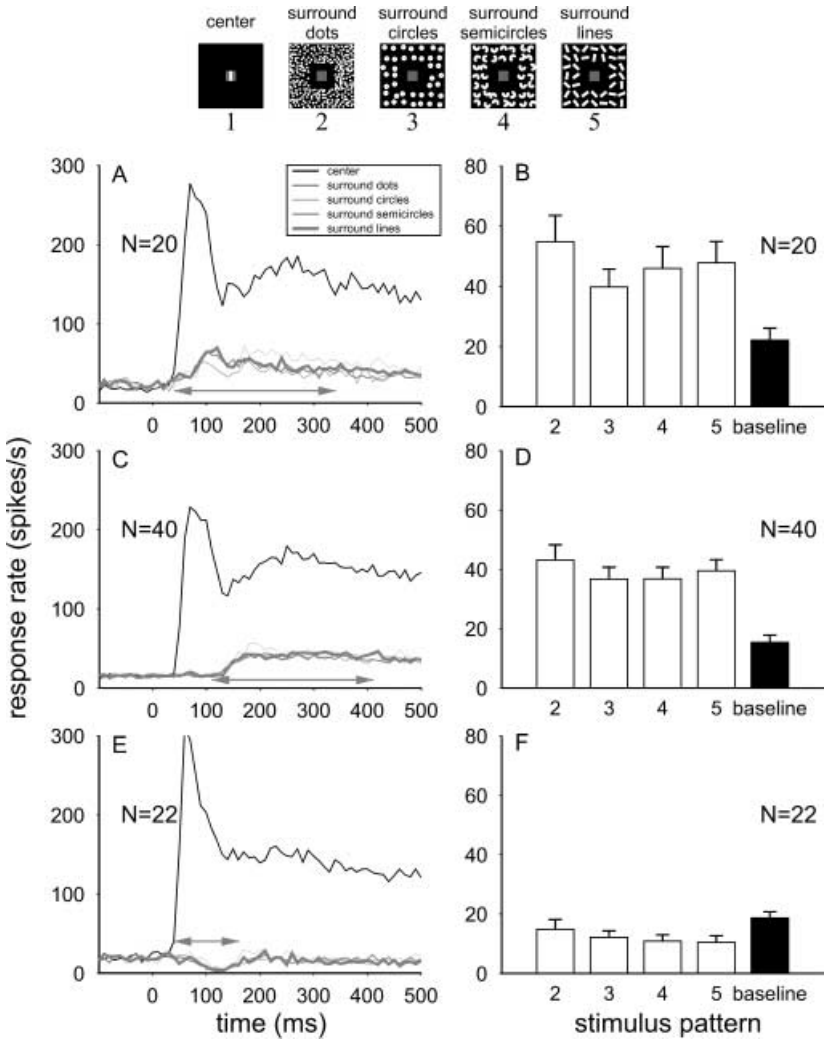

Fig. 6A–F Effects of different types of stimulus elements on surround responses. Stimuli are shown schematically at the top (*insets 1–5*). The *small gray squares* in the center of stimuli denote the CRF. The surround stimuli (*insets 2–5*) consisted of random dots, circles, semicircles, and straight lines, respectively. The total length of stimulus elements was kept constant, so was the mean luminance. In *3–5*, the whole 4.9°×4.9° (can be up to 7.0°×7.0° depending on CRF size) stimulus area was divided into 7×7 (can be up to 10 × 10 depending on the CRF size) equally spaced compartments (0.7°×0.7° each) for holding individual elements. In *3*, some spatial jitter (from zero to one-quarter the size of a compartment) was introduced to randomize the circle position. In *4 and 5* the orientation of each element was randomized in each trial. A blank window of minimum size at least twice the size of CRF was put in the center of stimuli. *Inset 1* shows the control condition in which only a line was presented inside the CRF at the optimal orientation. The *top and middle rows* show the two subgroups of cells in excitatory class whose latencies of surround responses are shorter (**A, B**) or longer (**C, D**) than 110 ms, respectively. The *bottom row* (**E, F**) shows the inhibitory class of cells. The plots in the *left column* show the population PSTHs. The plots in the *right column* show the mean cell responses. The mean surround responses (*empty bars*) were calculated for the time period indicated by the *gray horizontal arrows* on the corresponding PSTHs in the *left column* (40–340 ms in **A**; 110–410 ms in **C**; 40–160 ms in **E**). The baseline (*black bar*) was determined based on a time period of 500 ms before stimulus onset. *Error bars* represent 1 SEM

