

Recurrent networks in human visual cortex: psychophysical evidence

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To study the neuronal circuitry underlying visual spatial-integration processes, we measured the effect of short and long chains of proximal Gabor-signal (GS) flankers ($\sigma = \lambda = 0.15^\circ$) on the contrast-discrimination function of a foveal GS target. We found that the same pattern of lateral masks enhanced target detection with low-contrast pedestals and strongly suppressed the discrimination of a range of intermediate pedestal contrasts (pedestal contrast $<30\%$). Increasing the number of the flankers reversed the suppressive effect. The data suggest that the main influence of the proximal flankers is maintained by activity-dependent *interactions* and not by linear spatial summation. With an increased number of flankers, we found a nonmonotonic relationship between the discrimination thresholds and the number of flankers, supporting the notion that the discrimination thresholds are mediated by excitatory-inhibitory recurrent networks that manifest the dynamics of large neuronal populations in the neocortex [Proc. Natl. Acad. Sci. USA **94**, 10426 (1997)].

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1. INTRODUCTION

A large body of psychophysical and physiological evidence coherently supports the notion that the basic visual mechanisms in primates include local, contrast-responding filters that are position, orientation, and size specific.¹⁻⁴ The way in which these local mechanisms interact to produce a more global, low-level description of the visual world has been the subject of increasing scientific effort in recent years. Here we address this question by measuring the contextual influence of systematically changed chains of lateral maskers on the thresholds for contrast discrimination. Using maskers of fixed contrast while varying the target contrast enabled us to characterize the lateral interactions as a function of the target contrast. In addition, using chains of maskers enabled us to explore interactions of the maskers among themselves as well as the interactions between maskers and the target.

Contextual influences on the thresholds for contrast discrimination have been reported by an accumulating mass of studies. The visibility of short bars and Gabor patches was found to be either enhanced or suppressed by laterally placed flanking stimuli of similar orientation and spatial frequency.⁵⁻¹¹ However, for proximal, partially overlapping stimuli, it was not clear whether the observed visibility changes were the result of lateral interactions or merely reflected linear spatial summation by local filters. Linear summation by a local filter assumes that the filter has some sensitivity profile that differs from zero for a limited extent of the visual field (its perceptive field).¹² The sensitivity profile of the visual local filters has been suggested to be a circular or an elongated two-dimensional Gabor function,¹³⁻¹⁶ resembling the receptive field of simple cells in the visual cortex. The filter is assumed to sum up (or integrate) the product of its sensitivity profile and the intensity profile of the input stimuli. Thus visibility changes of Gabor-signal (GS) tar-

gets in the context of lateral maskers, which are due to linear summation, are expected to be sensitive to the relative polarity, the contrast, and the proximity of the stimuli. Such a dependency was psychophysically found. Proximal, low-contrast flankers at 0 or 1λ target-flanker distance were found to enhance the detection of the target. Proximal, high-contrast flankers suppress the detection of the target.^{6,8,11} Increasing the target-flanker distance (optimally to $2-3\lambda$ distance) turns the suppressive effect into a facilitative one. These observations support the possibility that at short range, the contextual effects are the result of linear summation. According to this viewpoint, high-contrast stimuli at a decreased sensitivity region of the perceptive field have an effect on target visibility similar to that of low-contrast stimuli at a higher-sensitivity region of the perceptive field. Thus the enhancement that was found with high-contrast flankers at $2-3\lambda$ may be equivalent to the decreased thresholds found with low-contrast, overlapping pedestals. However, other studies suggest that spatial integration is mediated by lateral interactions between the local filters, and these interactions dominate even at relatively short ranges.^{5,11} Long-range spatial interactions, at distances above 3λ , were shown to be insensitive to the contrast and phase of the flankers,^{6,8,11,17} suggesting nonlinear processes. We tested the linear summation hypothesis for short-range interactions. We measured the contrast-discrimination function for a foveal GS target in the context of proximal high-contrast lateral flankers. Linear filters predict a horizontal shift of the contrast-discrimination function when a fixed input from flankers is added. Failure of this prediction implies a dominance of nonlinear lateral interactions at early stages of the visual processing.

Models for spatial integration can be broadly classified as belonging either to hierarchical or to "fully recurrent" models. Hierarchical models can be classified as belong-

ing to strictly feed-forward models or to feed-forward models with recurrent normalization process. The basic phase of the hierarchical (or feed-forward) models includes the processing of the image by local filters that project to a second-order set of filters that integrate (linearly or not) their outputs.^{8,17-22} The properties of the local filters are described by models that were devised to account for human performance of masking and contrast-discrimination tasks under different states of adaptation.^{8,23-25} Such models include a local linear summation circuit followed by a nonlinear transformation and then by a divisive inhibition (normalization) process.²⁴ Normalization models, with *recurrent* divisive inhibition, were suggested to account for the visually driven responses of cat and monkey simple cells.²⁶⁻²⁸ The other class of spatial-integration models includes fully recurrent models. These models suggest that spatial integration is mediated by a network with both excitatory and inhibitory recurrent interactions.^{5,29} Moreover, they assume that the local interactions among the different channels and the long-range spatial integration take place at the same stage of visual processing. Recurrent networks were suggested to include nonlinear transformations of both the excitatory and inhibitory inputs and the subtractive inhibitions. Such networks were used to explain surround modulation on contrast-masking performances.^{5,29} Having both local and spatial influences at the same level of processing, the recurrent model predicts that the effect of remote maskers on the threshold for contrast discrimination depends on the activity at the more proximal nodes and can be changed according to the context presented.

In this study we demonstrate that lateral interactions, rather than linear spatial summation, dominate even at short ranges (2λ distance) and support the recurrent-network model.

2. METHODS

We conducted contrast-discrimination experiments under different contextual conditions (Fig. 1). The results were described by a threshold-versus-contrast (TvC) function.

