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The effect of spatial frequency on peripheral collinear facilitation

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ABSTRACT

The detection of a Gabor patch (target) can be decreased or improved by the presence of co-oriented Gabor patches (flankers) having the same spatial frequency as the target. These phenomena are thought to be mediated by lateral interactions. Depending on the distance between target and flankers, commonly defined as a multiple of the wavelength (λ) of the carrier, flankers can increase or decrease a target's detectability. Studies with foveal presentation showed that for target-to-flankers distances $<2\lambda$ contrast thresholds for the central target increase, while for target-to-flankers distances $>3\lambda$ contrast thresholds decrease. Earlier studies on collinear facilitation at the near-periphery of the visual field (4° of eccentricity) showed inconsistent facilitation (Shani & Sagi, 2005, *Vision Research*, 45, 2009–2024) whereas more recent studies showed consistent facilitation for larger separations ($7–8\lambda$) (Maniglia et al., 2011, *PLoS ONE*, 6, e25568; Lev & Polat, 2011, *Vision Research*, 51, 2488–2498). However, all of these studies used medium-to-high spatial frequencies (3–8 cpd). In this study we tested lower spatial frequencies (1, 2, and 3 cpd) with different target-to-flankers distances. The rationale was that near-peripheral vision is tuned for lower spatial frequencies and this could be reflected in collinear facilitation. Results show consistent collinear facilitation at 8λ for all the spatial frequencies tested, but also show collinear facilitation at shorter target-to-flanker distance (6λ) for the lowest spatial frequencies tested (1 cpd). Additionally, collinear facilitation decreases as spatial frequency increases; opposite to the findings of Polat (2009, *Spatial Vision*, 22, 179–193) in the fovea, indicating a different spatial frequency tuning between foveal and peripheral lateral interactions.

1. Introduction

At early stages of visual analysis, information is processed locally and for specific features of the input (Hubel & Wiesel, 1963). Moreover, there are excitatory and inhibitory interactions between neurons (Gilbert & Wiesel, 1985; Kapadia et al., 1995). For example detection thresholds for a Gabor stimulus can be modulated by placing two high-contrast flanking Gabor stimuli collinearly aligned (Polat & Sagi, 1993, 1994a). This phenomenon is thought to be mediated by lateral interactions; that is, depending on the distance between the central target and flankers modulation can be facilitatory or suppressive. Indeed, there is psychophysical evidence that collinear facilitation peaks around a target-to-flankers distance corresponding to 3 times the carrier's wavelength (λ) of the Gabor, while for shorter distances (e.g., $1.5–2\lambda$) there is suppression (Polat & Sagi, 1993, 1994a). The most prominent hypothesis is that these modulations are mediated by long-range interactions between units in the primary visual cortex paired by orientation preference (Bolz & Gilbert, 1989; Gilbert, 1992; Gilbert & Wiesel, 1985; Grinvald et al., 1994; Malach et al., 1993; Malonek, Tootell, & Grinvald, 1994; Polat & Norcia, 1996; Polat et al., 1998; Ts'o, Gilbert, & Wiesel, 1986).

Interestingly there is physiological evidence that these connections span outside of the visual cortex area that represents the fovea, encompassing part of the periphery (Gilbert & Wiesel, 1989; Malach et al., 1993; Ts'o et al., 1986). Single cell recording studies in monkeys and cats showed extrafoveal contextual modulation for distances up to 10° of eccentricity (Kapadia et al., 1995; Polat et al., 1998).

To date several studies on lateral interactions have focused on foveal presentation while few studies have dealt with peripheral lateral interactions; that is, presenting the collinear configuration (target and flankers) at a certain eccentricity (4°–6°; Shani & Sagi, 2005; Williams & Hess, 1998; Zenger-Landolt & Koch, 2001). Most of the studies that investigated peripheral lateral interactions tested peripheral collinear facilitation with stimuli presented in the near-periphery (eccentricity up to 4°) showing a

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greater amount of suppression with respect to the fovea and no evidence of consistent facilitation. For example, Giorgi and colleagues (2004) provided evidence for collinear facilitation, but the authors compared the collinear condition in which target and flankers were iso-oriented along the vertical axis with a no-flankers condition. In this case it was not possible to assess whether the flankers acted either as collinear modulatory elements or more generally as spatial cues, reducing the spatial uncertainty. Shani and Sagi (2005) adopted a more precise paradigm comparing the collinear configuration with an orthogonal configuration (i.e., with flankers orthogonally oriented with respect to the vertical target) under the assumption that a greater than 45° orientation difference between target and flankers does not produce collinear facilitation (Polat & Norcia, 1996; Polat & Sagi, 1994). With this method lower contrast thresholds for the collinear condition with respect to the orthogonal condition are considered evidence for peripheral facilitation. However, for target-to-flankers distance of 4λ, typically facilitatory in foveal vision, the authors failed to find consistent collinear facilitation.

Recently two studies (Maniglia et al., 2011; Lev & Polat, 2011) attempted to establish some possible relationships between psychophysical results and physiological evidence of inter-layer connections outside the cortical area representing the fovea. In particular these studies reported consistent collinear facilitation for eccentric (near-peripheral) presentation at target-to-flankers distances larger than the separation that produces facilitation in fovea (i.e., 8λ and 7λ). Lev and Polat (2011) used a yes–no paradigm with a "mix trial" procedure (i.e., orthogonal and collinear configurations were presented randomly within the same block at different target-to-flankers distances) previously used in the fovea by Polat and Sagi (2007), and measured Hits, False Alarms and Criterion. The authors considered the increase of Hits and False Alarms and the negative value of the Criterion as indicators of collinear facilitation. The rationale of the "mix procedure" paradigm is that by presenting stimuli with different features (e.g., orientation, eccentricity, separation) within the same experimental block, observers cannot adapt their Criterion in order to reduce the False Alarm rates. Thus producing a genuine sensitivity measure not affected by compensative strategies (Polat & Sagi, 2007).

Polat and Sagi (2007) reported that collinear facilitation produces filling-in, resulting in higher Hits and False Alarm rates and negative Criterion values. The underlying neuronal explanation is that flankers placed within the facilitatory distance produce higher neuronal baseline activation leading to more reporting for the central target even when it was not present. Consistent with this, Meirovithz et al. (2010) showed using fMRI that collinear flankers produce not only facilitation for the target response but also increase the baseline activity at the target location even when the target was not present. Crucial for the emergence of this pattern of results is the "mix procedure", since it does not allow observers to compensate for the increase of target reporting by changing their response Criterion that is a subjective measure of sensitivity.

