

# **Contrast adaptation improves spatial integration**

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## **Abstract**

The effects of contrast adaptation and contrast area summation (spatial integration) were investigated using a contrast discrimination task. The task consisted of a target of variable size, and a pedestal with a fixed base contrast. Discrimination performance was examined for a condition in which the pedestal size was fixed, equal to the largest target size, and for a condition in which the pedestal size matched the target size and thus varied with it. Repeated performance of the task produced rapid within-session improvements for both conditions. For stimuli with a matching size of target and pedestal, the performance improved only for the larger targets, indicating the development of spatial integration, which was initially absent for these stimuli. However, the improvements were mostly temporary, and were not fully retained between subsequent sessions. The temporary nature of the sensitivity gains implies that they resulted, at least in part, from rapid adaptation to the stimulus contrast. We suggest that adaptation decorrelates and thus reduces the spatial noise generated by a high-contrast pedestal, leading to improved spatial integration (area summation) and better contrast sensitivity. A decorrelation model successfully predicted our experimental results.

## Introduction

Visual adaptation is a stimulus-driven process that continuously adjusts the neural responses to the statistics of the current visual environment. Contrary to perceptual learning, which leads to long-term improvements in performance, adaptation effects are generally short termed, tracking the current visual input to the eyes. However, both are thought to reflect neuronal plasticity, short-term in adaptation, and long-term in learning, possibly interacting (Sagi, 2011; Webster, 2015). One approach to visual pattern adaptation assumes that coding efficiency can be improved via short-term plasticity. According to this view, visual adaptation adjusts the limited dynamical range of individual neurons or a population of neurons to the statistics of the recent visual input (Wainwright, 1999; Wark et al., 2007). Coding efficiency can also be enhanced by reducing redundancy in sensory signals, possibly by decorrelating neuronal responses across processing channels (Barlow & Földiák, 1989). This was supported by studies showing that adaptation decorrelates population responses in V1 of cats and monkeys (Benucci et al., 2013; Gutnisky & Dragoi, 2008). These continuous adjustments are expected to improve discriminability. However, previous studies that tested how adaptation affects contrast discrimination found only weak and mixed evidence for improved discriminability using target stimuli similar to the adapter (Barlow et al., 1976; Greenlee & Heitger, 1988; Määtänen & Koenderink, 1991a; Ross et al., 1993). In a recent study we found large improvements in a grouping discrimination task, which were attributed to visual adaptation (Pinchuk-Yacobi & Sagi, 2019). Perceptual grouping was suggested to rely highly on spatial correlations and spatial integration (Ben-Av & Sagi, 1995); therefore, it should be most affected by adaptation-induced spatial decorrelation. On the other hand, contrast discrimination, which is also influenced by spatial configuration (Adini & Sagi, 2001; Snowden & Hammett, 1998), does not benefit from spatial integration when the base contrast (pedestal) and the increment contrast (target) are over an equal spatial extent, explained by balanced excitation and inhibition interactions (Bonneh & Sagi, 1999b; Legge & Foley, 1980; Meese, 2004). However, spatial integration in contrast discrimination was observed for varying target sizes when a large, fixed, base contrast was used (Bonneh & Sagi, 1999b).

Here we aimed at testing the dynamics of contrast discrimination while varying target size, using stimuli in which the pedestal was either fixed at a maximal size, or of varied size, matching the size of the target. We tested for changes in observers' performance, both repeatedly within a session as well as across several daily sessions. Repeated stimulation during an experimental session leads to both adaptation and learning. For learning, we assume long-term persistence, across days, of performance changes (Sagi, 2011). Adaptation effects are assumed to follow recent stimulation, accumulate with repeated stimulation, and decay after stimulation has ended (Greenlee et al., 1991). Basing on previous studies showing adaptation to brief stimuli (sub-second) to affect detection thresholds (Pavan et al., 2012), and to generate tilt aftereffects (Dekel & Sagi, 2020; Pinchuk-Yacobi, Harris, et al., 2016), we expect the many (~600) short duration (0.1 sec) high contrast stimuli used here to develop adaption. We found that repeated performance of the task produced rapid within-day improvements, which were largely transient, and were not fully retained when tested on subsequent days. For stimuli with a matching size of target and pedestal, the performance improved only for the larger targets, indicating the development of spatial integration (area summation), which was initially absent for these stimuli. We assumed that the transient nature of the gains implies that they resulted from rapid adaptation to the visual stimuli. Our results were predicted by a simple model, assuming that adaptation decorrelates spatial noise, thus leading to improved spatial integration and better contrast sensitivity. Practice with the task, over several days, resulted in faster adaptation, in accordance with previous findings (Yehezkel et al., 2010), supporting the idea that adaptation involves short-term plasticity, which with repetition, may consolidate and result in long-term effects.

