

Specificity and generalization of perceptual learning in low myopia

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Abstract.

Purpose: In this study we investigated in observers with low myopia: (i) the pattern of lateral interactions between stimuli activating early cortical analyzers and its modulation by perceptual learning (PL), and (ii) whether PL transferred to untrained stimuli and tasks and whether it exhibits interocular transfer.

Method: Participants (seven adults with low myopia) performed 12 training sessions. Participants were trained on a contrast detection task of a central Gabor target flanked by two co-oriented and co-aligned high contrast Gabor patches. Target-to-flankers separation along the vertical axis was varied from 2 wavelengths (λ) to 8λ .

Results: The results showed that before PL facilitatory lateral interactions in the myopic eye were reduced in strength, but PL increased contrast sensitivity and improved facilitatory lateral interactions. However, PL did not transfer to different local/global orientations and lower spatial frequencies. On the other hand, PL resulted in an enhancement of the contrast sensitivity function (CSF) and of the uncorrected visual acuity (UCVA) both in the trained and untrained eye.

Conclusions: Such improvements seem to be associated to a modulation of lateral interactions between target and flankers and it is likely to take place at a level in which the inputs from the two eyes converge.

Keywords: Low myopia, perceptual learning, lateral interactions, contrast sensitivity, visual acuity

1. Introduction

It is well known that performance on perceptual tasks is improved by practice. This practice effect is known as perceptual learning (PL). PL in adult human observers has been shown for several tasks, such as hyper-acuity (McKee and Westheimer, 1978; Poggio, Fahle et al., 1992) phase discrimination in compound gratings (Fiorentini and Berardi, 1981), motion discrimination (Ball and Sekuler, 1982, 1987; Ball, Sekuler, et al., 1983), texture discrimination based on

simple and combined features differences (Ahissar and Hochstein, 1996; Casco, Campana et al., 2004; Casco and Campana, 1999; Campana and Casco, 2003; Karni and Sagi, 1991), and contrast polarity (Grieco, Casco et al., 2006). The finding that the effect of training on simple visual features was highly specific for location in the visual field (Ahissar and Hochstein, 1996; Karni and Sagi, 1991; Grieco, Casco et al., 2006; Fiorentini and Berardi, 1980), spatial frequency (Fiorentini and Berardi, 1980), contrast polarity (Grieco, Casco et al., 2006), local and global orientation (Ahissar and Hochstein, 1996; Casco and Campana, 1999; Campana and Casco, 2003; Karni and Sagi, 1991; Fiorentini and Berardi, 1980; Casco, Caputo et al., 2001) and in some case even the eye of origin (Karni and Sagi, 1991;

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Fahle 2004; Schoups, Vogels et al., 2001) suggests that neurons or population of neurons are modified at the earliest stage of visual processing. However, other studies reported that practicing in spatial frequency discrimination (Fiorentini and Berardi, 1981) and contrast detection of Gabor patches yields only weak or no improvements (Doshier and Lu, 2005; Snowden, Rose et al., 2002; Mayer, 1983; Dorais and Sagi, 1997; Maehara and Goryo, 2007).

Similarly, the ability to discriminate between two contrast levels of otherwise identical grating patches does not improve with practice (Dorais and Sagi, 1997; Maehara and Goryo, 2007; Adini, Sagi et al., 2002). On the other hand, it has been shown that the addition of high contrast and collinear Gabor flankers enabled learning contrast detection, thus reducing lateral suppression and increasing lateral facilitation by flankers; such modulations are usually obtained with target-to-flankers separations of 2 and 3-4 wavelengths (λ) (Adini, Sagi et al., 2002; Polat and Sagi, 1993; Polat and Sagi, 1994a, 1994b; Shani and Sagi, 2005; Polat, 2009; Maniglia, Pavan et al., 2011).

These results support the hypothesis that PL strengthens facilitatory interactions and reduces inhibitory interactions between laterally displaced Gabor patches. Indeed, cortical anatomy reveals that long-range horizontal interactions exist in all brain regions, including the visual cortex (Gilbert and Wiesel, 1983; Rockland and Lund, 1983) that are modulated by perceptual learning (Gilbert, Li et al., 2009). Indeed, there is recent psychophysical evidence of training-dependent reduction of low-level inhibitory lateral interactions that weaken a peripheral suppressive effect known as crowding (Maniglia, Pavan et al., 2011). PL also induces faster processing (for example, it increases reading speed) and overcomes the reduction of facilitation caused by background masking (Polat, Schor et al., 2012). The effect of PL is preserved when the contextual flankers are removed, leading to an enhanced contrast sensitivity function (CSF) (Polat, 2009). This suggests that the learning dependent modulation of excitatory and inhibitory connections between neurons improves the response of visual channels selective to spatial frequencies (Adini, Sagi et al., 2002), increasing signal-to-noise ratio in neural activity (Geisler and Albrecht, 1997). In addition, an outstanding study has provided evidence that abnormal neuronal interactions in amblyopia, i.e., reduced facilitation and increased suppression, can be improved by PL (Polat, Ma-Naim et al., 2004). In this study the

authors reported a transfer between different categories such as training on contrast detection and improvement of visual acuity. This result raises two important questions:

(i) whether PL improves high level processing that does not involve specificity for basic features

(ii) whether improvement in contrast sensitivity is essential and precedes improvement in visual acuity (e.g., letter recognition task).

The improvement of contrast sensitivity and visual acuity following PL has also been demonstrated both in observers with low myopia (Durrie and McMinn, 2007; Tan and Fong, 2008) and presbyopia (Polat, 2009; Polat, Schor et al., 2012; Durrie and McMinn, 2007). The vision of myopic and presbyopic individuals is blurred without optical correction, and their corrected contrast sensitivity is reduced (Liou and Chiu, 2001). Therefore, in the case of myopia and presbyopia it is possible that repeated practice in an adapted state to blur produces an improvement in contrast sensitivity.

An open question is whether myopia and presbyopia induce abnormal lateral interactions. Indeed, since facilitatory and inhibitory lateral interactions strengthen as a consequence of co-activation of pre- and post-synaptic units, similarly to a Hebbian learning mechanism, it is possible that non-optimal activation of spatial frequency visual channels in observers with myopia and presbyopia also weaken lateral interactions. A second question concerns the level at which PL operates. The transfer of learning to visual acuity suggests that visual acuity task share a common mechanism operating either at low or high level.

To shed light on these issues we have used a PL paradigm in monocular vision of myopic observers and asked whether:

(i) the pattern of lateral interactions in observers with low myopia differs from observers with normal vision. This should be regarded as maladaptive plasticity; that is, a long-term reduced efficiency of neural communication which limits the capability of representing the details of the input regardless it comes from corrected or uncorrected vision (Webster, Georgeson et al., 2002).

(ii) PL allows overcoming such modified pattern of lateral interactions.

(iii) such possible modulation is specific for the spatial frequency and orientation of the trained stimulus.

(iv) the modulation of lateral interactions by means of PL enhances contrast sensitivity and visual acuity.

(v) the enhancement of contrast sensitivity and visual acuity is specific for the trained eye.

2. Methods

2.1. Participants

Myopic participants, all suffering from functional low myopia with relatively late onset during childhood, were seven healthy volunteers (five males and two females), aged 20–25 years. Observers were selected on the basis of optometric evaluation that included: manifest subjective and objective refractions, best spectacle-corrected visual acuity (BSCVA) and uncorrected visual acuity (UCVA) using 4 m distance Early Treatment Diabetic Retinopathy Study (ETDRS) charts. Table 1 shows the refraction of each observer.

Inclusion criteria were low myopia of cycloplegic spherical equivalence (SE) within the range of 0.75–1.75 diopters (D) in the worst eye and with astigmatism not exceeding 0.75 D in either eye. Inclusion criteria were also a stable refractive state with no increase beyond ± 0.5 D over the previous 6 months, uncorrected visual acuity better than 0.7 logMAR, with no more than 0.3 logMAR difference between the two eyes, and best spectacle-corrected visual acuity better than 0.05 logMAR (ETDRS logMAR charts). Exclusion criteria included ocular condition or cause of reduced visual acuity other than simple myopia and/or astigmatism. The control group consisted of seven normal sighted participants (four males and three females), aged 20–26 years, with uncorrected visual acuity better than 0.05 logMAR. The participants sat in a dark room at a distance of 57 cm from the screen. Viewing was monocular with the non-dominant eye and without optical correction for both groups. The dominant eye was patched with a black occluder. It

should be noted that at the viewing distance of 57 cm, in myopic observers visual acuity is almost corrected to normal.

