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Flanker effects in peripheral contrast discrimination—psychophysics and modeling

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Abstract

We studied lateral interactions in the periphery by measuring how contrast discrimination of a peripheral Gabor patch is affected by flankers. In the psychophysical experiments, two Gabor targets appeared simultaneously to the left and right of fixation (4° eccentricity). Observers reported which contrast was higher (spatial 2-alternative-forced-choice). In different conditions, Gabor flankers of different orientation, phase, and contrast were present above and below the two targets, at a distance of three times the spatial Gabor period. The data show that *collinear flanks* impair discrimination performance for low pedestal contrasts but have no effect for high pedestal contrasts. The transition between these two result patterns occurs typically at a pedestal contrast which is similar to the flanker contrast. For *orthogonal flanks*, we find facilitation at low pedestal contrasts, and suppression at intermediate contrasts. We account for this complex interaction pattern by a model that assumes that flankers can provide additive input to the target unit, and that they further contribute to the target's gain control, but only in a limited range of pedestal contrasts; once the target contrast exceeds a critical value, inhibition becomes subtractive rather than divisive. We further make specific propositions on how this model could be implemented at the neuronal level and show that a simple integrate and fire unit that receives time-modulated inhibition behaves in a fashion strikingly similar to the model inferred from the psychophysical data.

Keywords: Lateral inhibition; Gain control; Attention; Contrast discrimination; Contrast detection; Masking; Subtractive inhibition; Divisive inhibition

1. Introduction

Visual images of Gabor patches are thought to excite a small and specific subset of neurons in the primary visual cortex and beyond. By measuring psychophysically in humans the contrast detection and discrimination thresholds of peripheral Gabor targets, one can estimate the sensitivity of this subset of neurons. If additional Gabor patches (masks) are presented, they can stimulate the target neurons either directly and/or indirectly (by first stimulating mask units, which then stimulate target units). By measuring the effects of these masks on target detection, spatial interactions between different neuronal populations can be probed (Polat & Sagi, 1993; Kapadia, Ito, Gilbert, & Westheimer, 1995) The interpretation of psychophysical thresholds in terms of activities of units and spatial interactions between them is, of course, model-dependent. Current models usually describe the response behavior of one or several neuronal units, and their interactions. Two stimuli are typically considered discriminable if some constant—often assumed to be 1 for simplicity—response difference is obtained in the decision unit, or one of several decision units (Foley, 1994; Snowden & Hammet, 1998; Solomon & Morgan, 2000).

Results of psychophysical masking experiments often cannot be accounted for by assuming only a simple within-receptive field summation of target and mask. Instead, these results indicate the existence of a network with a highly configuration-specific pattern of excitatory (Polat & Sagi, 1993; Kapadia et al., 1995) and inhibitory (Campbell & Kulikowski, 1966; Legge &

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Foley, 1980; Ross & Speed, 1991) spatial interactions. Facilitatory interactions might arise from long-range connections in primary visual cortex (Kapadia et al., 1995) and can be modeled as additive (Zenger & Sagi, 1996), whereas inhibitory interactions can be attributed to short-range interactions (Bonds, 1989; Van Essen et al., 1989; Levitt & Lund, 1997; Das & Gilbert, 1999) and are commonly modeled as divisive (Foley, 1994; Zenger & Sagi, 1996; Snowden & Hammet, 1998; Lee, Itti, Koch, & Braun, 1999)

While most psychophysical studies have focused on detection of foveal targets (Polat & Sagi, 1993, 1994; Morgan & Dresp, 1995; Zenger & Sagi, 1996; Solomon & Morgan, 2000) we studied peripheral targets. Differences between foveal and peripheral interactions have previously been reported; for example, the flanker facilitation found in the fovea (Polat & Sagi, 1994) is not observed in the periphery (Williams & Hess, 1998), and surround inhibition is stronger in the periphery than in the fovea (Xing & Heeger, 2000). A second difference to many other studies is that we measured not only contrast detection thresholds but also discrimination thresholds. In a typical contrast discrimination task, observers have to discriminate patches of contrast c and $c + \Delta c$. The curve that plots discrimination thresholds Δc as a function of the pedestal contrast, c, is often referred to as TvC (threshold vs. contrast) function.

Similar to the conditions, which we investigated here, Wilkinson, Wilson, and Ellemberg (1997) have measured contrast increment thresholds for a peripheral Gabor patch presented in a string of Gabor patches. They found that increment thresholds were higher when flanks were present, as opposed to when only a single Gabor target was presented in isolation. However, in this study, discrimination thresholds were measured only for one fixed pedestal contrast. The goal of our study was to learn more about the nonlinear characteristics of the underlying spatial interactions by testing an extensive range of pedestal contrasts.

This rationale has been used before by Snowden and Hammet (1998), who have compared contrast discrimination, contrast detection and apparent contrast measurements in both foveal and peripheral vision. Their data suggest that the surround has considerable suppressive effects on discrimination performance but that the data can be accounted for in a parsimonious fashion by assuming that the surround provides divisive inhibition to the target (at least for the data obtained in the periphery), similar to the mechanism that has been suggested for foveal masking with oblique masks (Foley, 1994).

Other models, developed for foveal data, suggest that in other situations, surrounds may have also additive effects (Zenger & Sagi, 1996) or that the surround has a subtractive effect on the divisive inhibition (Yu & Levi, 2000). Though all these models differ slightly in the assumed mechanisms, we would like to point out that in any model in which decision relies on a single mechanism (target unit), most of the effects expected from a surround of a specific contrast and configuration (additive, divisive, subtractive, etc.) would not change the fact that the contrast–response function of the target unit is sigmoidal. Hence, these models predict dipper-shaped TvC functions.

Here, we report a new effect that is inconsistent with this prediction; we find that, in the presence of collinear flanks, contrast discrimination thresholds first decrease with increasing pedestal contrast, then increase (like in the classical dipper function), then decrease again, and finally often increase again, resulting in a W-shaped curve. To account for these data, we propose a model which assumes that flankers provide divisive inhibition to the target unit for low target contrasts, but provide subtractive inhibition for higher target contrasts. The transition between divisive and subtractive inhibition occurs at a target contrast similar to the flanker contrast. We further make specific suggestions on how the proposed transition from divisive to subtractive inhibition might be implemented at the neuronal level.

2. General methods

2.1. Apparatus

Experiments were controlled by an O2 Silicon Graphics workstation, and stimuli were displayed on a 19 inch raster monitor. Mean luminance, L_m, was set to 40 cd/m^2. We used color-bit stealing to increase the number of gray levels that can be displayed (Tyler, 1997). A gamma correction ensured linearity of the gray levels.