## **Methods**

### **Pilot experiment**

A pilot experiment was performed prior to the main experiment. The pilot included eleven observers, out of which one continued to the main experiment. Analysis of the

pilot's results revealed two methodological issues that were modified in the main experiment: (1) the target in the pilot was subtracted from (decrement), instead of added to (increment), the pedestal. Detecting a contrast decrement was not intuitive and was very difficult, especially in the 'Non-matched' condition, resulting in very high threshold, often saturated. This result is consistent with previous reports comparing detection of contrast increments and decrements (Bowen, 1997). (2) the adaptive staircase method made temporal tracking of performance difficult – changing to a constant stimuli method in the main experiment allowed for more accurate temporal tracking of performance. See the Appendix section for detailed results of the pilot experiment.

## **Apparatus**

The stimuli were presented on a 23.6'' VIEWPixx/3D monitor (1920 x 1080, 10bit, 120Hz, with 'scanning backlight mode') viewed at a distance of 100 cm. The mean luminance of the display was 47.26 cd/m<sup>2</sup>, in an otherwise dark environment.

## **Observers**

Seventeen observers with normal or corrected-to-normal vision participated in the experiments described in the Results section. All observers were naïve to the contrast discrimination task and gave their written informed consent. The work was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki), and was approved by the Institutional Review Board (IRB) of the Weizmann Institute of Science.

## **Stimuli and task**

### Contrast discrimination task (CD):

The stimuli consisted of two peripheral Gabor patterns (5.3° eccentricity left and right of fixation, 100 ms duration) presented simultaneously (Figure 1). Both patterns contained a pedestal signal (Gabor patch with  $\lambda = 0.53^\circ$ ; phase = 0) with a constant base contrast (Michelson contrast = 55%). One of the patterns, either on the left or on the right, contained an additional target signal (a Gabor patch with  $\lambda = 0.53^\circ$ ; phase = 0) that was added to the pedestal. The size of the target (defined as the standard deviation of the

Gaussian envelope,  $\sigma$ ) was one of four values:  $0.37^\circ$ ,  $0.56^\circ$ ,  $0.84^\circ$ , or  $1.3^\circ$ , which were randomly interleaved across trials. The size of the pedestal was either fixed at a maximal size ( $\sigma = 1.3^\circ$ , ‘Non-matched’ condition) or changed in size in accordance with the size of the target ( $\sigma = 0.37^\circ$ ,  $0.56^\circ$ ,  $0.84^\circ$ , or  $1.3^\circ$ , ‘Matched’ condition). Contrast thresholds were measured using a spatial two-alternative forced-choice (2AFC) paradigm. After fixating a central fixation circle, observers, when ready, initiated a new trial, and reported which of the patterns (left or right) contained the target, that is, which of the Gabor patterns appeared to have a higher contrast. An auditory feedback was given for an incorrect response.

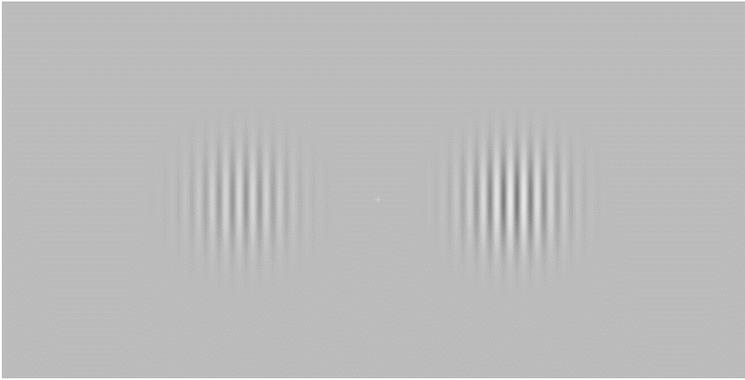


Fig. 1. *Stimuli and task. Observers fixated the white cross at the center of the screen and judged the location of a contrast increment (spatial 2AFC: left or right,  $5.3^\circ$  eccentricity, 100 ms duration).*

## **Procedure**

Seventeen observers participated in this experiment. Ten of them participated in the ‘Non-matched’ condition, and seven participated in the ‘Matched’ condition. The experiment included one introductory session and four testing sessions, on different days. Each session consisted of four blocks with 140 or 168 trials per block (4 target sizes,  $\times$  7 contrast values, and  $\times$  5 or 6 trials per contrast). The target contrast was one of seven values: 0.8%, 1.6%, 3.1%, 4.7%, 6.3%, 12.6%, and 25.2%, randomly intermixed across trials (constant stimuli method). The measured psychometric curves (the percentage of correct responses as a function of target contrast) were fitted with a Weibull function

distribution (lapse rate: up to 0.05). The discrimination threshold was defined as the contrast for which there were 79% correct responses. Fitting was performed using Psignifit 4.0 software for MATLAB (Schütt et al., 2016).

