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Multi-component correlate for lateral collinear interactions in the human visual cortex

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ABSTRACT

Perceptual facilitation, a decrease in detection threshold for low-contrast Gabor patches (GPs) occurs when the GP is flanked by collinearly oriented high-contrast patches. There is earlier evidence suggesting a spatial architecture of excitatory and inhibitory interactions. Here we used Visual Evoked Potentials (VEPs) to study the temporal structure of this process. We measured VEPs elicited by a foveal near-threshold target GP presented in isolation (T), T in the presence of two flanking collinear high-contrast GPs (lateral masking, LM), or the flankers alone (F). Stimuli were presented for 50 ms every 1000 ms. The choice of the set parameters elicited behavioral facilitation of T detection. Significant modulation of peak amplitudes in LM compared with linearly summed waveforms elicited by T and F was found for five alternating polarity components, ranging from 65 to 290 ms after stimulus onset. In the frequency domain, suppression at lower frequencies (up to 0.8 log units) was followed by facilitation at higher frequencies (4–6 Hz, up to 0.8 log units). Although no differences in the latencies were found, lateral interactions were reflected by non-linear waveform modulation of multiple components and frequencies, including components as early as 65–75 ms. Spectrum analysis suggests that both suppression and facilitation may be found for the same configuration of stimuli, simultaneously, distributed at different temporal frequencies and/or sources. The physiological correlates of lateral interactions may thus originate at multiple sources, only some of which are explicitly facilitatory. The final perceptual outcome of this complex spatio-temporal representation is determined by combining sensory and cognitive factors.

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1. Introduction

Visual processing is based on integrating spatially localized inputs according to relevant contextual information, the results being a cohesive percept of object borders and contours. One perceptual manifestation of such a process is the lateral masking effect, measured as a decrease in detection thresholds for low-contrast Gabor patches (GPs) when flanked by collinearly oriented high-contrast patches, which was previously reported (Polat & Sagi, 1993, 1994a, 1994b). Detection facilitation is found when a low-contrast target is presented simultaneously with the maskers (Adini & Sagi, 2001; Adini, Sagi, & Tsodyks, 1997; Bonneh & Sagi, 1998; Cass & Alais, 2006; Cass & Spehar, 2005; Levi, Hariharan, & Klein, 2002; Polat & Sagi, 1993, 1994a, 1994b; Solomon & Morgan, 2000; Williams & Hess, 1998; Woods, Nugent, & Peli, 2002) or with a delay (Tanaka & Sagi, 1998) and occurs preferentially in collinear configurations (Chen & Tyler, 1999; Polat, 1999; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998). The facilitation of target

detection is most prominent when flankers are separated from the test by three wavelengths (λ), decreasing for longer distances. Thresholds are elevated for shorter target-to-flanker separations (Polat & Sagi, 1993). Collinear facilitation is found in the early visual cortex (Crook, Engelmann, & Lowel, 2002; Kapadia, Ito, Gilbert, & Westheimer, 1995; Khoe, Freeman, Woldorff, & Mangun, 2004; Mizobe, Polat, Pettet, & Kasamatsu, 2001; Polat & Norcia, 1996; Polat et al., 1998), suggesting that early stages of visual processing are involved in the effect. On the other hand, flanker facilitation benefits from focused attention in human observers (Freeman, Driver, Sagi, & Zhaoping, 2003; Freeman, Sagi, & Driver, 2001; Giorgi, Soong, Woods, & Peli, 2004; Khoe, Freeman, Woldorff, & Mangun, 2006) and monkeys (Ito & Gilbert, 1999), suggesting that higher levels of processing are involved in collinear facilitation.

The physiological basis of the observed lateral interactions may be the result of a network of long-range connections that exist between similar orientation columns (Bolz & Gilbert, 1989; Gilbert & Wiesel, 1985; Grinvald, Lieke, Frostig, & Hildesheim, 1994; Ts'o, Gilbert, & Wiesel, 1986; Stettler, Das, Bennett, & Gilbert, 2002). These connections extend for long distances and may convey contextual information (Fitzpatrick, 1996; Gilbert & Wiesel, 1983;

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Schmidt, Goebel, Lowel, & Singer, 1997). However, several studies have argued that the horizontal connections are too short and/or too slow to explain the observed patterns of lateral interactions and have suggested a mechanism based on top-down feedback mechanisms (e.g., Angelucci, Levitt, Walton, Hupe, Bullier, & Lund, 2002; Levi et al., 2002; Rockland & Lund, 1982; for a review, see Angelucci & Bressloff, 2006).