However, the "mix procedure" in Polat and Sagi (2007) did not produce the expected increase of d' (the sensitivity index obtained by the standardized difference between the means of the Signal Present and the Signal Absent distribution within the Signal Detection Theory framework) for facilitatory target-to-flankers distances (Polat & Sagi, 1993), probably because of the lack of the shift in Criterion apparently necessary for the induction of the facilitation. In a subsequent experiment Polat and Sagi (2007) used a temporal 2AFC task which restored the classical finding of collinear facilitation for target-to-flankers distance of 3λ (Polat & Sagi, 1993). The authors argued that in a temporal 2AFC paradigm, there is no need for a pre-stored strategy to choose from because the most efficient strategy is to compare the stimulus in the first interval with that in the second temporal interval. In conclusion Polat and Sagi (2007) proved that collinear facilitation produces filling-in but that this can be properly observed and measured only when the Criterion does not shift by mixing different condition in the same experimental block.

As aforementioned, Lev and Polat (2011) using a yes–no paradigm with a "mix procedure" and the configuration presented at 4°, showed higher Hits and False Alarms whilst lower Criterion for the collinear condition with respect to the target-alone and the orthogonal conditions. For the fovea, no difference in terms of d' between collinear and orthogonal conditions were found. This is somewhat in contrast with our previous study (Maniglia et al., 2011) in which we reported lower contrast thresholds and higher d' for the collinear configuration with respect to the orthogonal configuration with a yes–no task. However, we used a "fixed procedure" so the observers had the possibility to adjust their Criterion. Thus, similarly to what Polat and Sagi (2007) showed for the fovea, such difference in d' might be due to different strategies between fixed and mixed trial procedures. On the other hand, whilst Polat and Sagi (2007) showed collinear facilitation in fovea using a temporal 2AFC instead of the yes–no task, Lev and Polat (2011) did not test for this possibility in the periphery, assumed a bidirectional correspondence instead.

In our previous study (Maniglia et al., 2011) we measured collinear facilitation as the difference in contrast thresholds between collinear and orthogonal conditions and found a significant reduction of contrast thresholds at a target-to-flankers distance of 8λ.

Taken together our previous results (Maniglia et al., 2011) and those of Lev and Polat (2011) suggest the presence of collinear facilitation at the near periphery of the visual field but at larger target-to-flankers distances than in fovea.

It should be noted that all previous studies on peripheral collinear facilitation used Gabor stimuli with medium to high spatial frequencies (i.e., 3–8 cpd) that, while ideal for foveal vision, may not be suitable for studying peripheral facilitation since the visual periphery is more selective for low spatial frequencies. Indeed, the periphery of the visual field is subject to cortical magnification and scaling for eccentricity. Tailby, Cubells, and Metha (2001) using a collinear configuration of Gabor patches with the same contrast found evidence for contrast summation when the collinear configuration was presented at 4.8° of eccentricity and using Gabor patches with a spatial frequency of 3 cpd. However, they did not find evidence for spatial summation when using 6 cpd. The authors argued that the different results are associated with the low spatial frequency tuning of neurons processing the peripheral space.

In order to investigate the spatial frequency selectivity of collinear facilitation at the periphery of the visual field we used a temporal two alternative forced-choice task (2AFC) with triplets of stimuli randomly presented at 4° with respect to a central fixation point, either to the left or to the right visual hemi-field. The task of the observers was to judge in which temporal interval the target was present.

In contrast to Lev and Polat (2011) and our previous study (Maniglia et al., 2011) we avoided the yes–no task for two main reasons, because: (i) it seems more suitable for measuring filling-in than collinear facilitation (Lev & Polat, 2011; Polat & Sagi, 2007), and (ii) as Giorgi et al. (2004) reported, collinear facilitation in the periphery can be found with a temporal but not spatial two-alternative forced choice (2AFC). Probably because in the spatial 2AFC subjects are forced to attend competing stimulus configurations, reducing the facilitation. In this context Freeman, Sagi, and Driver (2001) showed that the allocation of attention is an important factor for collinear facilitation, and a spatial 2AFC task, in which subjects are forced to split their attention between two different spatial locations, could be detrimental for collinear facilitation. As Polat and Sagi (2007) pointed out a temporal 2AFC task is a more robust procedure because it does not require choosing between pre-stored strategies and it is suitable for replicating classical findings of collinear facilitation. In addition we estimated contrast thresholds instead of d′.

The results of the present study show that at 2 and 3 cpd contrast thresholds estimated in the collinear configuration are significantly lower than contrast thresholds estimated in the orthogonal configuration at 8λ. At 1 cpd facilitation is already present at 6λ, suggesting selectivity for low spatial frequencies. This is consistent with the spatial characteristics of the visual periphery (Banks, Sekuler, & Anderson, 1991). Further, we showed that collinear facilitation decreases as spatial frequency increases, the opposite of what Polat (2009) found in the fovea.

2. Experiment 1

The aim of Experiment 1 was to measure collinear facilitation in the near periphery (4° of eccentricity) with low spatial frequencies (i.e., 1, 2, and 3 cpd) in order to assess whether the magnitude of collinear facilitation is associated with spatial frequency selectivity also for non-foveal presentation. Since the periphery of the visual field is selective for low spatial frequencies stronger collinear facilitation for the lowest spatial frequency (i.e., 1 cpd) was expected.

2.1. Methods

2.1.1. Apparatus

Stimuli were displayed on a 17″ Dell M770 CRT monitor with a refresh rate of 60 Hz. We generated the stimuli with Matlab Psychtoolbox (Brainard, 1997; Pelli, 1997). The screen resolution was 1024 × 768 pixels. Each pixel subtended 1.89 arcmin. The minimum and maximum luminance of the screen were 0.98 cd/m^2 and 98.2 cd/m^2 respectively and the mean luminance was 47.6 cd/m^2. Luminance was measured with a Minolta CS110 (Konica Minolta, Canada). A digital-to-analogue converter (Bits#, Cambridge Research Systems, Cambridge UK) was used to increase the dynamic contrast range (12-bit luminance resolution). A 12-bit gamma-corrected lookup table (LUT) was applied so that luminance was a linear function of the digital representation of the image.

