



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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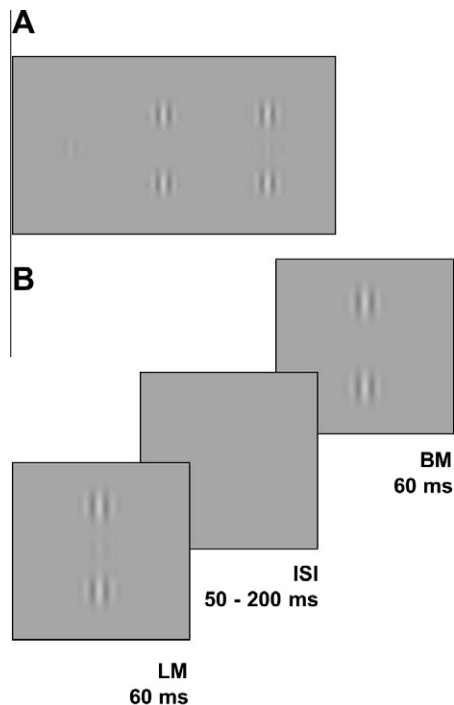


Fig. 1. Stimuli and backward masking paradigm. (A) Stimuli. Target alone – a single Gabor patch at a contrast of 6% (contrast increased for presentation); mask alone – two flanking collinear GPs at a contrast of 40%, separated by 6 λ ; target in the presence of flankers (lateral masking, LM). (B) Sequence 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-

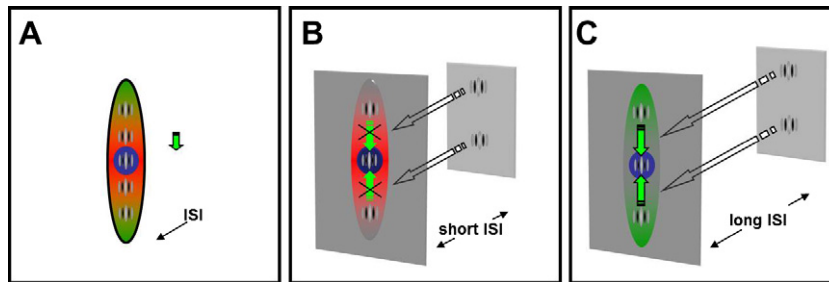


Fig. 2. Schematic illustration of the BM effect on lateral interactions. (A) Spatial arrangement of lateral interactions between the target and the masks. Suppression (red) is evoked when the mask is positioned within a close range of the target (blue circle), whereas facilitation (green) is evoked when the mask is presented at a larger spatial separation (green). The green arrow denotes the propagation of the activity evoked by the masks to the vicinity of the target via lateral interactions; the black arrow denotes the propagation of the activity evoked by BM at different ISIs. (B) For short ISI, the activity evoked by BM coincides with the time-window of the propagation of lateral interactions and thus cancels the facilitation (black crosses). (C) For long ISI, the activity evoked by BM fails to interfere with facilitation evoked by lateral interactions because it is presented after the propagation of lateral interactions is accomplished. The Figure is adapted from Sterkin, Yehezkel, Bonneh et al. (2009a).

surements (Polat & Sagi, 2006; Polat, Sterkin, & Yehezkel, 2007; Sterkin, Yehezkel, Bonneh, et al., 2009). Here we asked whether excitatory interactions supporting collinear lateral facilitation reinforced by perceptual learning can overcome the inhibitory effects induced by backward masking. We used the spatial separation of two wavelengths (λ) in order to take advantage of the larger shift between facilitation and suppression observed under LM and BMLM conditions, respectively, compared with the 3λ separation as was reported earlier (Polat & Sagi, 2006; Polat, Sterkin, & Yehezkel, 2007). Although the improvement in performance after training is well established, its neural mechanisms are not fully understood. We used ERP recording with simultaneous perceptual measurements, in order to measure the neuronal changes underlying the perceptual improvement. We show that changes in N1 amplitude and latency provide a signature for perceptual learning. Following incremental reinforcement, collinear facilitation could overcome the suppressive effects of backward masking. Moreover, we show that changes in RT reflect improvements in early stages of visual processing.

2. Methods

The paradigm in this study is reminiscent of the one used in our earlier backward masking VEP study (Sterkin, Yehezkel, Bonneh, et al., 2009) in terms of behavioral task and temporal conditions.

2.1. Subjects

ERPs were recorded in eight volunteers (two females, mean age 22) with normal or corrected-to-normal vision in both eyes. All participants signed the informed consent form.

2.2. Stimuli

The stimuli were localized vertically oriented gray-level gratings (Gabor patches, GPs) with a spatial frequency of 6 cycles per degree (wavelength, λ) and equal distribution (STD, σ , allowing a minimum 2 cycles in the GP), modulated from a background luminance of 40 cd m⁻² (Fig. 1A). Stimuli were presented on a Philips 107P color monitor, using a PC (1024 × 768 pixels at a 100 Hz refresh rate; gamma correction was applied). The effective size of the monitor screen was 32 × 24 cm, which, at a viewing distance of 150 cm, subtended a visual angle of 9.1° × 12.1°. The experiment was conducted in a dark environment, wherein the only ambient light came from the monitor.