In humans, physiological measurements of the behavioral facilitation of target detection by flankers at 3λ separation were performed for the first time using the VEP (Polat & Norcia, 1996). The evidence for facilitation came from deviations from linear summation of responses to targets and flankers presented alone or in combination. The results indicated that the effective contrast of the target GP was increased when it was presented in the context of collinear high-contrast flankers. In another particularly relevant study, event-related potentials (ERPs) were recorded to investigate the neural bases of collinearity effects in the time domain (Khoe et al., 2004). Early (80–140 ms after stimulus onset) waveform modulations were observed at the midline occipital scalp-recorded ERPs as a function of collinearity, whereas later (245–295 and 300–350 ms) effects were focused at lateral occipital scalp sites. From the cortical distribution and the latencies, the authors inferred that whereas the earlier effects are consistent with a generator in the primary visual cortex, the later pattern reflects activity in the extrastriate visual cortex. However, because perifoveal GP target stimuli with high-contrast pedestals were used in Khoe et al.'s study, no direct comparison regarding the facilitation of low-contrast target representation in isolation can be drawn from these findings. The study of Polat and Norcia (1996) was performed using steady-state recordings that showed that phase shifts accompanied the facilitation effect, but absolute latencies were not determined.

We aimed to study the responses in both the time and the frequency domains in order to more completely characterize the lateral interactions induced by collinear configuration. To this end, VEPs were recorded under conditions that produce the most prominent behavioral facilitation of foveal GP detection. Non-linear summation of the responses evoked by target and flankers, when presented together, compared to their presentation in isolation, was used to detect the presence and sign of lateral interactions. Waveform modulations, which are different from those predicted by linear summation, were found for multiple components and frequencies, including latencies as early as about 65–75 ms, compatible with generators in early visual cortex (Li, Piech, & Gilbert, 2006). We also found much later effects of up to about 300 ms. Spectrum analysis suggests that the perceptual outcome reflects a combination of both suppressive and facilitatory effects distributed at different frequencies. Thus, lateral interactions may originate at multiple sources, which are just partly facilitatory.

2. Methods

2.1. Participants

VEPs were recorded in 12 volunteers (6 females, mean age 31.6) with normal or corrected-to-normal vision in both eyes. All participants signed the informed consent form.

2.2. Stimuli

The stimuli were localized gray-level gratings (Gabor patches, GP) with a spatial frequency of six cycles per degree (wavelength, λ) and equal distribution (STD, σ , allowing minimum two cycles in the GP), modulated from a background luminance of 40 cd m^{-2} (Fig. 1). Stimuli were presented binocularly on a Richardson Electronics MR200HBM monochrome monitor, using a Power Macintosh G4 computer (800×600 pixels at a 72 Hz refresh rate). The effective size of the monitor screen was 34×26 cm, which, at a viewing distance of 150 cm, subtended a visual angle of 9.9×12.9 deg. The experiment was conducted in a dark environment, wherein the only ambient light came from the monitor.

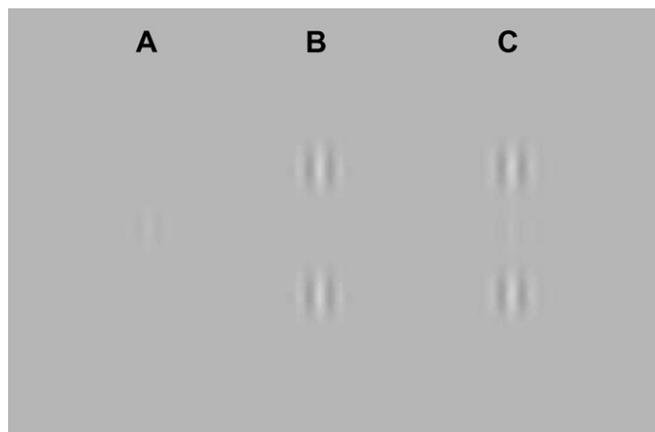


Fig. 1. Stimuli. (A) Target alone (T)—a single Gabor patch at a contrast of 6% (contrast increased for presentation). (B) Mask alone—two flanking collinear GPs at a contrast of 40%, separated by 3λ (flankers, F). (C) T in the presence of flankers, each separated from T by 3λ (lateral masking, LM).