2.1.2. Participants

One of the authors and five naïve participants took part in the experiment. All participants had normal or corrected to normal visual acuity. They sat in a dark room at a distance of 57 cm from the screen. The participant's heads were stabilized using a chinrest. Viewing was binocular. They were instructed to fixate at the center of the screen. All participants took part voluntarily with no compensation. In addition, all participants gave written informed consent prior to their inclusion in the experiment. We have performed the study in accordance with the ethical standards laid down by the Declaration of Helsinki (1964).

2.1.3. Stimuli

Stimuli were Gabor patches consisting of a cosinusoidal carrier enveloped by a stationary Gaussian. Each Gabor patch was characterized by its sinusoidal wavelength λ, phase φ, and SD of the luminance Gaussian envelope (σ) in the (x, y) space of the image:

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

In all experiments, $\sigma = \lambda$ and $\varphi = 0$ (even symmetric). Gabors had a spatial frequency of 1, 2 and 3 cycles per degree (cpd). A vertical Gabor target was presented flanked above and below by two high-contrast Gabor patches (0.6 Michelson contrast) (Fig. 1). In the orthogonal configuration flankers were always orthogonally oriented with respect to the target and located at various distances from the target (i.e., 3λ, 4λ, 6λ, and 8λ). The location of the target relative to the fixation point (0.18 °) was 4° either in the left or in the right visual hemi-field.

2.2. Procedure

We measured and compared the contrast detection thresholds of a vertical Gabor target flanked by either two vertically oriented Gabor patches (collinear configuration; Fig. 1) or two orthogonally oriented Gabor patches (orthogonal configuration; Fig. 1) with target-to-flankers distances of 3λ, 4λ, 6λ, and 8λ. The spatial frequencies tested were 1, 2 and 3 cpd. Contrast detection thresholds were measured at 4° of eccentricity. We used a temporal two-alternative forced choice task (temporal 2AFC). After an initial

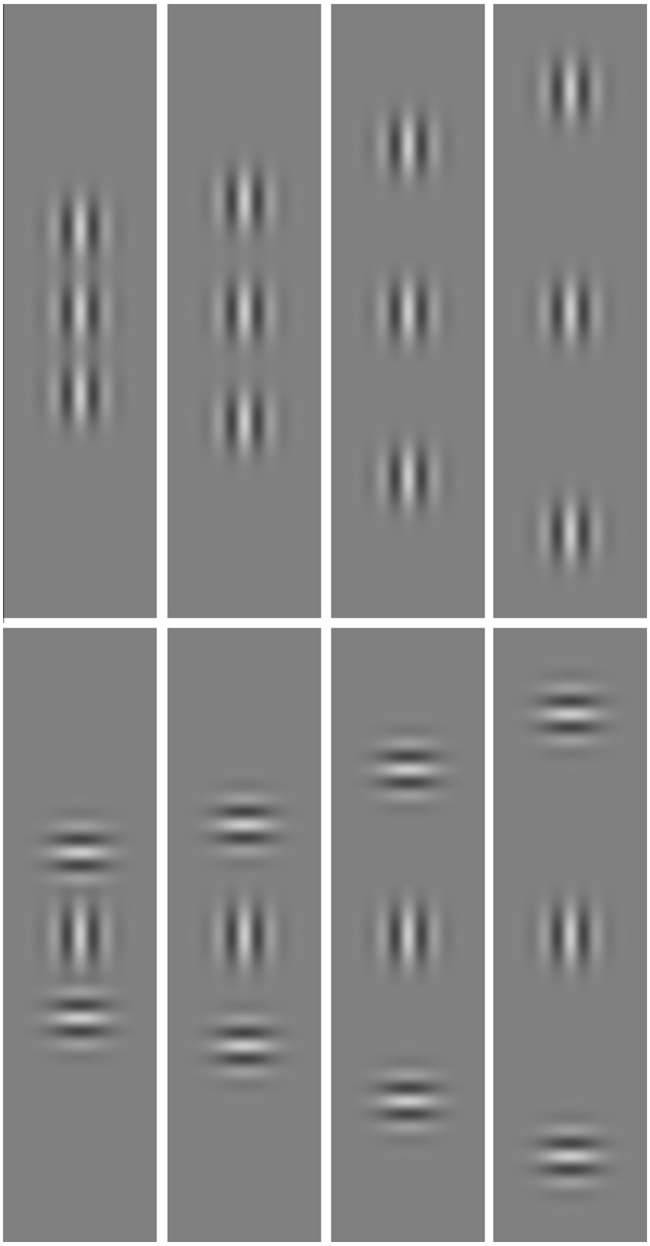

Fig. 1. Gabor patches used in Experiment 1. The first row represents collinear configurations of 1 cpd with target-to-flankers distances of 3λ, 4λ, 6λ, and 8λ (from left to right). The second row represents orthogonal configurations of 1 cpd with a target-to-flankers distance of 3λ, 4λ, 6λ, and 8λ. However, in the experiment we also used Gabor patches of 2 and 3 cpd. The contrast of the central Gabor patch (i.e., the target) is increased for demonstrative purposes.

fixation of 1 s the first temporal interval was presented for 80 ms, and after a further delay of 500 ms the second temporal interval was presented always for 80 ms. The target was presented either in the first or second temporal interval and participants were required to choose which of the two temporal intervals contained the target. In addition the target could be presented either in the left or right visual hemi-field (Fig. 2). We used a stimulus duration of 80 ms to prevent eye movements toward the stimuli (Carpenter, 1988; Martinez-Conde, Macknik, & Hubel, 2004). The temporal interval and the visual hemi-field were randomized on a trial basis with the constraints that the target could not be presented in the same temporal interval or in the same visual hemi-field for more than three consecutive trials.

The contrast of the central Gabor target was varied according to a simple 1up-3down staircase (Levitt, 1971). The starting contrast of the target Gabor was set at 0.1 Michelson contrast increasing by 0.1 log units for each wrong response and decreasing by the same value after three consecutive correct responses. The staircase terminated after either 120 trials or 16 reversals. Contrast threshold corresponding to 79% correct responses was calculated averaging the contrast values in correspondence to the last 8 reversals. Acoustic feedback (50 ms tone at 500 Hz) was given following a wrong answer. Participants performed the task on three consecutive days. A daily session consisted of 8 blocks in which the target-to-flankers distance and the flankers' orientation were varied while the spatial frequency was kept constant. Each day was devoted to one spatial frequency starting from the lower (i.e., 1 cpd).