2.2. Stimuli

Stimuli were Gabor patches. The luminance distribution $L(x, y)$ of a single patch as a function of spatial coordinates x and y is given by

$$L(x,y) = L_m + L_m C \cos(\omega[(x-x_0)\cos\theta + (y-y_0)\sin\theta] + \phi) \times \exp\left(-\frac{(x-x_0)^2 + (y-y_0)^2}{2\sigma^2}\right). \quad (1)$$

The location of the Gabor patch is described by (x_0, y_0), $\sigma = 0.18°$ is S.D. of the Gaussian envelope, $\omega = 4$ cpd is the spatial frequency of the grating, θ is its orientation, ϕ is its spatial phase, and C is the contrast of the Gabor patch (ranging between 0 and 1).

The task was a spatial 2AFC task. Two vertical Gabor patches were presented at 4° eccentricity left and right of fixation, and observers had to report which patch had the higher contrast. Pedestal contrast levels tested were 0%, 1%, 2%, 4%, 6%, 8%, 12%, 16%, 20%,

Fig. 1. Example stimulus. Observers fixated a white fixation cross. Two targets appeared at 4° eccentricity left and right of fixation. In the flanker conditions, Gabor patches of fixed contrast, here 40%, appeared above and below each target. Targets and flanks were presented simultaneously for 83 ms and were then replaced by a gray blank screen (i.e. there was no masking). Subjects had to indicate which central patch had the higher contrast (here the one on the right hand side).

30%, 40%, 50%, 60%, 70%, and 80%. In some conditions, the two probes were flanked by two Gabor patches, presented above and below the target (at a distance of 0.75°, i.e. three times the spatial period of the Gabor). No mask was used.

Flanker parameters were varied between conditions. Each of these conditions is described by a letter followed by two digits. The letter indicates the configuration of the flanker; in particular, we use P for vertical in-phase flankers (i.e. positive phase), N for vertical flankers that are 180° phase-shifted (negative phase), and O for orthogonal (i.e. horizontal) flanks. The two digits denote the flanker contrast. In-phase flanks of 40% contrast (as in Fig. 1) are, for example, denoted by P40. The absence of flankers is abbreviated with NON.

2.3. Procedure

After fixating a central fixation cross, observers initiated each trial by pressing the space bar on the computer keyboard. Two gray circular cues appeared for 180 ms to indicate the target location (to minimize spatial uncertainty). A blank stimulus of randomized length (500 ± 100 ms) was followed by an 83 ms stimulus presentation. Observers indicated their response ('left' or 'right') by specified keys. Auditory feedback was provided.

We used an adaptive 3:1 staircase, i.e. the contrast level of the target decreased after three consecutive correct responses (contrast level was divided by 1.1) and increased after each mistake (contrast level was multiplied by 1.1). This staircase converges at a level of 79.3% correct (Levitt, 1971). A block was ended after 20 contrast reversals, and the geometric mean of the reversals served as the threshold estimate (first two reversals were ignored). In conditions without flanks, only 14 reversals were required. Whenever the staircase procedure showed a ceiling effect (asking for producing contrasts above 100%), the data for this pedestal contrast in this condition were not considered, even if, on other days, valid threshold estimates were obtained, because considering only the 'good days' would have introduced a bias. For some observers, valid threshold estimates were obtained across the whole range tested (up to 80%); others sometimes did not obtain valid estimates for pedestal contrasts as low as 50%.

Each observer participated in 28 sessions. In the first five sessions, observers performed the no-flanker (NON) conditions. Then, each observer tested three different flank conditions for six sessions each. One observer group tested different flank contrasts (conditions P20, P40, and P70); the other observer group tested different configurations: P40, N40, and O40 (Fig. 2). The session order was systematic (condition 1, condition 2, condition 3, condition 1, and so on). In the last five sessions of the experiment, observers repeated again the no-flanker condition (NON).

2.4. Observers

Seven observers with normal or corrected-to-normal vision participated in the experiment. The observers were divided into two different groups, both containing observer BZ (an author) and three naïve observers who were unaware of the purpose of the experiment.

To reduce inter-observer variability, we first subtracted from each threshold measurement the observer's mean performance across all conditions (which we wanted to average) and all pedestal contrast levels, and only then computed the mean and S.E. across observers. Finally, the mean performance of all observers was added again, to retain information about absolute performance levels.

2.5. Modeling

The model suggested below has been implemented in C code. Error minimization was achieved by a multidi-

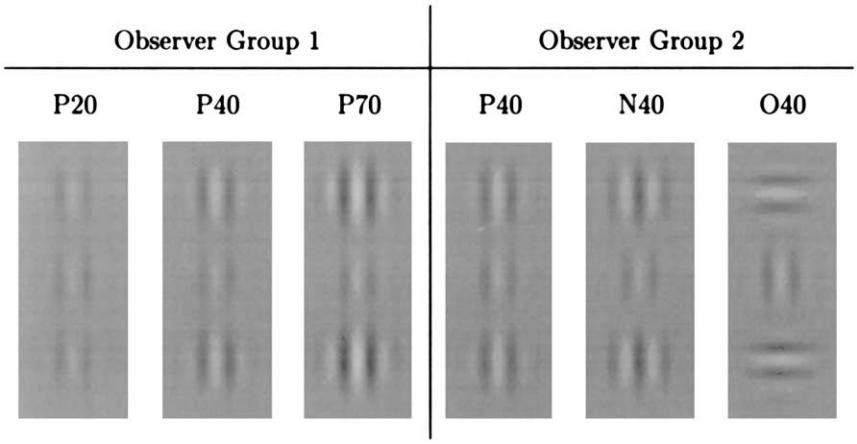

Fig. 2. For observer group 1, we varied the contrast of the collinear flanks between sessions (20%, 40% or 70%). For observer group 2, the flank contrast was always 40% and flanks were either collinear with target and of same phase (P40), collinear with target and of negative phase (N40), or orthogonal to the target (O40). All observers were tested in the no-mask (NON) condition.

