

# Eccentricity effects on lateral interactions

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## Abstract

We attempted to resolve an apparent conflict between the lack of psychophysical evidence of collinear facilitation at the near-periphery and physiological evidence from the monkey showing collinear effects extra-foveally. We compared collinear and orthogonal configurations to discount facilitation due to reduced positional uncertainty. Detection thresholds were measured for Gabor targets at eccentricities of  $0^{\circ}$ – $4^{\circ}$ , flanked by collinear or orthogonal flankers. Like in previous reports in the literature, results varied among subjects when the stimulus position was off-fixation. We found reduced facilitation at eccentricities as small as  $1^{\circ}$ – $2^{\circ}$ . Moreover, facilitation did not increase when the stimuli were M-scaled or when observers received more practice. However, a larger proportion of subjects showed collinear facilitation when attention was directed to the tested configurations. The results suggest that differences in allocation of attention along the visual field may affect the underlying lateral interactions, consequently resulting in eccentricity effects as well as inter-observer variability.

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## 1. Introduction

A large body of psychophysical and physiological studies supports the findings that in early visual areas, the responses of cells to a stimulus are modulated by stimuli that are located outside their classical receptive field. This sort of modulation is suggested to be mediated by a mass of lateral and feedback connections (Grinvald, Lieke, Frostig, & Hildesheim, 1994; Kapadia, Ito, Gilbert, & Westheimer, 1995; Knierim & van Essen, 1992; Levitt & Lund, 1997; Li, Their, & Wehrhahn, 2000, 2001; Polat & Norcia, 1996; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Zipser, Lamme, & Schiller, 1996). Such networks may serve to link local elements into global percepts. An example of such a contextual modulation is the phenomenon of collinear facilitation, in which the contrast detection threshold for a

local element (such as a short bar or Gabor stimulus) is reduced when it is flanked by nearby co-aligned elements with similar orientation and spatial frequency (Morgan & Dresch, 1995; Polat & Sagi, 1993, 1994a; Solomon, Watson, & Morgan, 1999; Williams & Hess, 1998). The specificity of the collinear facilitation effect to orientation and spatial frequency suggests an early level of processing in the cortex where the cells and the interactions possess such fine tuning to these features.

Collinear facilitation is a robust phenomenon for Gabor targets that are located at the fixation point (Polat & Sagi, 1993, 1994a; Solomon et al., 1999; Williams & Hess, 1998; Woods, Nugent, & Peli, 2002). However, some studies showed that when the stimulus is presented at  $3^{\circ}$ – $4^{\circ}$  of visual angle, facilitation is not observed for the majority of the subjects (Williams & Hess, 1998; Zenger-Landolt & Koch, 2001). Assuming that the facilitation is mediated by lateral interactions, the lack of facilitation may suggest a different pattern of connectivity at the fovea and periphery. However, this suggestion

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is in conflict with anatomical and physiological findings from the cat and the monkey, since anatomically, the long-range horizontal connections have not been reported to be restricted to those cortical areas that represent the fovea (Gilbert & Wiesel, 1989; Malach, Amir, Harel, & Grinvald, 1993; Ts'o, Gilbert, & Wiesel, 1986). Moreover, physiological recordings taken from the cat and the monkey show extra foveal contextual modulation, up to around  $10^\circ$  eccentricity (Kapadia et al., 1995; Polat et al., 1998). Also, the reports on the existence of lateral facilitation at the near-periphery in some subjects (Levi, Hariharan, & Klein, 2002; Polat & Sagi, 1994b; Zenger-Landolt & Koch, 2001; Williams & Hess, 1998), supports the hypothesis that the fovea–periphery difference is not in the connectivity but rather in its functional expression. It is possible that the pattern of connectivity is the same at the fovea and the periphery, but the interactions are modulated differently in these two regions by some factor. Indeed, contrast summation experiments provide evidence for excitatory lateral interactions in the near-periphery when stimulus contrast is at the detection threshold (Bonneh & Sagi, 1998; Tailby, Cubells, & Metha, 2001). A modulator that may act differently on foveal and peripheral targets is visual attention. Recently, it has been shown that attention modulates lateral interactions in the fovea (Freeman, Sagi, & Driver, 2001). Moreover, the resolution of attention is reduced along eccentricity (He, Cavanagh, & Intriligator, 1996; Intriligator & Cavanagh, 2001). Hence, it is possible that reduced resources of attention at the periphery are responsible for the absence of facilitation around  $4^\circ$ , as measured psychophysically.

In the current study we tried to understand the reasons for the failure to find consistent collinear facilitation at the periphery. Previous studies compared detection thresholds of collinear and no-flank configurations to test for facilitation at the near-periphery (Levi et al., 2002; Williams & Hess, 1998; Zenger-Landolt & Koch, 2001). However, we found it problematic since spatial uncertainty is greater at the periphery, and hence the no-flank condition can suffer from it more than the collinear one. Here we defined collinear facilitation as the advantage of the collinear over the orthogonal configuration at threshold, noting that due to increased spatial uncertainty at the periphery, orthogonal flankers may also facilitate detection relative to detection of a non-flanked target by signaling the target position. We chose the orthogonal configuration as a reference because at the fovea orthogonal flankers were shown not to affect detection thresholds of an unflanked Gabor target (Polat & Sagi, 1993). Nevertheless, if collinear flankers would still facilitate detection relative to orthogonal at the periphery, this facilitation would be orientation-specific and could be attributed to lateral interactions. Therefore, the subjects needed to detect a Gabor target,

flanked from above and below by similar, high-contrast Gabor signals, in either collinear or orthogonal configurations. First, we looked for the eccentricity at which collinear facilitation falls off (we tested at  $0^\circ$ ,  $1^\circ$ ,  $2^\circ$  and  $4^\circ$  eccentricity). Then, several manipulations were carried out in an attempt to find collinear facilitation at  $4^\circ$ : (1) scaling the stimuli by the cortical magnification factor, (2) training on the collinear configuration, and (3) manipulating attention similarly to Freeman et al. (2001) by means of a dual task in order to affect the lateral interactions between the target and the flankers. In the dual task experiment the subjects performed a Vernier acuity task on the flankers concurrent with target detection, presumably better distributing their attention along the stimulus configuration. We found that collinear facilitation diminished with eccentricity. Scaling the stimuli according to the cortical magnification factor did not produce facilitation. Moreover, training also did not generate facilitation. However, for some subjects, collinear facilitation was observed when attention was manipulated. Nevertheless, several subjects showed facilitation under various conditions with no special manipulation. To conclude, we have found evidence for facilitating lateral interactions at the near-periphery. Apparently, the conditions needed to generate the peripheral facilitation are more subject-specific than those for foveal facilitation. The difference between foveal and peripheral lateral interactions can be partially explained by differences in the individual strategy of allocation of attention.

## 2. General methods

### 2.1. Apparatus

Stimuli were displayed as a gray-level modulation on a 22" Mitsubishi Diamond Pro 2060u color monitor using an ATI Radeon Graphic card. The video format was 85 Hz non-interlaced. An 8-bit RGB mode was used and Gamma correction was applied to produce a linear behavior of the displayed luminance. The mean display luminance was  $30 \text{ cd/m}^2$  in an otherwise dark environment.

### 2.2. Subjects

The subjects were 13 paid high-school and undergraduate students with normal or corrected-to-normal vision. Some of them participated in more than one experiment.

### 2.3. Stimuli

The stimuli were Gabor signals, which are luminance-modulated sinusoidal gratings that were added to a

uniform gray background. Each Gabor patch is characterized by its sinusoidal wavelength  $\lambda$ , phase  $\varphi$  and SD of the luminance Gaussian envelope  $\sigma$ , in the  $(x, y)$  space of the image:

$$G(x, y) = \cos((2\pi/\lambda)x + \varphi) \exp(-(x^2 + y^2)/\sigma^2) \quad (1)$$

In all experiments  $\sigma = \lambda$  and  $\varphi = 0$ . The stimulus was placed at  $4^\circ$  unless otherwise noted. A vertical Gabor target was either presented by itself (no-flank) or flanked, above and below, by two high-contrast (60%) Gabor patches, with either the same local orientation (collinear) or rotated by  $90^\circ$  (orthogonal) (Fig. 1a). In one of the experiments, there was a neutral condition in which the flankers were two black circular contours, 1 pixel wide, of the same size as the flankers' sigma, which provided an orientation-free spatial reference termed "cue" condition (see Fig. 1a). The spatial frequency (SF) of the Gabor patches and target-flank distance are specified for each experiment separately.

#### 2.4. Procedures

The task studied was contrast detection. Two measurement methods were used: (i) a temporal 2 alternative forced choice (2AFC) using a 3-down 1-up staircase method, in steps of 0.1 log units, with eight reversals (the first 2 were ignored), to estimate the threshold that corresponds to 79% correct; and (ii) a single presenta-

tion interval of a constant stimulus followed by a "yes/no" answer, from which  $d'$  was calculated.

##### 2.4.1. Spatial layout of the stimulus

In all experiments, except for those in which their results are described in Figs. 4 and 6, the stimuli (target and flankers) appeared randomly on one side of the fixation cross (1-sided presentation, Fig. 1b, left) either to the right or left in each trial (in the 2AFC paradigm the second presentation was on the same side as the first). In the experiments corresponding to Figs. 4 and 6, the flankers appeared on both sides of the fixation cross simultaneously (2-sided presentation, Fig. 1b, right), while the target appeared on the left or on the right either in the first or second stimulus intervals. The subject's answer indicated the stimulus interval in which the target appeared in all the 2AFC experiments.

