



Learning to be fast: Gain accuracy with speed

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ABSTRACT

Our recent neurophysiological findings provided evidence for collinear facilitation in detecting low-contrast Gabor patches (GPs) and for the abolishment of these collinear interactions by backward masking (BM) (Sterkin et al., 2008; Sterkin, Yehezkel, Bonne, et al., 2009). We suggested that the suppression induced by the BM eliminates the collinear facilitation. Moreover, our recent study showed that training on a BM task overcomes the BM effect, hence, improves the processing speed (Polat, 2009). Here we applied training on detecting a target that is followed by BM in order to study whether reinforced facilitatory interactions can overcome the suppressive effects induced by BM. Event-Related Potentials (ERPs) were recorded before and after ten training sessions performed on different days. Low-contrast, foveal target GP was simultaneously flanked by two collinear high-contrast GPs. In the BM task, another identical mask was presented at different time-intervals (ISIs). Before training, BM induced suppression of target detection, at the ISI of 50 ms, in agreement with earlier behavioral findings. This ISI coincides with the active time-window of lateral interactions. After training, our results show a remarkable improvement in all behavioral measurements, including percent of correct responses, sensitivity (d'), reaction time (RT) and the decision criterion for this ISI. The ERP results show that before training, BM attenuated the physiological markers of facilitation at the same ISI of 50 ms, measured as the amplitude of the negative N1 peak (latency of 260 ms). After the training, the sensory representation, reflected by P1 peak, has not changed, consistent with the unchanged physical parameters of the stimulus. Instead, the shorter latency (by 20 ms, latency of 240 ms) and the increased amplitude of N1 represent the development of faster and stronger facilitatory lateral interactions between the target and the collinear flankers. Thus, previously effective backward masking became ineffective in disrupting the collinear facilitation. Moreover, a high-amplitude late peak (P4, latency of 610–630 ms) was not affected by training, however its high correlation with RT (95%) before training was significantly decreased (to 76%), consistent with a lower-level representation of a trained skill. We suggest that perceptual learning that strengthens collinear facilitation results in a faster processing speed.

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1. Introduction

1.1. Lateral interactions

During the last decade, it was demonstrated that contrast-driven neural response is robustly affected by lateral interactions in the visual cortex of humans (Bonne & Sagi, 1999; Cass & Alais, 2006; Cass & Spehar, 2005; Ellenbogen, Polat, & Spitzer, 2006; Herzog & Fahle, 2002; Polat & Norcia, 1996; Polat & Sagi, 1993, 1994a, 1994b, 2006; Shani & Sagi, 2006; Solomon & Morgan, 2000; Tanaka & Sagi, 1998; Woods, Nugent, & Peli, 2002) and of animals (Chen et al., 2001; Crook, Engelmann, & Lowel, 2002; Kapadia et al., 1995; Kasamatsu et al., 2010; Mizobe et al., 2001; Polat et al., 1998; Series, Lorenceau, & Fregnac, 2003), suggesting that early stages of visual processing

are involved in inducing this effect. 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 et al., 1998; Sterkin 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, 2008) and is superimposed on a suppressive area surrounding the filters.

Perceptual modulation of detecting low-contrast Gabor patches (GPs) induced by spatially separated collinearly oriented high-contrast flanking patches is sometimes termed “lateral masking” (LM, Fig. 1A). An important masking factor is the overlap between the receptive fields of the responding units. The size of the

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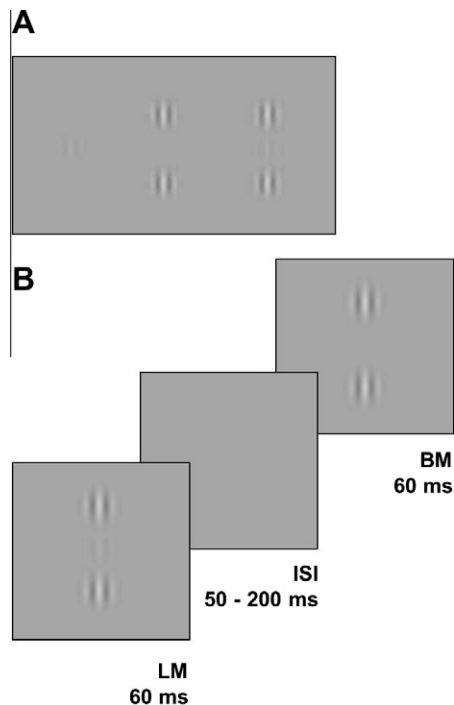


Fig. 1. Stimuli and backward masking paradigm. (A) Stimuli. Target alone – a single Gabor patch at a contrast of 6% (contrast increased for presentation); mask alone – two flanking collinear GPs at a contrast of 40%, separated by 6 λ ; target in the presence of flankers (lateral masking, LM). (B) Sequence of presentation. Backward masking (BMLM) condition: LM followed by a mask with a temporal delay (at four different ISIs: 0, 50, 150, and 250 ms). Duration of presentation for each stimulus: 60 ms.

receptive fields in V1 is estimated to be about 2–3 λ (Mizobe et al., 2001; Polat, 1999; Polat & Norcia, 1996; Polat & Sagi, 1993, 2006; Watson, Barlow, & Robson, 1983; Zenger & Sagi, 1996).