2.3. Paradigm

Three conditions were tested: (1) a foveal target GP presented in isolation at a contrast of 6% (at or very close to the detection threshold) (T), (2) T in the presence of two flanking collinear GPs at a contrast of 40% (lateral masking, LM), and (3) the flankers alone (F). A comparison between the collinear and orthogonal configurations was performed in a subgroup of five subjects. The orthogonal configuration was similar to the collinear in all parameters besides the orientation of the flankers was orthogonal to the orientation of the target (i.e., 90 deg difference). Stimuli were presented for 50 ms every 1000 ms, with no change in the average background luminance. The spatial distance between the target and the flankers was three wavelengths (λ), which is thought to be outside the receptive fields (RF) (Mizobe et al., 2001; Polat, 1999; Polat, Norcia, Mizobe, & Kasamatsu, 1996; Polat & Sagi, 1993, 2006; Zenger & Sagi, 1996). Each condition consisted of 10 trials (10 s each), during which all the parameters were kept constant. Conditions were presented in random order. A small, 2-min arc fixation point, located at the center of the screen, indicated the T location. Participants were instructed to maintain their fixation and to avoid eye movements during the trials. The set of parameters used for the VEP recording was tested psychophysically and elicited significant facilitation of T detection (mean d' improvement of 1.83, from 0.23 (± 0.49 , STD) for T and 2.06 (± 0.94 , STD) for LM ($p = .001$, paired t -test), tested in a subgroup of eight subjects, as previously described (Polat & Sagi, 1993)).

2.4. VEP recording and signal processing

The EEG was sampled at 432 Hz (filtered between 0.1 and 1000 Hz, amplified by 50,000 with Grass Model 12 amplifiers) from a cruciform array of five electrodes centered at a midline occipital site (O_2), spaced by 3 cm (referenced to the midline frontal site, F_2). For every condition, the averaged VEPs were computed over a 1000-ms period, for 100 trials per condition. Runs composed of 10 trials were recorded; for each run the mean of additional two periods of 1000 ms each, at the beginning and at the end of each run, was taken as the baseline for the run and was not included in averaging. Trials containing artifacts were rejected (thresholded at $200 \mu\text{V}$), as were trials containing eye movements (detected by visual inspection, less than 5% of trials).

The waveforms of all the subjects were first entered into a within-subject ANOVA and the standard deviation in the stimulated periods was compared against the standard deviation of the baseline (Greenhouse–Geisser correction was applied to correct for non-sphericity), to insure significance of the VEPs. Next, the waveforms of the evoked responses were analyzed separately for each subject. Peak amplitudes were measured for five alternating polarity components: P0, N0 (i.e., C1), P1, N1, and P2 (for mean peak latencies, see Table 1). “Local peak amplitude”

Table 1
Latencies of the five tested components

	LM	F	T + F (linear prediction)
P0	73.4 \pm 24.3	66.6 \pm 29.1	57.8 \pm 28.2
N0	97.6 \pm 26.4	101.0 \pm 33.3	92.5 \pm 32.9
P1	160.1 \pm 26.7	162.4 \pm 24.9	164.6 \pm 25.8
N1	222.4 \pm 22.5	225.7 \pm 20.9	223.2 \pm 20.6
P2	293.4 \pm 16.1	294.0 \pm 21.5	288.4 \pm 27.2

Mean peak latency \pm STD (ms after stimulus onset).

within a constant time-window of 50 ms was used to detect the maxima and minima; the “local peak” is defined as having greater voltage than the average of the 3–5 points on either side (as opposed to the “simple peak” that may occasionally produce an artifact on the edge of the time-window) (Luck, 2005). Due to variability in the latencies between subjects we chose the least variable peak (P1, the most salient peak in the time course) as the reference component. Next, the individual latencies of the remaining four peaks, relative to the P1 latency within each subject were detected. The N1 peak (also known as N250) with a latency that is within the range reported in the literature was detected. The negative peak preceding the P1 peak (also known as C1 in the literature) was termed N0, the positive peak following the N1 peak was termed P2, and the positive peak preceding the N0 peak was termed P0.

A linear prediction of the LM response was calculated as a sum of the time courses evoked by T and F, each presented alone (T + F) (see Fig. 2). Comparison of the peak amplitudes between the LM and the linear prediction response was performed using within-subject ANOVA (2 conditions × 5 peaks × 12 subjects), followed by pair-wise comparisons per peak performed using paired *t*-tests.

On average, there was a slightly higher signal-to-noise ratio (SNR) in the left electrode compared with O₂; however, there were no significant differences in the peak amplitudes under the LM condition between the O₂ and the two electrodes located left and right of it (within-subject ANOVA, $F(4,2) = 0.3, p = .7$). The electrode with the maximal SNR varied among subjects (either left or right). To avoid selection bias between the electrodes in different subjects, the central recording channel was selected for the group averages (O₂).