However, although the visual input is only partially degraded, communication amongst neurons should be affected if myopia produces a long-term plasticity that reduces the strength of interconnections between neurons (Webster, Georgeson et al., 2002).

Informed written consent was obtained from all observers before the study was initiated. The study and protocol conformed to the tenets of the Declaration of Helsinki.

2.2. Stimuli

2.2.1. PL stimuli

PL stimuli were displayed on a 19-inch LCD Asus monitor with a refresh rate of 60 Hz, and generated using Matlab Psychtoolbox (Brainard, 1997; Pelli, 1997). The screen resolution was 1280×1024 pixels. The mean luminance was 50 cd/m^2 , measured using a Minolta LS-100 photometer. Stimuli were generated using a gamma-corrected lookup table (LUT) to ensure display linearity.

Stimuli were Gabor patches consisting of a cosinusoidal carrier enveloped by a stationary Gaussian. Each Gabor patch was characterized by its wavelength (λ), phase (φ), and standard deviation (σ) of the luminance Gaussian envelope in the (x , y) space of the image. Formally each Gabor patch can be expressed as follows:

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

Gabors had a spatial frequency of 6 and 12 cpd with $\sigma = \lambda$ and $\varphi = 0$ (even symmetric). During the learning sessions a vertical and centrally presented Gabor target was flanked above and below by two high-contrast Gabor patches (0.6 Michelson contrast), originating a configuration of collinear Gabors. Flankers were always vertically oriented and located at various distances from the target: 2λ , 3λ , 4λ , and 8λ , corresponding to 0.33, 0.49, 0.66 and 1.33 deg for 6 cpd, and 0.16, 0.25, 0.33 and 0.66 deg for 12 cpd (Fig. 1).

In the learning sessions, the target was presented in only one of two intervals, each lasting 130 ms and separated by 500 ms. We used a two-interval forced choice task (2IFC) in which the observer was required to choose which of the two temporal intervals con-

Table 1

Refraction (in diopters) of each myopic observer for the trained and untrained eye

Observer	Trained eye	Untrained eye
MV	-1.00	-0.75 -0.25 \times 90
AP	-1.25	-1.75
SE	-1.75	-1.75
MC	-1.50	-2.0
MB	-1.25	-1.25
LB	-0.75	-0.75
SC	-1.25	-1.50

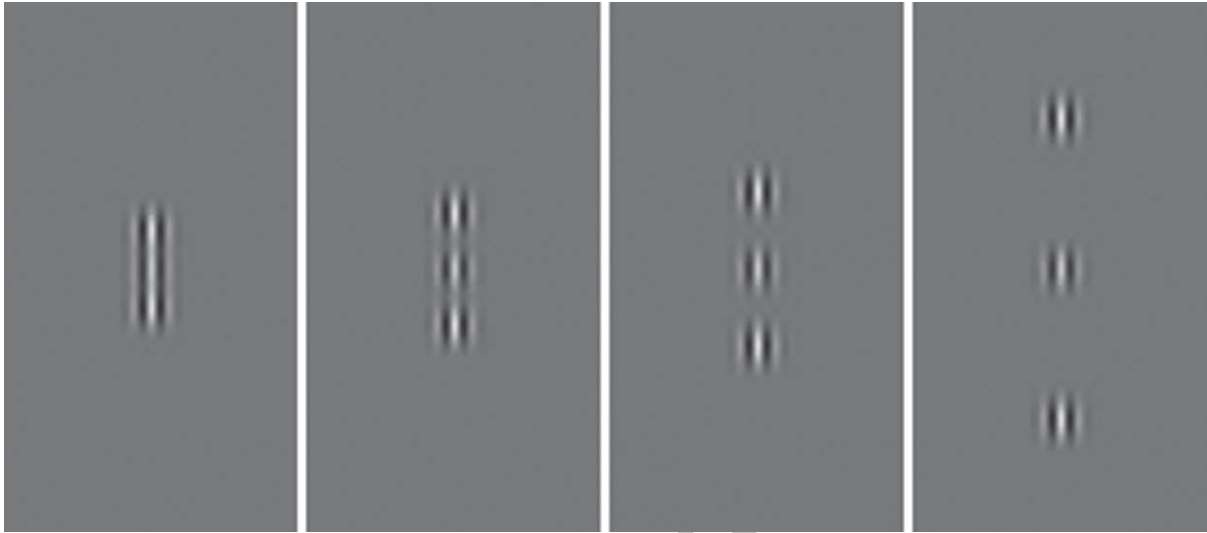


Fig. 1. Stimuli used in the learning sessions. A central target Gabor is flanked by two high-contrast Gabor patches of the same orientation. The figure shows only Gabor patches with a spatial frequency of 6 cpd, but in the learning sessions 12 cpd Gabor patches were also employed. Panels from left to right show the four target-to-flankers distances trained: 2λ , 3λ , 4λ and 8λ , respectively. For demonstrative purposes the contrast of the central target Gabor is exaggerated.

219 tained the target. Contrast detection thresholds were
 220 estimated using a 1-up/3-down staircase (Levitt, 1971),
 221 with contrast varying in steps of 0.1 log units. The ses-
 222 sion terminated after either 120 trials or 24 reversals.
 223 Threshold was calculated averaging the contrast values
 224 in correspondence of the last 18 reversals. Threshold
 225 corresponded to the stimulus strength at 79% accuracy.
 226 A fixation point (0.18 deg) indicated the location of
 227 the target during the interval between the two presen-
 228 tations. Observers activated the presentation of each
 229 pair of images at their own pace. They were informed
 230 of a wrong answer by an auditory feedback.

231 2.2.2. Baseline PL stimuli

232 Lateral interactions and the transfer to other stimu-
 233 lus characteristics were tested by comparing contrast
 234 detection thresholds in the pre- and post-test sessions.
 235 In the pre- and post-test sessions stimuli were a verti-
 236 cal collinear configuration of vertically oriented Gabor
 237 patches and a vertical configuration of Gabor patches
 238 with flankers orthogonally oriented with respect to the
 239 central target (i.e., orthogonal condition). The spatial
 240 frequency was 6 cpd for both groups and 12 cpd only
 241 for the myopic observers. Four target-to-flankers dis-
 242 tance levels were used: 2λ , 3λ , 4λ , and 8λ . In addition,
 243 the following conditions were tested: (i) a collinear
 244 vertical configuration of 1.5 cpd, to test the transfer to
 245 a different spatial frequency, (ii) a horizontal collinear

246 configuration of 6 and 12 cpd to test the transfer to a
 247 different orientation of the triplet.

248 2.2.3. Visual acuity stimuli

249 Visual acuity (ETDRs and Landolt-C) was measured
 250 before and after PL by using a remote-controlled visual
 251 and ophthalmic test chart monitor (Vision Chart by
 252 Costruzione Strumenti Oftalmici; CSO) placed at 4 m
 253 of viewing distance on a 19-inch screen with a res-
 254 olution of 1280×1024 pixels, contrast of 500:1 and
 255 maximum lightness of 280 cd/m^2 .

256 2.2.4. Eccentric visual acuity and crowding 257 stimuli

258 Eccentric visual acuity (eccentric-VA) and crowding
 259 were measured before and after PL. Stimuli were gen-
 260 erated using E-Prime software and presented at 57 cm
 261 from the same screen used for the PL. The stimuli were
 262 10 SLOAN letters (D, N, S, C, K, R, Z, H, O and V),
 263 randomly presented for 100 ms. In the eccentric-VA
 264 test, the location of the target letter was 4 deg either to
 265 the left or the right (randomly chosen on a trial basis)
 266 with respect to the fixation point. The size of the letters
 267 varied according to a 1-up/3-down staircase (Levitt,
 268 1971). The step size was 1 font size corresponding
 269 to streak width of 0.19 arcmin the character type was
 270 Arial, and the starting font size was 20 (streak width of
 271 3.72 arcmin). Observers had to say the letter displayed

and the experimenter registered the answer. The session terminated after either 100 trials or 18 reversals. The acuity threshold, expressed as the font size for 79% correct identifications, was the mean of the last eight reversals.