2.3. Results

2.3.1. Collinear facilitation

The results show that the contrast thresholds estimated in the collinear condition are significantly lower than in the orthogonal configuration at 8λ for 2 and 3 cpd (paired-sample *t*-tests between collinear and orthogonal contrast thresholds; 2 cpd: $t_5 = -2.818$, $p = 0.037$, $d = 1.15$[2]; 3 cpd: $t_5 = -5.314$, $p = 0.003$, $d = 2.16$) (Lev & Polat, 2011; Maniglia et al., 2011). For spatial frequency of 1 cpd collinear thresholds were significantly lower at both 6λ ($t_5 = -4.216$, $p = 0.008$, $d = 1.72$) and 8λ ($t_5 = -2.9$, $p = 0.034$, $d = 1.18$) (Fig. 3, panels A–C).

In order to allow comparisons with previous studies (see the Discussion section) we report the averaged contrast thresholds expressed in percentage contrast and the relative standard deviation (SD) for the three spatial frequencies tested. In addition we report only the percentage contrast relative to the statistically significant conditions. In particular, for 1 cpd: Collinear at 6λ = 0.98 ± 0.45%, orthogonal at 6λ = 1.28 ± 0.39%, collinear at 8λ = 0.96 ± 0.41%, orthogonal at 8λ = 1.23 ± 0.44%. For 2 cpd: collinear at 8λ = 2.11 ± 0.54%, orthogonal 8λ = 2.48 ± 0.44%. For 3 cpd: collinear 8λ = 3.48 ± 0.67%, orthogonal = 4.36 ± 0.91%.

In Fig. 3 we also report the normalized thresholds which were computed by taking the difference between the contrast thresholds obtained in the collinear configuration and in the orthogonal configuration for each target-to-flankers distance (λ) and for each spatial frequency (Fig. 3, panels D–F). We also express in percentage the difference (absolute values) between the contrast thresholds estimated in the collinear and orthogonal conditions: 0.27 ± 0.23%, 0.37 ± 0.29% and 0.87 ± 0.4% for 1, 2 and 3 cpd at 8λ respectively, while for 1 cpd at 6λ it was 0.29 ± 0.17%.

In addition we tested whether normalized thresholds differed significantly from zero (i.e., no modulation), thus indicating facilitation for negative values or suppression for positive values. Results on normalized thresholds confirmed the results reported above for the contrast thresholds obtained in the collinear and orthogonal configurations showed that normalized contrast thresholds are significantly below zero at 8λ for 1, 2 and 3 cpd (1 cpd: $t_5 = 3.89$, $p = 0.011$, $d = 1.58$; 2 cpd: $t_5 = 3.14$, $p = 0.025$, $d = 1.28$; 3 cpd: $t_5 = 5.35$, $p = 0.003$, $d = 2.18$) indicating consistent collinear facilitation, and at 6λ for 1 cpd ($t_5 = 3.98$, $p = 0.01$, $d = 1.62$) (Fig. 3, panels D–F).

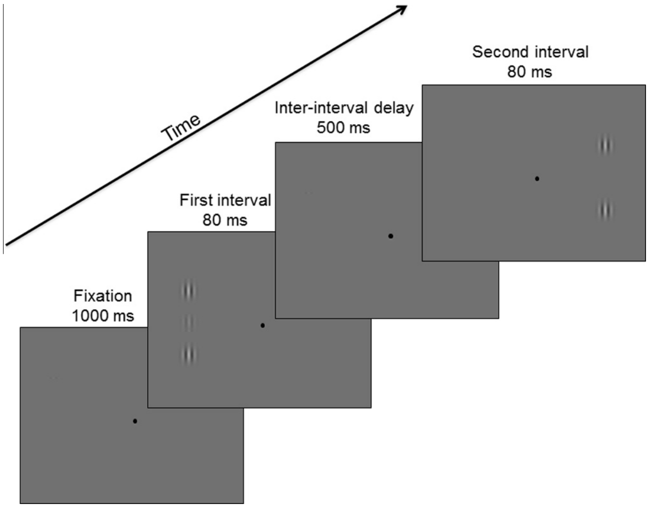

Fig. 2. Schematic representation of the procedure used in Experiment 1. The target is shown in the first temporal interval. The contrast of the target is increased for demonstrative purposes. See text for more details about the procedure.

3. Experiment 2: collinear facilitation with higher spatial frequencies

In Experiment 2 we tested collinear facilitation for higher spatial frequencies (i.e., 4 and 6 cpd) in order to better understand the role of spatial frequency in the magnitude of collinear facilitation with peripheral stimuli. Contrast thresholds were measured only for 8λ since in Experiment 1 we found facilitation for the higher spatial frequencies (i.e., 2 and 3 cpd) only at this target-to-flankers distance. Thus, in Experiment 2 we investigated whether with increasing spatial frequency in the near periphery collinear facilitation is strongly diminished or even absent.

3.1. Methods

Nine naïve participants took part in Experiment 2. Stimuli were the same as used in Experiment 1 except that the spatial frequencies were 4 and 6 cpd. We measured contrast thresholds at a target-to-flankers distance of 8λ. Apparatus and procedure were the same as used in the previous experiment.

3.2. Results

3.2.1. Collinear facilitation at 4 and 6 cpd

Fig. 4 shows the contrast thresholds estimated in the collinear and orthogonal conditions as a function of the spatial frequency. Paired sample *t*-tests showed that for both spatial frequencies contrast thresholds measured in the collinear condition are significantly lower than in the orthogonal configuration (4 cpd: $t_8 = -2.53$, $p = 0.035$, $d = 0.84$; 6 cpd: $t_8 = -2.64$, $p = 0.03$, $d = 0.88$). As in Experiment 1 we reported the average percentage contrast (and standard deviation) for the spatial frequencies tested: 4 cpd,

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[2] *d* refers to the Cohen's *d* effect size, calculated for paired samples *t*-tests as $d = \frac{t}{\sqrt{n}}$, where *t* is the *t*-value and *n* is the sample size. Cohen's *d* of 0.2 represents a small, 0.5 medium and >0.8 large effect size.