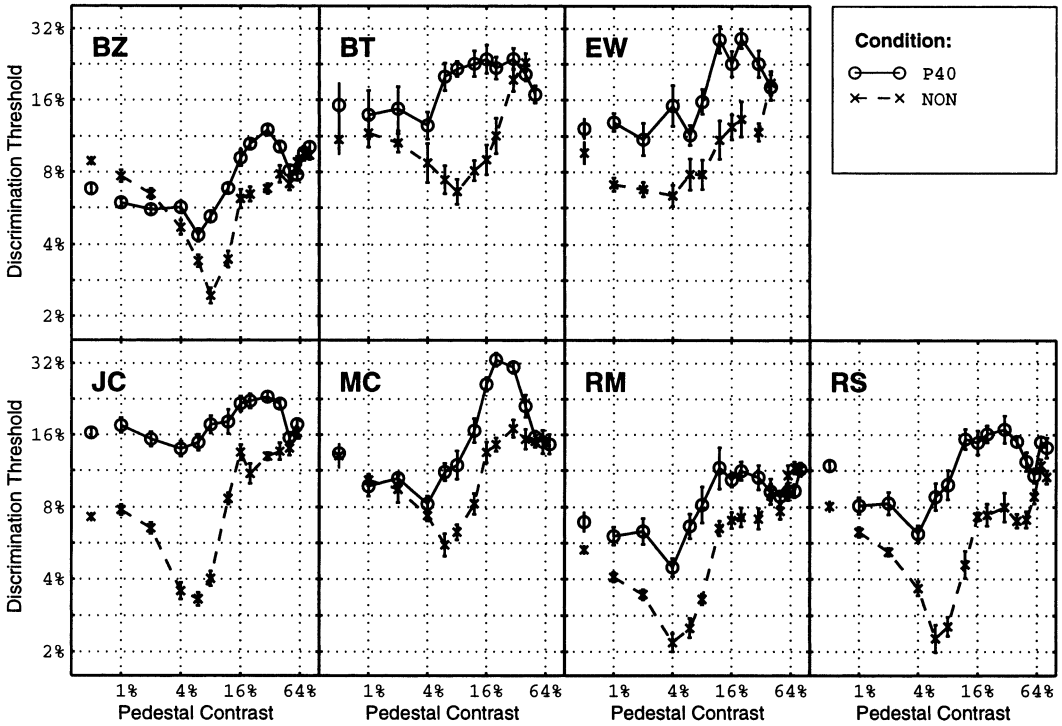

Fig. 3. Contrast discrimination thresholds of all observers for isolated targets (NON) and for targets with collinear in-phase flanks of 40% contrast (P40). Error bars represent the S.E.M. across sessions. Discrimination thresholds for isolated targets follow the common dipper-shaped function. In the presence of flanks, thresholds are highly nonmonotonic and first decrease, then increase, and then decrease again. In those observers where threshold measurements at high pedestal contrasts were possible (without ceiling contrast being reached), thresholds rise again, producing an overall W shape. In each graph, the isolated, left-most point corresponds to zero pedestal contrast, i.e. detection threshold.

mensional simplex method (Press, Teukolsky, Vetterling, & Flannery, 1992). Separate fits were obtained for three different data subsets: (1) the average across all observers (conditions NON and P40); (2) the average across observer group 1 (NON, P20, P40, P70); and (3) the average across observer group 2 (NON, P40, N40, O40).

3. Results

Both observer groups performed in the conditions with 40% in-phase flanks (P40), and with isolated targets (NON). Fig. 3 shows the data of all individual observers, while Fig. 4AC displays the mean across all observers. Consistent with many previous reports in the

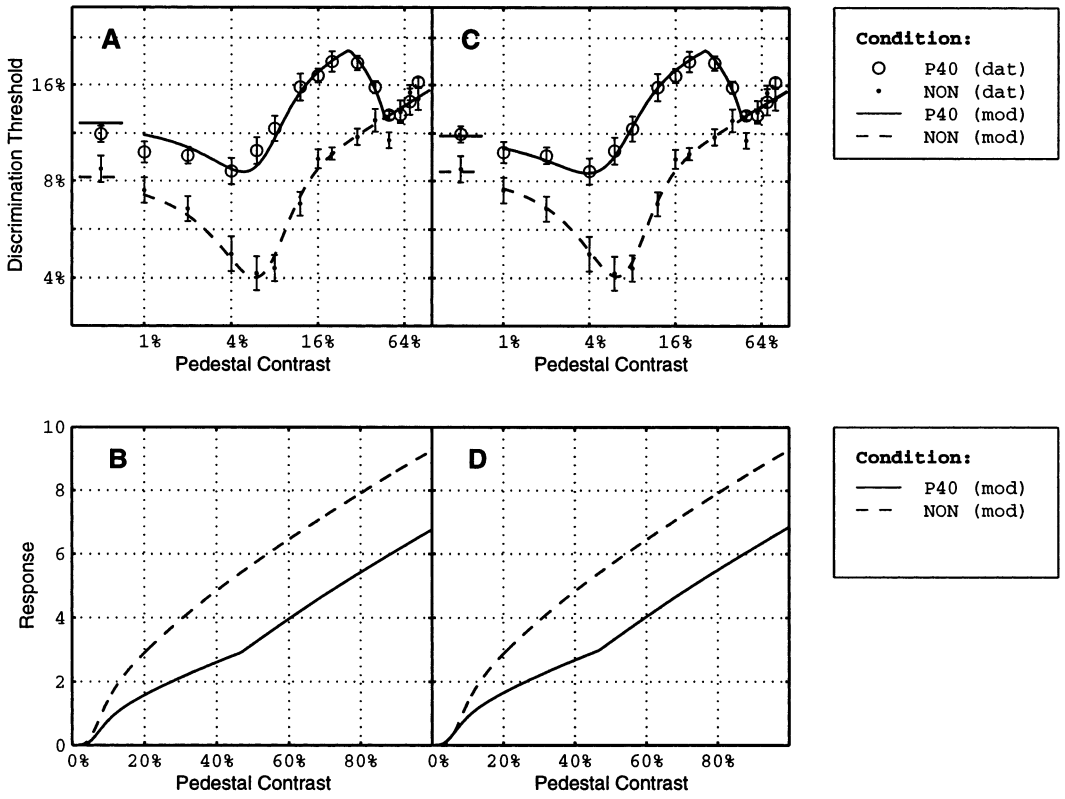

Fig. 4. Data of conditions NON and P40 averaged across all observers, together with two different model fits. (A) Data (circles and dots) together with the fit of model 1 ($a = 0.360$; $c_{th} = 7.15\%$; $p = 4.51$; $q = 0.705$; $b = 1.85$; $c_o = 46.9\%$). The corresponding contrast response functions are shown in (B). The model assumes that flankers provide divisive inhibition to the target unit for target contrasts below c_o (here 46.9%), and provide subtractive inhibition for target contrasts above c_o. While the overall fit is satisfactory, there is a systematic error at low pedestal contrasts, where thresholds for isolated targets are consistently underestimated, and the flanked thresholds are consistently overestimated. The simulation in (C) and (D) shows that this problem disappears when flankers are assumed to provide also additive input to the target unit (model 2; parameters in Table 1).

literature (Legge & Foley, 1980; Wilson, 1980; Bradley & Ohzawa, 1986; Foley, 1994), we find that for the isolated targets (×), discrimination thresholds first improve as a function of pedestal contrast, but deteriorate when pedestal contrast is further increased, resulting in a dipper function. Sometimes, a second dip seems to occur at high pedestal contrasts (e.g. MC and RS), but this effect is small and not consistent across observers[1].