##### 2.4.2. Temporal sequence

The subjects initiated each trial by pressing a mouse button. When the target was not at  $0^\circ$ , a fixation sign (+) was present during the entire trial at the center of the screen. When the target was at  $0^\circ$ , the fixation sign was present for 300 ms and disappeared 200 ms before stimulus onset. The presentation sequence started with 500 ms in which there was no stimulus, continued with the first stimulus interval of 90 or 100 ms (specified for each experiment separately) in the 1-sided experiments, and 150 ms in the 2-sided experiments, in which the flankers with or without the target appeared, followed by an inter-stimulus interval (ISI) of 900 ms (1-sided) or 1000 ms (2-sided). In the 2AFC experiments there was a second stimulus interval of the same duration as the first. The specific procedure and stimulus duration are specified for each experiment separately. In all experiments, the subjects completed two sessions a day of 15–25 min each, with a 10-min break between sessions.

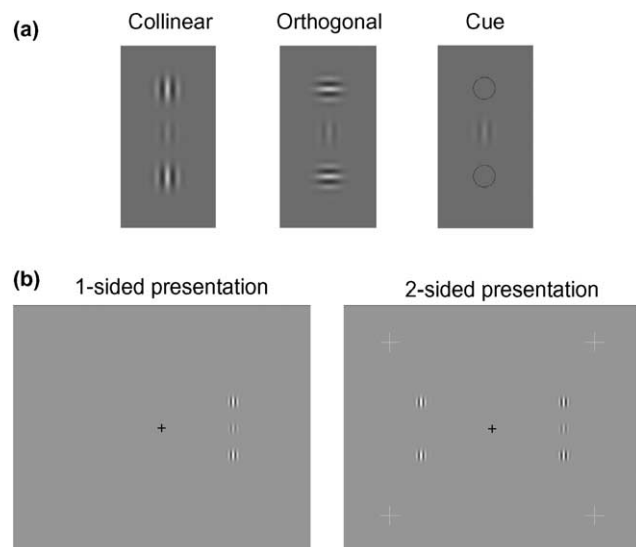


Fig. 1. (a) The stimulus configurations used in the experiments. Left to right: a Gabor target with collinear, orthogonal, and neutral-orientation flankers we refer to as "cue". (b) The spatial layouts used: Left—flankers with or without a target appeared on either side of the fixation sign. This layout was used with both the constant stimulus (1-interval) and the temporal 2AFC paradigms. Right—flankers appeared on both sides of the fixation sign, while the target appeared on one of the sides either in the first or second stimulus intervals. This layout was used only with the temporal 2AFC paradigm.

### 3. Part I—Lateral interactions as a function of eccentricity

In order to determine the eccentricity at which collinear facilitation falls off, subjects performed a detection task of a Gabor target at eccentricities of  $0^\circ$ ,  $1^\circ$ ,  $2^\circ$  and  $4^\circ$  of visual angle. The Gabor targets were flanked by collinear or orthogonal Gabor flankers (Fig. 1a). We compared collinear with orthogonal thresholds and not with no-flank thresholds (except for the  $0^\circ$  target in the first experiment) in order to see if there is orientation depended facilitation that could arise from orientation specific lateral interactions, and not a general facilitation of the flankers that could arise from reducing positional uncertainty.

We used two experimental methods, 2AFC and yes–no. Each of the methods has its benefits and disadvantages.

When using the 2AFC method with a staircase procedure one gets the actual threshold relatively fast, while in the yes–no method a single target contrast is being tested with some guesswork required to find the working contrast range. The major advantage of the yes–no method is that in a single stimulus interval the subject does not benefit from eye-movements.

Finally, using the same constant stimulus procedure, we tested stimuli at 4° eccentricity that were scaled by the cortical magnification factor in order to see if cortical magnification can account for the previous result of no facilitation at the near-periphery.

### 3.1. Comparing detection thresholds of targets flanked by collinear or orthogonal flankers at several eccentricities

#### 3.1.1. Stimulus and procedure

The task was contrast detection of a vertical Gabor stimulus flanked from above and below by high-contrast Gabor stimuli, either collinear or orthogonal to the target orientation. The experiment was carried out using two experimental methods, 2AFC and yes–no. Detection thresholds were measured with a staircase procedure in the 2AFC method. In the yes–no method target contrast was set to the mean threshold of collinear and orthogonal, as determined by a staircase method in a preceding 2AFC experiment. The observer had to determine on each trial whether a target was present or not, and  $d'$  was calculated from the resulting false alarm and hit rates. In the 2AFC experiment a target with no flankers was also tested at 0°. In both methods, the stimulus appeared randomly on each trial either to the right or left of the fixation-cross when the target was not present at fixation. The target–flank separation was four times the Gabor period, a choice made to minimize effects from within the classical receptive field (Zenger & Sagi, 1996). In the 2AFC experiment the SF of the target and flankers was 8 cycles per degree (cpd) and stimulus duration was 90 ms. Each threshold was repeated 2–4 times. In the yes–no experiment SF was 4 cpd, stimulus duration was 100 ms, and  $d'$  was calculated based on 100 trials/condition.

#### 3.1.2. Results and discussion

Collinear facilitation (as measured relative to orthogonal) declined or diminished, with eccentricity (Fig. 2a). For subject DK there was no collinear facilitation already at 1° eccentricity, which is still inside the fovea. Subject YG showed facilitation at 4° although for this subject facilitation declined gradually at 1° and 2°. Both subjects showed collinear facilitation relative to the no-flank condition at 0° (Fig. 2a striped bars).

In order to make sure the result is not due to the high thresholds (24–63% contrast) obtained with an 8 cpd SF stimuli at 4°, we repeated the experiment with Gabor

stimuli of a 4 cpd SF. In this experiment we used the yes–no method with a constant stimulus contrast as described above. Collinear facilitation (relative to orthogonal) diminished at 2° for subject KS and at 4° for subject UE (Fig. 2b).

To conclude, there was no consistent “border” between fovea and periphery; rather, the fall of collinear facilitation occurred at different eccentricities for different subjects. However by 4°, the sensitivity for collinear targets was smaller than that for orthogonal targets (except for subject YG). The orthogonal advantage at 4° may arise from inhibitory interactions between the collinear flankers and targets at  $4\lambda$  distance or from cross-orientation surround facilitation. Such cross-orientation facilitation was observed at the fovea with low-contrast flankers (Yu, Klein, & Levi, 2002).

#### 3.2. Scaling the stimuli by the cortical magnification factor

Because the central visual field is magnified in the cortex relative to more eccentric locations, we tested the possibility that the decrease in facilitation with increasing eccentricity is due to the cortical magnification.

##### 3.2.1. Stimulus and procedure

The stimulus was scaled at 4° according to Rovamo and Virsu (1979). Following the scaling, the Gabors' SF was 1.84 cpd (equivalent to 4 cpd at the fovea), the Gabor patches were larger ( $\sigma = \lambda = 0.54^\circ$ ), and the target–flank distance was kept at  $4\lambda$ , thus resulting in an increased retinal distance of  $2.16^\circ$ . The task was contrast detection using the yes–no method. The procedure was as before.

##### 3.2.2. Results and discussion

With the scaled parameters, we found no collinear facilitation, that is:  $d'$  for target detection in the collinear configuration was similar or worse than  $d'$  for the orthogonal configuration (Fig. 2b, gray bars). However, at 4°, detection thresholds (measured by a 2AFC method using a staircase procedure to determine target contrast for the yes–no experiment) for scaled targets were better than those for non-scaled targets in both orthogonal and collinear configurations, as expected from larger stimuli (average thresholds [ $N = 4$ ]  $\pm$  standard error [%contrast] for subject UE scaled: (C)ollinear =  $1.7 \pm 0.0$ ; (O)rtogonal =  $1.9 \pm 0.3$ ; non-scaled:  $C = 16.5 \pm 0.6$ ,  $O = 14.2 \pm 1.1$ ; for subject KS scaled:  $C = 2.1 \pm 0.2$ ,  $O = 1.8 \pm 0.1$ , non-scaled:  $C = 7.5 \pm 0.7$ ,  $O = 6.3 \pm 0.5$ ). Overall, scaling by the cortical magnification factor did not restore the advantage of a collinear arrangement over orthogonal as occurs at the fovea.

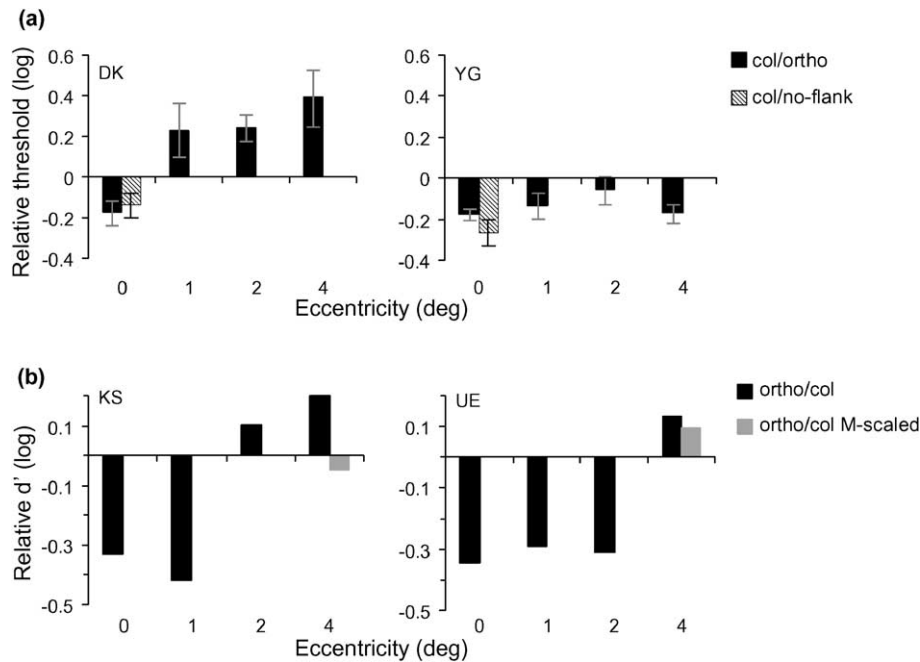


Fig. 2. (a) Ratio of detection thresholds of Gabor targets flanked by high-contrast collinear or orthogonal flankers as a function of eccentricity (black bars). Striped bars—collinear versus no-flank thresholds ratio at 0° eccentricity. Stimulus parameters: SF—8 cpd, target–flank distance— $4\lambda$ , presentation duration—90 ms. Data average of 2–4 repeats for each configuration. Error bars are  $\pm 1$  standard error. (b) Ratios of detection sensitivity ( $d'$ ) for orthogonally versus collinearly flanked targets as a function of eccentricity. Stimulus parameters: SF—4 cpd, target–flank distance— $4\lambda$ , presentation duration—100 ms. There were 100 trials for each configuration at each eccentricity. Gray bars are the results for stimuli scaled by the cortical magnification factor (see text for details). Negative values represent collinear facilitation and positive—orthogonal superiority. Collinear facilitation diminishes with eccentricity.