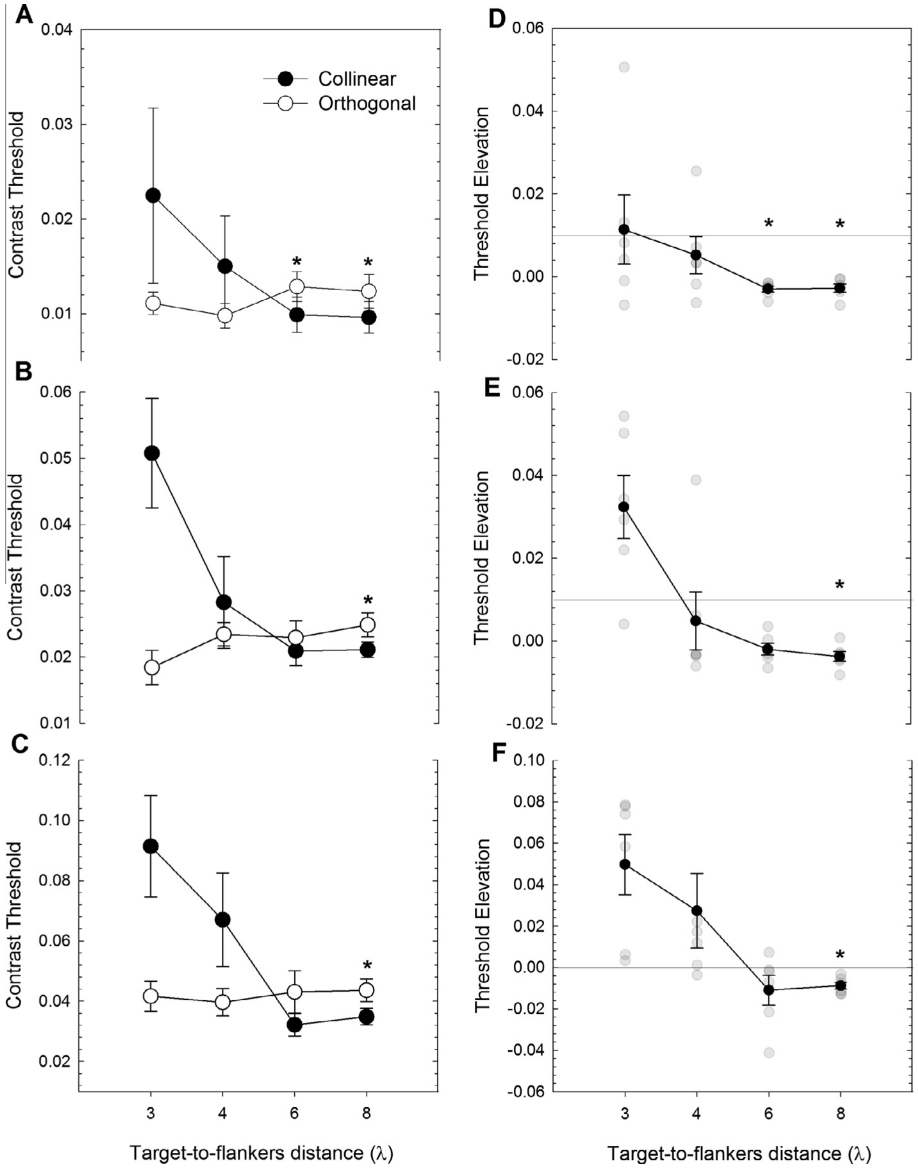

Fig. 3. Panels A–C show the mean contrast thresholds obtained of the collinear and orthogonal configurations as a function of target-to-flankers distance for the three spatial frequencies tested: panel A for 1 cpd (contrast thresholds for the collinear condition: 0.022 [SEM: 0.009], 0.015 [SEM: 0.005], 0.0098 [SEM: 0.001], and 0.0095 [SEM: 0.001]; contrast thresholds for the orthogonal condition: 0.011 [SEM: 0.001], 0.0097 [SEM: 0.001], 0.013 [SEM: 0.0015], 0.012 [SEM: 0.0018], respectively for 3λ, 4λ, 6λ, and 8λ), panel B for 2 cpd (contrast thresholds for the collinear condition: 0.051 [SEM: 0.008], 0.028 [SEM: 0.0069], 0.020 [SEM: 0.002], and 0.021 [SEM: 0.001]; contrast thresholds for the orthogonal condition: 0.0184 [SEM: 0.0025], 0.023 [SEM: 0.0017], 0.022 [SEM: 0.002], and 0.024 [SEM: 0.001], respectively for 3λ, 4λ, 6λ, and 8λ), and panel C for 3 cpd (contrast thresholds for the collinear condition: 0.091 [SEM: 0.016], 0.067 [SEM: 0.015], 0.032 [SEM: 0.003], and 0.034 [SEM: 0.002]; contrast thresholds for the orthogonal condition: 0.041 [SEM: 0.005], 0.039 [SEM: 0.004], 0.043 [SEM: 0.007], and 0.043 [SEM: 0.0036], respectively for 3λ, 4λ, 6λ, and 8λ). Asterisks represent a significant difference between the collinear and orthogonal condition for a specific target-to-flankers distance. Panels D–F show the threshold elevation (difference between contrast threshold estimated in the collinear and orthogonal configurations) as a function of target-to-flankers distance for the three spatial frequencies tested. Points represent normalized thresholds for each observer. On average normalized threshold were: panel D 1 cpd: 0.011 (SEM: 0.008), 0.005 (SEM: 0.004), −0.003 (SEM: 0.0007), and −0.002 (SEM: 0.0009), panel E 2 cpd: 0.032 (SEM: 0.007), 0.005 (SEM: 0.007), −0.0019 (SEM: 0.0014), and −0.0037 (SEM: 0.0011), and panel F 3 cpd: 0.049 (SEM: 0.014), 0.027 (SEM: 0.018), 0.01 (SEM: 0.007), and −0.008 (SEM: 0.001), respectively for 3λ, 4λ, 6λ, and 8λ. Asterisks represent threshold elevation values significantly below zero (i.e., collinear facilitation). Some sub-panels have a different ordinate scale. This is to highlight some differences in terms of contrast thresholds between the collinear and orthogonal conditions (panels A–C) and differences between normalized thresholds and zero (panels D–F). Error bars ± SEM.

collinear = 7.64 ± 6.29%, orthogonal = 10.6 ± 7.95%; 6 cpd, collinear = 11.9 ± 4.01%, orthogonal = 14.81 ± 6.07%.