groups of cells. The top and middle rows show the two subgroups of cells in the excitatory class whose latencies of surround responses are shorter (Fig. 6A, B) or longer (Fig. 6C, D) than 110 ms, respectively. Figure 6E, F shows the inhibitory class of cells. The plots in the left column show the PSTHs averaged for all recording sites in each group of cells. Time zero indicates stimulus onset. The plots in the right column show the mean cell responses averaged for all the recording sites in each corresponding group of cells. The mean surround responses are calculated for the time period indicated by the gray horizontal arrows on the corresponding PSTHs in the left column (40–340 ms in Fig. 6A; 110–410 ms in Fig. 6C; 40–160 ms in Fig. 6E). The baseline is determined based on a time period of 500 ms before stimulus onset.

One-way ANOVA reveals that the stimulus pattern is not a significant factor in surround responses (P=0.65 for the excitatory subgroup of cells shown in Fig. 6A, B; P=0.57 for the subgroup in Fig. 6C, D; P=0.19 for the inhibitory class in Fig. 6E, F).

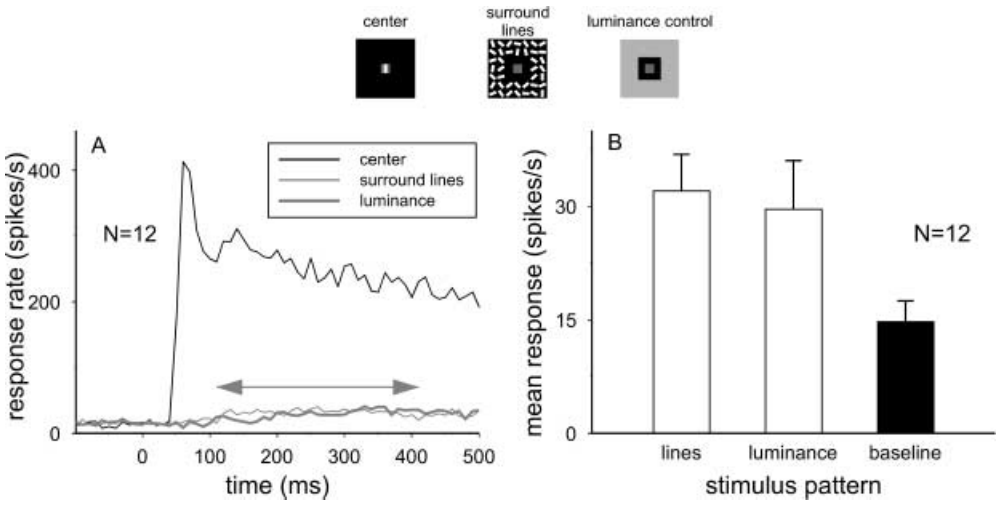

Fig. 7A, B Effects of homogeneous surround whose luminance was the same as the mean luminance of all textured patterns used in this study. Results from stimulation of randomly oriented surround lines are also shown here for comparison. **A** Population PSTHs. **B** Mean surround responses. For details, see Fig. 6