Once the flanks are added, the behavior is more complex. Like Williams and Hess (1998), we almost never observe detection facilitation for flanked peripheral targets, i.e. at a pedestal contrast of zero, the flanks do not enhance performance; rather, there is usually a significant suppression. This inhibition could potentially mask any underlying facilitation. Note that for one out of seven observers, the author BZ, there is some consistent detection facilitation, possibly reflecting the extensive practice that observer BZ had in these and similar tasks, and consistent with the notion that perceptual learning reduces divisive inhibition (Zenger & Sagi, 1996; Dorais & Sagi, 1997).

Suppression is not only found (for most observers) at zero pedestal contrast, but is consistently observed for a whole range of pedestal contrasts up to about 40%. For higher pedestal contrasts (above 50%), thresholds with and without flanks are very similar. The transition from flanker suppression to no-flanker-effect with increasing pedestal contrast is marked in all seven observers by a threshold improvement with increasing flanker contrast, which is opposite to what one would expect according to a power-law behavior (Legge, 1981). This improvement occurs typically in the pedestal range from about 20%–30% to 50%. As a result, the threshold behavior is highly non-monotonic; thresholds first decrease, then increase, and then decrease again. In those observers where thresholds could be measured at high pedestal contrasts, thresholds increased again (consistent with a power law), suggesting an overall W-shaped curve.

[1] Similar second dips at high pedestal contrasts have been reported previously by Kingdom and Whittle (1996), who attributed them to light adaptation processes; however, this effect was observed only at spatial frequencies lower than that used in the present study. Future research will be necessary to test whether a similar mechanism is at work under the conditions of our experiment.

3.1. Effect of Flanker contrast

For flanker contrasts of 20% and 70%, we find that discrimination performance is again well described by a W function (see Fig. 5A). The central peak (and the second dip) in the W curve shift rightwards with increasing flank contrast: for a flank contrast of 20%, the peak occurs at 12% contrast, for a flank contrast of 40%, the peak moves to a contrast of 20%, and for a flank contrast of 70%, the peak is around 40%. Overall, thresholds are higher for higher flanker contrasts.

3.2. Effect of Flanker phase

Negative-phase flanks produce a W-shaped curve as well, although it is somewhat less pronounced compared with the positive-phase condition (see Fig. 5B). The most obvious difference between the positive and negative phase condition is a difference in the detection thresholds, and in the discrimination thresholds with subthreshold pedestals.

3.3. Effect of Flanker orientation

Orthogonal flankers shift the dipper function leftwards (see Fig. 5C), leading to a significant facilitation for low pedestal contrasts, and suppression for higher pedestal contrasts. The detection facilitation is surprising, given that Gabor detection at fixation is not affected by orthogonal flanks (Polat & Sagi, 1994). The condition for orthogonal flanks is the only flanker configuration we tested where we did not observe a convincing W shape.

4. Modeling

As is common in sensory psychopyhsics, we assume that the contrast discrimination thresholds can be derived from an underlying sigmoidal contrast–response function $r(c)$ (see Fig. 4B, dashed curve), together with the assumption that some fixed response difference, $\Delta r = 1$, is required for correct discrimination (Foley, 1994). In other words, for any fixed pedestal