A. Apparatus

Stimuli were displayed as gray-level modulation on a Philips color monitor, using a personal computer with an Intel Pentium II processor. The video monitor specifications were 61 Hz noninterlaced, with 1280×1024 pixels occupying a $15^\circ \times 12^\circ$ area. The mean display luminance was 50 cd/m^2 in an otherwise dark environment. The stimuli were viewed from a distance of 125 cm.

B. Stimuli

The stimuli consisted of one target signal (at the fixation point), one pedestal signal (at the target location) and 0, 2, 4, 8, or 10 lateral masks. The spatial luminance distribution of each of the target, pedestal, and mask signals was described by a Gabor function (a cosine grating multiplied by a Gaussian envelope¹³), with a vertical orientation, and $\sigma = \lambda = 0.15^\circ$. The mask-signal amplitude, C_m , and the pedestal-signal amplitude, C_p , were changed according to the different experimental conditions. Note that a GS does not have a fixed contrast across the stimu-

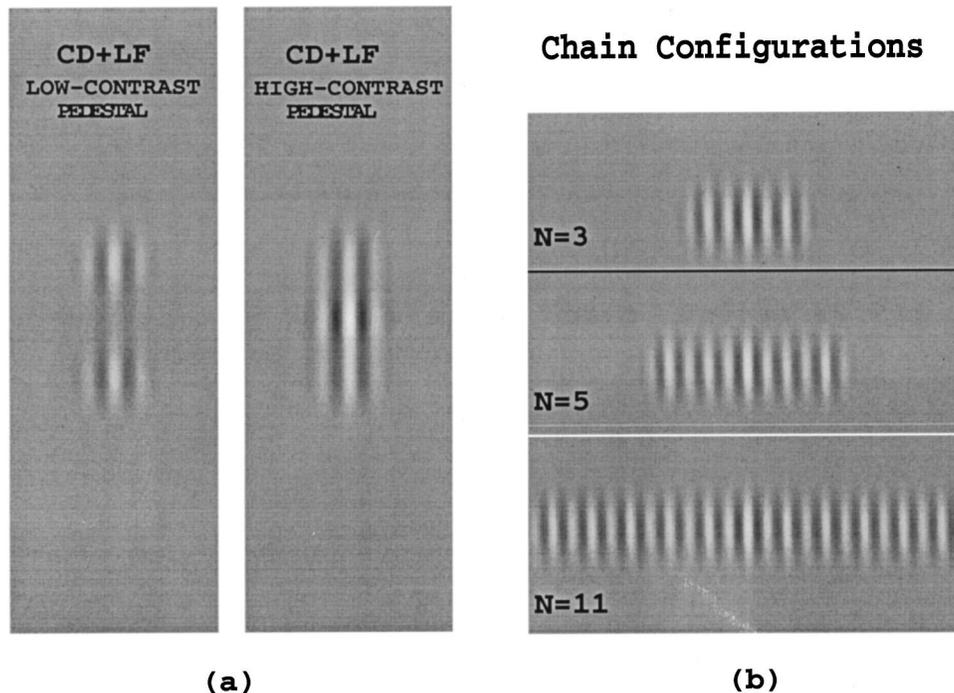


Fig. 1. Examples of stimuli used in our experiments. (a) Different experimental conditions used in Experiment 1 (the collinear configuration), in which the thresholds for contrast discrimination (CD) were measured with and without high-contrast lateral flankers (LF). (b) Different experimental conditions used in the chain experiment (the parallel configurations). N is the number of the masks in the chain: 1 pedestal at the center of the chain and $N - 1$ lateral flankers.

lus, and the amplitude of the signal represents its maximum contrast. The target and masks were aligned with 2λ (0.3°) spacing.

C. Experiment 1

Contrast-discrimination thresholds were measured for a foveal target, flanked on each side by 0, 1, 2, or 4 high-contrast masks. We carried out experiments for two global configurations: (1) a parallel configuration of side-by-side vertically oriented GSs, and (2) a collinear configuration of vertically oriented GSs [Fig. 1(a)]. The range of the pedestal contrasts varied from zero to 50% ($C_p = 0, 1.5, 3, 6, 12.5, 25, \text{ and } 50\%$) during each daily session, whereas the flankers' contrast ($C_m = 30\%$) was held fixed throughout the experiment. We used a single number of flankers in each of experimental session.

D. Experiment 2

We measured the threshold for contrast discrimination for a foveally centered GS target masked by a foveally centered chain of 1 to 11 GSs [1 pedestal at the target location and 2–10 lateral flankers; Fig. 1(b)]. We used just the parallel (and not the collinear) configuration. The lateral flankers and the pedestal had the same contrast: either the threshold for contrast discrimination (observer EC, 6.5%; VR, 3%; AR, 4.5%) or a suprathreshold contrast (30%). The length of the chain varied from 1 (just the pedestal) to 11 during each session, whereas the GSs' contrast was held fixed throughout the experiment.

E. Experimental Procedure

A temporal two-alternative forced-choice procedure was used. Each trial consisted of two stimuli presented sequentially, only one of which contained a target. Before each trial a small fixation circle was presented at the center of the screen. The observers, when ready, pressed a key to activate the trial sequence, which consisted of (1) a no-stimulus interval (500 ms), (2) a stimulus presentation (90 ms), (3) a no-stimulus interval (1,000 ms), and (4) a second presentation (90 ms). The observers' task was to determine which of the stimuli contained the target. The decision was indicated by pressing a key, and an auditory feedback was given for an incorrect response. A staircase method⁸ was used to determine the contrast threshold at a level of 79% correct³⁰: The contrast of the target was increased by 0.1 log unit after every incorrect response and decreased by 0.1 log unit after three consecutive correct responses. A block was terminated after eight reversals of the staircase procedure, and the mean of the last six reversal points in log units was used as a threshold estimate. A session lasted approximately 30 min. Observers usually participated in two successive sessions on each day that they came to the lab, with a 20-min break between the sessions.