The power spectra in the 2–10 Hz frequency band were calculated separately for each subject and then averaged across subjects. Signal spectrum had an exponential profile and energy content at higher frequencies was insignificant; therefore, frequencies beyond 10 Hz were not analyzed. Thus, data presentation is consistent with the study of Polat and Norcia (1996), focusing on 4 Hz, and it includes surrounding frequencies. The first count of the spectrum, mainly representing the DC (i.e., the mean of the originating time course; 1 Hz), was disregarded. Similarly, the power spectra for the linear prediction waveforms were calculated per subject. The frequency domain comparisons between conditions were performed using paired *t*-tests on the grand averages. A spectral modulation index (i.e., the interaction index) was calculated as the log₁₀ of the ratio between the power spectrum of the linear prediction and LM at each frequency. Thus, ratios above zero indicate suppression, whereas ratios below zero indicate facilitation. The interaction indices obtained in the collinear and orthogonal configurations were compared using a paired *t*-test.

3. Results

3.1. Waveform analysis

The evoked voltage deflections under all conditions were significantly different from baseline, as demonstrated by comparison of

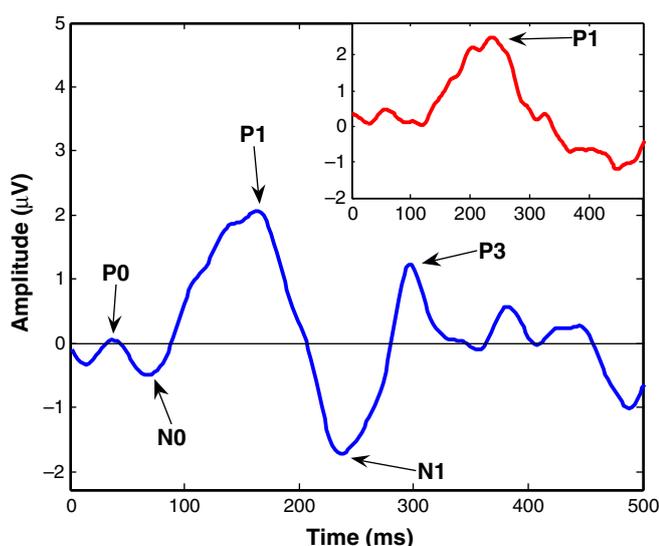


Fig. 2. Representative waveforms. The average waveform (time courses of 1000 ms, 12 subjects) of the VEPs, under the LM condition, is presented (blue line). Arrows indicate the five alternating components (positive and negative) that were analyzed: P0, N0, P1, N1, and P2. The average waveform under the T condition is presented in the inset (red line). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the standard deviation in the stimulated periods against the baseline across conditions (within-subject ANOVA, three conditions, $F(2,22) = 14.823, p < .001$; corrected $p < .001$, Greenhouse–Geisser $\epsilon = 0.77$) and per condition, including T that was near threshold and produced a lower amplitude response than that evoked by F and LM ($p = .034, .011, \text{ and } .001$, Bonferroni corrected, T, F, and LM, respectively). Five alternating polarity components were detected in the waveforms evoked under the conditions containing high-contrast (40%) GPs, F, and LM (P0, N0 (i.e., C1), P1, N1, P2; Fig. 2; for latencies, see Table 1). The response evoked by a low-contrast (6%) target has a much longer latency of the P1 component (224.2 ± 24.0 , mean \pm STD) than is observed under the F or LM conditions (162.4 ± 24.9 and 160.1 ± 26.7 , mean \pm STD, F and LM, respectively). In addition, the high-amplitude components N1 and P2 are missing in the waveform evoked by T (Fig. 2).

The overall waveform elicited by LM was largely dominated by the high-contrast flankers; however, comparison of LM vs. the linear prediction showed significant differences with all five tested components (within-subject ANOVA, two conditions, main effect of condition, $F(1,11) = 10.024, p = .025$; condition × peak interaction, $F(4,44) = 6.04, p = .002$; for *p*-values of the paired *t*-tests, see Table 2; Figs. 3 and 4). There were no significant differences in latency in any of the components except P1, the latency of which is shorter by 4.5 ms in LM (for *p*-values, see Table 2). The N1 component showed higher absolute amplitude in LM, whereas the remaining components showed higher absolute amplitudes in the prediction compared with LM (Figs. 3 and 4). Comparison between the collinear and orthogonal configurations in a subgroup of five subjects showed that the difference between LM and the linear prediction is significantly larger for the collinear configuration for all peaks excluding P1 ($p = .035$, paired *t*-test).