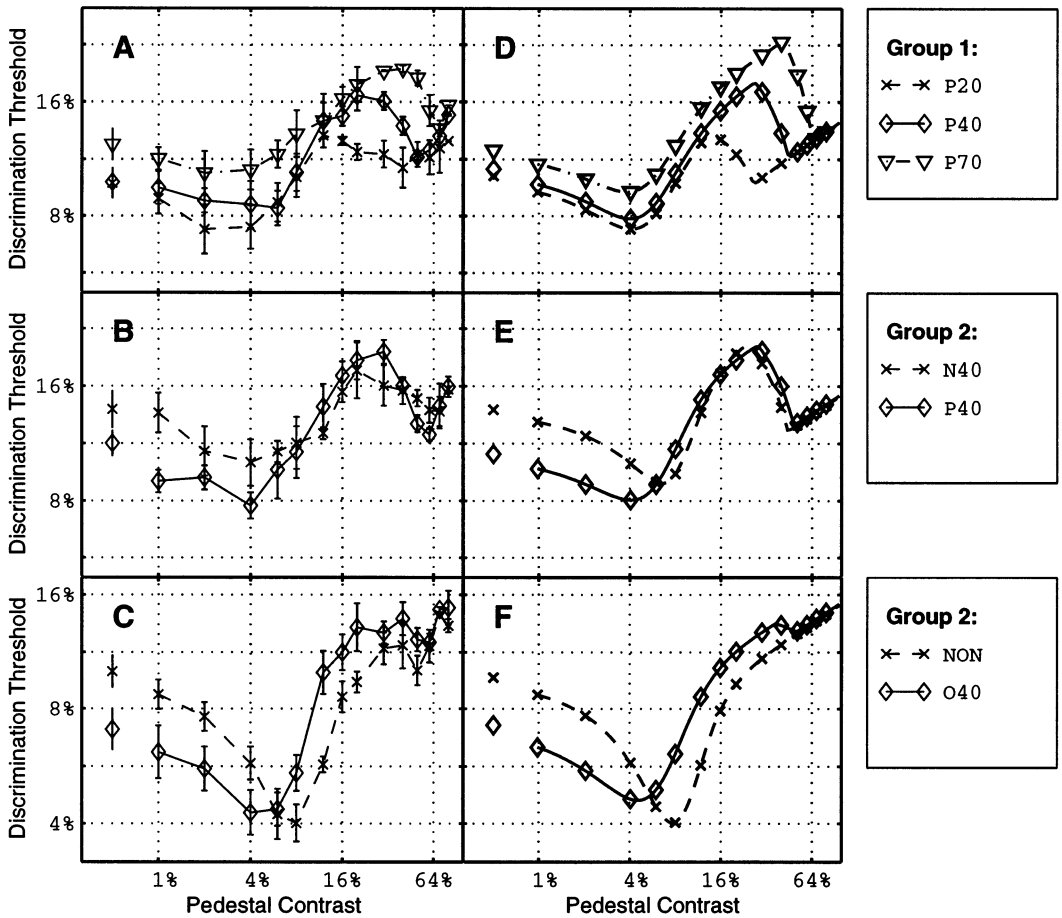

Fig. 5. (A, B, C) Mean data and S.E.M. across observers for different flanker contrasts and configurations. (D, E, F) Best model fits in the least-square sense. The model assumes that flankers provide additive input to the target unit, and that flankers contribute to the target's gain control in a limited target–contrast range. The parameters used for these simulations are given in Table 1.

contrast, c, the discrimination threshold, Δc, satisfies, $r(c+\Delta c) = r(c) + 1$.

To describe the response, r, of the system to a single, well-isolated target as a function of its contrast, c, we adopt the function suggested by Foley (1994).

$$r_{\text{isolated}}(c) = \frac{ac^p}{c^{p-q} + c_{\text{th}}^{p-q}}. \quad (2)$$

For plausible parameters (c, $c_{\text{th}} > 0$), this function is proportional to c^p for $c \ll c_{\text{th}}$ and is proportional to c^q for $c \gg c_{\text{th}}$, consistent with a modified Weber law (Legge, 1981).

4.1. Flanker effects on target-gain-control

How can we model the flanker effects? Our results indicate that the flankers impair discrimination for low target contrasts. Such impairment has often been attributed to a divisive inhibition of the target response by the flanker response; in other words, the impairment of discrimination may simply arise from the fact that the flanker units contribute to the target's gain control (Heeger, 1992; Foley, 1994). Once the target contrast is above a certain level, however, the flanks cease to contribute to the target's gain control and have no effect on performance.

Following this concept, we define two model parameters to describe the effects of the flankers: the first parameter, c_{o}, determines the maximal target contrast at which gain control is still effective; the second parameter, b, determines the strength of the gain control. Formally written, we obtain

Model 1:

$$r_{\text{flanked}-1}(c) = \begin{cases} r_{\text{isolated}}(c)/b & \text{for} \quad c \le c_{\text{o}}, \quad \text{(gain control)} \\ r_{\text{isolated}}(c) - d & \text{for} \quad c \ge c_{\text{o}}, \quad \text{(no gain control)} \end{cases} \quad (3)$$

In the low-contrast range, the contrast–response functions with and without flankers are multiples of each other (factor b); in the high-contrast regime, the two curves are shifted vertically (offset d) with respect to each other (see Fig. 4B). The subtractive constant, d, is not a free parameter but is determined by imposing that r be continuous at $c = c_{\text{o}}$, i.e. $r_{\text{isolated}}(c_{\text{o}})/b = r_{\text{isolated}}(c_{\text{o}}) - d$.

The model fit to the experimental data in the two conditions run by all observers is shown in Fig. 4A. The overall fit is good, and the average error is only 7.7%. The model behavior is easily understood: for low pedestal contrasts, gain control leads to a vertical upward shift of the dipper function. For high pedestal contrasts ($> c_{\text{o}}$), the unflanked and flanked discrimination are identical, since flanks do not affect the target gain and thus do not affect discriminability. Finally, there is an intermediate pedestal range (30–50%) where we find a transition between the two types of behavior. The good fit of model and data in this range comes somewhat as a surprise and indicates that the assumed sharp transition between divisive and subtractive inhibition at contrast c_{o} was adequate.

4.2. Additive Flanker effects

While the overall fit is not bad, it is clear that a simple upward shift of the dipper function in the low pedestal range is not what we find in all observers. In many cases, there is, in addition, a clear leftward shift of the dip (see Fig. 3). Moreover, the current model clearly cannot encompass the data for orthogonal flanks, which also lead to a leftward shift in the dipper curve. To explain the leftward shift, we assume that the flanks provide also additive input, c_{add}, to the target unit.

Model 2:

$$r_{\text{flanked}-2}(c) = \begin{cases} r_{\text{isolated}}(c + c_{\text{add}})/b & \text{for} \quad c \le c_{\text{o}} \\ r_{\text{isolated}}(c + c_{\text{add}}) - d & \text{for} \quad c \ge c_{\text{o}} \end{cases} \quad (4)$$

The result of the fits of the second model (Fig. 4CD) show that with this additional assumption, the data are accounted for even better; the mean error decreases from 7.7% to 5.0%. The price we pay for this superior fit is one additional parameter. Note that the assumed additive input is consistent with models previously developed for Gabor detection at fixation (Zenger & Sagi, 1996; Adini, Sagi, & Tsodyks, 1997). Further note that assuming additive flanker input does not automatically imply detection facilitation, as we have at the same time a strong inhibition.

Using this model, we can account fairly well for all the results obtained with different flank contrasts and flank configurations. The best fits are shown in Fig. 5DEF next to the experimental data.

The model characterizes each flanker configuration and contrast with three parameters. The first parameter, b, reflects the strength of gain control provided by the flanks. The gain-control strength is found to increase with flanker contrast. Gain control is particularly weak for orthogonal flanks. The second parameter, c_{o}, describes the target contrast at which the transition from gain control to no-gain control occurs. This parameter is similar in all cases to the flank contrast. Finally, the parameter c_{add} gives an estimate of the amount of additive input that the flankers or flanker units provide to the target unit. Clearly, one would expect this additive input to increase with the flanker contrast, but this trend is not observed. However, the estimated additive inputs seem too small ($\le 3\%$) and too variable to conclude anything. If the additive