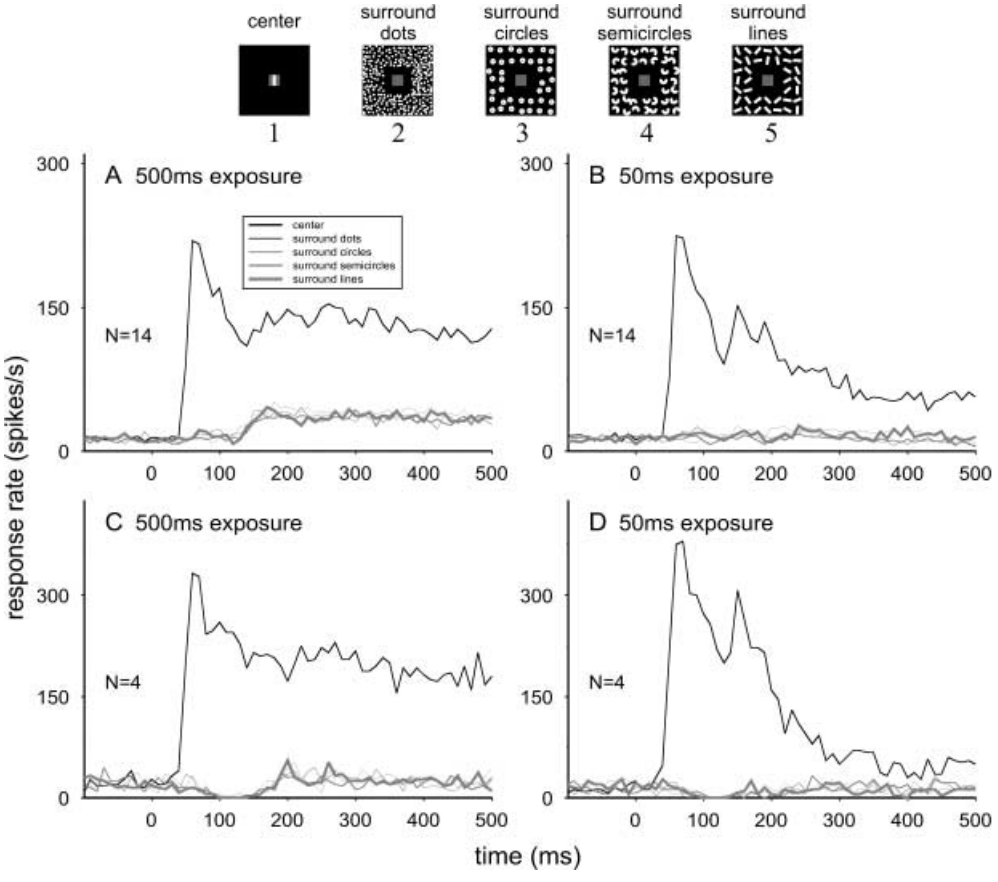

Fig. 8A–D Effects of exposure duration of stimuli on direct surround responses. Stimulus configurations (see *insets 1–5* at the *top*) are the same as described in Fig. 6. Population responses of 14 excitatory recording sites (*top panel*) and 4 inhibitory recording sites (*bottom panel*) to these stimuli under exposure duration of 500 ms (*left panel*) and 50 ms (*right panel*) are shown. Time zero indicates stimulus onset. Bin width is 10 ms. Note that with 50 ms stimulus exposure, the excitatory surround responses are almost eliminated, whereas the outburst of responses to the center line and the inhibitory surround responses are not affected

For a further comparison, we tested the effect of a featureless homogeneous surround, whose luminance is the same as the mean luminance of all textured patterns. Twelve V1 recording sites showing excitatory surround responses are tested (Fig. 7). Very similar to the other textured patterns, a homogeneous surround yields the same late responses as an array of random lines of equal mean luminance (paired *t*-test: t=0.51, P=0.62).

Late excitatory surround responses are dependent on exposure duration of stimuli

We demonstrated in Figs. 5, 6, 7 the nonstimulus-specific properties of the direct surround responses activated by stimulation of regions outside the CRF. For the majority of recording sites in the excitatory class, the latencies of surround responses are much longer than the center responses. For most recording sites in the inhibitory class, the latencies of suppression are also longer than

the center responses. In those experiments, an exposure duration of 500 ms is used. One question arising from here is whether the long presence of surround stimuli is necessary to activate the late surround responses.

For 14 recording sites showing excitatory responses to stimuli outside their CRFs under exposure duration of 500 ms (Fig. 8A), we recorded their responses to the same stimulus patterns with a shorter exposure duration of 50 ms (Fig. 8B). By comparing Fig. 8A with B, we see that, with 50 ms stimulus exposure, the late surround responses are almost eliminated. The outburst of cell responses to a line in the RF center, however, is not affected at all by reducing the duration of center stimulus. Only the sustained firing around 150 spikes/s in Fig. 8A depends on maintained center stimulation. These data suggest that, unlike the center responses, the activation of late excitatory surround responses depends on the continuous signal input from the surround regions.