F. Observers

Thirteen observers participated in the experiments. All observers were with normal or corrected-to-normal vision and were naïve as to the purpose of the experiments. Seven observers participated in Experiment 1. Three (YS, MR, and SH) with the parallel configuration (YS and MR with 0, 2, and 4 lateral masks and SH with 0 and

2 lateral masks). Three (ZE, AS, and YO) performed the experiment with the collinear configurations (0, 2, and 4 lateral masks) and one observer (OH) with 0, 4, and 8 lateral masks.

Six observers participated in Experiment 2. Three performed the task with low-contrast masks (EC, VR, and AR), and three performed the task with high-contrast masks (GG, GL, and IB).

3. RESULTS

Contrast-discrimination thresholds for a GS target were measured as a function of the pedestal contrast C_p . In Fig. 2 we compared the TvC curves that were obtained in the presence of two high-contrast lateral flankers with those measured without the flankers. We found that the same pattern of lateral masks enhanced the target detection with the low-contrast pedestals and strongly suppressed the discrimination of a range of intermediate pedestal contrasts (pedestal contrast $<$ lateral-flanker contrast). The enhancement was maximal, a 20% decrease in the contrast-detection threshold, for zero pedestal contrasts near zero. The suppression increased with the pedestal contrast, reaching its maximum, a 150–200% increase in the threshold for contrast discrimination, for pedestals having contrasts of $1.3C_{th}$ (C_{th} , threshold for detection). The configuration had an interesting effect on the thresholds for discrimination. Collinear flankers strongly suppressed the discrimination of intermediate pedestal contrasts and had a small suppressive effect on the contrast-discrimination thresholds with high-contrast pedestals ($C_p \geq 0.8C_m$). In contrast, parallel lateral flankers (the parallel configuration) were found to decrease (by 20%) the contrast-discrimination thresholds for pedestals having a contrast \geq the mask contrast.

To test the linear-summation hypothesis, we assumed that the lateral flankers contributed a fixed linear input ($\Delta C = 8\% = 1.5C_{th}$) to the target location. Under the linear-summation hypothesis, the thresholds measured in the presence of the lateral masks are predicted to be $T_m(C) = T_0(C + \Delta C)$, where $T_0(C)$ is the TvC function obtained without the flankers. As can be seen from Fig. 3, $T_m(C)$ does not fit the TvC curves that we measured in the presence of the flankers (the “shifted” versus the “CD+flanks” curves in Fig. 3). The amount of ΔC we chose ($1.5C_{th}$) can explain the thresholds obtained with both the parallel and the collinear lateral flankers for low-contrast pedestals. However, it fails to predict the thresholds that were found with higher pedestal contrast. With the parallel configuration, for high-contrast pedestals ($4\text{--}9.5C_{th}$), the linear-summation hypothesis predicts 40–5% increase (respectively) in the threshold for discrimination, whereas the actual data show 40–10% decrease (respectively) in the thresholds. With the collinear configuration, the decreased detection threshold found with the lateral flankers can be achieved by assuming that the lateral flankers add $\Delta C = 8\%$ contrast to the target location. However, this small amount of added contrast cannot explain the high thresholds found with pedestals of $1\text{--}2.5C_{th}$ (5–12% contrast). Thus for both configurations our results demonstrate that a linear-

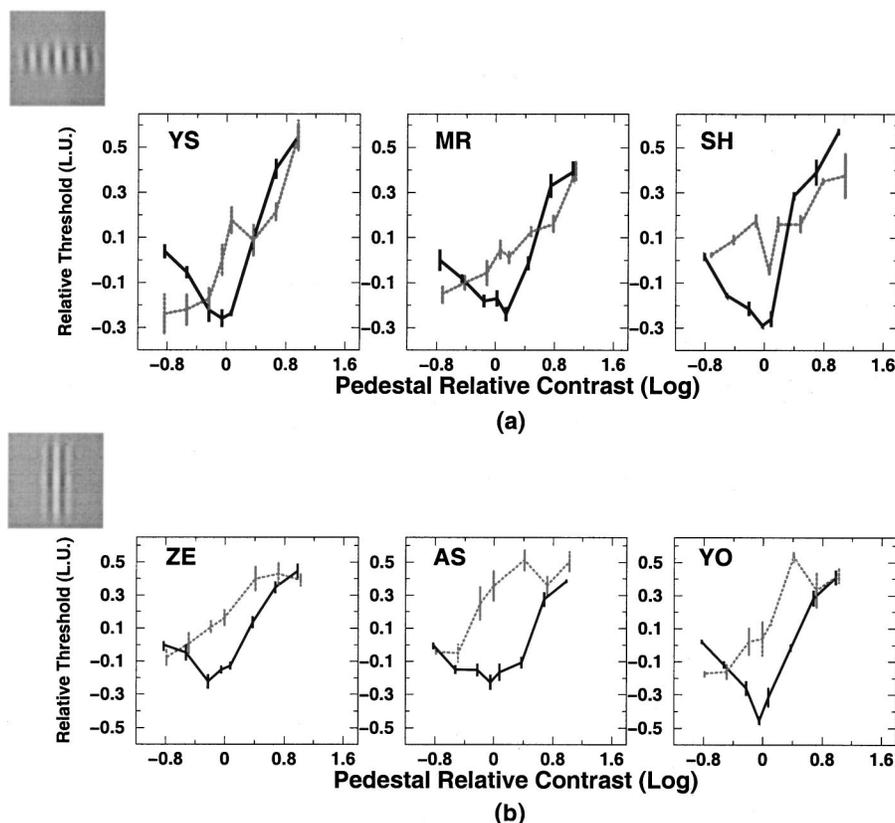


Fig. 2. TvC curves that were obtained with (dotted curves), and without (solid curves) two flankers, for (a) the parallel and (b) the collinear configurations. Each datum point is the average of 3–5 threshold estimates that were taken on different days. Both the discrimination thresholds and the pedestal contrasts were normalized to the observer's average threshold for detection. The flankers acted to decrease the threshold for contrast discrimination and to increase greatly the threshold for discrimination of a range of intermediate target contrasts. High-contrast parallel flankers enhanced the discrimination with high-contrast pedestals. Note that the thresholds for discriminating a contrast C , $[C_{th}(C)]$, were normalized by the threshold for detection $C_{th}(0)$. $\text{Log}[C_{th}(C)/C_{th}(0)] = 0 \Rightarrow C_{th}(C) = C_{th}(0)$; L.U. stands for log unit.