#### 4. Part II—Manipulating target–flank distance

The size of the receptive fields (RF) of cells in early visual areas increases with eccentricity. Thus, at more peripheral locations, the flankers may activate the target's RF and cause inhibition at a distance that is facilitative at the fovea; whereas, facilitation may occur at larger separations. To test the possibility that at 4° facilitation appears at larger separations between target and flankers, we manipulated their distance in the following experiments.

##### 4.1. Comparing lateral-masking curves at different eccentricities

Detection thresholds were measured for several target–flank distances within the range  $2\lambda$ – $12\lambda$  at 0°, 2°, and 4° eccentricity. We used a relatively high SF of 8 cpd in order to achieve reasonable thresholds at 0° and still use the same parameters across eccentricities.

##### 4.1.1. Stimulus and procedure

Detection thresholds were measured for a Gabor target flanked by collinear or orthogonal flankers and for targets without flankers, in separate blocks of trials, using a staircase procedure in a temporal 2AFC para-

digm. The stimulus (target and flankers) appeared either to the right or to the left of the fixation cross, randomly in each trial though on the same side in both intervals of a trial. The task was to determine the interval in which the target appeared. The SF of the target and flankers was 8 cpd and stimulus duration was 90 ms. Each threshold was repeated 2–4 times.

##### 4.1.2. Results and discussion

Fig. 3a shows the lateral masking curves (thresholds versus target–flank distance) of two subjects at 0° and 4° eccentricity. Each datum point is normalized by the threshold for the no-flank condition. At 0°, the known effect of collinear facilitation is seen for both subjects, whereas at 4° only subject YG shows collinear facilitation relative to orthogonal at a target–flank distance of  $4\lambda$ . Note that subject YG showed facilitation also at another experiment (Fig. 2a). At 2° (data not shown) there was a small collinear facilitation relative to orthogonal (0.1–0.15 log units), about half the typical foveal facilitation, for each of the three subjects who were tested. Interestingly, at 4° eccentricity, detection thresholds for targets with flankers were lower than thresholds for non-flanked targets (the normalized thresholds were negative) regardless of the flankers' orientation, suggesting that this orientation-independent facilitation arise

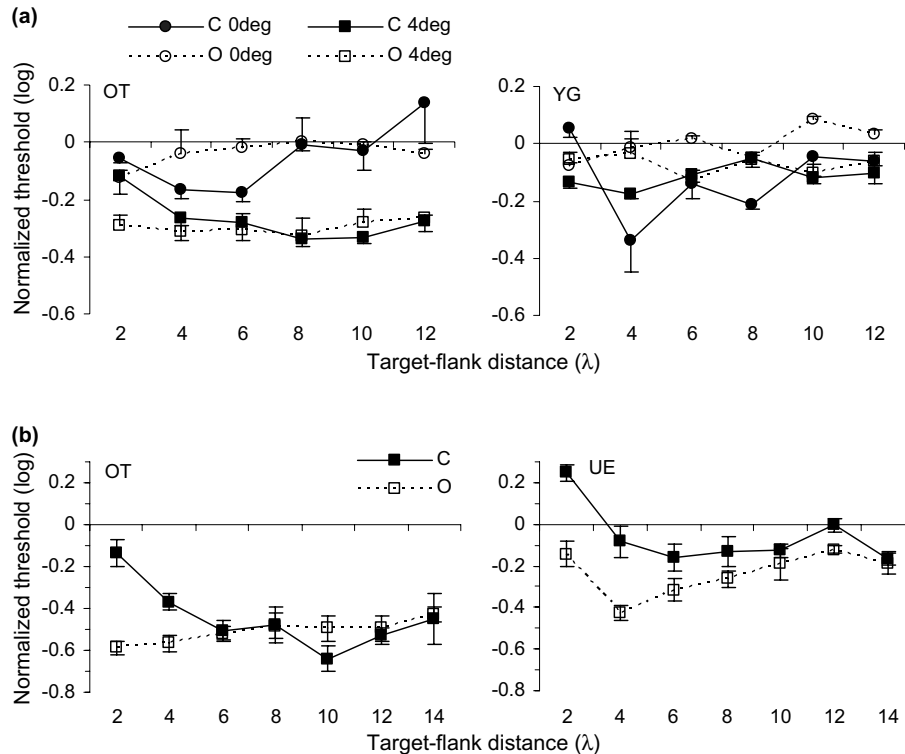


Fig. 3. (a) Normalized detection thresholds (by no-flank threshold, log units) as a function of target–flank distance ( $\lambda$  units) at 0° (circles) and 4° (squares) eccentricity, for targets flanked by collinear (filled symbols) or orthogonal (open symbols) flankers. Stimulus parameters: SF—8 cpd, presentation duration—90 ms. Each point averages 2–4 measurements. Error bars are 1 standard error. Collinear facilitation (relative to orthogonal) is present at 0° and disappears at 4° (except for subject YG at 4 $\lambda$ ). Note that at 4° both collinear and orthogonal thresholds are better than no-flank. (b) Same as (a) but for SF of 3 cpd measured only at 4° eccentricity. Each point averages four measurements. Error bars are  $\pm 1$  standard error.

from reduced spatial uncertainty at the periphery. Only when facilitation is orientation specific may a mechanism of lateral interactions be considered.

#### 4.2. Checking for spatial frequency effect

The above experiment was done with Gabor signals of high spatial frequency (8 cpd). However, Tailby et al. (2001) found contrast summation with the collinear configuration at 4.8° eccentricity using Gabor signals of 3 cpd SF, but not with 6 cpd (in their study the flankers were also at low contrast and the subjects detected the whole configuration). They argued that the different results between the 3 cpd and 6 cpd stimuli is associated with the low SF tuning of cells at more peripheral sites. To test such spatial frequency effects we had two subjects perform lateral masking experiments with Gabor patches of 3 cpd SF.

##### 4.2.1. Stimulus and procedure

The stimulus and procedure were the same as in the previous experiment, except that SF was 3 cpd and we tested only at 4° eccentricity. A target–flank distance of 14 $\lambda$  was also included. Each threshold measurement was repeated four times.

#### 4.2.2. Results and discussion

The results are shown in Fig. 3b. Decreasing the SF of the Gabor patches did not reveal collinear facilitation relative to orthogonal. Nevertheless, there was facilitation relative to no-flank for both configurations as was shown for the 8 cpd stimuli (Fig. 3a)—a general facilitation probably arising from reduction in positional uncertainty. Moreover, at 2 $\lambda$  and 4 $\lambda$  target–flank distance, orthogonal thresholds were lower than collinear ones. Here it is clearly seen that the orthogonal advantage is due to increased thresholds with the collinear configuration at small separations. Thus, these orientation-specific increased thresholds are better explained by inhibitory interactions between the collinear elements at small separations rather than by cross-orientation facilitation.

#### 4.3. Effect of stimulus spatial layout

In all the experiments presented above, the stimuli (target and flankers) appeared in each trial randomly either to the left or right sides of the fixation sign. We repeated the experiment at 4° in a second paradigm, where flankers appeared on both sides of the fixation cross simultaneously, while the target was present only

on one side, either in the first or second stimulus intervals. This configuration is more similar to the stimulus spatial layout used by others (Williams & Hess, 1998; Zenger-Landolt & Koch, 2001). Note that the task in this experiment was still a temporal 2AFC and not a spatial 2AFC, as used by Williams and Hess (1998) and Zenger-Landolt and Koch (2001).

In order to isolate the effect of reduced positional uncertainty that is caused by the flankers, from their possible orientation-dependent interactions with the target, we also measured detection thresholds with neutral-orientation flankers, which were small, black circles (Fig. 1a). This condition was termed “cue”.

#### 4.3.1. Stimulus and procedure

Detection thresholds were measured with a staircase procedure using a 2AFC paradigm. Differently from the previous experiments, the flankers appeared on both sides of the fixation cross, while the target appeared on either side, either in the first or second stimulus intervals. The task was to determine the interval in which the target appeared. The Gabors' SF was 4 cpd (to be comparable to previous work), and the presentation time was raised from 90 ms to 150 ms. The rationale behind a longer presentation time was to increase the flankers' influence, as lateral interactions seem to show their effect relatively late in the response of the cells (150–250 ms; Bauer & Heinze, 2002). Detection thresholds for each target–flank distance were repeated twice, as an initial measure before training (described in Section 5, the *Practice* experiments).