In the crowding test the target letter was flanked on the left and the right sides by two different letters. The triplets could appear randomly either to the left or to the right of the fixation point, but the target letter was always at 4 deg from the fixation spot. In the crowding test, the size of both the target letter and flanking letters was set 30% bigger than the VA threshold. We measured critical spacing, i.e., inter-letter distance that did not produce threshold elevation, using a 1-up/3-down staircase (Levitt, 1971). The initial distance between letters was set at 95 arcmin. The step size was 5.7 arcmin for the first 5 reversals, and 1.9 arcmin for the remaining reversals. The session terminated either after 100 trials or 18 reversals. At the end of the procedure, we calculated the threshold by averaging the critical spacing values in correspondence of the last eight reversals.

2.2.5. CSF stimuli

We measured contrast sensitivity functions (CSF) by using sinusoidal gratings generated by a VSG2/3 graphics card with 12-bit luminance resolution. Gratings were displayed on a 17-inch Philips Brilliance 107P CRT monitor with a refresh rate of 70 Hz and a spatial resolution of 1024×768 pixels. The stimuli were vertical gratings displayed on the whole screen area (26×20 deg). Contrast thresholds were measured with the method of Limits for each of the eight spatial frequencies tested (i.e., 0.1, 0.2, 0.4, 0.9, 2.0, 4.5, 10.2, and 20.4 cpd).

2.3. Procedure

2.3.1. Pre- and post-training evaluation

Participants performed a monocular and a binocular evaluation of central visual acuity (ETDRS; Landolt C), eccentric visual acuity, crowding, and finally the central contrast sensitivity function was measured. All of these tests were repeated after the training sessions. Moreover, participants were tested in the baseline conditions before and after the training.

2.3.2. PL procedure

A typical daily session consisted of 4 blocks, in which the target-to-flanker distance was varied starting

from the higher distance (i.e., 8λ) and with the spatial frequency of the Gabor patches varying across daily sessions. Each treatment session was approximately 30 minutes in duration and was administered twice a week. To probe specificity effects (Harris, Gilksberg, and Sagi, 2012), each of the two daily sessions was devoted to one of the two spatial frequencies, starting from the lower spatial frequency (i.e., 6 cpd). The PL was completed after six weeks.

3. Results

Overall, the results show weak facilitatory interactions in myopia, which are strengthened by PL. The training of facilitatory lateral interactions enhanced the contrast sensitivity function and increased visual acuity but did not reduce crowding. Moreover, the results show that these learning effects transferred to the untrained eye but not to either the horizontal collinear configuration of 6 cpd or an orthogonal configuration (i.e., vertical triplet but with flankers orthogonal to the central target). In addition, the results did not show any transfer of learning to a collinear vertical configuration made up by Gabor patches with a lower spatial frequency (i.e., 1.5 cpd).

3.1. Lateral interactions in myopia

Figure 2 shows normalized thresholds (log units) as a function of the target-to-flanker distances for both normal sighted observers and myopic observers. Contrast thresholds, obtained in the collinear configuration of 6 cpd at each target-to-flanker distance, were normalized for each individual observer by the baseline threshold obtained using an orthogonally flanked target with the same spatial frequency and target-to-flanker separation (i.e., $\log_{10}[\text{collinear/orthogonal}]$).

The results of the repeated measures ANOVA performed to compare the two groups at the different levels of λ showed a significant effect of Target-to-Flankers Separation ($F(3,36)=9.7$, $p=0.0001$). Bonferroni corrected pairwise comparisons showed that mean normalized thresholds at 2λ were significantly different to those at 3λ and 4λ . Moreover, normalized thresholds at 3λ significantly differed to those at 8λ . Neither the effect of the Group nor the interaction between Group and Target-to-Flankers separation resulted significant. However, Bonferroni corrected one-sample t -tests revealed that normal-

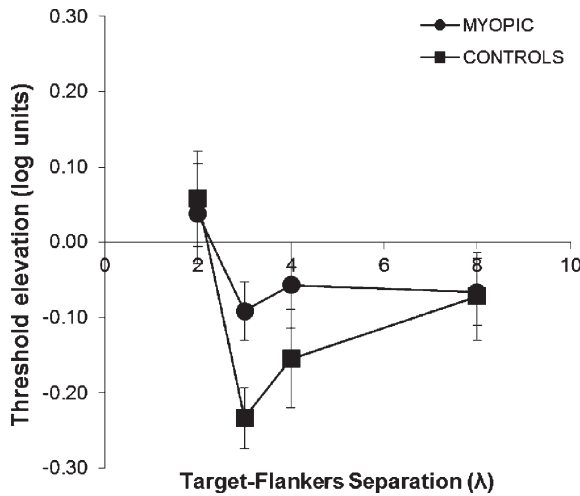


Fig. 2. Mean normalized thresholds (log units) for 6 cpd target as a function of the target-to-flanker distances for both normal sighted observers and myopic observers. Thresholds in the collinear configurations were normalized by the baseline threshold of orthogonally flanked target. The mean normalized thresholds for target-to-flanker separations of 2λ , 3λ , 4λ and 8λ were equal to 0.037 (SEM: 0.066), -0.091 (SEM: 0.039), -0.056 (SEM: 0.057) and -0.066 (SEM: 0.044) for the myopic observers and were equal to 0.037 (SEM: 0.063), -0.23 (SEM: 0.04), -0.15 (SEM: 0.065) and -0.07 (SEM: 0.058) for the control observers, respectively. Error bars \pm SEM.

363 ized thresholds obtained at 3λ by the normal sighted
 364 observers ($t(6) = -5.7$, $p = 0.001$) were significantly
 365 different from zero. On the other hand, normalized
 366 thresholds obtained at 3λ by the myopic observers
 367 ($t(6) = 2.32$, $p = 0.059$) did not differ from zero. This
 368 result indicates facilitatory interactions at this target-
 369 to-flankers separation only for the sighted observers. At

370 4λ normalized thresholds of neither group significantly
 371 differed from zero (controls: $t(6) = -2.3$, $p = 0.056$;
 372 myopic: $t(6) = 0.992$, $p = 0.36$). The amount of facil-
 373 itation in the sighted observers was very similar to
 374 that reported in previous studies (Polat and Sagi, 1993,
 375 1994a, 1994b; Shani and Sagi, 2005; Polat, 2009),
 376 whereas the amount of facilitation found in the myopic
 377 observers was significantly reduced. These results indi-
 378 cate a reduced strength of facilitatory lateral interaction
 379 in myopic observers.

3.2. Perceptual learning

381 The mean normalized thresholds obtained before
 382 and after the training by myopic observers are shown
 383 in Table 2 and Fig. 3. Table 2 also reports the
 384 contrast thresholds estimated in the pre- and post-
 385 training sessions for the two spatial frequencies used
 386 and for the collinear and orthogonal conditions (i.e.,
 387 baseline contrast thresholds). A three-way repeated
 388 measures ANOVA conducted on normalized thresh-
 389 olds before and after learning showed a significant
 390 effect of Learning ($F(1,6) = 12.34$, $p = 0.013$), but nei-
 391 ther a significant effect of the Spatial Frequency
 392 ($F(1,6) = 0.01$, $p = 0.97$), nor a significant effect of the
 393 Target-to-Flanker Separation ($F(1,6) = 2.3$, $p = 0.14$).
 394 Since we did not obtain a significant effect of the
 395 Spatial Frequency, data for the two spatial frequen-
 396 cies (i.e., 6 and 12 cpd) were collapsed to increase
 397 statistical power (see Fig. 3). The repeated measures
 398 ANOVA did not point out any significant interac-
 399 tion. Moreover, after training, normalized thresholds
 400 for the myopic observers were significantly lower

Table 2

Top panel: Mean contrast thresholds of the myopic observers obtained before (pre-) and after (post-) the training separately for 6 and 12 cpd, and for the collinear and orthogonal configurations. Bottom panel: Mean normalized thresholds of the myopic observers obtained in the pre- and post-training sessions separately for 6 and 12 cpd. SEM in brackets. * Introduce " . "