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 (BM). 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 BM affected the lateral interactions and not the detection of the target *per se*.

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 et al., 2004; Mizobe et al., 2001; Polat et al., 1998; Polat & Norcia, 1996). 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, 1985; Grinvald et al., 1994; Schmidt, Goebel, Lowel, & Singer, 1997; Ts'o, Gilbert & Wiesel, 1986). On the other hand, flanker facilitation benefits from focused attention in human observers (Freeman et al., 2003; Freeman, Sagi, & Driver, 2001; Giorgi et al., 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, Hariharan, & Klein, 2002; Rockland & Lund, 1982); for a review, see (Angelucci & Bressloff, 2006). An insight into the neuronal basis of lateral interactions was made by our recently published VEP studies. We have identified a neuronal marker for facilitatory lateral interactions, recorded over the central occipital electrode – the N1 peak (latency above 200 ms) (Sterkin et al., 2008). Moreover, in a subsequent study we have shown that this neuronal marker is specifically sensitive to temporal load produced by backward masking (Sterkin, Yehezkel, Bonneh, et al., 2009; Sterkin, Yehezkel, Zomet, et al., 2009), in correlation with the perceptual deterioration of lateral facilitation shown earlier (Polat & Sagi, 2006; Polat, Sterkin, & Yehezkel, 2007). Another mask, identical to LM, was presented at different delays (Inter-Stimulus-Intervals, ISIs) after LM (backward masking on lateral masking, BMLM). The responses were compared to separate waveforms evoked by target-alone and mask-alone at different ISIs. BM attenuated the physiological markers of facilitation at an ISI of 50 ms, with no effect with longer ISIs, in agreement with earlier psychophysical findings, whereas no effect of backward masking on target presented alone was observed. Specifically, 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. These results indicted an active time-window for the lateral interactions falling within 50 ms after onset of presentation, suggesting that spatial interactions are affected by temporal masking as long as the integration of target and mask is in progress (Fig. 2). We have also shown that pharmacologically induced intracortical inhibition modifies the amplitude of N1 peak (Sterkin, Yehezkel, Zomet, et al., 2009).

1.2. Perceptual learning

Visual plasticity is the ability of the visual system to adapt to changes in the visual input. Evidence for plasticity in the adult visual system has been reported in human studies that have demonstrated that training in specific visual tasks leads to improvement in performance or sensitivity (for a review, see (Fahle & Poggio, 2002; Sagi, 2010; Sasaki, Nanez, & Watanabe, 2010). Improvement after perceptual learning was demonstrated using a variety of visual tasks showing that the adult visual system can change according to behavioral demands (Fahle, 2002, 2005; Fahle & Poggio, 2002; Fiorentini & Berardi, 1980; Gilbert, Sigman, & Crist, 2001; Polat, 2008, 2009; Polat et al., 2004; Polat & Sagi, 1994b; Sagi, 2010; Sagi & Tanne, 1994). A prominent aspect of perceptual learning is the specificity of the improvement to stimulus features, however improvement generalization to different stimulus features is also found (for a review, see (Fahle, 2002, 2005; Fahle & Poggio, 2002; Fiorentini & Berardi, 1980; Gilbert, Sigman, & Crist, 2001; Polat, 2008, 2009; Polat et al., 2004; Polat & Sagi, 1994b; Sagi, 2010; Sagi & Tanne, 1994; Tartaglia, Aberg, & Herzog, 2009). Thus, the specificity of the perceptual learning may pose constraints on the methodology when it is employed to improve basic visual functions, such as contrast sensitivity (CS) in individuals with normal vision. Because CS is a fundamental function that reflects the output of the neurons in the primary visual cortex, improvement in CS may facilitate the performance of visual processing during the next stages of the visual cascade. Improvement in contrast sensitivity by training that induces lateral interactions was previously reported, including generalization to higher visual functions (Polat, 2008, 2009; Polat et al., 2004; Polat & Sagi, 1994b). However, the neural mechanisms underlying these changes are not clear.

1.3. Aim and summary

Inhibitory effects induced by backward masking abolished collinear facilitation, both in behavioral and electrophysiological mea-

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