Unlike the excitatory surround responses of the excitatory class of cells, the suppression of spontaneous activity in the inhibitory class of cells seems to be unaffected by the reduction of exposure (compare Fig. 8C with D). Only the rebound or afterdischarge following the inhibitory period is weakened with 50 ms of exposure.

Discussion

The effects of contextual stimuli on the responses of neurons in the primary visual cortex have been extensively studied for more than two decades (for reviews, see Allman et al. 1985; Gilbert 1998; Lamme et al. 1998a). Little attention has been paid, however, to the direct responses activated by stimulation of regions outside the CRF. In the present study, for the first time, the properties of neuronal responses in V1 of alert monkeys to stimuli placed well outside the CRF are investigated. Using responses to static patterns outside the CRF as a criterion, we demonstrate three classes of cells. Our data also show that the late surround responses are not selective for stimulus orientation as compared to the responses evoked by stimuli inside the CRF, and that they are not selective for the stimulus patterns in contrast to the contextual modulation effect induced by surround stimuli. Moreover, long exposure of stimuli is necessary to activate the late excitatory surround responses.

Possible neural substrate

Our data show that the inhibition of neuronal responses to a center test line by contextual patterns occurs almost from the beginning of cell responses, in accordance with Knierim and Van Essen (1992). The fast contextual inhibition is orientation-specific (Blakemore and Tobin 1972; Knierim and Van Essen 1992; DeAngelis et al. 1994; Li and Li 1994; Sengpiel et al. 1997; Nothdurft et al. 1999; Li et al. 2000). It could have its neural substrate in the long-range horizontal connections between cells in V1 revealed in some anatomical studies (Gilbert and Wiesel 1983; Blasdel et al. 1985; Fitzpatrick et al. 1985; McGuire et al. 1991). Feedback from V2 may also play a role in the surround inhibition (Knierim and Van Essen 1992; Lamme et al. 1998a, 1998b).

For the direct inhibitory surround responses, the response latencies fall within the range of response latency in V1 reported in the literature. Their underlying neural basis could also be the intrinsic connections in V1 or feedback from prestriate cortex. The nonstimulus specificity of the direct inhibitory surround responses is distinct from the fast contextual inhibition. This suggests that these responses could result from pooling input from cells of a wide range of selectivity rather than from cells with similar selectivity.

It is difficult to explain the late excitatory surround responses in terms of intrinsic connections in V1 as their latencies are on average about 3 times longer than center responses. The fact that the activation of late excitatory surround responses needs the continuous signal input from the surround regions independently suggests that a special neural circuit is involved.

Zipser et al. (1996) have reported in their V1 study that, when any cues defined a textured figure centered on the RF, there is always an enhancement of neuronal responses 80–100 ms after stimulus onset. In a recent study, Lamme et al. (1999) further demonstrated a clear 3-phase time course of cell responses to figure-ground stimuli by positioning the figure pattern at different locations relative to the CRF. They observed that the initial stage (less than 70 ms after stimulus onset) of cell responses to local features is followed by a figure-ground edge enhancement stage that peaks at 115–125 ms, and this stage is then followed by another even later figure surface enhancement stage. This figure surface enhancement is at full strength between 150 and 160 ms after stimulus onset. Moreover, this enhancement persists for as long as the stimulus is on. The late facilitation of neuronal responses caused by stimulation of figure surfaces has about the same latency as the late direct surround responses observed in our study. Besides, of the cells showing direct late responses to stimuli outside the CRF, most showed sustained responses to surround stimuli as long as the stimuli were on. The similarities between the late enhancement of neuronal responses by figure surfaces and the late direct responses by extra-CRF stimulation alone suggest that the underlying neural substrate could be the same. The only difference is that, in their experiments (Lamme 1995; Zipser et al. 1996; Lamme et al. 1999), the CRF was always covered with stimuli to drive the cells continuously, as is a usual procedure in studying contextual modulation effects. Our experiments unequivocally show that in around 50% of the V1 sites recorded no spatiotemporal alteration of contrast in the RF center is required to activate the late excitatory surround responses. In the latter case, the dark stimulus-free region over the CRF (blank window) could be perceived as a figure (dark square) against a textured or luminance background. We show in this study that many V1 cells