2.3. Paradigm for testing at pretest and posttest, with ERP recording

ERPs were recorded during the pretest (before training) and posttest (after training) sessions. The tested conditions included lateral masking (LM) and backward masking applied on lateral masking (BMLM). LM condition: a foveal target GP at a contrast of 6% (at or very close to the detection threshold) in the presence of two flanking collinear GPs at a contrast of 40%; BMLM condition: LM followed by another mask, identical to the two flanking collinear GPs used in LM, presented at different time intervals (ISIs) after LM. ISIs of 50, 100, 150, and 250 ms were tested in BMLM (Fig. 1B). Under all conditions, the target GP was present in 50% of the trials and the task was to report the detection of the target using a standard computer mouse. A yes/no paradigm was used: response was required in each trial – left button for a “yes” and right button for “no” response. The rates of hits and false alarms were measured to calculate sensitivity (d') and decision criterion (Cr) measurements. Reaction time (RT) of hits was also measured. No feedback was provided. Stimuli were presented for 60 ms each (not including the ISIs) in 2 s trials. The spatial distance between the target and the flankers was two wavelengths (λ) – spatial separation producing the largest shift from facilitation under LM to suppression under BMLM. Each condition was repeated in 100 trials. All conditions were mixed in a random order. A small, 2-min arc fixation point, located at the center of the screen, indicated the target GP location. Participants were instructed to maintain their fixation and to avoid eye movements during the trials.

2.4. Training paradigm

The subjects were trained for 10 sessions at different days (not including the days of pretest and posttest), with no ERP recording. A yes/no paradigm, identical to the one used in pretest and posttest, was used for training. However, as opposed to posttest and pretest sessions, each condition was trained in a separate block and negative auditory feedback was provided. A total of three sets were used, each consisting of seven blocks of 40 trials (target presented alone, LM, BMLM with five different ISIs). Thus, each set consisted of 280 trials and lasted for about 15 min. 1st and 3^d set used a target–flanker separation of 2λ , whereas the 2nd set used a target–flanker separation of 3λ . Up to 15 min break separated between the sets, resulting in a training session of about 1 h. The contrast of the target was kept close to the detection threshold level, individually for each subject and was decreased, once the percent of correct responses in the preceding session reached 90% for target presented alone and 80% for BMLM with the ISI of 50 ms. The contrast ranged between 4% and 8%.

Table 1

Peak latencies. Averaged peak latencies under all conditions, for pretest and posttest (peak latency in ms; sem, standard error of the mean).

	Pretest					Posttest				
	LM	BMLM-50	BMLM-100	BMLM-150	BMLM-200	LM	BMLM-50	BMLM-100	BMLM-150	BMLM-200
PI	189	185	189	196	188	190	184	190	188	184
PI sem	14	12	14	12	13	12	11	14	13	14
NI	260	244	249	257	258	239	240	237	233	241
NI sem	23	21	15	20	19	18	21	17	17	21
P4	616	634	665	644	675	613	633	640	673	691
P4 sem	40	22	23	82	92	28	36	31	17	29

2.5. ERP recording and signal processing

The EEG was sampled at 1032 Hz (filtered from 0.1 to 100 Hz, amplified by 50,000 with Grass Model 12 amplifiers) from a cruciform array of five electrodes centered at a midline occipital site (O_z), spaced by 3 cm (referenced to the midline frontal site, F_z). For every condition, the average ERPs were computed over 2000 ms period per trial, for 100 trials per condition. For each trial the mean of 500 ms before the onset of the stimulus was taken as the baseline for the trial. Trials containing artifacts were rejected (thresholded at 200 μ V), as were trials containing eye movements (detected by visual inspection, less than 5% of trials). Trials with the target present were averaged for further analysis. The waveforms of the evoked responses were analyzed separately for each subject. Peak amplitudes and latencies were measured for a positive component, P1, a negative component, N1, (for details, see (Sterkin et al., 2008, Sterkin, Yehezkel, Bonne, et al., 2009)) and a late positive peak, termed P4. Peak latencies under all conditions are summarized in Table 1. The central recording channel was selected for the group averages (O_z). The results were first entered into ANOVA; pairwise comparisons were performed using paired *t*-tests, unless specified differently. For the behavioral data, percent of correct responses, reaction times (RT), decision criterion (Cr) and d' were measured. Significance of correlation was calculated using a non-directional hypothesis.