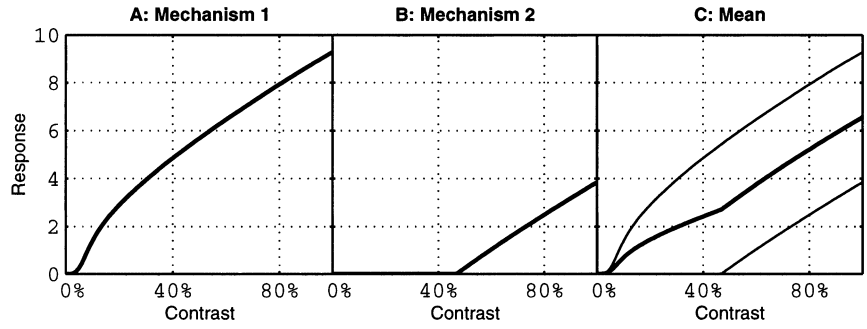

Fig. 6. (A) Responses of mechanism 1 are unaffected by the flanks, and the contrast response function is the same as that for isolated targets. (B) Mechanism 2 is strongly inhibited by the flanks (subtractive inhibition) and fires only after a relatively high threshold is crossed. (C) The weighted average of mechanisms 1 and 2 exhibits a transition from subtractive to divisive inhibition.

flanker input were to arise entirely from the fact that the flanks are presented within the linear receptive field of the target, one would expect that the c_{add} values for negative and positive flanker phase add up to zero. This is not the case, but again, the data seem too noisy to draw any conclusions at this stage. The main reason warranting inclusion of this additive parameter is the data for orthogonal flanks, which show a strong facilitation of detection.

4.3. Neuronal implementations

While the contrast–response functions with and without flanks give a reasonably good account of the psychophysical data, one may wonder how these functions can be computed by the brain. Here, we suggest that the transition between divisive and subtractive inhibition may reflect two distinct mechanisms with different thresholds.

4.3.1. Distinct neuronal populations

One way in which this can be implemented is by two different neural populations. Assume that there is one population of target neurons, which do not care about the flankers, and fire normally (Fig. 6A). Another population of neurons receives a strong subtractive inhibition and thus has a relatively high threshold (Fig. 6B). This second population would respond only once the target contrast exceeds the flanker contrast and pops out perceptually. Assuming that decision relies on both neuronal populations, the contrast response function that predicts decision is a weighted average of the two population responses (Fig. 6C); this function shows the required transition from divisive to subtractive inhibition.

4.3.2. Delayed inhibition

Alternatively, the two different mechanisms (Fig. 6A and B) may not reflect different populations but different stages in the response behavior of the same neuron. Specifically, we suggest that at response onset, inhibition is weak (Fig. 6A), but that at a later stage, inhibition is strong (Fig. 6B). Note that delayed surround effects have been repeatedly described in electrophysiological studies (Zipser, Lamme, & Schiller, 1996; Nothdurft, Gallant, & Van Essen, 2000; Rossi, Desimone, & Ungerleider, 2001). If the decision depends on the mean response over time (Fig. 6C), we expect to observe a transition from gain control to no-gain control with increasing target contrast.

4.3.3. Flanker synchronization

Finally, the low- and high-inhibition state may alternate rapidly within a neuron. This could reflect synchronicity in the flanker units (Singer & Gray, 1995), which provides high inhibition when the flankers fire synchronously, and provides low inhibition when the flankers do not fire.

To illustrate that this would indeed work, we have simulated a simple integrate-and-fire neuron that receives time-modulated inhibition. To model individual neurons, we use a variant of the leaky integrate-and-fire unit (battery $E_e = 70$ mV, capacitance $C = 200$ pF, leak conductance $g_{pass} = 10$ nS, and firing threshold $V_{th} = 20$ mV; see Fig. 7A).

Excitatory and inhibitory synaptic input are modeled as changes in the conductances g_e and g_i, respectively. Whenever the membrane potential, V_m, exceeds the threshold (V_{th}), a spike is initiated, and the membrane potential, V_m, is reset to $V_{rest} = 0$. No refractory period was assumed. The model was implemented on a PC using the programming language C.

Firing rates for increasing excitation (g_e) at various levels of inhibition (g_i) are shown in Fig. 7B. For low excitatory input, the cell never fires, because the input current is counter-balanced by the leakage current, thus preventing the cell from reaching its firing threshold. Once the cell does start firing, firing rates first increase very rapidly, but then rapidly converge against a linear function, whose slope is independent of g_i (Holt & Koch, 1997).

When the inhibitory input is modulated in time and switches between a low ($g_i = g_{low}$) and a high inhibition state ($g_i = g_{high}$), the results look different (Fig. 7C). The cell behaves part of the time like when receiving weak inhibition and part of the time like when receiving strong inhibition. This explains why the overall firing rates resemble weighted averages of the curves for constant g_i. As can be seen, inhibition switches from a divisive mode to a subtractive mode. The level at which the switch occurs depends on the level of inhibition in the high-inhibition state (here, $g_{high} = 20$ nS). The strength of divisive inhibition depends on the percentage of time R that the cell spends in the high-inhibition state; in the example shown as a dashed line in Fig. 7C, the cell spends on average half of the time in the high-inhibition stage (thus, $R = 50\%$) and remains the rest of the time in the low-inhibition stage.

Making the connection between psychophysics and biophysics explicitly requires that a number of assumptions be made: (1) the excitatory input, g_e, to the target unit increases with increasing target contrast; (2) increasing the flank contrast leads to an increase in g_{high} (to account for the fact that the transition from divisive to subtractive inhibition occurs at higher contrasts c_o; see Fig. 5B and Table 1); (3) the relative time spent in the g_{high} state (R) increases with flanker contrast (leading to a stronger divisive inhibition, b, that is reflected in the overall performance decrease with increasing flanker contrast). All these assumptions are quite plausible. The remaining differences between the psychophysically estimated contrast–response functions (Fig. 4BD) and the firing rates of the circuit model (Fig. 7C) seem to reflect mainly over-simplifications in the biophysical model, as discussed in more detail elsewhere (Zenger & Koch, 2001).

5. Discussion

We have measured contrast-discrimination thresholds in the presence of flankers of different configurations and contrasts. We find that collinear flanks impair performance at low pedestal contrasts, but have no consistent effect on discrimination performance at higher pedestal contrasts.