summation process cannot explain the effects of the proximal flankers on the contrast-discrimination thresholds.

The refutation of the linear spatial-summation hypothesis suggested the lateral interaction as the main source of the above findings. To explore the nature of these interactions, we compared the TvC curves that we measured for a GS target in the context of 0, 2, 4, and 8 lateral flankers. We found that short chains of flankers increased the thresholds for contrast discrimination for pedestal contrasts less than the flankers' contrast. Increasing the number of the flankers reversed this effect. With two parallel lateral masks (the parallel configuration) the maximum suppression was a 150% increase in the threshold for contrast discrimination. Adding two more flankers at 4λ (0.6°) distance from the target canceled this suppression [Fig. 4(a)]. With the collinear configuration, further increasing the length of the chain of masks led to decreased thresholds, although the observers differed in the size of the reversing effect. The effect of an increased number of lateral flankers was more dominant with the high-contrast pedestals, where for two of the observers the suppressive effect measured with short chains of flankers turned into a facilitative effect with the longer chains [Fig. 4(b)]. Note that this finding provides more evidence to disprove the linear spatial-summation hypothesis, which predicts that increasing the number of

flankers should lead to an increased leftward shift of the contrast-discrimination function.

To explore further the unmasking effect found with an increased number of masks, we conducted Experiment 2. In this experiment we measured the contrast-discrimination thresholds for a foveal GS in the context of a chain of parallel flankers. The pedestal and the flankers had the same contrast. We tested two contrast conditions: low contrast (3–6.5%, the threshold for detection depending on the subject) and high contrast (30%). We varied the length of the chain during each daily session. With both contrasts we found a nontrivial, nonmonotonic relationship between the discrimination thresholds and the number of simultaneously presented lateral flankers (Fig. 5). For all three observers the high-contrast pedestal increased the threshold for detection by an average amount of 58% (0.20 ± 0.08 , log units \pm standard error (SE), averaged across three observers). Adding two lateral flankers ($N = 3$ masks) was found to increase further the discrimination thresholds up to twice the threshold for detection. However, as the chain length increased ($3 < N < 9$), the thresholds decreased, showing an oscillatory behavior. The maximum threshold peaks (twice the threshold for detection) were measured with 3 and 9 masks. The minimum contrast-discrimination thresholds ($1.3C_{th}$) were measured in the presence of 7 and 11

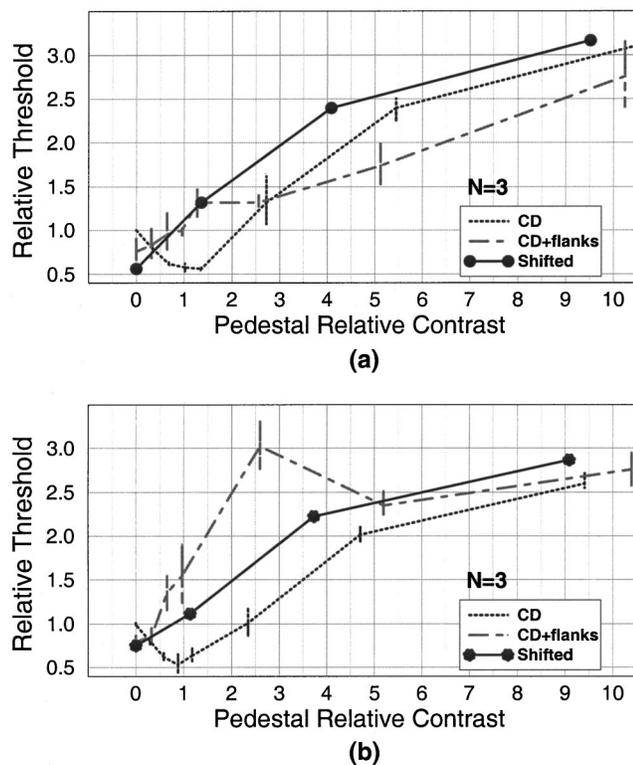


Fig. 3. Average (across $N = 3$ subjects) TvC curves that were obtained with and without two lateral flankers for (a) the parallel and (b) the collinear configurations. Assuming that the flankers contributed the same constant input (ΔC) to each pedestal contrast (C_p), we replotted the thresholds for contrast discrimination obtained without the flankers versus the $C_p + \Delta C$ and obtained leftward-shifted TvC curves. The thresholds and the pedestal contrasts were normalized by the average threshold for detection ($C_{th} = 4.6\%$ with the parallel configuration; $C_{th} = 5.3\%$ with the collinear configuration). To fit the thresholds measured with the flankers for low-contrast pedestals, we chose ΔC to be $1.5C_{th}$. As can be seen in the graphs, the constant spatial-summation assumption (shifted curves) fails in predicting the psychophysical data (CD+flanks curves).

masks. The average difference between any two successive peak-threshold points (either minima or maxima points), was 0.21 ± 0.006 , log units \pm SE. A similar nonmonotonic effect was found when both the pedestal and the flankers were at a contrast as low as the threshold for contrast detection. For all three observers the low-contrast pedestal decreased the threshold for detection by an average amount of 50% (0.3 ± 0.05 , log unit \pm SE; $N = 3$). Adding 2–4 lateral flankers canceled this enhancement (the thresholds returned to the baseline). As the chain length increased, the enhancement increased again, reaching its minima ($0.58C_{th}$) with 10 lateral flankers ($N = 11$ masks). The average difference between any two successive peak-threshold points (either minima or maxima points) was 0.20 ± 0.04 , log unit \pm SE, similar to what was found with the high-contrast masks.