3. Results

3.1. Behavior

The percent of correct (PC) responses was significantly increased after training; ANOVA (2 tests \times 5 conditions) showed a significant learning effect ($F(1,7) = 10.1, p = 0.016$), a significant effect of the ISI ($F(4,28) = 5.6, p = 0.002$) and a significant interaction (test \times condition, $F(4,28) = 4.4, p = 0.024$) (Fig. 3A). Pairwise comparisons show that PC became significantly higher in BMLM with the ISI of 50 ms (BMLM-50, $p = 0.001$), whereas remained unchanged in LM and the rest of the ISI in BMLM ($p > 0.05$) (Fig. 3A). Moreover, PC was significantly lower in BMLM-50 ($p = 0.001$) compared to LM in pretest – a difference that became non-significant after training ($p > 0.05$). Therefore, only the ISI of 50 ms showed a significant effect of BM and, following the training, a significant improvement. The other ISIs did not show effective BM in pretest and no improvement in posttest.

There was also a significant effect of learning on the sensitivity (d') (learning effect: $F(1,7) = 5.2, p = 0.05$; effect of the ISI: $F(4,28) = 4.7, p = 0.005$; interaction: (test \times condition) $F(4,28) = 2.508, p = 0.022$) (Fig. 3B). Pairwise comparisons show that sensitivity became higher in BMLM-50 following the training ($p = 0.02$), but not in LM or BMLM with other ISI ($p > 0.05$). However, even after training, d' is still lower in BMLM-50 compared to LM (although the difference became non-significant, $p > 0.05$),

suggesting that improvement did not reach saturation and may have needed more than 10 training sessions.

Similarly, there was a significant change in the decision criterion (Cr) (learning effect: $F(1,7) = 3.1, p = 0.03$; effect of the ISI: $F(4,28) = 4.7, p = 0.005$; interaction: (test \times condition) $F(4,28) = 1.809, p = 0.015$) (Fig. 3C). The number of reports for “target present” (“Yes” responses) after the training increased as opposed to the tendency for “No” responses before the training, thus the Cr became less positive. These results are consistent with our earlier suggestion that collinear facilitation increases the number of reports of “target present” (Polat & Sagi, 2007; Zomet, Amiaz, Grunhaus, & Polat, 2008). The significant difference in the decision criterion between BMLM-50 and LM in pretest ($p = 0.009$) disappeared in the posttest ($p > 0.05$), indicating attenuated BM effect and suggesting that processing of collinear facilitation was almost accomplished within 50 ms. The comparisons between LM and BMLM with the rest of the ISIs were non-significant in both pretest and posttest ($p > 0.05$).

Reaction time (RT) also benefited from training ($F(1,7) = 12.2, p = 0.01$; effect of the ISI: $F(4,28) = 5.9, p = 0.001$) (Fig. 3D). RT became faster for both LM and BMLM-50 (by 85 ms with $p = 0.002$ for LM and by 84 ms with $p = 0.02$ for BMLM-50), yet stayed significantly shorter for LM than for BMLM-50 ($p = 0.02$ and $p = 0.009$ for pretest and posttest, respectively), possibly due to waiting with the motor response until the end of the stimulus presentation, which is longer for BMLM. RT improved for the longer ISIs as well after training ($p < 0.03$). Moreover, across all conditions, the gain in RT was correlated with the change in the Cr ($R = 0.69, p < 0.001$) (Fig. 4A), but completely uncorrelated with the gain in d' ($R = 0.05$) (Fig. 4B).

3.2. ERPs

Our earlier study has shown that the amplitude of N1 provides a signature for the lateral interactions (Sterkin et al., 2008). We have also shown that the amplitude of N1 is affected by backward masking and pharmacologically induced intracortical inhibition (Sterkin, Yehezkel, Bonne, et al., 2009; Sterkin, Yehezkel, Zomet, et al., 2009). The P1 peak denotes the sensory representation of the stimulus, modulated by physical parameters of input, such as contrast (Luck, 2005). Here we looked at the peak to peak differences in amplitude between P1 and N1 (the “delta”), while no changes in P1 amplitude or latency were observed following the training (ANOVA on amplitude: learning effect: $F(1,7) = 4.5, p > 0.05$; effect of the ISI: $F(4,28) = 0.7, p > 0.05$; ANOVA on latency: learning effect: $F(1,7) = 0.2, p > 0.05$; effect of the ISI: $F(4,28) = 1.07, p > 0.05$) (Fig. 5). We used the P1–N1 delta instead of reporting changes in N1 peak directly in order to account for amplitude differences between the two recording sessions (pretest and posttest).

In the amplitude domain, there was a significant change by 0.85 μ V in the delta following the training under the BMLM-50 condition ($p = 0.02$), with no change under the LM condition or BMLM with longer ISIs ($p > 0.05$) (Fig. 6A). The same result was