3.2. Spectrum analysis

Whereas a low-contrast target presented to the fovea (T) induces a response in the lower frequencies, as indicated by the spectrum, the response to the high-contrast flankers (F) has a more evenly distributed spectrum (Fig. 5A). The difference between the spectrum of the response elicited by LM and the linearly predicted one reflects both suppression and facilitation (Fig. 5B). The interaction index, calculated as the ratio between the spectrum of the linear prediction and LM at each frequency, was used to visualize the nature of the observed non-linear interactions (Fig. 5C). Suppression peaks at the lowest frequency (0.84 log units) were followed by facilitation at higher frequencies (4–6 Hz, peak at 6 Hz, -0.82 log units). Comparison between the collinear and orthogonal configurations in a subgroup of five subjects showed that the interaction index is significantly lower (i.e., more facilitatory) for the collinear configuration in the frequency range of facilitation (4–6 Hz, $p = .018$, paired *t*-test).

4. Discussion

The current study provides neuro-physiological evidence for a complex pattern of collinear interactions: both suppression and

Table 2
p-Values of comparisons for the five waveform components

	LM vs. prediction (waveform peak amplitude)	LM vs. prediction (waveform peak latency)
P0	0.01	0.14
N0	0.05	0.60
P1	0.01	0.05
N1	0.04	0.81
P2	0.03	0.49

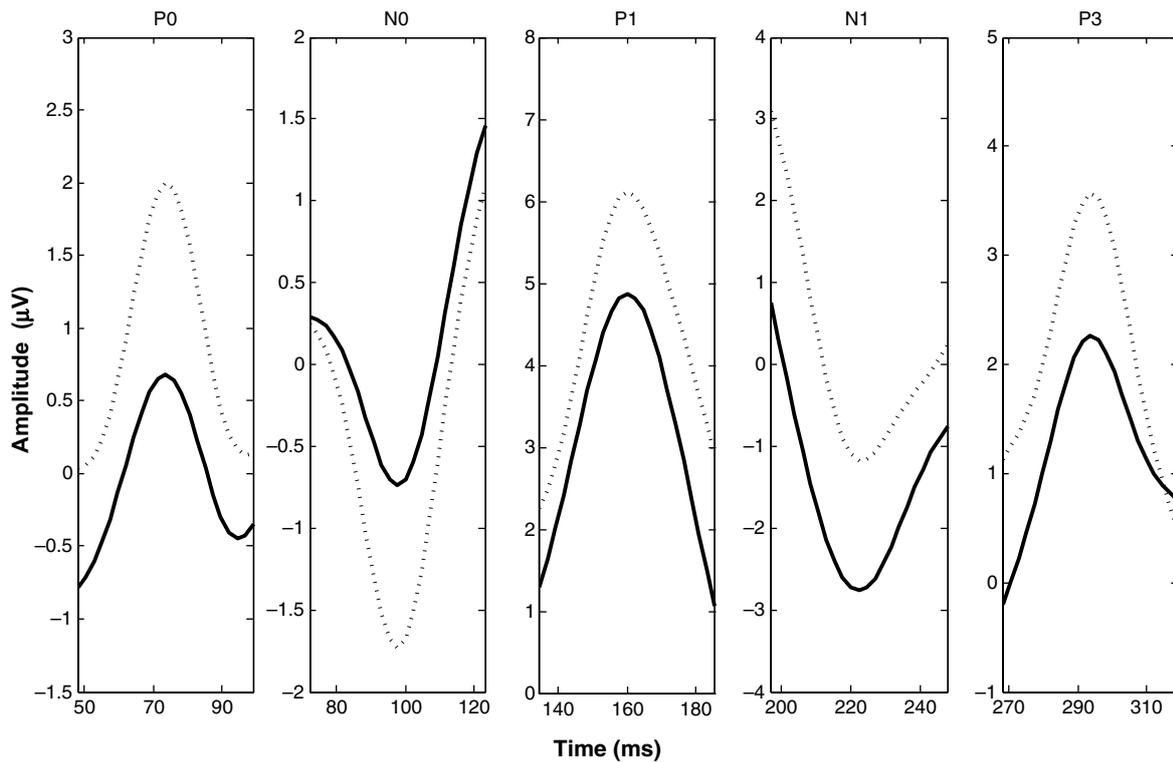


Fig. 3. The VEP components: LM vs. prediction. The averaged time courses (12 subjects) for the five detected components (for latencies, see Table 1). The peak amplitude values of LM and the linear prediction (T + F) were measured per subject, averaged and plotted within a constant time-window around the peak (i.e., ± 28 ms of the peak amplitude latency).