4. DISCUSSION

To explore the circuitry of local networks at early stages of visual processing, we measured the effect of short and

long chains of GSs on the thresholds for contrast discrimination for a range of pedestal contrasts [Experiment 1; Fig. 1(a)]. This paradigm enabled us to study the dependency of lateral interactions on the response level and the distribution of activity within the network of filters that are tuned to the same orientation and to different spatial locations. As a first step toward this goal, we tested the alternative hypothesis that at short ranges (2λ spacing), spatial integration is mediated merely by linear spatial summation (and not by lateral interactions). Using contrast-discrimination tasks in the presence of lateral flankers, we found that the same lateral masks can either facilitate or suppress the thresholds for contrast discrimination at the target location, depending on the target contrast. We reasoned that adding the lateral flankers may change the input to the filter at the target location either by spatial linear summation (an additive or a subtractive input, depending on the size of the receptive field), or through excitatory or inhibitory lateral interactions. Our results rule out the possibility of a linear spatial summation effect (Fig. 3). The decreased thresholds at the detection tasks with the lateral flankers implies a small lateral input ($I_l < 2C_{th}$), whereas the big increase in the thresholds for discriminating intermediate target contrasts requires a high additive lateral input ($I_l \geq 5C_{th}$). Thus our results suggest that the main influence of the flankers is maintained by contrast-dependent interactions: excitatory-dominated interactions from the high-contrast flankers into the lower-contrast targets, which are more pronounced with the collinear configuration,^{5–7,31–33} and inhibitory-dominated interactions between the high-contrast flankers and the high-contrast target, which are more dominant at the orthogonal axis.^{5,33} Note that excitatory-dominated interactions may act to increase the input to the local node, but, as is suggested by contrast-masking experiments, the increased input may act to decrease the slope of the response function of the local node and thus to increase the threshold for contrast discrimination of a range of pedestal contrast. On the other hand, inhibitory-dominated interactions may decrease the input to the local node and thus increase the slope of the response function of the local node, yielding decreased thresholds (as was found in this study).

Excitatory and inhibitory lateral interactions between high-contrast flankers and low- or high-contrast targets were suggested by several independent psychophysical studies. Both collinearly and parallelly aligned high-contrast GSs were found to enhance the detectability of a similar low-contrast GS target when the distance between them was 2λ or more,^{5–9,17,31,34–36} suggesting excitatory lateral interactions. Lateral inhibitions between high-contrast stimuli were suggested to be at the base of the pop-out phenomenon^{37,38} and of the masking and unmasking effects found with contrast detection and contrast discrimination tasks in the context of different numbers of maskers or different sizes of surroundings.^{5,18} Contrast-discrimination thresholds in the presence of flankers were measured in the periphery,³⁹ where only suppressive effects were found. These effects were pedestal-contrast dependent, as were the effects found here, and were explained by nonlinear inhibitory pro-