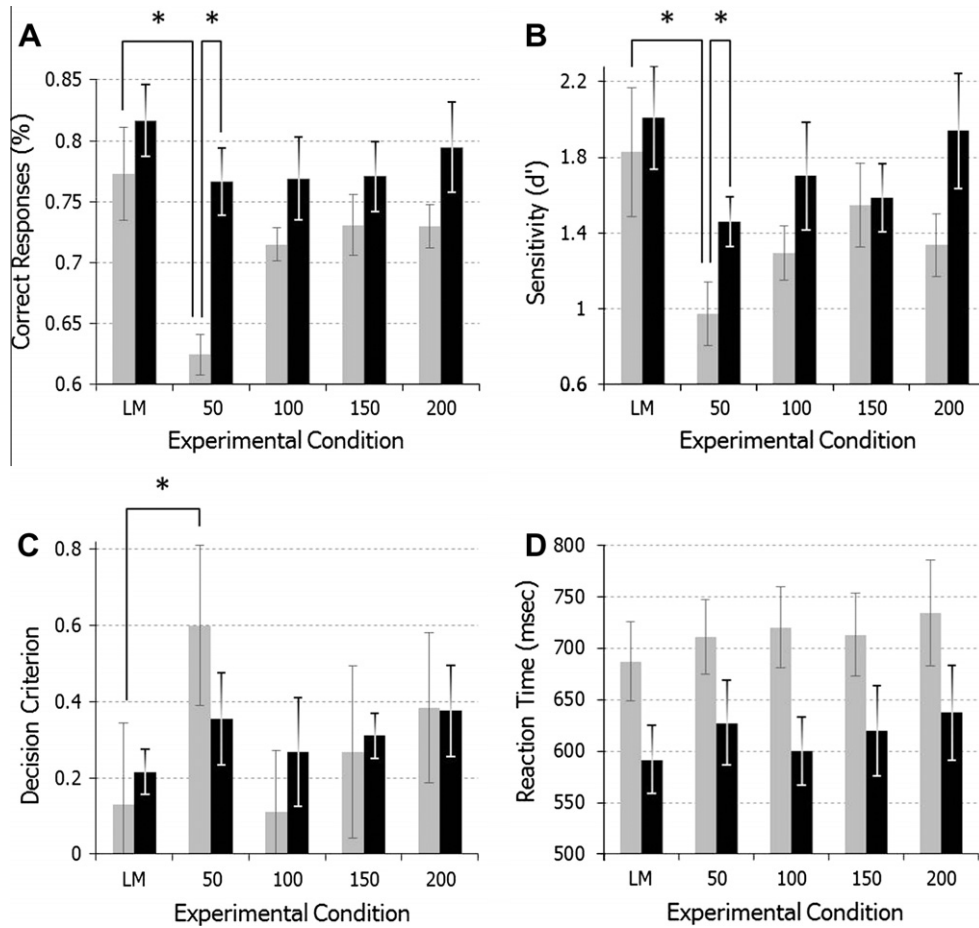


Fig. 3. Behavioral results. (A) Percent of correct responses (PC), (B) Sensitivity (d'), (C) Decision criterion (Cr) and (D) reaction times (RT) (mean \pm sem) as a function of condition (LM and BMLM with 4 ISIs: 50, 100, 150 and 200 ms). Gray bars, pretest; black bars, posttest. * p -value for paired t -tests below 0.05.

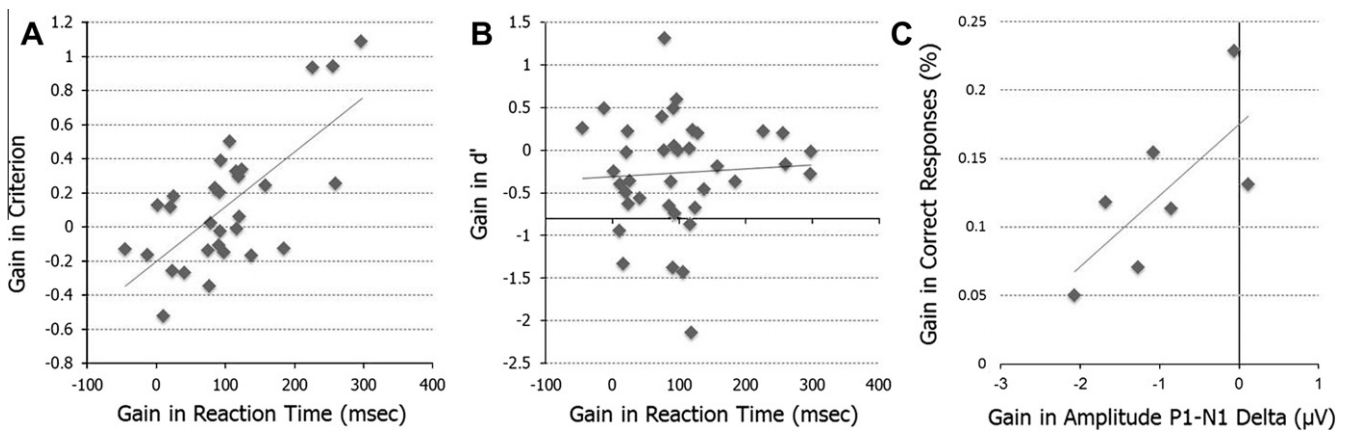


Fig. 4. Gain in RT and PC. (A) Change in the decision criterion plotted against the gain in reaction time (RT) (each datapoint represents a single subject results per condition; line, linear trendline). (B) Gain in the sensitivity (d') plotted against the gain in RT. (C) Gain in the percent of correct responses (PC) plotted against the gain in the amplitude P1–N1 delta.