	Contrast thresholds							
	Pre-6cpd		Post-6 cpd		Pre-12 cpd		Post-12 cpd	
	Coll.	Ortho.	Coll.	Ortho.	Coll.	Ortho.	Coll.	Ortho.
2λ	0.093 (0.03)	0.10 (0.04)	0.076 (0.02)	0.11 (0.04)	0.17 (0.04)	0.18 (0.04)	0.13 (0.02)	0.17 (0.02)
3λ	0.097 (0.04)	0.11 (0.04)	0.080 (0.02)	0.12 (0.03)	0.18 (0.06)	0.19 (0.04)	0.12 (0.02)	0.19 (0.03)
4λ	0.1 (0.04)	0.11 (0.04)	0.093 (0.03)	0.13 (0.03)	0.15 (0.03)	0.18 (0.04)	0.14 (0.03)	0.20 (0.03)
8λ	0.11 (0.04)	0.12 (0.03)	0.10 (0.04)	0.12 (0.03)	0.17 (0.03)	0.18 (0.04)	0.18 (0.02)	0.20 (0.03)
	Normalized thresholds							
	Pre-6cpd		Post-6 cpd		Pre-12 cpd		Post-12 cpd	
2λ	0.037 (0.07)		-0.13 (0.03)		-0.04 (0.06)		-0.12 (0.03)	
3λ	-0.091 (0.04)		-0.23 (0.07)		-0.07 (0.07)		-0.18 (0.05)	
4λ	-0.056 (0.06)		-0.19 (0.11)		-0.06 (0.04)		-0.21 (0.07)	
8λ	-0.066 (0.04)		-0.08 (0.07)		-0.01 (0.05)		-0.09 (0.03)	

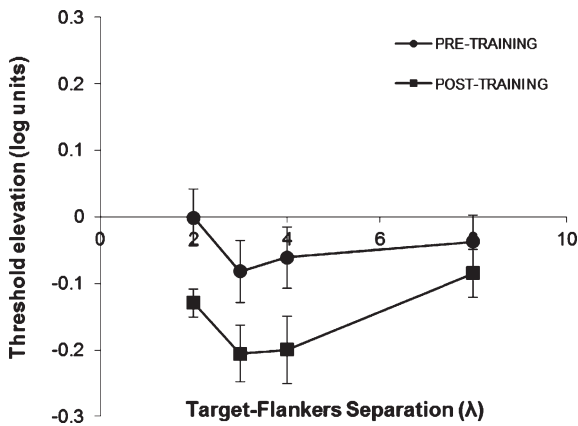


Fig. 3. Mean normalized thresholds (log units) obtained by the myopic observers before and after learning. Data relative to the 6 and 12 cpd were collapsed (see Table 2 for actual values). Thresholds are shown as a function of target-to-flankers separation (λ). Error bars \pm SEM.

than zero at 2λ ($t(6) = -6.2$, $p = 0.001$), 3λ ($t(6) = -4.8$, $p = 0.003$) and 4λ ($t(6) = -3.9$, $p = 0.007$), but not at 8λ ($t(6) = -2.362$, $p = 0.056$). These results indicate that training the contrast detection of a collinearly flanked target resulted in a significant decrease of contrast thresholds. In addition, this improvement is specific for the trained stimulus, indeed learning effect did not transfer to a target of the same orientation flanked by orthogonal Gabors. These results suggest that perceptual learning improves visual performance specifically for the trained collinear stimulus, pointing to a general increase of facilitatory interactions in the visual cortex during training.

Since learning specificity is viewed as the main indicator of the level of processing at which learning takes place, we also tested the specificity of learning for spatial frequency, target-flankers global orientation (i.e., orientation of the triplet) and interocular transfer.

3.3. Transfer of learning to lower spatial frequencies

Figure 4 shows the contrast thresholds obtained by the myopic observers in the pre- and post-training sessions. We did not find any transfer of perceptual learning to the vertical collinear configuration with low spatial frequency Gabors (i.e., 1.5 cpd). A repeated measures ANOVA conducted on the contrast thresholds before and after learning did not report

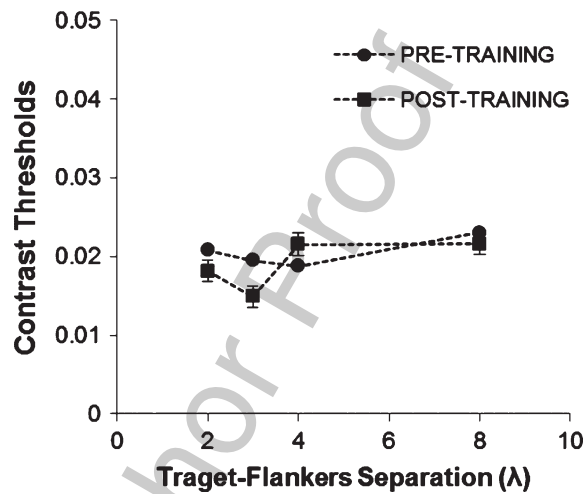


Fig. 4. Mean contrast thresholds (Michelson contrast) obtained in the untrained configuration of 1.5 cpd, as a function of target-to-flankers separation (λ). The average thresholds for target-to-flanker separations of 2λ , 3λ , 4λ and 8λ were respectively equal to 0.02 (SEM: 0.0013), 0.019 (SEM: 0.0013), 0.019 (SEM: 0.0014) and 0.023 (SEM: 0.0013) before the training and equal to 0.018 (SEM: 0.0014), 0.015 (SEM: 0.0013), 0.022 (SEM: 0.0023) and 0.022 (SEM: 0.002) after training higher spatial frequencies. Error bars \pm SEM. In some conditions error bars are smaller than the symbol size.

either a significant effect of Learning ($F(1,6) = 1.6$, $p = 0.252$), or an effect of the Target-to-Flanker Separation, though it was close to significance ($F(3,18) = 4.3$, $p = 0.051$), or a significant interaction between Learning and Target-to-Flankers Separation ($F(3,18) = 2.77$, $p = 0.102$). Indeed we found that, at every target-to-flanker separation, contrast thresholds before and after the training did not differ significantly ($p > 0.05$). The reason could be that contrast thresholds for 1.5 cpd Gabors were too low before training to be further decreased by PL (see Fiorentini and Berardi, 1980 for similar results). However, it should be noted that despite contrast modulation thresholds were estimated using a 8-bit luminance resolution, on average, the contrast modulation thresholds obtained before and after the training across all the target-to-flanker separations were significantly higher than the minimum contrast modulation displayed by the screen (i.e., 0.0098 Michelson contrast). One sample t -test revealed that thresholds were not significantly lower than 0.02 Michelson contrast, with except at 3λ after learning ($t(6) = -3.8$, $p = .01$), and that in this condition the threshold value did not differ from 0.015 (Michelson contrast). In addition, to assess whether the Gabor function was represented faithfully at the