In addition to the collinear and orthogonal Gabor-flankers, a third condition was tested, termed “cue”, in which the flankers were black, thin contours with a radius that equaled the standard deviation of the Gabor-target's envelope. This provided a ‘neutral’ control for the possibly orientation-dependent effects of the flankers.

Four peripheral plus signs ( $1.15^\circ \times 1.15^\circ$ ;  $0.82'$  width; located  $5.6^\circ$  to the left and right, and  $4.8^\circ$  above and below the center of the screen) were presented simultaneously with the stimulus to indicate stimulus presentation.

#### 4.3.2. Results and discussion

Fig. 4 presents lateral masking curves of four subjects for the three flanker-configurations: collinear, orthogonal, and neutral orientation (“cue”; Subject IK did not perform the cue condition but was additionally tested for smaller target–flank separations of  $0\lambda$ ,  $1\lambda$ , and  $2\lambda$ ). All the subjects showed collinear inhibition at the smallest distances they were tested on: UE and HT at  $4\lambda$ , OT at  $4\lambda$  and  $6\lambda$  and IK at  $0\lambda$ ,  $1\lambda$ , and  $2\lambda$ . Subjects HT and OT showed facilitation relative to the no-flank condition

with all flankers' type, but at a distance of  $4\lambda$  collinear thresholds were higher than no-flank, as reported in previous studies where only a single small distance was tested (except for subject BZ [Zenger-Landolt & Koch, 2001] and RD [Williams & Hess, 1998]).

Interestingly, the lateral masking curve of subject OT had a shape reminiscent of the typical foveal lateral masking curve, but facilitation was at larger separations. The collinear facilitation (relative to orthogonal) seen for her at  $12\lambda$  was due to an elevation of orthogonal thresholds with distance, which did not occur for collinear at separations of  $8$ – $12\lambda$ . Thresholds of the cue condition for subject OT also rose with target–flank distance, implying that this threshold elevation with distance cannot be attributed to orthogonal interactions, but rather to increased spatial uncertainty.

Thresholds with orthogonal flankers were similar to those with the neutral cue condition, and both did not increase at short distances like thresholds with collinear flankers. This shows that orthogonal flankers provide a proper control for testing lateral interactions at the near-periphery, serving as spatial cues. In addition and most importantly, this result shows that at the periphery it is no longer proper to conclude on lateral interactions from simply comparing collinear and no-flank thresholds, like done in the fovea, but that the important indication for lateral interactions comes from the orientation-dependent thresholds comparison.

Overall, despite the changes made in the paradigm, we could not find consistent collinear facilitation relative to orthogonal at  $4^\circ$ . On the contrary, the introduction of flankers on both sides of fixation, with the increased positional uncertainty, produced smaller facilitation (relative to no-flankers condition) when compared with the one-side presentation (compare results in Fig. 4 and Fig. 3b). This difference cannot be explained by changes of baseline (thresholds without flankers: 12.4% and 5.3% in the one-side condition, 8.1% and 7.7% in the two-sides condition, for OT and UE respectively). Thus it is possible that the change in facilitation rate is the result of the paradigm differences.

## 5. Part III—Practice

Inhibition is considered to be stronger at the periphery. It was suggested that this increased inhibition mask facilitation (Zenger-Landolt & Koch, 2001), and that facilitation itself is weak at the periphery (Levi et al., 2002; Xing & Heeger, 2000). On the other hand, practice was shown to increase the strength and range of facilitation with a foveal target (Polat & Sagi, 1994b). Practice may also improve the allocation of attention to the stimulus. In the third set of experiments, we tested whether practice can uncover or strengthen peripheral facilitation.

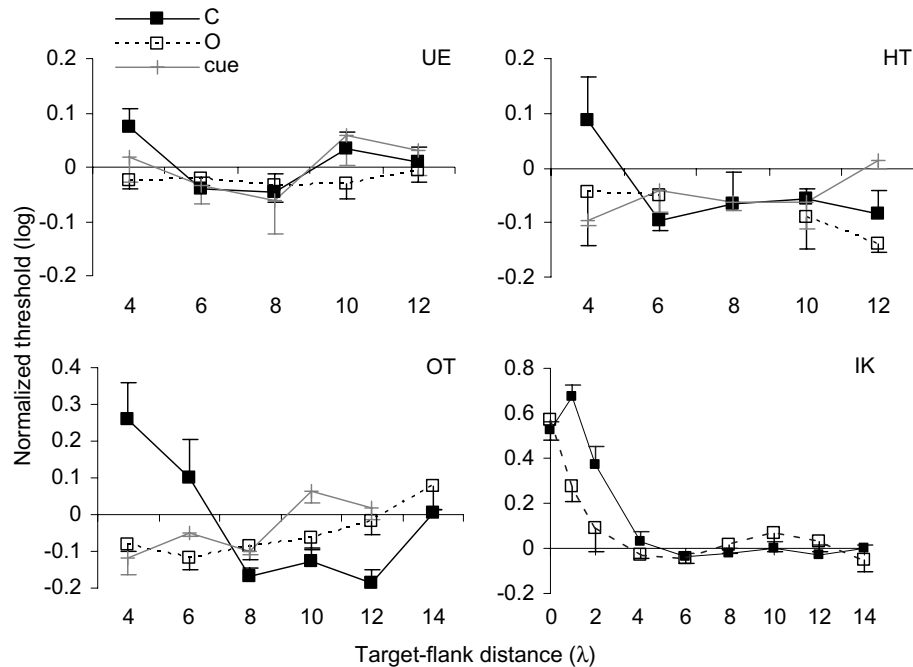


Fig. 4. Normalized thresholds (by no-flank, log units) as a function of target–flank distance ( $\lambda$  units) at  $4^\circ$ , for collinear (filled squares), orthogonal (open squares) and “cue” (+ sign) flankers. SF was 4 cpd, and presentation duration—150 ms. Flankers appeared on both sides of fixation and the task was a temporal 2AFC. Each point represents 2–4 measurements. Error bars are 1 standard error. There is no consistent collinear facilitation relative to orthogonal.

### 5.1. Basic practice

In the first practice experiment, two subjects had 6–8 practice sessions on detection of a Gabor target placed at  $4^\circ$  eccentricity with either collinear or orthogonal flankers. The goal here was to test whether the lack of facilitation in the peripheral task is due to insufficient experience with the more difficult peripheral stimulation.

#### 5.1.1. Stimulus and procedure

The target (8 cpd) appeared at  $4^\circ$  eccentricity on one side of the fixation point in a single interval (yes/no task) of 90 ms, and  $d'$  was calculated from the Hit and False-alarm rates. Target–flank distance was kept at  $4\lambda$  and several target contrasts were chosen to result in a  $d'$  between one and four. On each experimental day, collinear and orthogonal configurations were tested in separate, interleaved blocks of 200 trials (100 trials per side). There were 800–1000 trials per day.

#### 5.1.2. Results and discussion

Results are plotted in Fig. 5. Each datum point is from a block of 200 trials. In order to see some trend in practice we plotted blocks from the early (first 3–4 sessions) and late (last 3–4 sessions) phases of training in different symbols, as well as the linear fit for each training phase. Orthogonal  $d'$  was always higher than collinear  $d'$ , as seen also in the previous experiments at  $4\lambda$  distance, where collinear thresholds were increased.

Practice did not change the tendency of an orthogonal-flanked target being easier to detect than a collinear-flanked target. It may be that practicing on both configurations together created some interference between two opposing responses or that practicing only one distance was not effective as was shown by Polat and Sagi (1994b) for foveal targets. Hence, we tried practice on the collinear configuration, in a range of target–flank distances.

### 5.2. Practicing on a range of distances

In the second practice experiment only the collinear configuration was repeated at a range of target–flank distances. The initial measurements before practice are those reported in Fig. 4. In this experiment, the flankers appeared on both sides of the fixation point simultaneously, whereas the target appeared only on one of the sides, either in the first or second stimulus intervals. The task was to choose the interval that contained the target. Subject IK had 10 training sessions and subject UE had 22 training sessions (Fig. 6).

#### 5.2.1. Stimulus and procedure

The stimulus and procedure were the same as in Section 4.3.1 except that only the collinear configuration was repeated. After practice the orthogonal configuration was tested again.

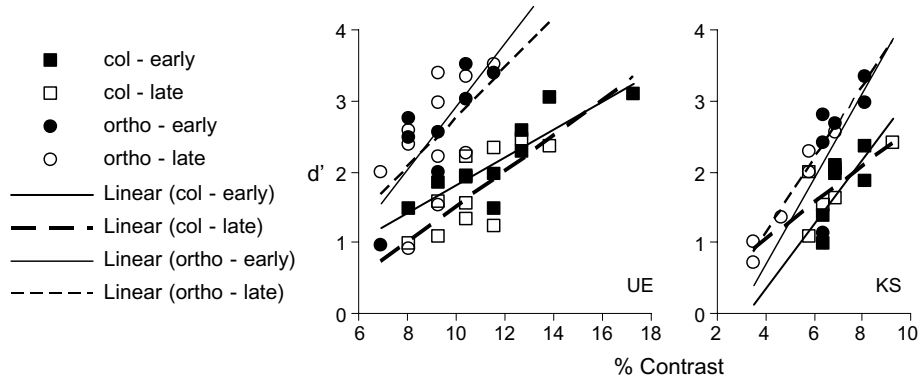


Fig. 5.  $d'$  as a function of target contrast (%) for collinear (squares) and orthogonal (circles) configurations at  $4^\circ$ . Closed symbols are taken from the first 3–4 practice sessions and open symbols from the last 3–4 practice sessions, for subjects KS and UE, respectively. Linear fits for the first (solid lines) and last (dashed lines) 3 or 4 sessions are plotted as well (thick and thin lines for collinear and orthogonal configurations, respectively). Stimulus parameters were: 8 cpd SF, and 90 ms stimulus duration. Each datum point is based on 200 trials. Practice did not change the pattern of higher orthogonal than collinear  $d'$ .