Additionally, we computed normalized thresholds and then we compared them with respect to zero. Consistent with Experiment 1 we found that normalized thresholds are significantly lower than zero for both spatial frequencies (one sample *t*-test; 4 cpd: $t_8 = -2.53$, $p = 0.035$, $d = 0.84$; 6 cpd: $t_8 = 2.64$, $p = 0.03$, $d = 0.88$). The differences in percentage contrast (absolute values) between collinear and orthogonal condition were 2.95% (SD: 3.4%) and 2.91% (SD: 3.3%), for 4 and 6, respectively.

3.2.2. Contrast sensitivity

Despite finding some facilitation for 4 and 6 cpd at 8λ (Fig. 4), the following analysis shows that in the near periphery contrast sensitivity decreases with increasing spatial frequency. In particular, based on Polat (2009) we calculated the contrast sensitivity (1/contrast threshold) for collinear and orthogonal configurations as a function of the spatial frequencies used in the previous experiments (i.e., 1, 2, 3, 4 and 6 cpd) (Fig. 5). We compared the collinear configuration with the orthogonal configuration at 8λ since for this target-to-flanker distance Maniglia et al. (2011) and Lev and Polat

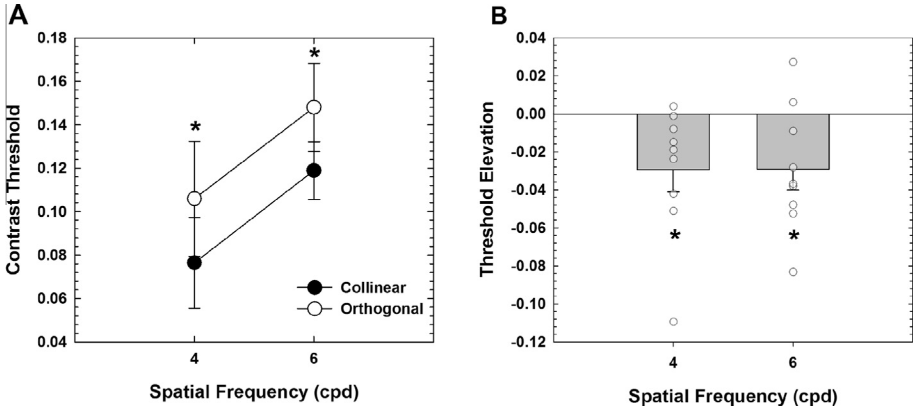

Fig. 4. (Panel A) Contrast thresholds for the collinear and orthogonal configurations as a function of the spatial frequency (cpd). For 4 cpd contrast thresholds are: 0.076 (SEM: 0.02) and 0.105 (SEM: 0.026) for collinear and orthogonal configurations, respectively. For 6 cpd contrast thresholds are: 0.12 (SEM: 0.013) and 0.14 (SEM: 0.02) for collinear and orthogonal configurations, respectively. Asterisks represent a significant difference between the contrast thresholds estimated in the collinear and orthogonal configurations for 4 and 6 cpd. (Panel B) Threshold elevation as a function of the spatial frequency (cpd). Points represent normalized thresholds for each observer (−0.0295 [SEM: 0.011] and −0.0291 [SEM: 0.011], for 4 and 6 cpd respectively). Asterisks represent threshold elevation values significantly below zero (i.e., collinear facilitation). Error bars ± SEM.

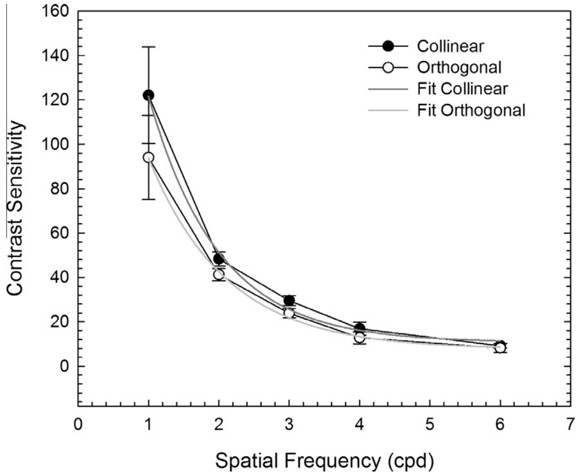

Fig. 5. Contrast sensitivity for collinear and orthogonal configurations is shown as a function of the spatial frequency. Dark gray continuous line represents the single exponential decay model fitted to the collinear configuration, whereas the bright gray continuous line represents the same single exponential decay model fitted to the orthogonal configuration. Error bars ± SEM.

(2011) found consistent collinear facilitation with stimuli presented in the near-periphery (4° eccentricity). Despite using different observers for the spatial frequencies, in this analysis we fitted a single exponential decay function to the contrast sensitivity values for the collinear configuration and the same model was fitted to the orthogonal condition. We then performed an F-test between the two fits to assess whether there was a difference between the two configurations (i.e., collinear vs. orthogonal). Non-linear fits and analysis were conducted using the OriginPro 8 software. The single exponential decay model was:

$$y = y_0 + Ae^{-x/t} \tag{2}$$

where y_0 is the y offset (i.e., the asymptote), A is the amplitude of the function and t is the decay constant. Table 1 reports the estimated parameters with the fitting procedure for the collinear and orthogonal configurations.

The F-test reported that the two configurations were statistically different ($F_{3,4} = 15.65$, $p = 0.011$). Thus, the results showed that in the near-periphery contrast sensitivity and collinear facilitation are statistically higher for low spatial frequencies (1 and 2 cpd).

Table 1
Estimated parameters of the simple exponential decay model fitted to the contrast sensitivity values for the collinear and orthogonal configurations.

Parameters	Value	SE
Collinear. Adjusted R-square = 0.992		
y_0	10.72272	3.492
A	302.632	34.673
t	0.995	0.119
Orthogonal. Adjusted R-square = 0.997		
y_0	7.634	1.734
A	212.528	12.874
t	1.108	0.0785

4. Experiment 3: flankers' visibility

The evidence that collinear facilitation at 8λ decreases with increasing spatial frequency could also depend on flankers' visibility. That is, the reduced visibility of flankers in the near-periphery of the visual field may decrease the effect of collinear facilitation. In order to test for this possibility we conducted a control experiment measuring the contrast threshold for a central Gabor flanked by two very high contrast flankers (i.e., 0.99 Michelson contrast).

4.1. Method

4.1.1. Stimuli and procedure

Five naïve participants took part in Experiment 3. The method was the same as described for the previous experiments except that the spatial frequencies tested were 4 and 6 cpd, and the flankers' contrast was either 0.6 or 0.99 (Michelson contrast). We compared contrast detection thresholds for collinear and orthogonal configurations at a target-to-flankers distance of 8λ. Contrast detection thresholds were measured at 4° of eccentricity. The procedure was the same as used in Experiments 1 and 2. Participants performed the task in one day.