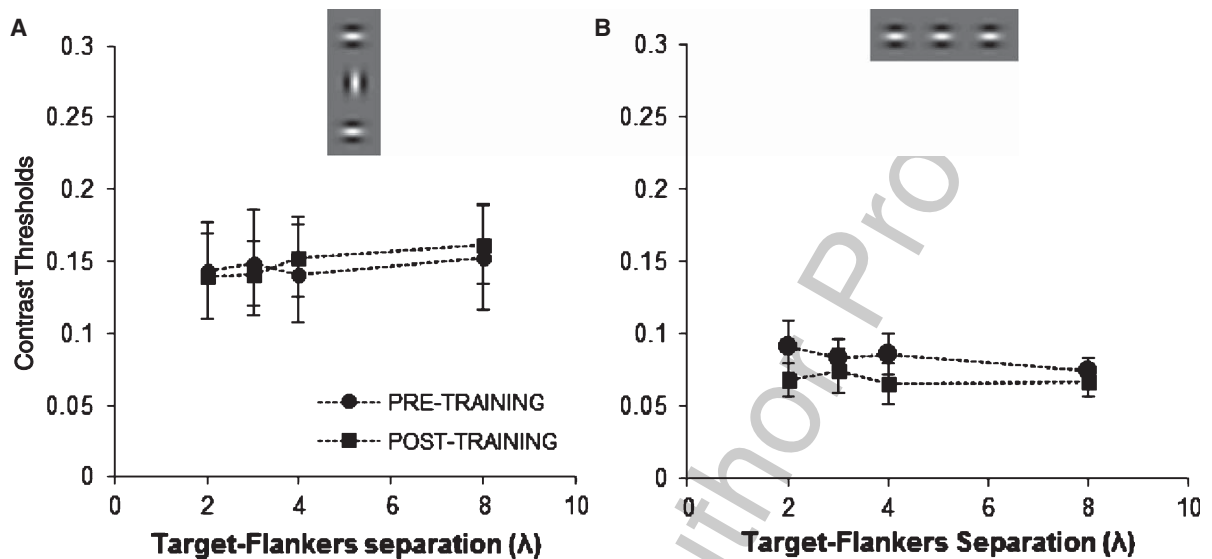


Fig. 5. Mean contrast thresholds (Michelson contrast) obtained in the following untrained configurations: (A) vertical configuration with vertical target and orthogonal flankers (data relative to the 6 and 12 cpd were collapsed), and (B) horizontal collinear configuration only for 6 cpd condition. Mean contrast thresholds are represented as a function of the target-to-flankers separation (λ). For target-to flanker separations of 2λ , 3λ , 4λ and 8λ , contrast thresholds in the orthogonal configuration are equal to 0.14 (SEM: 0.03), 0.15 (SEM: 0.03), 0.14 (SEM: 0.03) and 0.15 (SEM: 0.04) before the training and equal to 0.14 (SEM: 0.03), 0.14 (SEM: 0.02), 0.15 (SEM: 0.03) and 0.15 (SEM: 0.03) after training. In the horizontal configuration thresholds are equal to 0.09 (SEM: 0.02), 0.08 (SEM: 0.01), 0.08 (SEM: 0.01) and 0.07 (SEM: 0.01) before the training and equal to 0.07 (SEM: 0.01), 0.07 (SEM: 0.02), 0.06 (SEM: 0.01) and 0.07 (SEM: 0.01) after the training. Error bars \pm SEM.

* The symbol is wrong

454 minimum contrast modulation displayed by the screen
 455 (i.e., 0.0098 Michelson contrast), we performed a control
 456 experiment in which six naïve observers (normal
 457 sighted or corrected to normal) reported whether they
 458 perceive a number of stripes of the Gabor patch lower
 459 or equal/higher than three, by pressing one of two
 460 designated keys on a standard computer keyboard. A
 461 single Gabor patch was presented at the center of the
 462 screen. We used five contrast levels: 0.025, 0.02, 0.015,
 463 0.01, and 0.005 (Michelson contrast); each contrast
 464 level was repeated 15 times. The percentage of trials
 465 in which observers reported to perceive a number of
 466 stripes equal or higher than three was: 0.025:100%
 467 [SEM: 0%], 0.02:97.7% [SEM: 2.2%], 0.015:98.8%
 468 [SEM: 1.1%], 0.01:82.6% [SEM: 15.7], 0.005:0%.
 469 This suggest that at ~ 0.01 of contrast modulation the
 470 Gabor function was still visible. In sum, our results sug-
 471 gest that the learning effect is specific for the spatial
 472 frequency.

3.4. Transfer of learning to different configurations

473 A repeated measures ANOVA conducted on the
 474 contrast thresholds obtained before and after learn-

477 ing with orthogonal configuration did not report
 478 any significant main effect or interaction: Learning
 479 ($F(1,6) = 0.007$, $p = 0.94$), Target-to-Flanker Separation
 480 ($F(3,18) = 0.95$, $p = 0.42$), Learning \times Target-to-
 481 Flankers Separation ($F(3,18) = 0.77$, $p = 0.46$). Similarly,
 482 contrast thresholds obtained before and after learning
 483 with horizontal collinear configurations of 6 cpd Gabors
 484 (the 12 cpd data were not included because only four
 485 observed were tested in this condition) did not report
 486 a significant effect of Learning ($F(1,6) = 2.27$, $p = 0.19$),
 487 of the Target-to-Flanker Separation ($F(3,18) = 0.43$,
 488 $p = 0.61$) and of the interaction between Learning
 489 and Target-to-Flankers Separation ($F(3,18) = 0.76$,
 490 $p = 0.47$). These results indicate that there is not a
 491 transfer of learning to an orthogonal configuration (Fig.
 492 5A) and to the horizontally oriented collinear configura-
 493 tion (Fig. 5B), presented in the same retinal position
 494 as the learning stimulus. Note however that three out
 495 of four subjects that performed the horizontal collinear
 496 condition with a spatial frequency of 12 cpd showed
 497 transfer of learning, suggesting that training a vertical
 498 collinear configurations may transfer to horizontal
 499 collinear configuration, but only for high spatial frequen-
 500 cies. This second result was unexpected on the bases
 501 of previous results showing that, as task

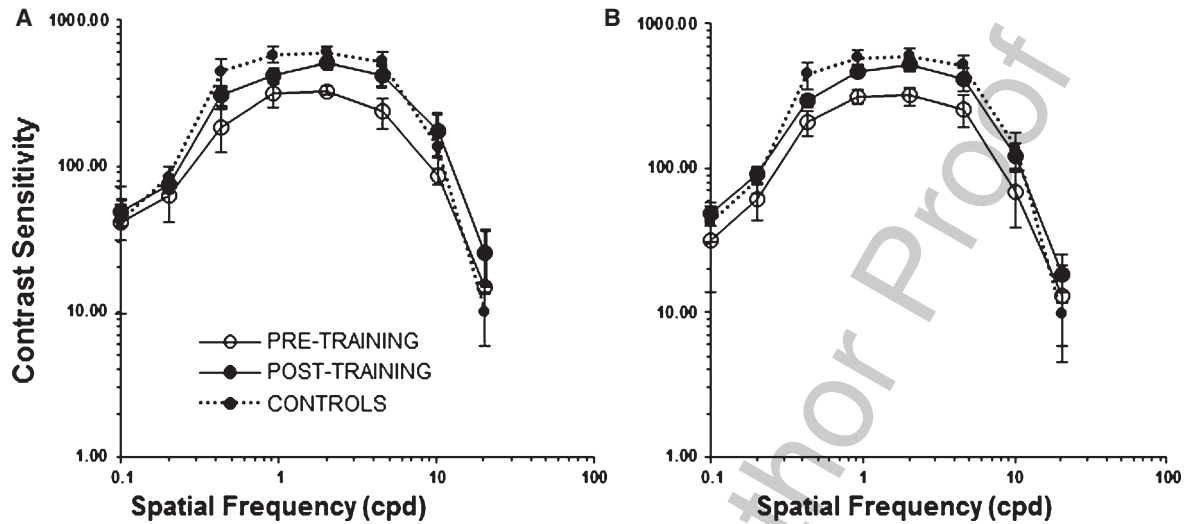


Fig. 6. Contrast sensitivity functions (CSFs) obtained in both the trained (A) and untrained (B) eye before and after training. The effect of training was significant at 2.04 cpd (trained: 330 [SEM: 47] vs. 512 [SEM: 45]; untrained: 325 [SEM: 47] vs. 513 [SEM: 44]), at 4.53 cpd (trained: 237 [SEM: 65] vs. 419 [SEM: 66]; untrained: 256 [SEM: 61] vs. 402 [SEM: 75]) and less consistently significant at 10.18 cpd (trained: 85 [SE: 30] vs. 172 [SE: 56]; untrained: 73 [SE: 32] vs. 114 [SE: 28]). Data are compared to those obtained by normal sighted observers. Error bars \pm SEM.

502 difficulty increases, learning becomes more specific
 503 with respect to orientation (Ahissar and Hochstein,
 504 1996). However, a larger sample size is need to clarify
 505 whether the transfer to a horizontal collinear configura-
 506 tion depends on spatial frequency in the myopic eye.
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508 The finding that transfer stimuli are immune to percep-
 509 tual learning of vertical collinear configurations
 510 strongly suggests that the modulation of lateral inter-
 511 actions through perceptual learning is functionally
 512 specific. Ts'o and colleagues (1986) investigated the
 513 relationship between lateral connections and the func-
 514 tional architecture of V1; in particular, they showed
 515 that V1 neurons establish connections only with cells
 516 that have the same functional specificity (i.e., respon-
 517 siveness to an iso-oriented line). Thus, our results are
 518 compatible with their findings.