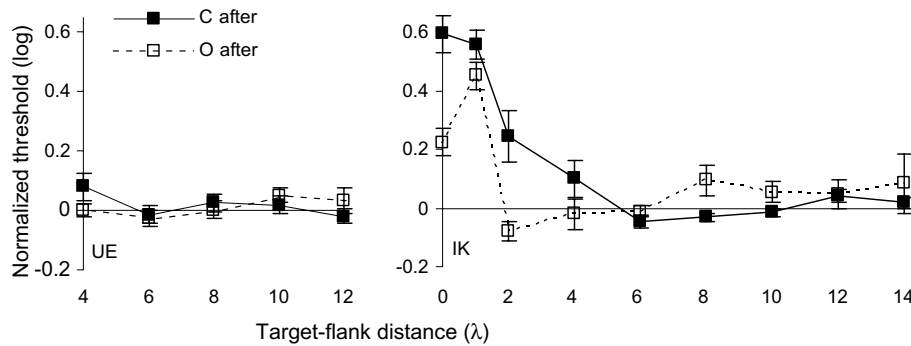


Fig. 6. Normalized thresholds (by no-flank, log units) as a function of target–flank distance for collinear (filled squares) and orthogonal (open squares) configurations after practice (4 cpd, 150 ms stimulus duration, flankers appeared on both fixation sides). Error bars are  $\pm 1$  standard error. Practice did not induce collinear facilitation.

5.2.2. Results and discussion

Results are plotted in Fig. 6. The extensive practice did not induce collinear facilitation relative to orthogonal. There was no facilitation relative to the no-flank condition either.

6. Part IV—Peripheral collinear facilitation induced by attention

In order to test the hypothesis that the lack of facilitation at the periphery is caused by a different distribution of attention, we applied the double task paradigm of Freeman et al. (2001) in which attention was directed to the flankers by a Vernier acuity task. In that study, four flankers surrounded a foveal target, two collinear and two orthogonal to it. Detection threshold was determined by the pair of flankers for which the Vernier task was applied to, in a way as if the other pair did not exist, i.e. when the collinear flankers were attended to, the thresholds were lower than those of the unflanked condition, and when attention was driven to the orthogonal

flankers, no facilitation was found, as if the collinear flankers were not present.

Here we thought to improve the distribution of attention over the stimulus configuration by employing the additional Vernier acuity task. In the current experiment we used only one pair of flankers at a time, either collinear or orthogonal to the target (Fig. 7), to eliminate any possible ambiguity as for the relevant flankers in the acuity task that may have resulted from the peripheral stimulation. When performing the double task, the subjects were first requested to determine whether the flankers had an offset of a pre-specified direction, and then to detect a Gabor target located between the flankers. In the single task condition, the subjects performed either the detection or the acuity task. Performing the single detection task requires focusing attention only on the target, whereas performing the double task, requires to direct attention to the flankers as well. Directing attention to the flankers in the Vernier acuity task was expected to increase the efficacy of the excitatory interactions between the target and the collinear flankers and hence to produce facilitation. We hypothesized that

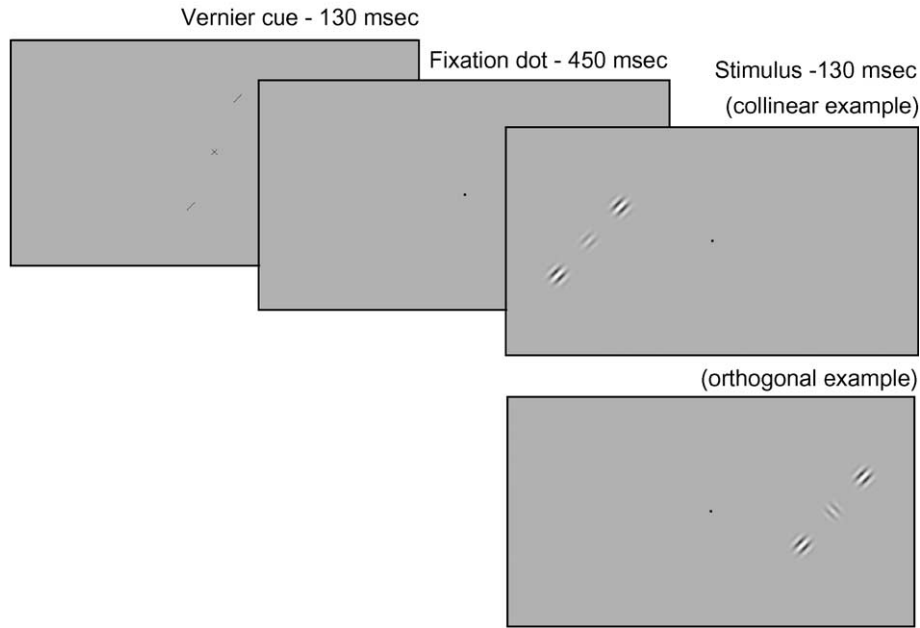


Fig. 7. The stimuli, presentation sequence and timing of the double task. A fixation cross with Vernier direction cues appeared for 130 ms. The cue turned off and a fixation dot appeared for 450 ms. The flankers (with or without the target) appeared for 130 ms on either side of fixation, with global orientation (left/right diagonal) randomized. The flankers were slightly displaced orthogonal to the axis on which they were laying. Configuration (collinear or orthogonal) was blocked. The subject gave two consecutive answers: first about the offset of the flankers (yes—like the cue offset, no—otherwise) and then target detection. Only the portions of the displays that contain the stimulus are shown, and target contrast is high, for demonstration purposes. Two example stimuli are shown. Upper stimulus panel: collinear configuration left to fixation; lower stimulus panel: orthogonal configuration right to fixation. In both examples global orientation is right-diagonal, Vernier offset is the same as the cue (1st answer: yes) and target is present (2nd answer: yes).

an effect of attention should cause the relationship between the psychometric curves of the collinear and the orthogonal conditions in the single task to be different from that in the double task.

### 6.1. Stimulus

The flankers and target were aligned on the  $45^\circ$  or  $135^\circ$  diagonal axis (either left or right diagonal), and the local orientation of each element was also  $45^\circ$  or  $135^\circ$ . Unlike the other experiments, the orthogonal flankers were co-aligned with each other, while the target was rotated by  $90^\circ$  (see Fig. 7). The flankers were slightly displaced on the axis orthogonal to their global orientation to allow for the acuity task. The flankers' offset was set individually for each subject, to maintain an acuity level of around 80% correct (ranged from 0.3 to  $0.5\lambda$ ). The Gabors' SF was 4 cpd and the flankers were located  $6\lambda$  from the target.

### 6.2. Procedure

In the double task, the subjects had to determine first whether the flankers' offset was in a pre-specified direction and then perform a contrast detection task on the central target. All four combinations of global and local orientations that form the collinear and orthogonal configurations in the left and right diagonal axis were tested

and averaged separately for each configuration. There was a single stimulus interval, to avoid eye movements. Presentation sequence and duration were as follows: fixation cross ( $0.023^\circ \times 0.023^\circ$ ) with Vernier direction bars ( $0.35^\circ \times 0.023^\circ$ ; placed  $1.86^\circ$  above and below the cross on a  $22^\circ$  or  $158^\circ$  axis)—130 ms; small fixation square ( $0.058^\circ \times 0.058^\circ$ )—450 ms, which remained until the end-of-trial; stimulus interval—130 ms. Hit and false-alarm rates were measured, from which  $d'$  was calculated and then converted to the equivalent percent correct of a 2AFC task, used to generate psychometric curves. In this way we could obtain a bias-free measurement and fit a Weibull function to the data. At least 300 trials (150 per side but usually much more) per contrast (8–9 different contrasts) were done for each configuration. Contrast detection and Vernier acuity were also measured in a single-task paradigm, in which all parameters were as in the double task. On each experimental day both collinear and orthogonal configurations were presented but in separate sessions. The configuration to be presented first was switched between days. All four conditions (right/left diagonal; right/left side) of either the collinear or the orthogonal configurations were randomized within a session. Detection and Vernier acuity single-tasks were done before the double task. For subjects AI and RD collinear and orthogonal configurations were presented on separate days. They performed first the double task and then the single tasks,

and completed all the experimental tasks with a right diagonal target and then repeated the experiments with a left-diagonal target.

### 6.3. Data analysis

The psychometric curves were fitted by a Weibull function ( $P_W$ ):

$$P_W(C) = 1 - 0.5 \exp[-(C/T)^\beta] \quad (2)$$

where  $T$  is the contrast threshold, equivalent to the contrast that results in 81.6% correct, for a 2AFC psychometric curve,  $C$  is contrast (0–1), and  $\beta$  corresponds to the steepness. A finger error (FE) parameter,  $P_{FE}$ , was incorporated into the fit. For each subject the finger error rate was determined by averaging the error rate (0–1) at the highest contrast across all conditions. This resulted in the following formula:

$$P(C) = 0.5P_{FE} + (1 - P_{FE})P_W(C) \quad (3)$$

The fitting was done in Matlab using a non-linear least-squares method.

## 6.4. Results and discussion

The psychometric curves for detection with collinear and orthogonal flankers, under both the single and the double task conditions, are compared in Fig. 8. Weibull fits to the data are plotted as well.