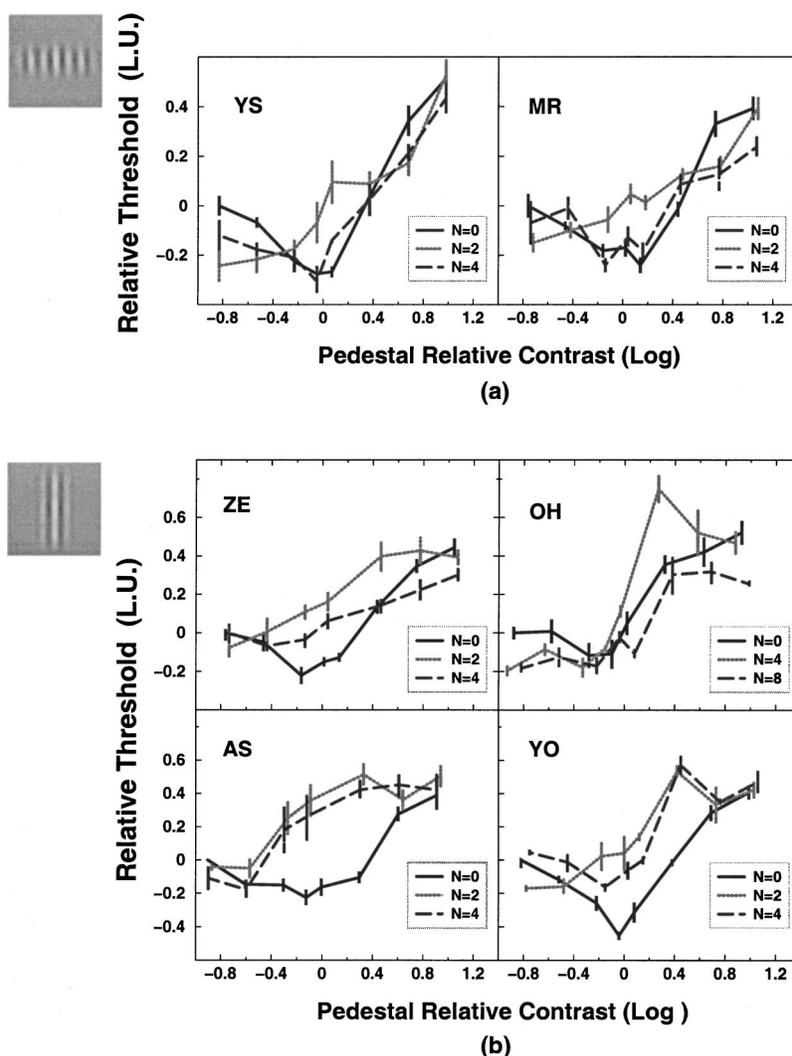


Fig. 4. Thresholds for contrast discrimination for a GS target masked by a pedestal of contrast C_p in the context of 0, 2, 4, and 8 lateral flankers. The thresholds and the pedestal contrasts were normalized by the threshold for detection (C_{th} that was measured separately for each observer). Short chains of flankers increased the thresholds for contrast discrimination for target contrasts less than the flankers' contrast. (a) With the parallel configuration, doubling the number of the flankers reversed this effect (observers YS and MR). (b) With the collinear configuration, the observers (ZE, OH, AS, and YO) differed in the size of the reversing effect. At the range of high-contrast pedestals, the suppressive effect found with short chains turned into a facilitative effect, with longer chains. Note that for observer OH the suppressive effect of the flankers occurred with four flankers and turned into facilitation with eight flankers. The influence of the configuration and practice on effects similar to this have been discussed elsewhere.⁵

cesses within a single neuron. Contrast-dependent influences were also found in apparent-contrast⁴⁰⁻⁴³ and rivalry³³ experiments. Recently it was proposed that the perceptual grouping phenomena can be explained by using neural networks with feedback and recurrent contrast-dependent interactions.⁴⁴ Such interactions might serve as the basis for creating dynamic, contrast-dependent receptive fields, a phenomenon reported in Ref. 45.

Interestingly, the notion of contrast-dependent interaction was also suggested by several physiological studies,⁴⁶⁻⁴⁹ showing that the responses of simple and complex cells in cats' and monkeys' cortices to a small patch of GS are changed in the presence of similar lateral masks. When the surrounding contrast was held fixed, the contrast at the target location was found to regulate the size and the sign of the effect.

The role of lateral interactions among the local filters was considered by several models for spatial integration. The decreased slope of the response-versus-contrast function, as measured with increased pedestal contrasts, and the contextual influence on both the thresholds for contrast discrimination and the shape of the response-versus-contrast functions, were suggested to reflect excitatory and inhibitory interactions that shape the cooperative neuronal activity of the local filters. One class of models suggests a feed-forward process and a normalization (inhibitory) process by a pool of nearby local filters, where the strength of inhibition is proposed to depend on the contrast of the input to the filters/cells (a contrast-gain-control process).^{8,18,23-25} Other models suggest a feedback process or a local circuit approach with use of recurrent networks.^{5,26,28,29,44} These models suggest a divisive or a subtractive inhibitory process that

depends on the responses of the different nodes in the network. While the feed-forward models succeed in giving a mathematical description to a wide range of results from masking experiments,^{18,24,25,50} they do not provide a whole framework that can explain the contrast dependency of the interactions. On the other hand, recurrent networks were demonstrated to be capable of accounting for the contrast-dependent influences. For example, in Ref. 29 Somers *et al.* suggested a local circuit module for spatial integration, where a local population of excitatory neurons recurrently interacts with a local population of inhibitory neurons, both populations getting both excitatory thalamo-cortical and long-range intracortical inputs. They assumed that there is a population-level bias among inhibitory neurons to have a higher-gain contrast threshold and a higher threshold than the excitatory cells. That is, the inhibition starts at a higher input than the excitation, but it increases faster with increased inputs. Depending on the activity level of the local inhibitory population, the lateral interactions can add just the needed amount of input so that the inhibitory population will exceed its threshold and enter into action. Note that in feed-forward models, the normalization process takes place before the long-range spatial integration and thus does not influence directly the normalization process.

Evidence supporting the recurrent-network model was found in two of our experiments. We showed that the thresholds for a range of pedestal contrasts were greatly increased when measured in the presence of two lateral flankers (four flankers, in the case of observer SH). However, when we further increased the number of lateral flankers, the effect reversed, and the thresholds measured with the increased number of flankers were similar

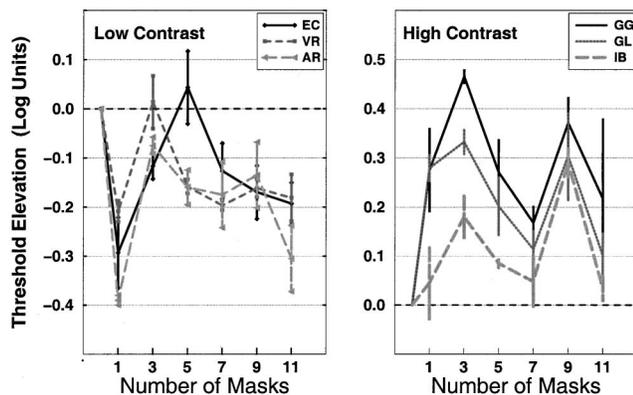


Fig. 5. Chain effect. Dependence of the contrast-discrimination threshold on the number of the masks in the chain for observers EC, VR, AR, GG, GL, and IB. The number of masks reflects the total number of the pedestal and the lateral flankers in the chain. The threshold elevation was computed relative to the threshold for detecting an isolated target. Each datum point is the average of three measurements. The pedestal and the flankers had the same contrast, either low (near the threshold for detection, of each observer) or high (near six times C_{th}). All observers show a similar nonmonotonic dependence of the discrimination threshold on the number of the masks. For high-contrast chains, the threshold first increases and then decreases and increases again. For low-contrast chains, the effect was with a reverse phase. The difference between the maximal and the minimal thresholds for CD was between 0.2 and 0.3 log unit.

to those measured for an isolated target. Thus the flankers at the short chains of flankers acted to increase the threshold for discrimination of a given pedestal contrast but had no such effect in the presence of more distal flankers. Consistent with this finding, the thresholds for contrast discrimination of a high-contrast GS target were found to have an oscillatory behavior, depending on the number of the simultaneously presented lateral flankers (Fig. 5). When the number of flankers increased, the threshold usually increased (reaching a maximum suppression) and then decreased (reaching a minimal suppression), and then increased and decreased again. Note that similar oscillatory behavior was found in our previous work,⁵ where we measured the threshold for contrast detection in the presence of different-length chains of high-contrast GSs.