519 3.5. Transfer of learning to contrast sensitivity 520 function (CSF)

521 Contrast sensitivity for sinusoidal gratings was mea-
 522 sured before and after training in order to derive
 523 CSFs (Fig. 6). Before training, the difference in con-
 524 trast sensitivity between myopic and control observers
 525 was significant ($F(1,10)=12.1, p=0.006$). The inter-
 526 action between Group and Spatial Frequency was

also significant ($F(1,10)=6.6, p=0.005$). Bonferroni
 corrected pairwise comparisons reported a significant
 difference in contrast sensitivity between control and
 myopic observers before Learning at 0.4 ($p=0.015$),
 0.9 ($p=0.005$), 2.0 ($p=0.005$) and 4.5 cpd ($p=0.021$).
 Training lateral interactions increased contrast sensi-
 tivity significantly in both the trained and untrained
 eye at 2.0 cpd ($p=0.002, p=0.02$), 4.5 cpd ($p=0.005$,
 $p=0.0001$) and less consistently at 10.18 cpd ($p=0.08$,
 $p=0.04$), indicating that Learning to detect flanked
 Gabor of 6 and 12 cpd selectively transfers to grat-
 ings of similar (ranging from 4.5 to 10 cpd) and lower
 spatial frequencies (2 cpd). However, we did not report
 a corresponding improvement for Gabor patches in the
 orthogonal configuration at the trained spatial frequen-
 cies and for collinear Gabor patches of 1.5 cpd. Thus,
 there is transfer from flanked Gabors to wide gratings
 but not to non-collinear Gabors of the same or lower
 spatial frequency with respect to those trained. The
 transfer from Gabor patches to gratings cannot be due
 to an enhanced focused attention which would bring
 to an improvement of different spatial frequencies
 and configurations (Carrasco, Eckstein et al., 2000).
 More likely, the transfer from Gabor patches to grat-
 ing may occur because training forces observers to
 simultaneously handle iso-oriented target and flankers
 so that it improves detection of the full screen grat-

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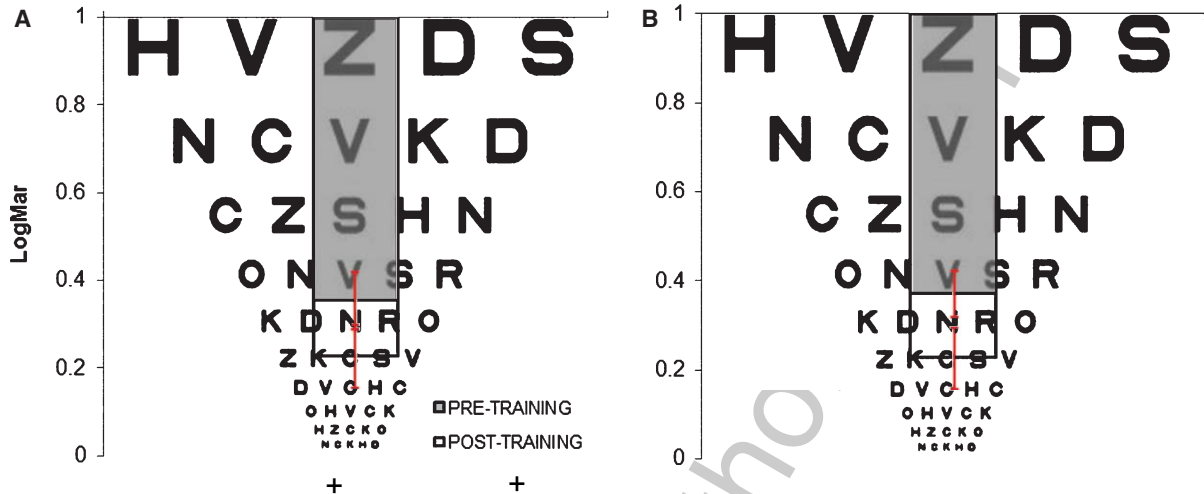


Fig. 7. Mean visual acuity (ETDRs), expressed in logMAR, measured before (gray bars) and after training (transparent bars) for the trained eye (A: 0.36 [SEM: 0.06] and 0.23 [SEM: 0.07] logMAR) and the untrained eye (B: 0.37 [SEM: 0.05] and 0.23 [SEM: 0.06] logMAR). Error bars \pm SEM.

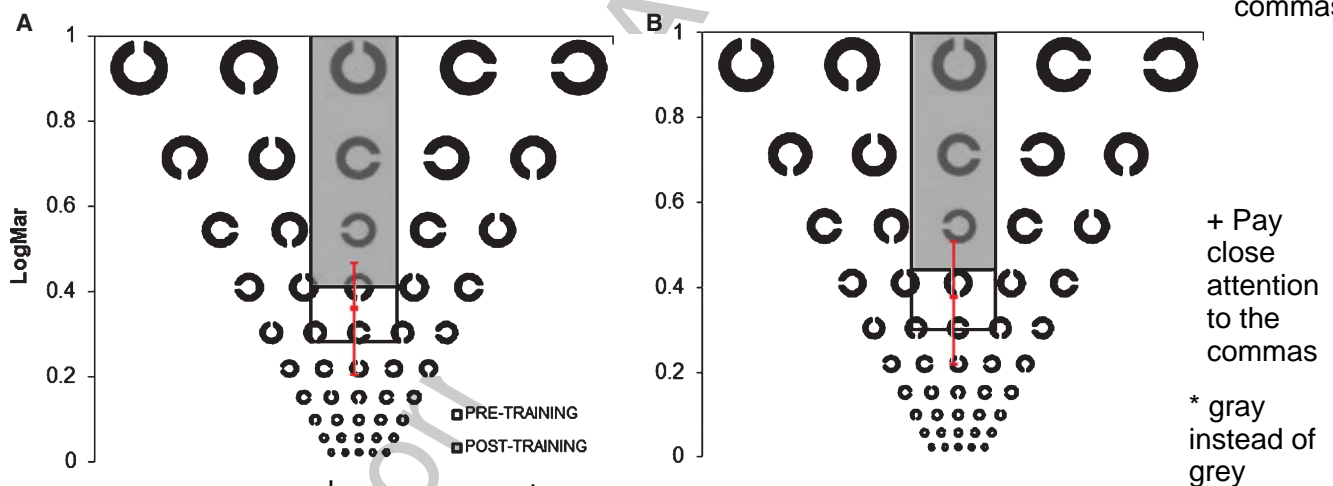


Fig. 8. Mean visual acuity (Landolt C), expressed in logMAR, measured before (gray* bars) and after training (transparent bars) for the trained eye (A: 0.41 [SEM: 0.05] and 0.28 [SEM: 0.08] logMAR) and the untrained eye (B: 0.44 [SEM: 0.06] and 0.3 [SEM: 0.08] logMAR). Error bars \pm SEM.

ings used to measure CSF, which stimulates several iso-oriented visual channels (Robson and Graham, 1981).