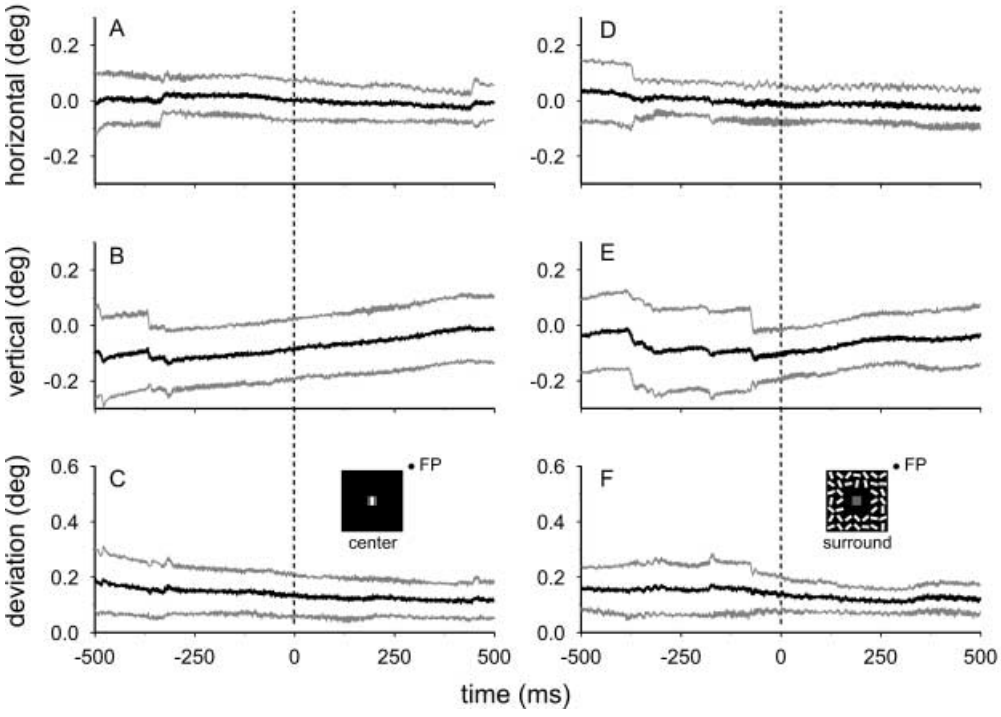

Fig. 9A–F Averaged (*N*=20 trials) eye position traces showing the relative eye positions with respect to the fixation spot for the conditions when the cell shown in Fig. 2D was tested with center and surround stimuli. Time zero indicates stimulus onset (*vertical dashed lines*), and eye position zero represents the location of the fixation point (*FP*) on the stimulus screen. The *dark middle traces* represent the mean eye positions, and the *gray traces above and below the thick traces* represent +1 SD and –1 SD from the mean positions, respectively. The *left panel* (**A–C**) corresponds to the center stimulus condition (see *inset* in **C**), and the *right panel* (**D–F**), the surround stimulus condition (see *inset* in **F**). *Top row* (**A, D**) horizontal eye positions. *Middle row* (**B, E**) vertical eye positions. *Bottom row* (**C, F**) the deviation of eye positions from the FP averaged for each trial, that is, the square root of the squared sum of the horizontal and vertical eye positions with respect to the FP. The fixation window size was 0.6°×0.6°

do respond to this special (degenerate) figure-ground pattern even though no "figure" pattern is inside the CRF. It has been shown that the late facilitation of cell responses by figure surfaces can only be observed in alert animals, and anesthesia suppresses this effect (Lamme et al. 1998a, 1998b). We would expect that the direct late surround responses could only be observed in alert animals as well. This also would explain why late surround responses have never been found in earlier experiments using anesthetized animals.