obtained when the gains in amplitude following the training were calculated as the difference between the delta in pretest and posttest: the gains were significantly higher under BMLM-50 compared to LM ($p = 0.05$) and to other ISIs ($p = 0.05, 0.02$ and 0.01 compared to the ISI of 100, 150 and 200 ms, respectively). Moreover, the gains under BMLM-50 were significantly different from zero ($p = 0.02$, one-sample t -test), whereas non-significant under LM or BMLM with longer ISIs ($p > 0.05$, one-sample t -test). Furthermore, the

gains were correlated with improvement in PC under BMLM-50 ($R = 0.71$), whereas no correlation was found under LM condition or BMLM with longer ISI (Fig. 4C).

In the latency domain, there was a significant change by 22 ms in the delta under the LM condition following the training ($p = 0.01$, from 71 ms in pretest to 49 ms in posttest), with no change under the BMLM-50 condition ($p > 0.05$, 60 ms in pretest and 56 ms in posttest) (Fig. 6B). The same result was obtained when the gains

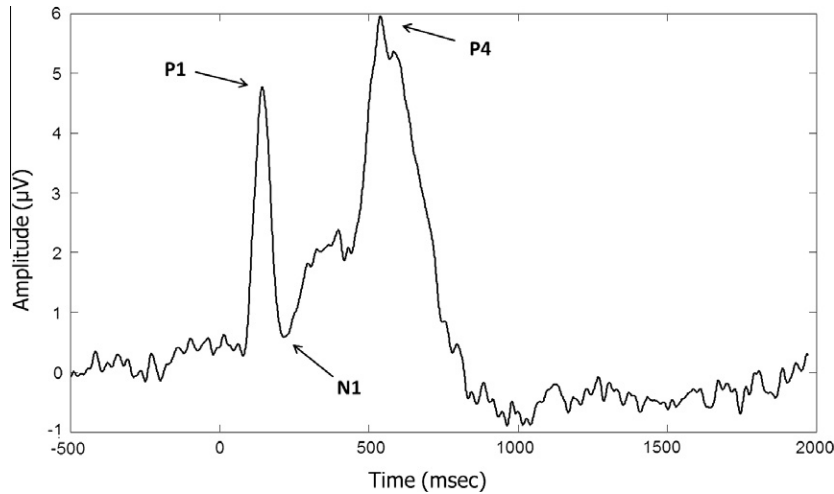


Fig. 5. Representative waveforms. The ERP time-course of a representative subject, under the LM condition. Arrows indicate the P1, N1 and P4 peaks.

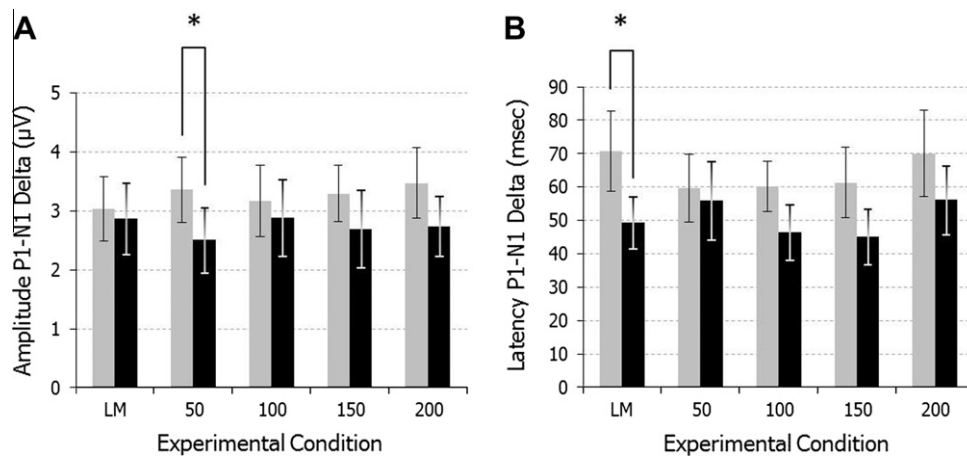


Fig. 6. ERP results. (A) Amplitude P1–N1 delta and (B) Latency P1–N1 delta (mean \pm sem) as a function of condition (LM and BMLM with 4 ISIs: 50, 100, 150 and 200 ms). Gray bars, pretest; black bars, posttest. * p -value for paired t -tests below 0.05.

in latency following the training were calculated (as the difference between the delta in pretest and posttest): the gains were significantly higher under LM compared to BMLM-50 ($p = 0.02$, 21 ms under LM vs. 4 ms under BMLM-50). Moreover, when these gains were normalized to the delta obtained under LM condition in pretest, the same result was observed, with a higher significance ($p = 0.003$, 28% under LM vs. 6% under BMLM-50).