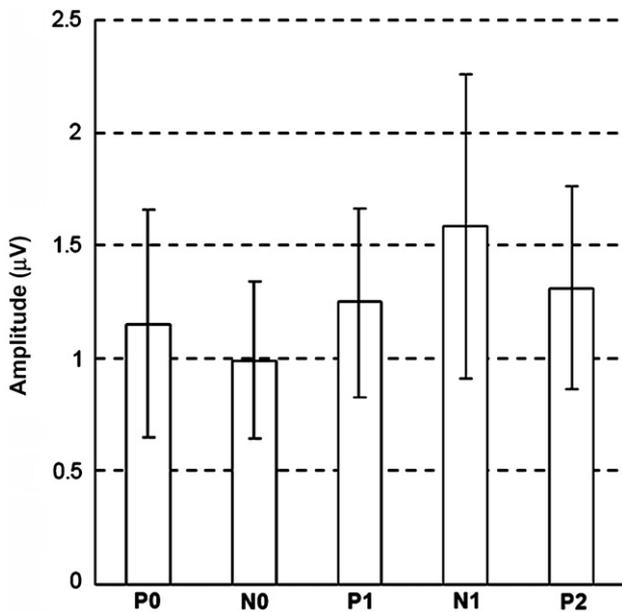


Fig. 4. Peak amplitude values of LM vs. prediction. The difference (absolute value) between peak amplitudes of LM and the linear prediction (T + F), measured per subject (mean \pm STD), for the five detected components (for latencies, see Table 1). The differences between the measured and the predicted amplitude are significant, with no significant differences in the latencies of all components except P1, the latency of which is shorter by 4.5 ms in LM (for *p*-values, see Table 2).

tion of signal amplitudes when a low-contrast target is presented in the context of two high-contrast flankers. While the latencies could be predicted linearly, there was a non-linear effect on the amplitude. However, because the waveform modulation, which either increases or decreases in amplitude, does not reflect the direction of interactions (Luck, 2005), the frequency domain was investigated. The spectrum analyses revealed a complex effect underlying the observed spatial interactions. Although the amplitude modulation at the lower frequencies indicates suppression, there is evidence for facilitatory effects at higher frequencies, in response to the same stimulus. Thus, the findings of the current study provide evidence for an architecture in the temporal domain, extending the architecture in the spatial domain suggested earlier (Adini & Sagi, 2001; Adini, Sagi, & Tsodyks, 2002; Adini et al., 1997; Kapadia, Westheimer, & Gilbert, 2000; Kapadia et al., 1995; Kasamatsu, Kitano, Sutter, & Norcia, 1998; Kasamatsu, Polat, Pettet, & Norcia, 2001; Polat, 1999; Polat & Bonneh, 2000; Polat & Sagi, 2006, 2007; Polat et al., 1998; Victor & Conte, 1991; for a review, see Angelucci & Bressloff, 2006; Series, Lorenceau, & Fregnac, 2003). The results suggest that temporal properties of the response may alter and even reverse the nature of the interaction, from suppression to facilitation and vice versa, as was also suggested earlier.

4.1. Comparison to previous studies

In an earlier particularly relevant study, event-related potentials (ERPs) were recorded to investigate the neural bases of collinearity effects in the time domain (Khoe et al., 2004). As in our data, early (80–140 ms after stimulus onset) waveform modulations were observed at the midline occipital scalp-recorded ERPs as a function of collinearity, whereas later (245–295 and 300–350 ms) effects were focused at lateral occipital scalp sites. However, the substantial differences in stimuli pose limits for comparing the

facilitation at different temporal frequencies. Significant differences were found between the linearly predicted and the measured waveform to target with flankers, in five components, including as early as 65–75 ms. This suggests a non-linear summa-

