



Backward masking suppresses collinear facilitation in the visual cortex

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ABSTRACT

Perceptual facilitation in detecting low-contrast Gabor patches (GPs) is induced by collinearly oriented high-contrast flankers. Our recent Visual Evoked Potentials (VEPs) study provided new physiological evidence for these collinear interactions, reflected by nonlinear modulation of multiple waveform components and frequencies [Sterkin, A., Yehezkel, O., Bonneh, Y. S., Norcia, A., & Polat, U. (2008). Multi-component correlate for lateral collinear interactions in the human visual cortex. *Vision Research*, 48(15), 1641–1647]. Here we used VEPs to study the temporal structure of this process. Low-contrast, foveal target GP (T) was simultaneously flanked by two collinear high-contrast GPs with a spatial separation that induces facilitation of T (lateral masking, LM). Another mask, identical to LM, was presented at different time-intervals (ISIs) after LM (backward masking, BM-on-LM). The responses were compared to separate waveforms evoked by T-alone and mask-alone at different ISIs. BM canceled the physiological markers of facilitation at an ISI of 50 ms, in agreement with earlier psychophysical findings, whereas no BM effect on T-alone was observed. This ISI coincides with the active time-window of lateral interactions, confirming our working model. The waveform amplitude of the negative N1 peak of LM was modulated toward the linear prediction of no interactions and the spectrum was shifted toward suppression, with no evidence of facilitation. Moreover, the P1 peak amplitude of BM was decreased at the same ISI, indicating that there is a mutual interference in cortical representation of both events. Waveform subtraction between BM-on-LM and LM suggests a mechanism of extended persistence of the target representation underlying facilitation in LM. We suggest an explanation for the role of improved detection of collinear stimuli in grouping of contours.

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1. Introduction

Neural representation of localized targets is modulated by context. Although the modulatory effect is mostly suppressive, it may also be facilitative in some spatio-temporal combinations (Bonneh & Sagi, 1998; Herzog & Fahle, 2002; Kovacs, 1996; Polat, 1999; Polat & Sagi, 1993; Polat & Sagi, 1994a) (Bauer & Heinze, 2002; Chavane, Monier, Bringuier, Baudot, Borg-Graham, Lorenceau, & Fregnac, 2000; Kapadia, Ito, Gilbert, & Westheimer, 1995; Kapadia, Westheimer, & Gilbert, 2000; Li & Gilbert, 2002; Mandon & Kreiter, 2005; Mizobe, Polat, Pettet, & Kasamatsu, 2001; Polat & Norcia, 1996; Schmidt, Goebel, Lowel, & Singer, 1997; Sugita, 1999), for a review, see (Series, Lorenceau, & Fregnac, 2003). The nature (either facilitation or suppression) and the strength of the context effect are determined by several parameters, such as proximity, similarity, contrast, and global configuration.

Several models of lateral interactions assume that excitatory and inhibitory connections form a neuronal network wherein each

unit receives three types of visual input: direct thalamic-cortical input, lateral input from other units within the network, and top-down feedback (Adini & Sagi, 2001; Adini, Sagi, & Tsodyks, 1997; Polat, 1999; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Sterkin, Yehezkel, et al., 2008). The lateral excitation is organized along the filters' optimal orientation, forming a collinear field (Chen & Tyler, 1999; Polat, 1999; Polat & Norcia, 1998; Polat & Tyler, 1999; Sterkin, Sterkin, & Polat, 2008a) and is superimposed on a suppressive area surrounding the filters.

The lateral masking (LM) effect is measured as a decrease in detection thresholds for low-contrast Gabor patches (GPs) when flanked by spatially separated collinearly oriented high-contrast patches (Polat & Sagi, 1993; Polat & Sagi, 1994a; Polat & Sagi, 1994b) (Adini & Sagi, 2001; Adini et al., 1997; Bonneh & Sagi, 1998; Cass & Alais, 2006; Cass & Spehar, 2005; Levi, Hariharan, & Klein, 2002; Polat & Sagi, 1993; Polat & Sagi, 1994a; Polat & Sagi, 1994b; Solomon & Morgan, 2000; Williams & Hess, 1998; Woods, Nugent, & Peli, 2002). An important masking factor is the overlap between the receptive fields of the responding units. It has been suggested that the size of the receptive fields in V1 is estimated to be about 2–3λ (Mizobe et al., 2001; Polat, 1999; Polat & Norcia,

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1996; Polat & Sagi, 1993; Polat & Sagi, 2006; Watson, Barlow, & Robson, 1983; Zenger & Sagi, 1996). Thus, separations of 3λ or more activate lateral interactions between different neurons responding to the target and the mask (lateral masking). Indeed, the collinear facilitation is most prominent for a target-to-flanker separation of 3λ , decreasing for longer distances, whereas suppression is found for shorter separations (Polat & Sagi, 1993).

The collinear facilitation is found in the early visual cortex, suggesting that the early processing stages are involved in the effect (Crook, Engelmann, & Lowel, 2002; Kapadia et al., 1995; Khoe, Freeman, Woldorff, & Mangun, 2004; Mizobe et al., 2001; Polat & Norcia, 1996; Polat et al., 1998). A network of long-range connections, extending for long distances that exist between similar orientation columns may underlie the observed lateral interactions (Bolz & Gilbert, 1989; Fitzpatrick, 1996; Gilbert & Wiesel, 1983; Gilbert & Wiesel, 1985; Grinvald, Lieke, Frostig, & Hildesheim, 1994; Schmidt et al., 1997; Ts'o, Gilbert, & Wiesel, 1986). 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) and monkeys (Ito & Gilbert, 1999), suggesting that higher levels of processing are involved in collinear facilitation. Consequently, a mechanism based on top-down feedback was proposed (e.g., Angelucci et al., 2002; Levi et al., 2002; Rockland & Lund, 1982; for a review, see (Angelucci & Bressloff, 2006).