How can the different approaches to spatial integration explain these findings? An obvious explanation for the above findings is that the oscillatory behavior reflects the activity of a linear feed-forward second-stage filter with both excitatory and inhibitory subregions.¹⁷ Assuming such a filter, the influence of the maskers on the target visibility or on the target discriminability should be the sum of the individual influences of the maskers at different target-to-mask distances that can be estimated by lateral masking data.⁶ However, lateral masking experiments give no indication for long-range inhibitory influences, as reported by Polat and Sagi⁶ for contrast detection and confirmed by us (preliminary data, not shown) for contrast discrimination. An alternative explanation for our findings suggests the existence of recurrent networks in the visual cortex. In such networks, the input to a local node depends on both the local input from earlier processing levels and the recurrent lateral input from its neighbors. A mutual inhibition process between two lateral nodes^{5,51} may change the response of these nodes and thus change their input to the target location and the threshold for discrimination (e.g., inhibition and disinhibition process). An example for a recurrent spatial-integration model can be found in Ref. 5, where the proposed model successfully accounted for human performance in detection experiments in the presence of chains of flankers. In the present study the oscillatory behavior of the threshold for contrast discrimination was also found with a low-contrast target and flankers (Experiment 2), suggesting that inhibitory processes may start at close to the thresholds for detection.

In summary, our results refute linear spatial summation as the main source of the short-range contextual influences found in the current study. Our data support the response gain-control notion^{48,52} and suggest that the contextual spatial influences on thresholds for contrast discrimination are the result of the dynamics of recurrent networks in the neocortex,⁵ with an important role assigned to the recurrent, activity-dependent lateral interactions.