### 6.4.1. Psychometric curves

A post-hoc analysis of the data shows three types of performance:

1. Attention-induced (or increased) collinear facilitation (Fig. 8a and b). Detection of the collinear-flanked target was better than detection of the orthogonal-flanked target in the double-task, whereas in the single-detection-task the performance in both the collinear and orthogonal configurations was similar. This result was observed for two subjects, RD and AI, for whom the different experimental conditions were not mixed in the same session (but blocked, see *Procedure* in Section 6.2). Thus, it may be suspected as an order effect. However, RD and another subject performed a similar experiment (results not shown), where the global orientation of the stimulus (i.e. target and flankers) was vertical instead of diagonal. In that experiment, the collinear and orthogonal configurations were presented on the same day, as for the other subjects. For both subjects the attentional effect was present.
2. Collinear facilitation was present without manipulation of attention (Fig. 8c and d). Target detection in the collinear configuration was better than in the orthogonal configuration under the single-task condi-

tion for subjects DY and SV. Performing the Vernier acuity task on the flankers under the double-task condition did not increase this difference.

3. Attention did not induce facilitation at threshold (Fig. 8e and f). Subjects HG and AC performed the experiment at 5° eccentricity because their contrast sensitivity at 4° were too high for a reliable estimate of the complete psychometric function. Detection performance of collinear and orthogonal flanked targets was comparable in both the single-task and the double-task conditions for both subjects, though subject HG had a somewhat steeper psychometric function with the orthogonal configuration in the dual-task condition.

### 6.4.2. Weibull fit parameters

Two parameters, threshold ( $T$ ) and steepness ( $\beta$ ) were obtained from the Weibull fits. Their values appear in the graphs for each subject separately. We also plotted all  $\beta$  and  $T$  pairs from the Weibull fits with mean values (Fig. 8g). The most salient observation was the increased steepness of the orthogonal curves under the double-task condition (paired  $t$ -test for  $\beta$  of collinear and orthogonal in the double-task:  $p < 0.001$ ). The average detection thresholds for collinear and orthogonal targets among subjects were not significantly different, in either the single or the double tasks. However, collinear facilitation was manifested (Fig. 8a and b—double task and Fig. 8c and d—single task), mainly at performance levels under the Weibull threshold, which is 81.6% correct. This change in steepness but not in threshold does not fit a change in the uncertainty level as an explanation of the effects of the collinear flankers (Pelli, 1985). However under the orthogonal configuration, both the threshold and steepness parameters were higher in the double than in the single task and hence this difference may be explained in terms of increased uncertainty in the double task (but only for orthogonal, not for collinear where steepness did not change between the single and double tasks).

Overall, orienting attention to the flankers triggered collinear facilitation (as compared to orthogonal) for some subjects, but not as a general rule. Those who showed facilitation in the single task may have the right strategy inherently. Possibly for those subjects who did not show facilitation even under the attentional manipulation, the specific parameters of the experiment (target–flank distance, Gabor envelope size, Vernier offset, etc.) were not optimal. For instance, they may have stronger collinear inhibition.

Acuity performance was comparable for collinear and orthogonal configurations in both the double and the single tasks. Hence, the advantage of collinear detection, when present, was not due to a trade-off between the detection and the Vernier acuity tasks.

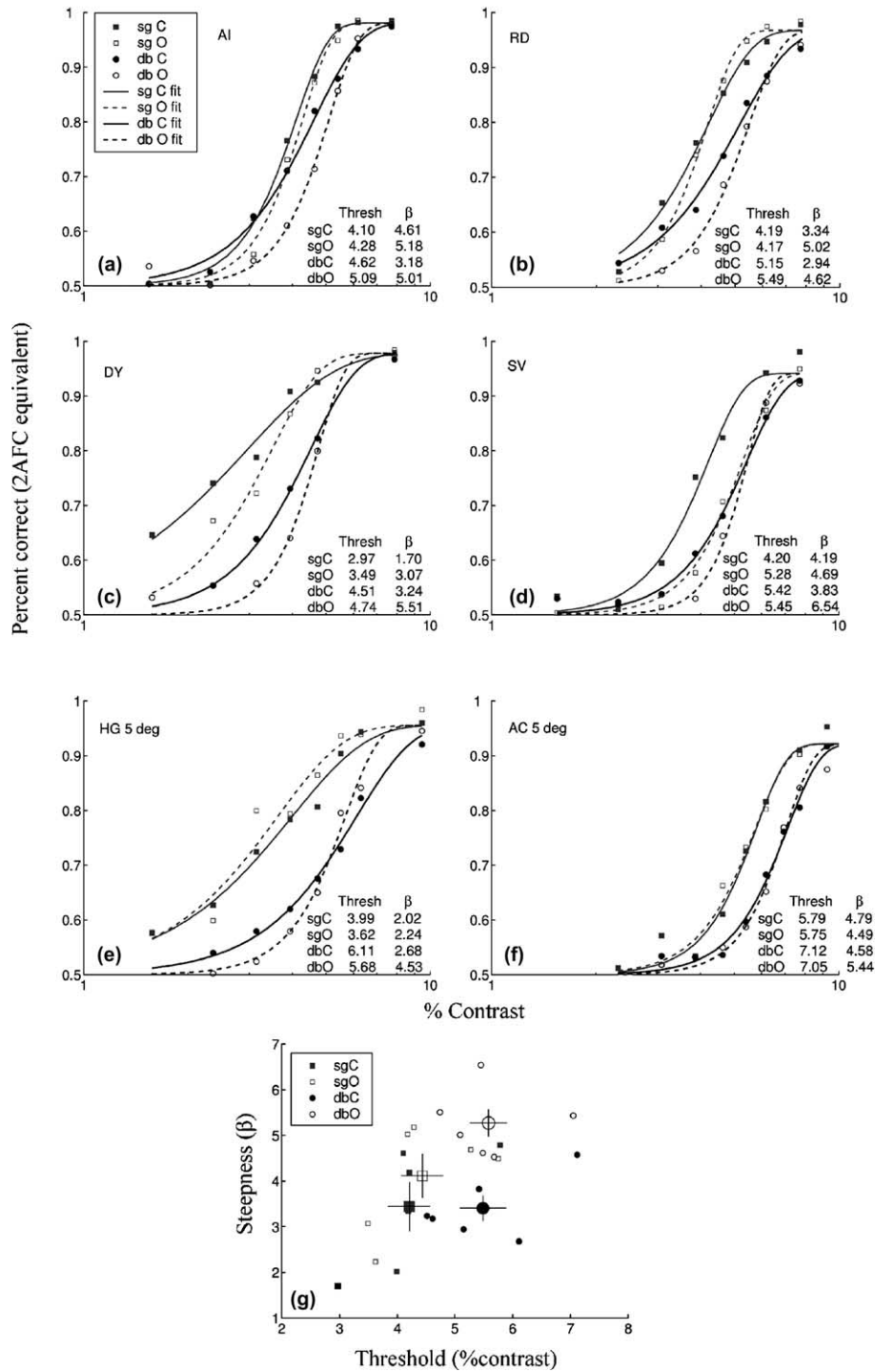


Fig. 8. (a–f) Data points and Weibull fits for contrast detection with collinear (filled symbols, solid lines) and orthogonal (open symbols, dashed lines) flankers in the single-task (squares) and the double-task (circles). Performance level (equivalent to 2AFC %correct) as a function of target contrast (%) for six subjects at 4° (a–d) and 5° (e, f) eccentricity. (a, b) Attention (double task) improves performance in the collinear configuration relative to orthogonal. (c, d) Collinear facilitation is evident without attentional manipulation (single task). (e, f) No collinear facilitation. (g) Steepness ( $\beta$ ) and threshold pairs (small symbols) of all subjects and their means ( $\pm$ standard error; large symbols) taken from the Weibull fits in a–f. The main effect of attention (performance in the double task) was raising the steepness of the psychometric curve of the orthogonal condition.

These results suggest that differences in allocation of attention between the fovea and periphery may cause, to some extent, the presence of collinear facilitation at the

fovea and its inconsistency at the periphery. Furthermore, the collinear facilitation found at 4° for some subjects suggests that lateral interactions can be activated at

the periphery similarly to the fovea, which is in agreement with physiological observations.

## 7. General discussion

This study demonstrates the existence of orientation-specific lateral interactions for peripheral Gabor presentations. We showed that the absence of collinear facilitation (as compared to orthogonal) is not a property of periphery and attribute it to an effect associated with attention. We found collinear facilitation to be less stable across subjects as the stimulus' distance from fixation increases. Collinear facilitation can be restored (mainly sub-threshold) to some extent with better control over the distribution of attention.

### 7.1. Fovea versus periphery

The striking result found here is the reduced collinear facilitation (as measured relative to orthogonal thresholds) at eccentricities as small as  $1^{\circ}$ – $2^{\circ}$  (Fig. 2). Scaling the stimulus to compensate for reduced peripheral spatial resolution did not restore facilitation. These results show that the change in collinear facilitation across eccentricity cannot be explained by known anatomical differences between the fovea and the periphery ( $1^{\circ}$  still stimulates the fovea). Basing on results reported here, we suggest an attention based explanation for the eccentricity effect (see Section 7.2 below).

An additional difference between foveal and peripheral facilitation is the effect of practice. Although practicing at the fovea increases the facilitation range (Polat & Sagi, 1994b), we did not find this result with peripheral practice. However, Tanaka et al. (2003) showed increased facilitation at  $3^{\circ}$  following training with a temporal cue.