4.2. Results

Fig. 6 shows the results of Experiment 3. We computed threshold elevation as the difference between collinear and orthogonal

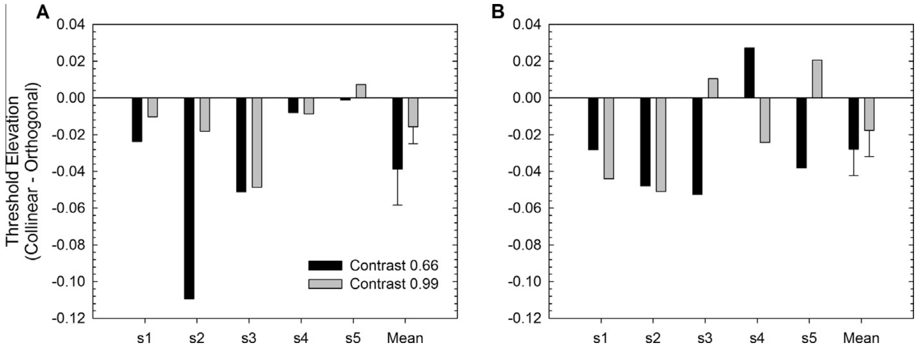

Fig. 6. Contrast threshold elevation computed as the difference between the contrast thresholds estimated in the collinear configuration and the orthogonal configuration, for 4 (panel A) and 6 cpd (panel B), and for flankers' contrast of 0.66 and 0.99 (Michelson contrast). Mean and individual data (s1–s5) are reported. Mean normalized thresholds for 4 cpd: -0.038 (SEM: 0.019) and -0.016 (SEM: 0.009) for 0.66 and 0.99 flankers' contrast, respectively. Mean normalized thresholds for 6 cpd: -0.028 (SEM: 0.014) and -0.018 (SEM: 0.014) for 0.66 and 0.99 flankers' contrast, respectively. Error bars ± SEM.

threshold at 8λ for each spatial frequency and separately for each flankers' contrast level (i.e., 0.6 and 0.99 Michelson contrast). A repeated measures ANOVA including the Spatial Frequency and the Flankers' contrast as factors did not report any significant main effect (Spatial Frequency: $F_{1,4} = 0.16$, $p = 0.71$, $partial\text{-}\eta^2 = 0.04$; Flankers' contrast: $F_{1,4} = 1.53$, $p = 0.28$, $partial\text{-}\eta^2 = 0.28$) or interaction ($F_{1,4} = 0.13$, $p = 0.74$, $partial\text{-}\eta^2 = 0.03$). Thus, the results show that normalized thresholds estimated in the high contrast condition (0.99) did not differ significantly from those obtained in the lower contrast condition (0.66) and this was the case for both spatial frequencies (i.e., 4 and 6 cpd).

To further confirm these results, we also performed paired samples *t*-tests between the low contrast flankers and the high contrast flankers separately for the two spatial frequencies: 4 cpd: $t_4 = 0.98$, $p = 0.38$, $d = 0.44$; 6 cpd: $t_4 = 0.46$, $p = 0.66$, $d = 0.21$. These results confirm that there was not a significant difference between the two contrast levels and further suggest that the reduction in magnitude of collinear facilitation for mid-high spatial frequencies was not due to flankers' visibility but more likely to the spatial frequency selectivity of neurons responding to peripheral stimuli.

5. Discussion

In a series of experiments we showed that collinear facilitation at the near periphery of the visual field (4° of eccentricity) is consistently present for a target-to-flankers distance of 8λ. Interestingly, for a spatial frequency of 1 cpd observers also showed facilitation at 6λ. The amount of collinear facilitation compared to the baseline (i.e., the orthogonal configuration) decreases exponentially with increasing spatial frequency, the opposite of what Polat (2009) reported for foveal presentation. Concerning collinear facilitation in fovea Polat (2009) reported threshold elevation, expressed as the log ratio between unflanked and flanked conditions, as a function of spatial frequency, showing that the highest reduction of threshold for the collinear condition with respect to the orthogonal condition (the baseline condition for peripheral collinear facilitation) was ~0.225 log units for the highest spatial frequency (12 cpd). Calculating threshold elevation in a similar manner (i.e., $\log_{10}$ ratio between orthogonal and collinear condition), we found that in general the effect of peripheral collinear facilitation is stronger for the lowest spatial frequency tested (1 cpd: 0.11 log units), while for the highest spatial frequency it is greatly reduced (6 cpd: 0.05 log units). This is similar to what happens in fovea for low spatial frequencies where the sensitivity for the collinear condition is between 0.03 and 0.015 log units (Polat, 2009).

To date, only Maniglia et al. (2011) have measured peripheral collinear facilitation using similar parameters (i.e., target-to-flankers distances) to those used in the present study. However, Maniglia et al. (2011) used a different procedure (i.e., method of constant stimuli; MCS), a yes/no task and only a spatial frequency of 4 cpd. In particular, they reported normalized thresholds ($\log_{10}$ ratio between orthogonal and collinear threshold) for "low contrast thresholds" (i.e., the contrast value that produced 60% detection) and "high contrast thresholds" (i.e., the contrast value that produced 80% detection) both showed a strong reduction of collinear facilitation at 8λ, with 0.04 and 0.08 log units respectively. Such reduced collinear effect could be attributed to the different methods used, with the filling-in effect inducing more false alarms in the one interval presentation with respect to the temporal 2AFC used in the present study.