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REFERENCES

1. D. H. Hubel and T. N. Wiesel, "Shape and arrangement of columns in the cat's striate cortex," *J. Physiol. (London)* **165**, 559–568 (1963).
2. F. Campbell and J. Robson, "Application of Fourier analysis to the visibility of gratings," *J. Physiol. (London)* **197**, 551–566 (1968).
3. C. Blakemore and F. Campbell, "On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images," *J. Physiol. (London)* **203**, 237–260 (1969).
4. R. L. DeValois and K. K. DeValois, *Spatial Vision* (Oxford U. Press, New York, 1990).
5. Y. Adini, D. Sagi, and M. Tsodyks, "Excitatory–inhibitory network in the visual cortex, psychophysical evidence," *Proc. Natl. Acad. Sci. USA* **94**, 10426–10431 (1997).
6. U. Polat and D. Sagi, "Lateral interaction between spatial channels: suppression and facilitation revealed by lateral masking experiments," *Vision Res.* **33**, 993–999 (1993).
7. U. Polat and D. Sagi, "The architecture of perceptual spatial interactions," *Vision Res.* **34**, 73–78 (1994).
8. B. Zenger and D. Sagi, "Isolating excitatory and inhibitory non-linear spatial interactions involved in contrast detection," *Vision Res.* **36**, 2497–2513 (1996).
9. J. Solomon, A. Watson, and M. Morgan, "Transducer model produces facilitation from opposite-sign flanks," *Vision Res.* **39**, 987–992 (1999).
10. M. K. Kapadia, M. Ito, D. C. Gilbert, and G. Westheimer, "Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in V1 of alert monkeys," *Neuron* **15**, 843–856 (1995).
11. B. Dresp, "Dynamic characteristics of spatial mechanisms coding contour structures," *Spatial Vision* **12**, 129–142 (1999).
12. L. Spillmann, A. Ransom-Hogg, and R. Oehler, "A comparison of perceptive and receptive fields in man and monkey," *Hum. Neurobiol.* **6**, 51–62 (1987).
13. D. Gabor, "Theory of communication," *J. Inst. Electr. Eng. (London)* **93**, 429–457 (1946).
14. A. Watson, H. Barlow, and J. Robson, "What does the eye see best?" *Nature* **302**, 419–422 (1982).
15. J. G. Daugman, "Uncertainty relation for resolution in space, spatial frequency, and orientation optimized by two-dimensional visual cortical filters," *J. Opt. Soc. Am. A* **2**, 1160–1169 (1985).
16. U. Polat and C. Tyler, "What pattern the eye sees best," *Vision Res.* **39**, 887–895 (1999).
17. J. Solomon and M. Morgan, "Facilitation from collinear flanks is canceled by noncollinear flanks," *Vision Res.* **40**, 279–286 (2000).
18. C. Yu and D. Levi, "Surround modulation in human vision unmasked by masking experiments," *Nat. Neurosci.* **3**, 724–728 (2000).
19. C. Chen and C. Tyler, "Spatial pattern summation is phase-insensitive in the fovea but not in the periphery," *Spatial Vision* **12**, 267–285 (1999).
20. L. Olzak and J. Thomas, "Neural recoding in human pattern vision: model and mechanisms," *Vision Res.* **39**, 231–256 (1999).
21. N. Graham and A. Sutter, "Spatial summation in simple (Fourier) and complex (non-Fourier) texture channels," *Vision Res.* **38**, 231–257 (1998).
22. N. Graham and A. Sutter, "Normalization: contrast-gain control in simple (Fourier) and complex (non-Fourier) pathways of pattern vision," *Vision Res.* **40**, 2737–2761 (2000).
23. J. Ross and H. D. Speed, "Contrast adaptation and contrast masking in human vision," *Proc. R. Soc. London* **246**, 61–69 (1991).
24. J. Foley, "Human luminance pattern-vision mechanisms: masking experiments require a new model," *J. Opt. Soc. Am. A* **11**, 1710–1719 (1994).
25. J. Foley and C. Chen, "Analysis of the effect of pattern adaptation on pattern pedestal effects: a two process model," *Vision Res.* **37**, 2779–2788 (1997).
26. D. Heeger, "Normalization of cell in cat striate cortex," *J. Neurosci.* **9**, 181–197 (1992).
27. D. J. Heeger, E. P. Simoncelli, and J. A. Movshon, "Computational models of cortical visual processing," *Proc. Natl. Acad. Sci. USA* **93**, 623–627 (1996).
28. M. Carandini and D. Heeger, "Summation and division by neurons in primate visual cortex," *Science* **264**, 1333–1336 (1994).
29. D. Somers, E. Todorov, A. Siapas, L. Toth, D. Kim, and M. Sur, "A local circuit approach to understanding integration of long-range inputs in primary visual cortex," *Cerebral Cortex* **8**, 204–217 (1998).
30. H. Levitt, "Transformed up–down methods in psychoacoustics," *J. Acoust. Soc. Am.* **49**, 467–477 (1971).
31. U. Polat and D. Sagi, "Spatial interactions in human vision: from near to far via experience-dependent cascades of connections," *Proc. Natl. Acad. Sci. USA* **91**, 1206–1209 (1994).
32. U. Polat and A. M. Norcia, "Neurophysiological evidence for contrast dependent long range facilitation and suppression in the human visual cortex," *Vision Res.* **36**, 2099–2109 (1996).
33. Y. Bonnef and D. Sagi, "Configuration saliency revealed in short duration binocular rivalry," *Vision Res.* **39**, 271–281 (1999).
34. C. Williams and R. Hess, "Relationship between facilitation at threshold and suprathreshold contour integration," *J. Opt. Soc. Am. A* **15**, 2046–2051 (1998).
35. E. Freeman, D. Sagi, and J. Driver, "Gabor contrast sensitivity depends on task relevance of collinear flankers," *Perception* **29** (Suppl.), 62 (2000).
36. R. Woods, A. Nugent, and E. Peli, "Bandwidth affects visual lateral interactions," *Invest. Ophthalmol. Visual Sci. Suppl.* **14**, S803 (2000).
37. D. Sagi and B. Julesz, "Short-range limitation on detection of feature differences," *Spatial Vision* **2**, 39–49 (1987).
38. M. Stemmler, M. Usher, and E. Niebur, "Lateral interactions in primary visual cortex: a model bridging physiology and psychophysics," *Science* **269**, 1877–1880 (1995).
39. B. Zenger and C. Koch, "Divisive and subtractive mask effects: linking psychophysics and biophysics," in *Advances in Neural Information Processing Systems*, T. K. Leen, T. G. Dietterich, and V. Tresp, eds. (MIT Press, Cambridge, Mass., 2001), Vol. 13, pp. 915–921.
40. D. Sagi and S. Hochstein, "Lateral inhibition between spatially adjacent spatial frequency channels?" *Percept. Psychophys.* **37**, 315–322 (1985).
41. C. Chubb, G. Sperling, and J. Solomon, "Texture interactions determine perceived contrast," *Proc. Natl. Acad. Sci. USA* **86**, 9631–9635 (1989).
42. M. Cannon and S. Fullenkamp, "A model for inhibitory lateral interaction effects in perceived contrast," *Vision Res.* **36**, 1115–1125 (1996).
43. R. J. Snowden and S. T. Hammett, "The effect of surround contrast on contrast thresholds, perceived contrast and contrast discrimination," *Vision Res.* **38**, 1935–1945 (1998).
44. S. Grossberg and R. Raizada, "Contrast-sensitive perceptual grouping and object-based attention in the laminar circuits of primary visual cortex," *Vision Res.* **40**, 1413–1432 (2000).
45. M. Sceniak, D. Ringach, M. Hawken, and R. Shapley, "Contrast effect on spatial summation by macaque V1 neurons," *Nat. Neurosci.* **2**, 733–739 (1999).

46. L. J. Toth, S. Rao, D. Kim, D. Somers, and M. Sur, "Sub-threshold facilitation and suppression in primary visual cortex revealed by intrinsic signal imaging," *Proc. Natl. Acad. Sci. USA* **93**, 9869–9874 (1996).
47. B. Roig, J. Kabara, R. Snider, and A. Bonds, "Non-uniform influence from stimuli outside the classical receptive field on gain control of cat visual cortical neurons," *Invest. Ophthalmol. Visual Sci. (Suppl.)* **37**, S2198 (1996).
48. J. B. Levitt and J. S. Lund, "Contrast dependence of contextual effects in primate visual cortex," *Nature (London)* **387**, 73–76 (1997).
49. U. Polat, K. Mizobe, M. W. Pettet, T. Kasamatsu, and A. M. Norcia, "Collinear stimuli regulate visual responses depending on cell's contrast threshold," *Nature* **391**, 580–584 (1998).
50. L. Itti, C. Koch, and J. Braun, "Revisiting spatial vision: towards a unifying model," *J. Opt. Soc. Am. A* **17**, 1899–1917 (2000).
51. H. B. Barlow, "A theory about the functional role and synaptic mechanism of visual after-effects," in *Vision: Coding and Efficiency*, C. Blakemore, ed. (Cambridge U. Press, Cambridge, UK, 1990), Chap. 32, pp. 363–375.
52. F. Sengpiel, R. J. Baddeley, T. Freeman, R. Harrad, and C. Blackmore, "Different mechanisms underlie three inhibitory phenomena in cat area 17," *Vision Res.* **38**, 2067–2080 (1998).