The P3 peak could not be analyzed because its latency overlapped with the latency of the mask representation. A later component with the dominating amplitude along the evoked response waveform was termed P4 (Fig. 5). Interestingly, despite the observed significant shift in the latency for the delta between P1 and N1 peaks under the LM condition, there was no effect on the latency of the P4 under either condition ($p > 0.05$, 616 ms in pretest and 612 ms in posttest under the LM; 633 ms in pretest and 632 in posttest under BMLM-50). There was also no significant effect of the training obtained when the gains in latency following the training were calculated and also when these gains were normalized to the delta obtained under LM condition in pretest ($p > 0.05$). Similarly, no effects of training on the amplitude of P4 were observed ($p > 0.05$).

However, an interesting pattern of results emerges when the latency of P4 is compared with RT. Before training, there was a remarkably high correlation between P4 latency and RT ($R = 0.95$, $p < 0.001$), that, however, became substantially reduced, but still significant, after the training ($R = 0.76$, $p = 0.028$).

4. Discussion

The results of the study show a robust improvement in behavioral measurements following perceptual training on a contrast detection task, measured as reaction time (RT), percent of correct responses (PC), sensitivity (d') and decision criterion (Cr). Changes in N1 amplitude and latency provide a neurophysiological insight for the observed perceptual learning. Amplitude modulation under backward masking with an ISI of 50 ms suggests strengthened collinear interactions in LM, whereas shorter latency in LM provides faster processing, essential for “escaping” from backward masking, relying on a faster representation of LM that became separated from the mask. Thus, previously effective backward masking became ineffective in disrupting collinear facilitation (Fig. 7). To sum up, we suggest that perceptual learning that strengthens collinear facilitation results in faster processing speed of the target.

4.1. Temporal characteristics of collinear facilitation

Lateral interactions are assumed to be relatively slow (Bringuier et al., 1999; Cass & Alais, 2006; Grinvald et al., 1994; Polat & Sagi, 2006; Polat, Sterkin, & Yehezkel, 2007; Series, Lorenceau, & Fregnac, 2003). Cass and colleagues have shown that psychophysical collinear facilitation is likely to be mediated by two sets of

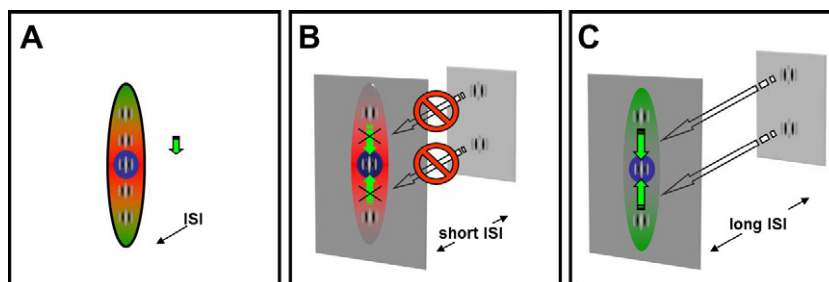


Fig. 7. Schematic illustration of learning modifying the BM effect on lateral interactions. (A) Spatial arrangement of lateral interactions between the target and the masks, as in Fig. 2. (B) For short ISI, at which BM was effective before training, “escaping” from backward masking became possible following perceptual learning, relying on a faster representation of LM that became separated from the mask. Thus, previously effective backward masking became ineffective in disrupting collinear facilitation. (C) As in Fig. 2, for long ISI, the activity evoked by BM is ineffective in interrupting collinear facilitation.

mechanisms: a fast integrative mechanism, possibly driven by synchronous onset of cortical response to collinear stimuli and another, involving slow, long-range horizontal transmission within V1 (Cass & Alais, 2006). It was suggested that excitation develops slowly and is sustained, lagging behind the stimulus both at the onset and offset, whereas inhibition is rapid and transient, following the onset and offset of the stimulus more precisely (Polat & Sagi, 2006; Polat, Sterkin, & Yehezkel, 2007; Sterkin, Sterkin, & Polat, 2008). This fundamental assumption is supported by the relatively slow time scale that characterizes lateral interactions (Bringuier et al., 1999; Grinvald et al., 1994; Series, Lorenceau, & Fregnac, 2003) and the strong, transient, and fast inhibition (Bair, Cavanaugh, & Movshon, 2003; Borg-Graham, Monier, & Fregnac, 1998), however see (Huang & Hess, 2008) for a different perspective. Our earlier backward masking study used VEPs to demonstrate that collinear facilitation is sustained, but also has a slow time constant: an active time window of lateral propagation of 50 ms, the time period during which collinear facilitation is disrupted by presentation of an additional mask (backward masking) (Sterkin, Yehezkel, Bonneh, et al., 2009). Here we show that perceptual learning overcomes these suppressive effects of backward masking, once a faster propagation via lateral connections is induced. We have proposed a theoretical framework of increased synchrony of collinear responses earlier as well as emphasized that increased sensitivity results in shorter latencies of neuronal response (Sterkin, Sterkin, & Polat, 2008). Moreover, a recent optical imaging study showed that the increased neuronal activity at the target site was synchronized over time, both locally and with neuronal population at the flanker’s site, with a higher synchronization for collinear than for orthogonal flankers (Meirovithz et al., 2010). Synchrony was revealed as a superior code over amplitude, for discriminating collinear from orthogonal pattern. However, one cannot dismiss the account of increased sensitivity induced by perceptual learning that, in turn, shortens response latencies. However, physiological measurements using a perceptual learning paradigm in animal models are needed to directly verify the suggested speeding of the lateral propagation as a likely mechanism of the observed effects of training.