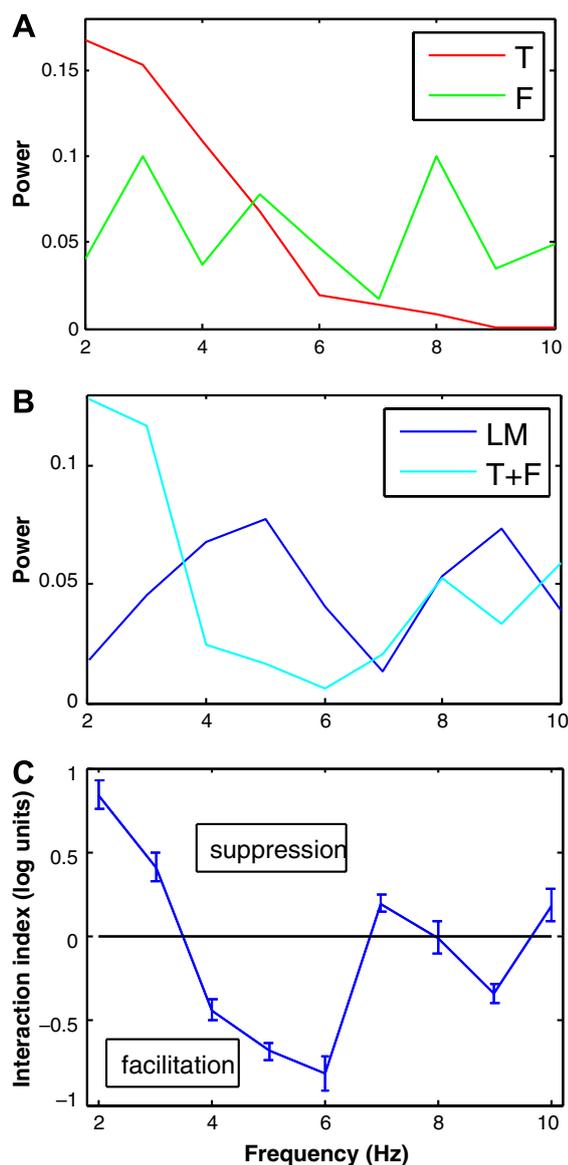


Fig. 5. Power spectrum and interaction index. The average power spectrum of the VEPs: (A) the target presented alone (T, red line) and mask presented alone (F, green line); (B) lateral masking (LM, blue line) and linear prediction (T + F, cyan line). The spectra were calculated per subject separately, in the 1–10 Hz frequency band, and averaged. (C) The interaction index was calculated as the log of the ratio between the amplitude spectrum of the linear prediction and LM, at each frequency. Thus, ratios above zero indicate suppression, whereas ratios below zero indicate facilitation. Error bars indicate SEM. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

two data sets. The calculation that was used in that study was based on difference waves between trials containing parafoveal collinear and orthogonal flankers, whereas no direct measurement of the response to a single foveal low-contrast target was provided. In this study, we focused particularly on measuring the lateral interactions provided by collinearity between the threshold-level central and the high-contrast flanking parts of a virtual contour. The results of the comparison between the collinear and orthogonal configurations in a subgroup of five subjects, both for the analysis of waveform and spectrum, suggest that the observed non-linear interactions are specific to collinear configurations. Other electrophysiological studies of contour perception showed VEP modulations with relatively late latencies for perceived illusory contours, e.g., (Mathes, Trenner, & Fahle, 2006; Murray, Imber, Javitt, & Foxe, 2006).

The non-linear summation of responses to target and collinear flankers in isolation during lateral masking was first measured in the frequency domain using VEP, providing the first correlation between physiological measurement and behavioral facilitation of Gabor target detection in humans (Polat & Norcia, 1996). Using a different type of stimulation and focusing the analysis primarily on the frequency at which the stimuli were presented at 4 Hz, the interaction index revealed a facilitatory effect of lateral masking. The current study extends this analysis and provides evidence for a more complex pattern of lateral interactions—shifting from suppression at lower frequencies toward facilitation at higher frequencies including 4 Hz.

4.2. Multiple sources of interactions

The differences between the time courses of the linear prediction and LM at different components, observed in our data, support the possibility of multiple stages of visual processing contributing in producing the lateral interactions, including both horizontal and feedback projections, whereas analysis of the frequency domain suggests that only part of the sources induces facilitation. Numerous studies suggested that early components recorded at the mid-line occipital electrodes are generated in the primary visual cortex, whereas later ones originate in extrastriate visual areas (Clark, Fan, & Hillyard, 1995; Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; Heinze et al., 1994; Jeffreys & Axford, 1972a, 1972b; Mangun, 1995; Woldorff et al., 1997), although some neurons in higher cortical areas were activated before neurons in striate cortex (Girard, Hupe, & Bullier, 2001; Nowak, Munk, Girard, & Bullier, 1995; Schmolesky et al., 1998). Extracellular recordings reported contextual modulation (Chen, Kasamatsu, Polat, & Norcia, 2001; Crook et al., 2002; Kapadia et al., 1995, 2000; Mizobe et al., 2001; Polat et al., 1998), effect of perceptual saliency (Li et al., 2006) and processing of global features (Fitzpatrick, 2000; Lamme, 2004; Roelfsema, 2006; Series et al., 2003; Tucker & Fitzpatrick, 2004) in early visual areas. On the other hand, there is fMRI evidence for processing of context information in the LOC (Altmann, Deubelius, & Kourtzi, 2004; Kourtzi, Tolias, Altmann, Augath, & Logothetis, 2003). Khoe et al. (2004) also reported late components of collinearity-related modulation.