3.6. Transfer of learning to visual acuity

Results (Figs. 7 and 8) show that the increase of facilitation after training significantly improved visual acuity both in the trained and untrained eye. Indeed, the result of the two-way repeated measures ANOVA on the ETDRS data (Fig. 7) pointed-out a significant effect of Learning ($F(1,6)=17.7, p=0.006$) but

not a significant effect of the Eye ($F(1,6)=0.02, p=0.89$), and of the interaction between Learning and Eye ($F(1,6)=0.07, p=0.80$). Similar results were obtained in the Landolt-C task (Fig. 8) in which we obtained a significant effect of Learning ($F(1,6)=13.02, p=0.01$), but not a significant effect of the Eye ($F(1,6)=0.3, p=0.6$) nor a significant interaction between Learning and Eye ($F(1,6)=0.3, p=0.6$). The average learning dependent improvement in visual acuity was 1.3 and 1.4 logMAR lines in the trained and untrained eye, respectively. This effect is lower than that reported in previous studies (Durrie and McMinn,

+ Pay close attention to the commas

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* gray instead of grey

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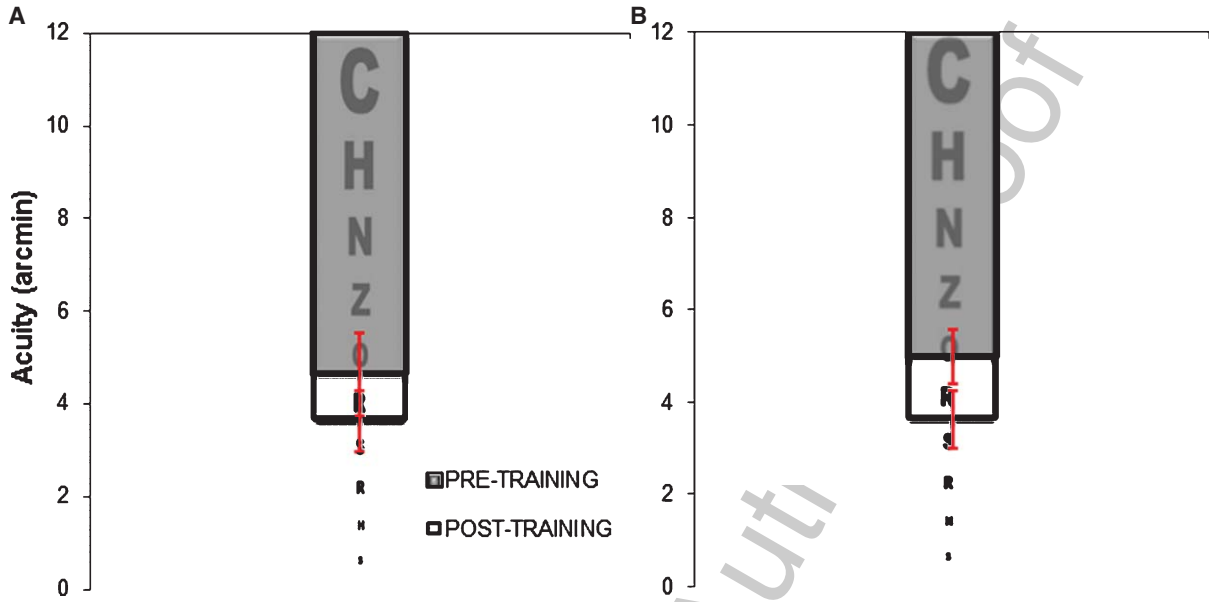


Fig. 9. Mean visual acuity, expressed in arcmin, obtained before (gray bars) and after training (transparent bars) for the trained eye (A: 4.7 [SE: 0.91] and 3.6 [SE: 0.67] arcmin) and the untrained eye (B: 5 [SE: 0.6] and 3.6 [SE: 0.62] arcmin). Stimuli were presented at 4 deg of eccentricity. Error bars \pm SEM.

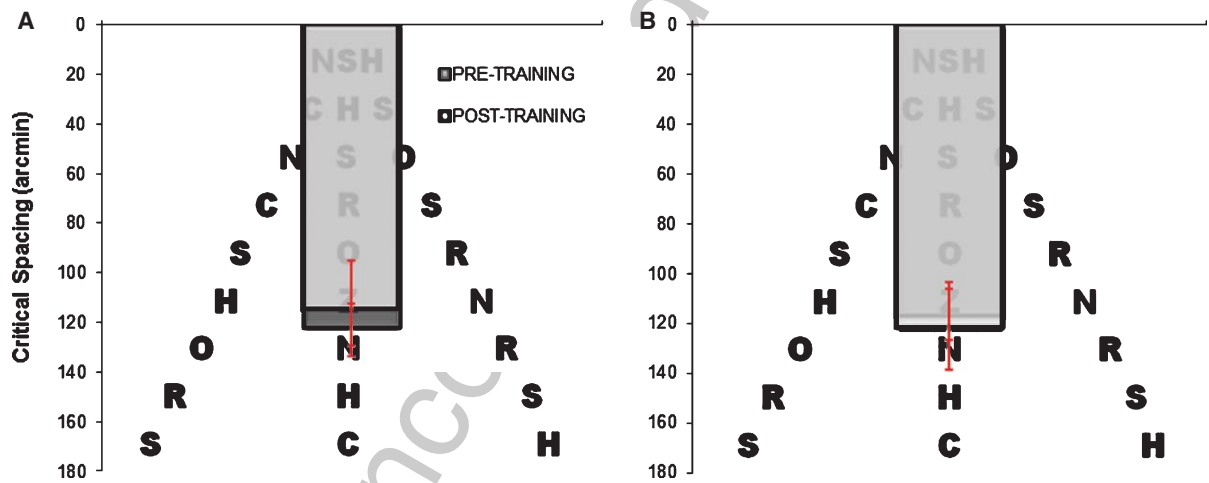


Fig. 10. Mean critical spacing (i.e., the target-to-flankers spacing at which the flankers did not reduce acuity), expressed in arcmin, obtained before (gray bars) and after training (transparent bars) for the trained eye (A: 121.1 [SEM: 8.5] and 114.4 [SEM: 19.1] arcmin) and the untrained eye (B: 116.9 [SEM: 10.1] and 121.2 [SEM: 17.7] arcmin). Stimuli were presented at 4 deg of eccentricity. Error bars \pm SEM.

2007; Tan and Fong, 2008), probably because we used only a vertically oriented training stimulus.

The transfer of learning with vertically oriented Gabors to complex stimuli such as Sloan letters and Landolt-C could be explained by assuming that these visual acuity tasks can be performed by detecting intensity changes (Westheimer, 2001), a task similar to the (trained) contrast detection.

3.7. Transfer of learning to crowding

Before Learning, eccentric visual acuity was significantly reduced in myopic with respect to control observers ($F(1,11) = 8.9, p = 0.012$), whereas crowding was not ($F(1,11) = 0.18, p = 0.9$). In myopic observers, training-dependent increased facilitation improved eccentric visual acuity (Fig. 9) but did not affect crowd-

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ing (Fig. 10). Indeed, a two-way ANOVA performed on the acuity data revealed a significant effect of Learning ($F(1,6) = 11.6, p = 0.014$), but not a significant effect of Eye ($F(1,6) = 2.5, p = 0.17$) nor a significant interaction between Learning and Eye ($F(1,6) = 0.10, p = 0.98$). On average visual acuity after Learning increased by 24% for the trained eye and 28% for the untrained eye reaching the normal level ($F(1,11) = 3.6, p = 0.07$), indicating that learning transferred to a more eccentric stimulus. On the other hand, a two-way repeated measures ANOVA performed on the crowding data did not report a significant effect of Learning ($F(1,6) = 0.5, p = 0.5$), Eye ($F(1,6) = 1.9, p = 0.22$) and of the interaction between Learning and Eye ($F(1,6) = 2.3, p = 0.18$). This is expected since in normal vision critical spacing (i.e., the target-to-flankers distance at which the flankers no longer interfere with target identification) is equal to $\sim \frac{1}{2}$ the eccentricity (Bouma, 1970; Pelli, Palomares et al., 2004). That is, before Learning the crowding effect was within the range of normal vision in the myopic eye.

4. Discussion

In the present study we investigated the pattern of lateral interactions in observers with low myopia and its modulation by perceptual learning (PL). We used a contrast detection task of a central Gabor patch flanked above and below by two collinear high contrast Gabor patches. Observers had to report whether the central target was present in the first or second temporal interval of a two-interval display sequence (2IFC task). We assessed whether PL transferred to untrained stimuli and tasks, and whether it exhibits interocular transfer.