4.2. Physiological correlates of perceptual learning

Improvement in contrast sensitivity by training of lateral interactions was previously reported (Polat, 2008, 2009; Polat et al., 2004; Polat & Sagi, 1994b). The behavioral improvement in contrast detection found here is consistent with earlier studies in normally sighted subjects (Polat & Sagi, 1994b, 1995) and in amblyopic and presbyopic subjects (Polat, 2009; Polat et al., 2004). However, here we demonstrate the neurophysiological evidence for perceptual learning of contrast detection in normal young population with good visual acuity (6/6 or 20/20 on the

ETDRS chart). Moreover, the ERP amplitude changes are correlated with improvement in performance, similarly to a recent ERP study (Censor et al., 2009). The often-observed specificity of learning is generally interpreted as evidence for training-induced plasticity in early cortical areas, including physiological evidence for training-induced changes in early visual cortical areas, such as reports of learning-induced changes of cortical activities in fMRI and ERP studies (for a review, see (Sagi, 2010). Censor and colleagues reported in a recent ERP study with two training sessions that practice seems to reduce the temporal interactions between the successive stimuli, revealing brain processes underlying perceptual learning in texture discrimination (Censor et al., 2009). Previous studies have also reported modulated electrophysiological responses following learning of texture segmentation (Casco et al., 2004; Pourtois et al., 2008), discrimination (Crist, Li, & Gilbert, 2001) and contour integration (Gilbert, Li, & Piech, 2009; Gilbert, Sigman, & Crist, 2001; Li, Piech, & Gilbert, 2008). A highly relevant recent study explored the physiological bases of perceptual learning by combining psychophysical measurements with extracellular single-unit recording in cats and showed that neuronal contrast gain in area V1 underlies behaviorally determined perceptual contrast sensitivity improvements (Hua et al., 2010). Training significantly improved perceptual contrast sensitivity of the cats to gratings with spatial frequencies near the “trained” spatial frequency, with stronger effects in the trained eye. Consistent with behavioral improvement, the mean contrast sensitivity of neurons recorded from V1 of the trained cats was significantly higher than that of neurons recorded from the untrained cats, confined to the trained spatial frequency. Furthermore, in the trained cats, the contrast sensitivity of V1 neurons responding preferentially to stimuli presented via the trained eyes was significantly greater than that of neurons responding preferentially to stimuli presented via the “untrained” eyes. Both eye and spatial frequency specificity of the observed perceptual learning suggest that perceptual learning in contrast detection is likely mediated through spatial frequency channels in the primary visual cortex in cats, although mixed results on eye specificity of visual perceptual learning have been reported in the literature (Gilbert, 1994; Karni & Sagi, 1991; Liu & Vaina, 1998; Sowden, Rose, & Davies, 2002; Zhou et al., 2006).

4.3. Speed vs. accuracy

The finding that the gain in RT is correlated with the change in Cr but is completely uncorrelated with the gain in d' suggests that RT became driven by a more aggressive response strategy following training. One possible explanation for the fact that both RT and PC improved is that no speed–accuracy tradeoff occurred, but rather a more efficient mechanism of contrast representation was formed, providing higher d' . However, there is evidence (e.g., Liu & Watanabe, 2012; Petrov, Van Horn, & Ratcliff, 2011) of strong