The effect of orthogonal flankers also differs between the fovea and periphery. High-contrast orthogonal flankers reduce detection thresholds of a Gabor target relative to the no-flankers condition at the periphery, in contrast to the fovea (Polat & Sagi, 1993; Zenger-Landolt & Koch, 2001). This orthogonal facilitation (relative to no-flank) seems to be best attributed to spatial uncertainty reduction, as orientation-neutral cues also reduce detection thresholds (“cue” condition Fig. 4). In addition, orthogonal thresholds were better than collinear ones at  $4^{\circ}$  eccentricity, only at short target-flank distances of  $2\lambda$ ,  $4\lambda$  and in some cases  $6\lambda$ , which may be explained by the rise of collinear thresholds at short distances due to short-range inhibition (Figs. 2–6).

Reduced orientation selectivity with increasing eccentricity may explain in part the attenuated facilitation with collinear configuration relative to orthogonal at

the periphery. However, physiological studies in cat and monkey show that peripheral cells are still orientation-selective (De Valois, Yund, & Hepler, 1982; Schiller, Finlay, & Volman, 1976; Wilson & Sherman, 1976). Schiller et al. (1976) reported only a slight decrease in the orientation selectivity of complex cells, with increasing eccentricity in the range of  $0^{\circ}$ – $20^{\circ}$ . At  $4^{\circ}$ – $5^{\circ}$  eccentricity, where we measured detection, there should be no effect of eccentricity on orientation selectivity (De Valois et al., 1982). Moreover, we compared the different effects of the  $0^{\circ}$  and  $90^{\circ}$  flankers, for which orientation information is surely processed by separate filters at the periphery. From the perceptual aspect, evidence of preserved orientation signals at the periphery comes from many psychophysical studies using paradigms such as pop-out (Sagi, 1990; Meinecke & Donk, 2002; Yeshurun & Carrasco, 1998), contour integration (Bonneh & Sagi, 1998, 1999a, 1999b; Hess & Dakin, 1997; Nugent, Keswani, Woods, & Peli, 2003), and orientation discrimination (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001; Sally & Gurnsey, 2003), some of which explicitly support integration of orientation information in the periphery.

Detection facilitation can be a result of the nonlinearity of the transducer function around threshold (Legge & Foley, 1980; Usher, Bonneh, Sagi, & Herrmann, 1999; Zenger & Sagi, 1996). On this account, the flankers change the operating point of the target filter, resulting in a change of gain. Thus, differences in facilitation between the fovea and periphery may arise also from differences in the transducer function. It is possible that at the periphery, thresholds increase because of increased noise; thus, the system is not limited by the transducer nonlinearity.

### 7.2. The effects of attention

Attention restored collinear facilitation in the periphery in 2 out of 4 subjects that did not have facilitation in the standard experiment. Another two subjects had collinear facilitation with and without manipulation of attention. Thus it is reasonable to assume that the inter-subject variability observed here and in other studies (Gilbert & Wiesel, 1989; Giorgi, Soong, Woods, & Peli, 2004; Williams & Hess, 1998; Zenger-Landolt & Koch, 2001) is largely due to differences in attentional strategies. Overall, the main effect of attention (averaged across subjects) was an increased steepness of the psychometric curve of the orthogonal condition (Fig. 8g). The slope of the psychometric curve is determined by several factors. According to models of uncertainty, increased steepness together with increased threshold indicates more uncertainty (Pelli, 1985). In our case, the orthogonal curves were steeper than the collinear curves on the average, but the thresholds of the collinear and orthogonal configurations were the same. Thus, the

differences between the collinear and orthogonal configurations in the dual-task cannot be explained only by uncertainty reduction. However, uncertainty reduction may explain the difference between the single and dual task conditions with the orthogonal configuration. Another factor that determines the steepness is the noise level. Accordingly, collinear flankers introduce noise that reduces the slope of the psychometric curve. A third factor that affects the slope is the shape of the transducer function. Depending on the configuration (collinear or orthogonal) and the attentional condition, the transducer function may change, or the working point on the same transducer function may shift.

### 7.3. Increased inhibition and crowding

It was suggested that collinear facilitation is not found at the periphery due to increased inhibition (Zenger-Landolt & Koch, 2001). We found that some subjects show inhibition at flanker distances that are facilitative at the fovea ( $2-6\lambda$ ), but this is not so for others. It may be that those individuals who exhibit peripheral facilitation have less inhibition. Inhibition itself can indicate strong lateral interactions, so the lack of facilitation does not necessarily indicate a lack of interaction.

Another kind of peripheral masking is crowding. Recently it was shown that crowding and contrast-masking are separate phenomenon (Levi et al., 2002). According to Levi et al. (2002), crowding occurs for identification but not for detection. Moreover, both He et al. (1996) and Parkes et al. (2001) showed that local orientation signals from extra-foveal locations are averaged or pooled, which suggests that lateral interactions may take place before crowding.

The overall evidence can be viewed as follows: lateral interactions are at a different excitation–inhibition balance along with eccentricity, according to the functional needs and are prone to attentional modulation. However, whereas in the fovea lateral interactions produce facilitation, at the periphery they are often biased more toward inhibition, as expected from texture processing (Rubenstein & Sagi, 1990).

### 7.4. Contour integration

The question as to what extent does lateral interactions underlie contour integration remains open. Contours, by their nature, cannot fall as a whole at fixation, so integration should take place at extra-foveal locations. Although contours are usually high-contrast, thus making facilitation at threshold less relevant to contour integration (Williams & Hess, 1998), there is evidence of peripheral contour integration of high-contrast, smoothly arranged stimuli both psychophysically (Bonneh & Sagi, 1999a, 1999b; Hess & Dakin, 1999; Nugent et al., 2003) and physiologically (Bauer & Heinze,

2002). This high-contrast integration may utilize the same mechanism suggested for facilitation at threshold, i.e. activity propagation along the long-range connectivity between iso-oriented filters (Polat & Sagi, 1994b).

### 7.5. Spatial summation

Although collinear facilitation induced by high-contrast flankers at extra-foveal locations is not consistent among subjects, more evidence of extra-foveal facilitating lateral interactions at threshold contrasts comes from summation studies (Bonneh & Sagi, 1998; Tailby et al., 2001). Bonneh and Sagi (1998) found that spatial summation for a circular ( $2.5^\circ$  radius) or an ellipsoid ( $2.4^\circ \times 3.12^\circ$  radius) contour is proportional to the fourth root of the number of Gabor elements (12.5 cpd) present, but only for a smooth and not for a random arrangement of the elements. Moreover, summation decreases as inter-element spacing increases. They also found that detection thresholds for textured stimuli rise with increasing local randomization; Tailby et al. (2001) found a collinear 3-patch stimulus to be more detectable than an orthogonal 3-patch stimulus at  $4.8^\circ$  eccentricity (but only for a SF of 3 cpd, as mentioned before). The key difference between spatial summation experiments, which show clear evidence for excitatory collinear lateral interactions at the near-periphery, and lateral-masking experiments, which show between-subject variability, may lay in the fact that in summation experiments all stimuli elements are at threshold contrast while masking experiments contain high contrast flankers which may induce stronger inhibition at the periphery.

### 7.6. Comparison with other studies

A conceptual difference between the current and previous studies is the way we consider collinear facilitation. Whereas others determine facilitation by comparing the thresholds under the collinear and no-flank conditions (Giorgi et al., 2004; Williams & Hess, 1998; Zenger-Landolt & Koch, 2001), we compare thresholds under the collinear and orthogonal conditions. Most of our subjects show collinear facilitation relative to no-flank, but this facilitation is also present under the orthogonal condition. Only when detection in collinear and another flanker arrangement is compared, may the effect of lateral interactions be separated from that of uncertainty reduction.

There are methodological differences that may have prevented collinear facilitation from being found in other studies. First, in most of the experiments in the current study the stimulus (target and flankers) appeared on one side of the fixation point and a temporal 2AFC paradigm was always used (also when flankers

were on both sides of fixation), whereas in previous studies (Williams & Hess, 1998; Zenger-Landolt & Koch, 2001) a spatial 2AFC paradigm was used. Some recent reports indicate that psychophysical thresholds may be affected by the type of 2AFC method used, whether spatial or temporal (Giorgi et al. (2004)). Dividing attention between two locations may reduce the efficiency of the lateral connectivity, resulting in no facilitation, as reported in those studies. This may serve as additional evidence in support of the effect of attention on lateral interactions. Second, Zenger-Landolt and Koch (2001) tested only a target–flank distance of  $3\lambda$ , which may be inhibitory at  $4^\circ$  for most subjects. In our study, the facilitation (relative to orthogonal) found in the dual task experiment was at  $6\lambda$ . Yet, in each of the studies of Zenger-Landolt and Koch (2001) and Williams and Hess (1998) there was one subject who showed collinear facilitation relative to no-flank. In the Williams and Hess study the facilitation was at  $6\lambda$ .

Nevertheless, there are studies that report collinear facilitation relative to no-flank at the near periphery. Polat and Sagi (1994b) mentioned in a side comment that collinear facilitation relative to no-flank was found at  $3^\circ$  eccentricity. Giorgi et al. (2004) report collinear facilitation relative to no-flank at  $2^\circ$ – $6^\circ$  eccentricity, but only in a temporal 2AFC paradigm (not in a spatial 2AFC). Similar to our finding of collinear facilitation relative to no-flank, they also report inter-subject variability and attenuated peripheral facilitation at an optimal distance of  $4\lambda$  (which is larger than the foveal optimum at  $2$ – $3\lambda$ ). Levi et al. (2002) also showed collinear facilitation relative to no-flank at  $5^\circ$  eccentricity for one of their subjects (in a temporal 2AFC paradigm, lower visual field presentation). In their case there was facilitation also relative to a parallel arrangement of target and flankers, so facilitation can be attributed to lateral interactions. All together, there is evidence in the literature supporting collinear facilitation relative to no-flank at extra-foveal locations, which is in agreement with our results.