Shani and Sagi (2005) used a similar paradigm to that used in the present study (i.e., staircase with a temporal 2AFC with stimuli presented at 4° of eccentricity), but with a shorter target-to-flankers distance (4λ) and a spatial frequency of 4 cpd. The authors reported the percentage contrast of two subjects tested on collinear and orthogonal conditions: subject 1 obtained 16.5 ± 0.6% for the collinear configuration and 14.2 ± 1.1% for the orthogonal configuration, while subject 2 obtained 7.5 ± 0.7% and 6.3 ± 0.0.5%, for collinear and orthogonal configurations, respectively. In a subsequent experiment Shani and Sagi (2005) scaled the spatial frequency for the cortical magnification factor using a spatial frequency of 1.84 cpd. Despite finding lower contrast thresholds, authors did not find consistent collinear facilitation (subject 1: collinear configuration = 1.7 ± 0.0%, orthogonal configuration = 1.9 ± 0.3%; subject 2: collinear configuration = 2.1 ± 0.2%, orthogonal configuration = 1.8 ± 0.1%). In this study we tested target-to-flankers distances beyond 4λ and, in agreement with recent literature (Lev & Polat, 2011; Maniglia et al., 2011), we considered the optimal target-to-flankers distance for collinear facilitation in the near periphery to be 8λ. Indeed, the contrast thresholds we estimated at 8λ in the collinear and orthogonal conditions are, on average, lower than those measured by Shani and Sagi (2005) at 4λ. The difference between the contrast thresholds estimated in the collinear condition of the present study and those of Shani and Sagi (2005) is 3% measured at 8λ [Maniglia et al., 2011] and 4λ [Shani & Sagi, 2005]), whereas for the orthogonal condition the difference between thresholds is 9% (8λ [Maniglia et al., 2011] and 4λ [Shani & Sagi, 2005]). Such a difference may indicate that in the near periphery at 4λ lateral interactions are still suppressive and lead to higher contrast thresholds for the collinear configuration with respect to the orthogonal configuration. If we compare another similar condition we used to that of Shani and Sagi (2005) (i.e., 4 cpd and 6λ [present study] vs. 4 cpd and 4λ [Shani & Sagi, 2005]), the difference in contrast thresholds is reduced for the collinear condition (7%) but it is almost the same for the orthogonal condition (4%).

Similarly, Giorgi et al. (2004) measured peripheral collinear facilitation for a range of eccentricities and target-to-flankers distances with a temporal 2AFC. They reported a contrast threshold reduction of ~0.1 log units already at 4λ for 2°, 4° and 6° of eccentricity. However, the authors used a target-alone condition as baseline so it is not possible to determine whether this reduction of threshold is due to collinear facilitation or to spatial uncertainty reduction where collinear flankers acted as spatial cue for the central target. Interestingly the amount of threshold reduction reported by Giorgi et al. (2004) is the same as we found, with different target-to-flankers distances (4λ vs. 8λ) and different baseline conditions (no flankers vs. orthogonal flankers). However, further psychophysical investigations would be necessary to assess whether there is similar collinear facilitation at other eccentricities.

Overall, using a temporal 2AFC we showed consistent collinear facilitation in the periphery of the visual field (see Giorgi et al., 2004 for similar results). However, we argue that for future investigations it is important to consider that collinear facilitation at the periphery is sensitive to the methodological procedure (Giorgi et al., 2004) and the stimulus parameters, as well as being highly variable among subjects (Lev & Polat, 2011). Additionally, temporal 2AFC at the periphery may be limited by the subjects' ability to maintain fixation between the first and the second interval (Lev & Polat, 2011). Despite these possible limitations of the procedure employed our results seem to be consistent with previous studies that used a yes/no paradigm (Lev & Polat, 2011; Maniglia et al., 2011) and are also plausible when considering the spatial frequency tuning of the periphery of the visual field (Rovamo and Virsu, 1979).

Our results are consistent with the idea that collinear facilitation peaks between 3 and 6 cpd for the fovea and at lower spatial frequencies in the periphery (e.g., 0.5–1 cpd), where the spatial frequency selectivity is low-pass (Banks et al., 1991). In addition, the pattern of collinear facilitation we found cannot be explained by eye movements since the presentation of the vertical configuration was very brief (80 ms), i.e., less than the time required for a saccadic eye-movement (Carpenter, 1988; Martinez-Conde et al., 2004). In each trial we randomized both the temporal interval in which the target could be presented and the visual hemi-filed. Indeed, the trend of the amount of collinear facilitation follows a very different pattern to that observed in fovea (Polat, 2009).

Perceptual Fields (PF; the equivalent in visual perception to the Classical Receptive Field) are usually modeled as having 2 or 3 antagonistic subunits (Polat & Tyler, 1999; Watson, 1992; Watson, Barlow, & Robson, 1983). Psychophysical studies on lateral interactions support the idea that inhibition is the product of the integration of inputs within the same PF, while facilitation is a between-PFs interaction (Polat & Sagi, 1993; Zenger & Sagi, 1996). Lev and Polat (2011) proposed that the size of the suppressive zone can be considered as an index for estimating the size of the PF. Since peripheral vision is characterized by cortical magnification, in order to produce an optimal neural activation, visual stimuli must be rescaled in size as a function of the eccentricity (Daniel & Whitteridge, 1961). Thus, the center-to-center distance of the optimal collinear facilitation increases from the fovea to the periphery as a consequence of the increasing size of the PF (i.e., 3λ vs. 8λ). Moreover, our results suggest that in the near-periphery there is a shift of the optimal spatial frequency for collinear facilitation towards lower spatial frequencies (Gelb & Wilson, 1983a, 1983b; Graham, 1989). This observation is also consistent with electrophysiological studies in monkeys and cats. Devalois, Albrecht, and Thorell (1982) using single-cell recording in macaque's V1 found that foveal and parafoveal visual cortex have similar proportion of simple and complex cells, and similar selectivity for spatial frequency and orientation tuning. However, the sample of recorded parafoveal cells did not include cells tuned to high spatial frequencies. Moreover, the total range of spatial frequency peaks is narrower in the parafoveal region. Additionally, Movshon, Thompson, and Tolhurst (1978) in an electrophysiological study on cats' areas 17 and 18 showed that average preferred spatial frequency declines smoothly with increasing eccentricity.

Pooresmaeili and colleagues (2010), using single cell recording in the macaque' striate cortex, reported a lack of collinear facilitation for stimuli between 1.5° and 2.5° of eccentricity, and claimed that there is no perceptual enhancement from collinear flankers with peripheral presentation. Since the authors used parameters that are more suitable for eliciting collinear facilitation in fovea (high spatial frequency and short target-to-flankers distance), it is possible that the lack of facilitation they reported resulted from a non-optimal selection of parameters, in similarity to previous psychophysical results that did not report consistent collinear facilitation with stimulus presentation in the near-periphery (Shani & Sagi, 2005; Williams & Hess, 1998; Zenger-Landolt & Koch, 2001).

Future studies could apply this recently discovered scaling of target-to-flankers distance in order to re-establish peripheral collinear facilitation, bringing new insight to previous evidence for collinear suppression at the periphery of the visual field.

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