5.1. Flanker facilitation

Under the conditions tested in this study, collinear flanks did not improve contrast detection performance, in contrast to foveal data (Polat & Sagi, 1993). This does not mean, however, that there are no facilitatory interactions in the periphery; facilitatory flanker effects might simply be masked by the strong inhibition. Facil-

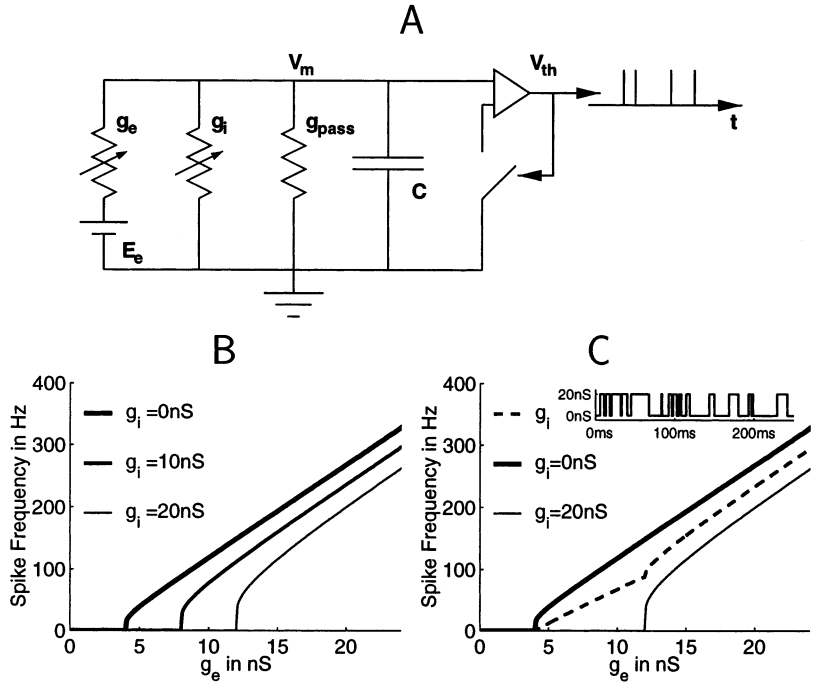

Fig. 7. (A) Standard circuit model (battery E_e, capacitance C, firing threshold V_{th}) to simulate the neurons behavior. Excitatory and inhibitory input regulate the conductances g_e and g_i, respectively. (B) Simulations of circuit model with constant inhibition of different levels. (C) Resulting curve (dashed line) showing a transition from divisive to subtractive inhibition with respect to the zero-inhibition curve when inhibition is time-modulated and switches between a low-inhibition state and a high-inhibition state. This behavior is remarkably similar to the contrast–response behavior inferred from the psychophysical data (Fig. 4B).

Table 1
Model parameters that minimize the least-square errors of model 2 for the data presented in Fig. 4C and Fig. 5ABC

Flanker configuration	a	c_{th} (%)	p	q	b	c_o (%)	c_{add} (%)	Details
Observer group 1 and 2								
	0.351	7.57	4.62	0.711				Free parameters, 7
P40					1.84	46.8	1.32	Data points, 30
								RMS error, 5.0%
								Mean S.E.M. in data, 7.7%
Observer group 1								
	0.385	6.48	3.89	0.710				Free parameters, 13
P20					1.68	26.1	1.02	Data points, 60
P40					1.77	44.8	0.566	RMS error, 7.7%
P70					2.01	64.3	0.346	Mean S.E.M. in data, 9.1%
Observer group 2								
	0.342	9.07	4.93	0.719				Free parameters, 13
P40					1.80	48.4	2.56	Data points, 60
N40					1.94	44.3	−0.0095	RMS error, 8.8%
O40					1.13	50.0	3.00	Mean S.E.M. in data, 10.0%

Minimization was carried out by a multi-dimensional simplex algorithm. In the first fit, we used seven free parameters to simultaneously fit two conditions (NON, P40). In the other two fits, we used 13 parameters to simultaneously fit four conditions (NON, P20, P40, and P70, or NON, P40 and O40, respectively).

itation has been observed in the periphery using line stimuli (Kapadia et al., 1995), and even our data provide some indication for the existence of facilitatory interactions. First, flankers sometimes lead not only to an upward shift of the TvC function but also to a leftward shift (Fig. 3). This leftward shift is indicative of additive input from flanks to the target unit, consistent with the existence of facilitatory interactions. Second, one out of seven observers showed consistent flanker facilitation (Fig. 3); this observer (BZ) was particularly practised and may have led to a reduction in flanker inhibition (Zenger & Sagi, 1996; Dorais & Sagi, 1997), thus revealing underlying facilitatory effects. Areal demonstration of facilitatory interactions, however, would require a systematic variation of target-to-flank distance, to ensure that flanks are completely outside the target's receptive field and, if possible, outside the suppressive region.

A consistent facilitation was observed for orthogonal flanks, which is again in contrast to results for foveal targets, where orthogonal flanks have no effect (Polat & Sagi, 1993). This facilitation was modeled as an additive input from the orthogonal flanks to the target unit. Although long-range connections in primary visual cortex are usually formed between units of similar orientation (Gilbert & Wiesel, 1989; Malach, Amir, Harel, & Grinvald, 1993), direct facilitation from an orthogonal surround has also been suggested (Sillito, Grieve, Jones, Cudeiro, & Davis, 1995), and might account for the facilitatory effects observed here. Alternatively, the orthogonal flanks may inhibit neighboring cells and thus reduce spurious activity in cells that inhibit the target, leading to a reduction in subtractive inhibition of the target. In this case, facilitation would be achieved indirectly through disinhibition (Sillito et al., 1995).

5.2. Segmentation and attention

The transition from suppression to no effect typically occurs around a pedestal contrast similar to the flanker contrast, suggesting that the transition may occur as soon as the target pops out from the flanks due to its higher contrast (contrast popout). Consistent with this, we do not find suppression with orthogonal flanks, where targets pop out due to their different orientation even at low contrasts. In other words, in the conditions tested here, we find that flankers reduce the target's gain whenever the target does not pop out, but flankers have no effect on target-gain control as soon as the target pops out.

Utilizing a dual-task paradigm, we have recently shown (Zenger, Braun, & Koch, 2000) that in conditions where the target has a higher contrast than the surround, attention is not required to detect the target, nor is it required to detect targets that are tilted sufficiently with respect to the surround, as in classical orientation popout (Sagi & Julesz, 1985; Treisman & Souther, 1985; Treisman & Gormican, 1988; Braun & Sagi, 1990; Nothdurft, 1991, 1993). Attention is required, however, to detect collinear targets with a contrast below the surround contrast. In both studies, we thus find a transition in behavior for target contrasts close to the surround contrast. In the first study (Zenger et al., 2000), we found a transition from attentional to preattentive processing, while here, we find a transition from divisive to subtractive flanker inhibition. This suggests that attentive processing and divisive inhibition are related to each other (Lee et al., 1999), and that the role of attention may be to reduce the effects of surround normalization and thus bias processing towards the target (Desimone & Duncan, 1995).