It has been reported that the size and position of RF in V1 can change dynamically (Pettet and Gilbert 1992; Das and Gilbert 1995; Gilbert et al. 1996). We do not think this is the cause of the late surround responses for two reasons. First, the dynamic change of RF properties reported in the studies above develops in a time scale of minutes, while the latencies of surround responses were between 100 and 150 ms. Second, although the expansion of RF or shift of RF position could cause some changes in RF properties, it is hard to explain the big difference between center and surround responses with respect to stimulus selectivity. Also there is no evidence showing that the expanded part of RF has much longer latencies than the center part. It has been reported also that extrastriate visual neurons show a filling-in effect when stimulated with textured patterns with a hole (De Weerd et al. 1995). This filling-in phenomenon takes seconds to appear and has not been observed in V1.

The long response latency and the weak or absent specificity to the orientation of the stimulus presented outside the CRF, together with the long exposure duration required to activate these responses, point to a mechanism of visual processing that is different from RF-based processing or fast intrinsic connection-based contextual modulation. One possible explanation is that feedback from higher cortical areas could be involved in this mechanism. Another possibility is the contribution of slow intrinsic connections within V1. A recent study (Bringuier et al. 1999) of intracellular recordings from orientation-selective neurons in area 17 of cats showed subthreshold synaptic depolarizing responses to stimuli flashed outside the CRF, and the delay of depolarization increased linearly with the stimulus distance from the RF center. It is proposed that these signals spread along slowly conducting horizontal connections within primary visual cortex. As yet no evidence shows whether the slow intrinsic connections are among cells with similar stimulus selectivity, as is the case of conventional long-range horizontal connections (Gilbert and Wiesel 1983, 1989).

Eye movements and cell responses

It has been reported that responses of visual cortical neurons can be profoundly influenced by even small eye

movements (Leopold and Logothetis 1998). One may argue that the late surround responses that we observed by stimulation of regions outside the CRF were caused by eye movements related to stimulus onset. The eye position traces, which we recorded during V1 recordings, exclude this possibility. As an example, Fig. 9 shows the averaged (N=20 trials) eye position traces for the conditions when the recording site shown in Fig. 2D was tested with center and surround stimuli. There was a transient afterdischarge peaked at 150 ms for this recording site (Fig. 2D). If these responses were related to any saccades due to stimulus onset, we would expect eye movements phase-locked around stimulus onset. Averaging across many trials, if the eye movements were always toward one direction, we would see this in either horizontal (Fig. 9A, D) or vertical (Fig. 9B, E) eye traces around time zero (stimulus onset). If the eye movements could be in any directions, we would see either an increase in the deviation (Fig. 9C, F) of eye positions from the fixation point (FP) after stimulus onset, or increases of standard deviation of all eye traces. On the basis of the example shown in Fig. 9, which is representative for our recordings, all these hypotheses can be excluded. Only during the first several hundreds of milliseconds after fixation started (time zero to 500 ms) fixation was a little worse (SD is bigger). After the fixation was already held for 500 ms (time zero, stimulus onset), we can see that the fixation is very stable with no discernible sudden change of eye position or standard deviation. There is a slow upward drift of about 0.1° of eye positions during the whole fixation period (Fig. 9B, E), but we do not think this would result in the late surround responses whose phase were locked, for this cell, at about 150 ms after the onset of surround stimulus (Fig. 2D).

Possible role of late surround responses in perception

Our recent study (Li et al. 2000) showed that the responses of most V1 neurons to center stimuli are diminished when larger contextual stimuli are added to the surround. We found that the contextual inhibition has two distinct temporal phases. It starts in the beginning of cell responses and increases rapidly to maximal values. Then the strong, fast initial inhibitory phase is followed by a disinhibitory or facilitatory phase between 100 and 200 ms after stimulus onset in which the contextual inhibition is getting weaker and even facilitation can be observed in some cells during this period. The late responses due to extra-RF stimulation alone also start during the latter phase. This indicates that the late surround responses reduces the inhibition caused by the contextual stimuli and may play an important role in figure-ground segregation.

Feedforward, intrinsic horizontal connections, and feedback play different roles in visual processing in V1 (for recent review, see Lamme et al. 1998a). While feedforward mainly contributes to the generation of RF properties, the horizontal connections contribute to the fast modulation of cell responses important in visual perception (Gilbert 1998). Our data suggest that further late modulation of cell responses could be mediated by other neural circuit such as feedback connections from higher cortical areas or some slow, long-range lateral interactions within V1.

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