The temporal properties of the collinear facilitation are less explored. It was found that lateral facilitation critically depends on the order of presentation of the target and flankers (Polat & Sagi, 2006; Polat, Sterkin, & Yehezkel, 2007). Whereas a typical pattern of lateral interactions was observed for forward or simultaneous masking, this was not the case for backward masking. More specifically, facilitation of the target detection was observed when collinear flankers were presented simultaneously with the target or preceding the target. However, this facilitation was canceled when followed by another presentation of the flankers with a temporal delay that corresponded with the time-window of active processing of the target. The observed pattern of results is incompatible with a feedforward account of lateral interactions, according to which the two temporal effects are linearly summed within a higher level receptive field. The results suggested that backward masking affected the lateral interactions and not the detection of the target *per se*. In humans, the physiological measurements of the behavioral facilitation showed a deviation of responses to targets and flankers presented in combination from the linear summation of responses when each stimulus was presented alone (Khoe et al., 2004; Polat & Norcia, 1996). The latter study suggested that generators at the earlier primary visual cortex and at the extrastriate visual cortex are involved. Our recent study provided new evidence for collinear interactions using VEPs (Sterkin, Yehezkel, et al., 2008). Although no differences in the latencies were found, collinear interactions were reflected by nonlinear waveform amplitude modulation of multiple components. Spectrum analysis revealed suppression at lower frequencies (up to 0.8 log units) and facilitation at higher frequencies (4–6 Hz, up to 0.8 log units), suggesting that the physiological correlates of collinear interactions may originate at multiple sources, only some of which are explicitly facilitatory. This is reminiscent of the recent findings of facilitated responses of V1 neurons by collinear contours, whereas additional context resulted in suppression (Li, Piech, & Gilbert, 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 spatio-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, Sagi, & Tsodyks, 2002; Adini et al., 1997; 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. Increased sensitivity to stimuli may arise from several possible non-linear interactions, such as a multiplicative increase in firing rate, an increase in the effective contrast of the stimulus (Reynolds, Pasternak, & Desimone, 2000), or a normalization mechanism that is contingent upon the relative contrast of the flankers and target (Cavanaugh, Bair, & Movshon, 2002; Sceniak, Hawken, & Shapley, 2001). Our study did not attempt to distinguish between these alternative mechanisms; however, any non-linearity should reflect the context effect of collinear flankers.

Here we extended our VEP paradigm to include temporal masking. Temporal masking is a tool that is widely used to study information processing and is sensitive to the physical parameters of the stimuli, such as duration, contrast, orientation, luminance and the temporal interval between the target and the mask (Breitmeyer & Ogmen, 2006). When a mask is presented, typically less than 100 ms before or after the target, the detection of the target is reduced (Breitmeyer, 1984; Breitmeyer & Ogmen, 2000, 2006; Enns & Di Lollo, 2000). The time-window (inter-stimulus interval, ISI) during which the target response is influenced by the mask can be interpreted as the time-window of interactions between the target and the mask. Physiological experiments provide an upper limit of 200 ms (Albrecht, 1995; Mizobe et al., 2001; Polat et al., 1998). Bridgeman's reanalysis of earlier data (Jeffreys & Musselwhite, 1986) revealed a U-shaped modulation of the VEP amplitude around 250 ms, corresponding to the behavioral U-shaped masking function, which is thought to reflect visual masking due to recurrent processing (Bridgeman, 1988). However, a recent study suggests that it may reflect temporal interactions between the target and mask that are unrelated to the visibility of the target (Van Aalderen-Smeets, Oostenveld, & Schwarzbach, 2006). A modulation around this latency has also been found in single neuron activity in the cat and monkey striate cortex (Bridgeman, 1975; Bridgeman, 1980).

The results of our earlier psychophysical and VEP experiments enabled us to develop a working model indicating that the effect of the masking is determined by a spatio-temporal combination of several factors: (1) the processing time of the target, (2) the order of presentation of the target and the mask, and (3) the spatial arrangement of the target and the mask. Suppression was observed when the mask was positioned within a range that evoked inhibition from the vicinity of the target, and when the temporal separation between the target and the mask was short (Polat & Sagi, 2006). In contrast, facilitation was observed when the mask was presented at a larger spatial separation and when presented simultaneously with or before the target, but not when the target preceded the mask. We propose that masking effects, either suppression or facilitation, reflect integration in the spatial and the temporal domains of the feedforward response to the target with the lateral inputs evoked by the mask (excitatory and/or inhibitory). The excitation evoked by the mask is relatively delayed since it develops and propagates slowly from the location of the mask outside the receptive field of the target through the lateral connections. In contrast, inhibition that is produced close to the target evolves rapidly and follows the onset and the offset of the stimulus more precisely. Therefore, facilitation is possible only if the propagation of the excitatory input from the mask to the target is not delayed by a longer period than the integration time of the feedforward input. Lateral excitation that overcomes the inhibition

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