### 7.7. Solving the discrepancy between animal physiology and human psychophysics

The underlying neuronal circuitry in humans and primates is assumed to be roughly the same. Thus, the human low-level initial physiological response should show contextual facilitation for peripheral presentations similar to that observed in primates. However, the effect of attention may act in a subsequent processing stage and thus affect the response (at any processing level by feedback connections) and lead to the inter-individual differences observed in human subjects for peripheral presentations. In contrast, foveal facilitation is less prone to inter-individual differences presumably because attention is more stable and localized at the fovea.

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## References

- Bauer, R., & Heinze, S. (2002). Contour integration in striate cortex. Classic cell responses or cooperative selection? *Experimental Brain Research*, *147*, 145–152.
- Bonneh, Y., & Sagi, D. (1998). Effects of spatial configuration on contrast detection. *Vision Research*, *38*, 3541–3553.
- Bonneh, Y., & Sagi, D. (1999a). Contrast integration across space. *Vision Research*, *39*, 2597–2602.
- Bonneh, Y., & Sagi, D. (1999b). Configuration saliency revealed in short duration binocular rivalry. *Vision Research*, *39*, 271–281.
- De Valois, R. L., Yund, E. W., & Hepler, N. (1982). The orientation and direction selectivity of cells in macaque visual cortex. *Vision Research*, *22*, 531–544.
- Freeman, E., Sagi, D., & Driver, J. (2001). Lateral interactions between targets and flankers in low-level vision depend on attention to the flankers. *Nature Neuroscience*, *4*, 1032–1036.
- Gilbert, C. D., & Wiesel, T. N. (1989). Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex. *Journal of Neuroscience*, *9*, 2432–2442.
- Giorgi, R. G., Soong, G. P., Woods, R. L., & Peli, E. (2004). Facilitation of contrast detection in near-peripheral vision. *Vision Research*, *44*, 3193–3202.
- Grinvald, A., Lieke, E. E., Frostig, R. D., & Hildesheim, R. (1994). Cortical point-spread function and long-range lateral interactions revealed by real-time optical imaging of macaque monkey primary visual cortex. *Journal of Neuroscience*, *14*, 2545–2568.
- He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature*, *383*, 334–337.
- Hess, R. F., & Dakin, S. C. (1997). Absence of contour linking in peripheral vision. *Nature*, *390*, 602–604.
- Hess, R. F., & Dakin, S. C. (1999). Contour integration in the peripheral field. *Vision Research*, *39*, 947–959.
- Intriligator, J., & Cavanagh, P. (2001). The spatial resolution of visual attention. *Cognitive Psychology*, *43*, 171–216.
- Kapadia, M. K., Ito, M., Gilbert, C. D., & Westheimer, G. (1995). Improvement in visual sensitivity by changes in local context: Parallel studies in human observers and in VI of alert monkeys. *Neuron*, *15*, 843–856.
- Knierim, J. J., & van Essen, D. C. (1992). Neuronal responses to static texture patterns in area VI of the alert macaque monkey. *The Journal of Neurophysiology*, *67*, 961–980.
- Legge, G. E., & Foley, J. M. (1980). Contrast masking in human vision. *Journal of the Optical Society of America*, *70*, 1458–1471.
- Levi, D. M., Hariharan, S., & Klein, S. A. (2002). Suppressive and facilitatory spatial interactions in peripheral vision: Peripheral crowding is neither size invariant nor simple contrast masking. *Journal of Vision*, *2*, 167–177.
- Levitt, J. B., & Lund, J. S. (1997). Contrast dependence of contextual effects in primate visual cortex. *Nature*, *387*, 73–76.
- Li, W., Their, P., & Wehrhahn, C. (2000). Contextual influence on orientation discrimination of humans and responses of neurons

- in V1 of alert monkeys. *The Journal of Neurophysiology*, 83, 941–954.
- Li, W., Their, P., & Wehrhahn, C. (2001). Neuronal responses from beyond the classic receptive field in V1 of alert monkeys. *Experimental Brain Research*, 139, 359–371.
- Malach, R., Amir, Y., Harel, M., & Grinvald, A. (1993). Relationship between intrinsic connections and functional architecture revealed by optical imaging and in vivo targeted biocytin injections in primate striate cortex. *Proceedings of the National Academy of Sciences USA*, 90, 10469–10473.
- Meinecke, C., & Donk, M. (2002). Detection performance in pop-out tasks: nonmonotonic changes with display size and eccentricity. *Perception*, 31, 591–602.
- Morgan, M. J., & Dresch, B. (1995). Contrast detection facilitation by spatially separated targets and inducers. *Vision Research*, 35, 1019–1024.
- Nugent, A. K., Keswani, R. N., Woods, R. L., & Peli, E. (2003). Contour integration in peripheral vision reduces gradually with eccentricity. *Vision Research*, 43, 2427–2437.
- Parkes, L., Lund, J., Angelucci, A., Solomon, J. A., & Morgan, M. (2001). Compulsory averaging of crowded orientation signals in human vision. *Nature Neuroscience*, 4, 739–744.
- Pelli, D. G. (1985). Uncertainty explains many aspects of visual contrast detection and discrimination. *Journal of the Optical Society of America A*, 2, 1508–1532.
- Polat, U., & Norcia, A. M. (1996). Neurophysiological evidence for contrast dependent long-range facilitation and suppression in the human visual cortex. *Vision Research*, 36, 2099–2109.
- Polat, U., & Sagi, D. (1993). Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments. *Vision Research*, 33, 993–999.
- Polat, U., & Sagi, D. (1994a). The architecture of perceptual spatial interactions. *Vision Research*, 34, 73–78.
- Polat, U., & Sagi, D. (1994b). Spatial interactions in human vision: from near to far via experience-dependent cascades of connections. *Proceedings of the National Academy of Sciences USA*, 91, 1206–1209.
- Polat, U., Mizobe, K., Pettet, M. W., Kasamatsu, T., & Norcia, A. M. (1998). Collinear stimuli regulate visual responses depending on cell's contrast threshold. *Nature*, 391, 580–584.
- Rovamo, J., & Virsu, V. (1979). An estimation and application of the human cortical magnification factor. *Experimental Brain Research*, 37, 495–510.
- Rubenstein, B. S., & Sagi, D. (1990). Spatial variability as a limiting factor in texture discrimination tasks: Implication for performance asymmetries. *Journal of the Optical Society of America A*, 7, 1632–1643.
- Sagi, D. (1990). Detection of an orientation singularity in Gabor textures: Effect of signal density and spatial-frequency. *Vision Research*, 30, 1377–1388.
- Sally, S. L., & Gurnsey, R. (2003). Orientation discrimination in foveal and extra-foveal vision: effects of stimulus bandwidth and contrast. *Vision Research*, 43, 1375–1385.
- Schiller, P. H., Finlay, B. L., & Volman, S. F. (1976). Quantitative studies of single-cell properties in monkey striate cortex. II. Orientation specificity and ocular dominance. *The Journal of Neurophysiology*, 39, 1320–1333.
- Solomon, J. A., Watson, A. B., & Morgan, M. J. (1999). Transducer model produces facilitation from opposite-sign flanks. *Vision Research*, 39, 987–992.
- Tailby, C., Cubells, O., & Metha, A. (2001). Enhanced sensitivity for peripherally-presented collinearly-aligned stimulus elements: contour detection or spatial summation? *Clinical and Experimental Optometry*, 84, 354–360.
- Tanaka, Y., Miyauchi, S., Imaruoka, T., Misaki, M., Matsumoto, E., & Tashiro, T. (2003). Transfer of long-range interaction across the visual hemifield by reversed visual input. *Journal of Vision*, 3, 166, Abstract.
- Ts'o, D. Y., Gilbert, C. D., & Wiesel, T. N. (1986). Relationships between horizontal interactions and functional architecture in cat striate cortex as revealed by cross-correlation analysis. *Journal of Neuroscience*, 6, 1160–1170.
- Usher, M., Bonneh, Y., Sagi, D., & Herrmann, M. (1999). Mechanisms for spatial integration in visual detection: a model based on lateral interactions. *Spatial Vision*, 12, 187–209.
- Williams, C. B., & Hess, R. F. (1998). Relationship between facilitation at threshold and suprathreshold contour integration. *Journal of the Optical Society of America A Optics Image Science and Vision*, 15, 2046–2051.
- Wilson, J. R., & Sherman, S. M. (1976). Receptive-field characteristics of neurons in cat striate cortex: Changes with visual field eccentricity. *The Journal of Neurophysiology*, 39, 512–533.
- Woods, R. L., Nugent, A. K., & Peli, E. (2002). Lateral interactions: size does matter. *Vision Research*, 42, 733–745.
- Xing, J., & Heeger, D. J. (2000). Center-surround interactions in foveal and peripheral vision. *Vision Research*, 40, 3065–3072.
- Yeshurun, Y., & Carrasco, M. (1998). Attention improves or impairs visual performance by enhancing spatial resolution. *Nature*, 396, 72–75.
- Yu, C., Klein, S. A., & Levi, D. M. (2002). Facilitation of contrast detection by cross-oriented surround stimuli and its psychophysical mechanisms. *Journal of Vision*, 2, 243–255.
- Zenger, B., & Sagi, D. (1996). Isolating excitatory and inhibitory nonlinear spatial interactions involved in contrast detection. *Vision Research*, 36, 2497–2513.
- Zenger-Landolt, B., & Koch, C. (2001). Flanker effects in peripheral contrast discrimination-psychophysics and modeling. *Vision Research*, 41, 3663–3675.
- Zipser, K., Lamme, V. A., & Schiller, P. H. (1996). Contextual modulation in primary visual cortex. *Journal of Neuroscience*, 16, 7376–7389.