The first new result of the present study is a reduced strength of facilitatory lateral interactions in the myopic eye. This supports our suggestion that non-optimal activation of high spatial frequency channels in individuals with myopia may also reduce the strength of facilitatory lateral interactions between them, in terms of the transmission of internal response via a cascade of local connections (Polat and Sagi, 1994b). This suggestion is indicative of maladaptive plasticity and it is also indirectly supported by the Hebbian rule, according to which mature visual cortical connections require temporal covariation, i.e., both pre- and postsynaptic activity within a defined time window (Karmarkar and Dan, 2006). It is also possible that cortical connections may not be mature at the

onset of myopia so that they cannot become adult-like. To this purpose Kovacs (2000) has shown that long-range interactions span a shorter spatial range until the end of childhood. Indeed, if long-range lateral interactions are a late maturing function, they would be mostly affected by deficiency with a relatively late onset (Kovacs, 2000). However, in our myopic sample, the onset of myopia was relatively late during childhood, thus it is not clear whether this could have prevented a complete development of the pattern of lateral interactions. To address this issue, the comparison of the pattern of lateral interactions at different target-to-flankers distances (λ) in myopic groups with different onset of myopia is needed.

Our second result is that training lateral interactions results into a significant facilitation induced by the flankers. In particular, we found lower contrast detection thresholds in the trained collinear configuration with respect to the untrained orthogonal configuration. This enhancement of facilitatory lateral interactions could result from learning dependent increments of the synaptic strength in response to repetitive co-activation of visual channels responding to target and flankers (Karmarkar and Dan, 2006). Co-activation of a network of visual channels could facilitate the recruitment of information within a large retinal area, thus explaining why Learning did not transfer to a vertically oriented target flanked by orthogonal Gabors but it enhanced contrast sensitivity function for large gratings. Indeed, we found that learning transfers to CSFs, and this occurs in both trained and untrained eye indicating that the mechanism involved in the collinear facilitation operates after the convergence of the visual input from the two eyes.

The third result is the evidence of specificity of learning effects. We found that training did not transfer to collinear configurations of low spatial frequency. The reason could be that CSF in myopic observers (Fig. 6) is slightly shifted towards low spatial frequencies for which there is little or no facilitation (i.e., contrast thresholds are slightly affected by target-to-flankers separation) (Fig. 4), possibly because of inefficient lateral interactions (Polat, 2009). Furthermore, the improvement of contrast sensitivity by training lateral interactions did not transfer orthogonal configurations of 6 and 12 cpd and to collinear configurations of 6 cpd Gabors with different orientation of the triplet (i.e., horizontal; see Polat and Sagi, 1994b for similar results), although we found transfer of learning in three out of four subjects who were tested before

688 and after the learning with a collinear horizontal con- 738
689 figuration of 12 cpd. The specificity of learning in 739
690 human adults for the low-level trained stimulus and 740
691 for the task has been previously reported by a num- 741
692 ber of studies (Maniglia, Pavan et al., 2011; Bao, Yang 742
693 et al., 2010; Gilbert, Sigman et al., 2001; Sagi and 743
694 Tanne, 1994) as well as the selectivity to global con- 744
695 figurations, both in normal sighted (Maniglia, Pavan 745
696 et al., 2011) and in amblyopic observers (Levi and 746
697 Polat, 1996; Levi, Polat et al., 1997; Li and Levi, 747
698 2004) and these results are consistent with the involve- 748
699 ment of neural processes at the level of the primary 749
700 visual cortex. It should be noted that the specificity 750
701 phenomena we have reported may be the consequence 751
702 of the procedure used that is likely to induce sensory 752
703 adaptation. Indeed, Harris et al. (2012) using a texture 753
704 discrimination task showed that location specificity is 754
705 a consequence of sensory adaptation; that is, location 755
706 specificity results from selective reduced sensitivity 756
707 due to repeated stimulation. Observers practiced the 757
708 texture discrimination task with the target presented 758
709 at a fixed location within a background texture. To 759
710 remove adaptation, the authors added task-irrelevant 760
711 trials with the background texture oriented 45° relative 761
712 to the target's orientation. The results showed com- 762
713 plete generalization to a new location when adaptation 763
714 was removed, suggesting that adaptation interferes 764
715 with invariant pattern-discrimination learning by 765
716 inducing network-dependent changes in local visual 766
717 representations. 767

718 The lack of transfer to the horizontal collinear con- 768
719 figuration and to the orthogonal configuration tested 769
720 with the same procedure, is indicative that learning 770
721 cannot be accounted by changes in the optical system 771
722 (e.g., refraction and accommodation). This is because 772
723 changes of the refraction and accommodation would 773
724 produce a non-specific improvement. Similarly, the 774
725 transfer of learning to the non-trained eye indicates 775
726 that its effect is neural and occurs after the informa- 776
727 tion from the two eyes is combined (Fahle, 2004; Sagi, 777
728 2011). Moreover, Polat et al. (2012) showed that the 778
729 learning dependent improvement of vision in the pres- 779
730 byopic eye is achieved without changing the optical 780
731 characteristics of the eye. 781

732 In agreement with previous findings (Polat, 2009; 782
733 Maniglia, Pavan et al., 2011; Polat, Ma-Naim et al., 783
734 2004; Durrie and McMinn, 2007; Tan and Fong, 2008) 784
735 we found that the improvement achieved by percep- 785
736 tual learning of collinear configurations generalizes 786
737 to complex tasks such as visual acuity with Landolt-

C and ETDRS, and such generalization occurs in the 738
untrained eye in a more eccentric retinal position. One 739
possible explanation for these transfer effects is that 740
the improvement in contrast sensitivity may facilitate 741
the performance of visual processing during the next 742
stages of the visual cascade, where neurons respond to 743
more complex input. To this purpose, a striking num- 744
ber of studies showed that PL can be transferred to 745
the letter recognition task (VA) that relies on contrast 746
detection (Chung, Legge et al., 2002; Chung, Mans- 747
field et al., 1998; Legge, Pelli et al., 1985; Levi, Song 748
et al., 2007; Majaj, Pelli et al., 2002; Patching and Jordan, 749
2005; Solomon and Pelli, 1994). Most of these 750
studies indeed pointed out that letter recognition task 751
is mediated by visual channels that rescale with letter 752
size, such that when the channel's frequency and letter 753
size are both expressed as retinal frequency (c/deg), 754
a change in letter size will lead to a corresponding 755
change in the underlying channel's frequency of the 756
same magnitude. The change in terms of spatial fre- 757
quency is usually described as a power function with 758
an exponent of 1.0 (Solomon and Pelli, 1994). 759

760 There is a major question regarding the improve- 761
762 ment of contrast sensitivity and visual acuity following 762
763 PL in low myopia. The vision of myopic and presby- 763
764 opic individuals is blurred without optical correction, 764
765 and their corrected contrast sensitivity is reduced (Liou 765
766 and Chiu, 2001). Despite blur had persisted for years, 766
767 myopic subjects seem immune from effects due to 767
768 adaptation to blur, that makes object to look sharper 768
769 (Webster, Georgerson et al., 2002), improve visual 769
770 resolution (Pesudovs and Brennan, 1993) and lead- 770
771 ing to unbiased perception (Yehezkel, Sagi et al., 771
772 2010). Instead, Perceptual Learning seems able to 772
773 reduce blur. Such improvement could rely on some 773
774 interaction between perceptual learning and visual 774
775 adaptation. McGovern and colleagues (2012), for 775
776 example, investigated the interaction between adap- 776
777 tation and perceptual learning in the motion domain. 777
778 The results showed that, while adapting to motion, 778
779 repeated practice of direction discrimination on the test 779
780 pattern led to an improvement in direction discrimi- 780
781 nation performance that was higher after the training 781
782 compared to the unadapted performance. Therefore, in 782
783 the case of myopia it is possible that repeated practice 783
784 in an adapted state to blur produces an improve- 784
785 ment in contrast sensitivity. On the other hand, blur 785
786 in myopia is long-lasting and the effects of Learning 786
787 that we and other authors have shown (Durrie and McMinn, 2007; Tan and Fong, 2008) may also 787

reflect learning-dependent modulation of a long-term maladaptive plasticity.

In conclusion, we showed that probing cortical interactions with a set of spatial frequencies and target-to-flankers separations can modulate the spatial interactions in the visual field of myopic adult observers. A relevant question is whether these results could have an important implication in the treatment of myopic individuals, improving their visual functions in everyday life. To this purpose learning effects should be retained. Although we did not collect follow-up data, this issue was addressed by other authors that used the same Learning paradigm in myopia. For example, Tan and Fong (2008) found a PL effect retained up to 12 months.

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