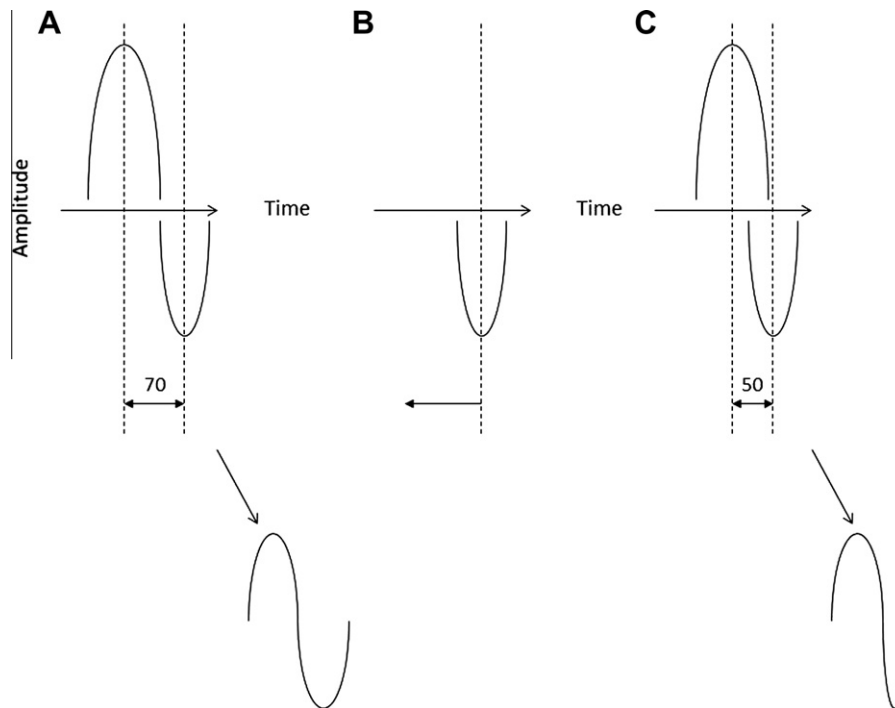


Fig. 8. Schematic illustration of suggested neuronal mechanisms underlying the observed learning effects. (A) The P1–N1 delta in latency under the LM condition (70 ms) was shortened after the training due to (B) a shift of 20 ms in the latency of the N1 peak, resulting in a (C) shorter P1–N1 delta in latency under the LM condition (50 ms).

changes in the speed–accuracy criterion during perceptual learning. The conclusion from these studies is that perceptual learning has two separate effects, both of which affect both PC (or d') and RT. On the one hand, the bottom-up sensory evidence improves, increasing the PC and decreasing the RT, in agreement with the explanation suggested above. However, observers often adopt more aggressive response policies as they gain practice and confidence, an effect leading to faster RTs but decreasing the PC, all else being equal. Typically, though, the stimulus-related improvement of the PC is greater than such “decision-related” decrement, and the observed PC increases with training. The correlation between the gain in RT and the gain in Cr (Fig. 4A) may thus reflect the increased confidence of the observers after training. More importantly, the lack of correlation between gains in RT and d' (Fig. 4b) may be due to individual differences in speed–accuracy tradeoff criteria as they get better at the task. This results in little or no d' gains but massive gains in RT. Other observers are more cautious, and maintain their mean RTs throughout. For them, the improvement is manifested predominantly in d' gains.

4.4. What is learned by the visual cortex?

One would expect changes in the sensory representation to underlie the observed improvement in contrast detection under temporal constraints induced by backward masking. However, there was no effect on the P1, the ERP component that is believed to be evoked by purely sensory representation (Luck, 2005). Rather, the N1 peak was modulated by training, the component that we have previously reported to provide the ERP correlate of lateral interactions (Sterkin et al., 2008; Sterkin, Yehezkel, Bonne, et al., 2009). A pronounced shortening of the N1 delay in the ERP evoked by LM indicates strong evidence for changes in the neuronal representation of lateral interactions (Fig. 8). This change in the LM representation is accompanied by an increase in N1 amplitude under

backward masking following the training, consistent with higher N1 amplitude for collinear facilitation reported earlier (Sterkin et al., 2008). Taken together, this pattern of results supports our working framework that propagation of collinear excitatory signals interrupted by backward masking may be restored by speeding up of the processing of collinear interactions, to complete the facilitatory conduction before the suppression induced by the mask affects the same neuronal population. This is an active process that has been induced by perceptual learning. A mechanism of synaptic plasticity, which involves strengthening or weakening of existing synapses as well as structural plasticity, including synapse formation and elimination may be considered (Holtmaat & Svoboda, 2009).

Interestingly, no effects of training on either amplitude or latency of the dominating late component, P4, were observed. This peak is probably related to the decision stage of processing. Before training, there was a remarkably high correlation between P4 latency and RT ($R = 0.95$), suggesting a common source of processing. After training, the correlation became substantially reduced, but still significant ($R = 0.76$), suggesting that before training the decision depended on a combination of low-level sensory representation and the higher-level executive function, whereas after the training, the bottom-up sensory evidence has improved, decreasing the RT and resulting in more aggressive responses that are less correlated with the higher-level processing stages. Because the task used in this study was simple target detection and did not involve any complicated judgment, it is rather expected that the P4 itself would not be affected by changes in the purely sensory representation of the stimulus induced by perceptual learning. The account of a more automatic lower-level sensory representation as a result of perceptual learning is consistent with earlier report of shifted representation following training found in multiple sensory systems (Hochstein & Ahissar, 2002, Karni et al., 1998, Lewis et al., 2009; Schwarzkopf, Zhang, & Kourtzi, 2009); for a review, see (Sagi, 2010). The reverse hierarchy of perceptual learning postulates a cascade from initial high-level to subsequent low-level learning (Hochstein & Ahissar, 2002).

5. Conclusions

Neuronal correlates of lateral interactions are modulated by perceptual training, shifting the balance towards facilitation. This learning effect is limited to the time-window of effective processing (ISI of 50 ms). We thus suggest that the speed of processing may be improved by incremental induction of facilitatory interactions.

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