One way to address the role of attention is to compare results for peripheral and foveal experiments, the underlying assumption being that it would be easier to attend to foveal than peripheral targets. Consistent with this view, Xing and Heeger have recently reported that surround inhibition is much stronger in the periphery than in the fovea (Xing & Heeger, 2000). Adini and Sagi have carried out experiments very similar to ours in the fovea (Adini & Sagi, 2000, 2001). Their data show a second dip in the contrast discrimination function (similar to that reported here) for two out of three observers. This suggests that the effects reported here do not disappear at the fovea (note, however, that in their study, flankers were located slightly closer to the target leading to a partial overlap that may make attentional isolation more difficult in spite of foveal presentation). Alternatively, attentional effects on the W-curve may be studied by varying the number of task-relevant targets in a visual search task (Palmer, Ames, & Lindsey, 1993), for example by having observers perform a forced choice between either two or eight precued targets (Zenger-Landolt & Koch, in press). This would appear as the cleaner approach since it does not confound attention and eccentricity.

5.3. Model architecture

The bump in the data (the central peak of the W curve) strongly suggests a transition between different processing mechanisms, or processing strategies. Such transitions between mechanisms are observed frequently when the target signals are close to detection threshold. For example, when a negative phase pedestal is increased, detection of the (positive phase) target first becomes more difficult, because the negative pedestal moves the target unit further away from its threshold. As soon as the pedestal is large enough to be detected, thresholds decrease again, because the presence or absence of the target can now be detected in the unit that detects the (negative phase) pedestal (Yang & Makous, 1995; Chen & Foley, 1999; Kontsevich & Tyler, 1999). The intermediate 'bump' reflects the contrast range where neither of the two mechanisms is particularly efficient at doing the task. Similarly, a recent model for detection of spatial chromoluminance patterns (Chen, Foley, & Brainard, 2000b) assumes that detection relies on several mechanisms with different spectral tuning, and that changes in pedestal contrast may lead to a switch in the mechanism that contributes most to detection. As a result, this model also produces bump, which reflects transitions between detection mechanisms (Chen, Foley, & Brainard, 2000a).

In our study, the transition occurs at contrasts well above detection threshold, and we thus need a contrast-dependent mechanism with a relatively high switch-point. An example of such a model was developed by Wilkinson et al. (1997). They assume that the target is monitored by both simple and complex cells. Simple and complex cells mutually inhibit each other such that in any given stimulus condition, only one of the two produces a response. Simple cells win for isolated stimuli, while complex cells win when the stimulus is embedded in a texture. This model might naturally extend to our conditions and produce a simple cell response whenever the target patch has a higher contrast than the flanks, and produce a complex cell response otherwise. While this general framework of switching between two to some degree independent networks might potentially be used to account for our data, the current implementation of their model will not be able to do so. Their complex cell model comprises two linear filtering stages, each followed by a pointwise nonlinearity. The observed impairment of target detection (pedestal contrast of zero) in the presence of flanks would imply that the flanks drive the operating point to the compressive region of the second-stage nonlinearity. Adding a pedestal contrast (in the contrast discrimination experiments) would drive the operating point even further into the compressive region and would reduce sensitivity (inconsistent with the initial dip we observe for low pedestal contrasts).

Solomon and Morgan (2000) have recently suggested a similar model, consisting of two consecutive filtering stages. Different decision strategies are considered where observers base their decision either on the first-stage response, or the second-stage response, or the stage which contains the larger target signal. While their model simulations demonstrate that bumps can be obtained, the model cannot account for our data, because it predicts, like the model by Wilkinson et al. (1997), that suppression by collinear flanks will increase with increasing pedestal contrast.

To account for our data, we have suggested here a model in which flanker inhibition is assumed to switch from divisive to subtractive at a target contrast close to the flanker contrast. The fact that flanker effects depend on the target contrast can be potentially explained also in the context of a recurrent network, where target response affects flanker response, which in turn affects 'flanker effects' (see, for example, Adini & Sagi, 2001). Here, however, we have favored a simpler feed-forward architecture. As outlined earlier, the model's contrast–response function can be viewed as a weighted average of two mechanisms: one mechanism that is not affected by the flankers, and one mechanism that responds only once the target contrast exceeds the flanker contrast (cf. Fig. 6). While the first mechanism can be understood as a simple contrast detector, the second mechanism acts as a spatial-contrast-increment detector. We have further outlined specific neuronal implementations in which the two mechanisms are implemented within a single neuron, by showing a striking analogy between

the psychophysics of flanker effects and the biophysics of time-modulated inhibitory synaptic input. Both the psychophysically derived and the simulated biophysical contrast–response functions show a switch from divisive to subtractive inhibition. This suggests that both evaluation of absolute contrast (a typical first-stage signal) and the evaluation of spatial contrast differences (a typical second-stage signal) might be carried out by the same functional unit, i.e. the switch in mechanism suggested by the central peak in our W-curves might not imply that the underlying computations are carried out by different units.

5.4. Predictions

Our model makes two clear predictions; first, the contrast–response functions should show—in the presence of flankers—a switch from divisive to subtractive inhibition (Fig. 4BD and Fig. 7C). Physiological studies have measured how stimuli outside the classical receptive field affect the absolute response level of the target unit (Levitt & Lund, 1997; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998). Distinguishing subtractive and divisive inhibition, however, requires that, in addition, surround effects on the *slope* of the contrast–response functions are estimated. Such experiments have been carried out by Sengpiel, Baddeley, Freeman, Harrad, and Blakemore (1998) in cat primary visual cortex. Their extracellular recordings show that when a target grating is surrounded by a high-contrast annulus, inhibition is indeed well described by a divisive effect on the response. It remains to be seen, however, whether surround annuli whose contrast is lower than the target contrast will act subtractively. Contrast response functions averaged over larger neuronal populations can also be measured using functional magnetic resonance imaging in human subjects (Boynton, Demb, Glover, & Heeger, 1999). Our model predicts that in the presence of flankers, this population response would show a transition from subtractive to divisive inhibition. Further insights on how flanker effects depend on target contrast might be gained by psychophysical apparent contrast measurements, which would presumably provide a more direct estimate of absolute responses evoked by a specific stimulus (Snowden & Hammet, 1998; Xing & Heeger, 2000), whereas the contrast discrimination experiments conducted here rather tell us something about the *slope* of the contrast response function.

The second prediction is that inhibition is bistable, i.e. that there are distinct low- and high-inhibition states. These states may alternate in time within the same neuron, or they may be represented by different subsets of neurons.

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