4.3. Type of interaction

Whereas the amplitude modulation at the lower frequencies indicated suppression, we found facilitatory effects at higher frequencies. This is reminiscent of the recent findings of facilitated responses of V1 neurons by collinear contours, whereas additional context resulted in suppression (Li et al., 2006). The source of this mixed pattern of interactions is a matter of debate. The effect of center-surround is mostly suppressive but may also be facilitative in some spatial–temporal combinations, according to previous psychophysical and physiological studies (Bauer & Heinze, 2002; Chavane et al., 2000; Kapadia et al., 1995, 2000; Li & Gilbert, 2002; Mandon & Kreiter, 2005; Mizobe et al., 2001; Polat & Norcia, 1996; Schmidt et al., 1997; Sugita, 1999, for a review, see Series et al., 2003). Network models of lateral interactions were proposed earlier (Adini & Sagi, 2001; Adini et al., 1997, 2002; Polat, 1999; Polat et al., 1998). The interplay between excitatory neurons, activated by the low-contrast target, and the complex excitatory and inhibitory effects with different spectral characteristics from the surround, indicate the involvement of multiple sources that interact with the center and modulate its response. Because we found evidence for both facilitation and suppression at different temporal frequencies, the final outcome was determined by the temporal and spatial integration of excitatory and inhibitory inputs (Polat & Sagi, 2006).

4.4. Spatial vs. temporal interactions

Is it possible to deduce the type of interaction from the amplitude modulation of the peaks? One can interpret the time course amplitude data in this study as suppression. However, waveform modulation per se, either an increase or decrease in amplitude, does not reflect the direction of interactions either facilitation or suppression (Luck, 2005). Our findings in the frequency domain are in line with this notion, showing both suppression and facilitation at different frequency ranges for the same time course.

We suggest two possible accounts for the observed findings: different temporal frequencies for inhibition and excitation or the contribution of different neuronal populations. Earlier it was proposed that inhibition has a faster time constant than facilitation (Bonneh, Sagi, & Polat, 2007; Polat & Sagi, 2006). This difference in the time constants may underlie the distribution of the suppressive and facilitatory effects at different frequencies, observed in LM in our study, thus extending the model of overall inhibition with a range of excitation into the temporal domain. Moreover, there is evidence showing that neurons induce different types of interactions: only facilitation, only inhibition, and a combination of both (Kasamatsu et al., 2001). The VEP measurements reflect the overall contribution of all the different types.

4.5. Global vs. local representation

The effect of lateral masking is typically inferred from a comparison of the target's visibility under two different conditions: the target alone and the target within the context of a mask. However, the neural representation of the same target under these two conditions may be different and, therefore, the masking should be probed by comparing between a local process (feedforward, target alone) and spatial integration that is context-dependent (feedforward and lateral interactions). The effects of context modulation, which may enable grouping of local elements into a global percept (Gestalt), were demonstrated in many psychophysical and physiological studies (for a review, see Series et al., 2003). It was also shown that facilitation may be observed for high-contrast targets as well, when surrounded by background noise (Polat & Bonneh, 2000). Our findings also suggest that a representation of an assembly of stimuli using a distributed network substitutes local representations of target and flankers—an effect that may play an important role in perception of contours. This implication is also consistent with findings in brain-damaged patients with visual extinction (Pavlovskaya, Sagi, & Soroker, 2000; Pavlovskaya, Sagi, Soroker, & Ring, 1997). However, an opposite view argues against the link between the integration of lower and higher collinear elements and contour perception (for a review, see Hess, Hayes, & Field, 2003).

5. Conclusions

Lateral interactions induced amplitude modulations of multiple components and frequencies different from a linear prediction, including components as early as about 70 ms, suggesting a non-linear mechanism of context modulation. Suppressive and facilitatory effects were found at different frequencies, implying that lateral interactions are generated by multiple sources, only some of which are explicitly facilitatory.

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Appendix

1. The spectrum of the responses to T and to F were added, generating the predicted response spectrum.

$$\Phi_T = \text{fft}(T) \text{—Fourier transform of T}$$

$$\Phi_F = \text{fft}(F) \text{—Fourier transform of F}$$

$$\Phi_{LM} = \text{fft}(LM) \text{—Fourier transform of LM}$$

$$\Phi_{\text{predict}} = \Phi_T + \Phi_F \text{—Linear prediction.}$$

2. Power spectra of the resulting prediction (calculated in step 1), T, F, and LM were calculated.

$$S_T = \Phi_T \times \Phi_T^* \text{—power spectrum of T}$$

(multiplying Φ_T by its complex conjugated)

$$S_F = \Phi_F \times \Phi_F^* \text{—power spectrum of F}$$

$$S_{LM} = \Phi_{LM} \times \Phi_{LM}^* \text{—power spectrum of LM}$$

$$S_{\text{predict}} = \Phi_{\text{predict}} \times \Phi_{\text{predict}}^* \text{—power spectrum of linear prediction.}$$

3. The interaction index was calculated as the log10 of the ratio between the power spectra of the predicted response and LM.

$$I = \lg \frac{S_{\text{predict}}}{S_{LM}}$$

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