## Results

Results for the group contrast discrimination thresholds (averaged across observers) for the 'Non-matched' group (fixed pedestal size) and the 'Matched' (varied pedestal size) groups are presented in Figure 2A and Figure 2B, respectively. To test for significant within-session improvements, we ran a repeated measures ANOVA with the within-observer factors including day (4 days), size (4 sizes), and block (first block vs last block) performed separately for the two groups. Performance within-session improved significantly in both groups, as indicated by a significant decrease in the threshold from the first block to the last block ( $5.2 \pm 0.8$ ,  $F(1,9) = 42.8$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.8$ ;  $2.2 \pm 0.6$ ,  $F(1,6) = 11.5$ ,  $p = 0.01$ ,  $\eta_p^2 = 0.7$ , mean  $\pm$  SEM in the 'Non-matched' group and the 'Matched' group, respectively). In the 'Non-matched' group, there was also a significant interaction between block threshold and day ( $F(3,9) = 3.4$ ,  $p < 0.05$ ,  $\eta_p^2 = 0.3$ ). To determine how the within-session improvements changed between days, we ran separate ANOVAs for each daily session. Results for the 'Non-matched' group show significant within-session improvements in every daily session ( $8.7 \pm 2.1$ ,  $F(1,9) = 17.1$ ,  $p < 0.01$ ,  $\eta_p^2 = 0.7$ ;  $4.0 \pm 0.8$ ,  $F(1,9) = 22.4$ ,  $p = 0.001$ ,  $\eta_p^2 = 0.7$ ;  $3.5 \pm 1.2$ ,  $F(1,9) = 8.2$ ,  $p < 0.05$ ,  $\eta_p^2 = 0.5$ ;  $4.4 \pm 0.9$ ,  $F(1,9) = 23.8$ ,  $p = 0.001$ ,  $\eta_p^2 = 0.7$ , improvements within the 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup>, and 4<sup>th</sup> daily sessions, respectively). However, in the 'Matched' group, only day 3 reached significant within-session improvement ( $2.2 \pm 1.5$ ,  $F(1,6) = 2.1$ ,  $p = 0.2$ ,  $\eta_p^2 = 0.3$ ;  $1.8 \pm 1.0$ ,  $F(1,6) = 3.5$ ,  $p = 0.1$ ,  $\eta_p^2 = 0.4$ ;  $3.2 \pm 1.3$ ,  $F(1,6) = 6.3$ ,  $p < 0.05$ ,  $\eta_p^2 = 0.5$ ;  $1.6 \pm 0.7$ ,  $F(1,6) = 5.7$ ,  $p = 0.06$ , ,  $\eta_p^2 = 0.5$ , mean  $\pm$  SEM, improvements within the 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup>, and 4<sup>th</sup> daily sessions, respectively). To determine how the within-session improvements changed between sizes, we ran separate ANOVAs for each stimulus size. Results for the 'Non-matched'

group show significant within-session improvements for all sizes ( $6.0 \pm 1.3$ ,  $F(1,9)=21.0$ ,  $p=0.001$ ,  $\eta_p^2=0.7$ ;  $7.1 \pm 1.9$ ,  $F(1,9)=13.9$ ,  $p<0.01$ ,  $\eta_p^2=0.6$ ;  $4.3 \pm 0.9$ ,  $F(1,9)=23.5$ ,  $p=0.001$ ,  $\eta_p^2=0.7$ ;  $3.2 \pm 1.4$ ,  $F(1,9)=5.1$ ,  $p=0.05$ ,  $\eta_p^2=0.4$ , improvements in the 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup>, and 4<sup>th</sup> target sizes, respectively). However, in the 'Matched' group, only the two large target sizes (sizes  $0.84^\circ$  and  $1.3^\circ$ ) reached significant within-session improvement ( $2.8 \pm 1.7$ ,  $F(1,6)=2.9$ ,  $p=0.1$ ,  $\eta_p^2=0.3$ ;  $0.8 \pm 0.9$ ,  $F(1,6)=0.7$ ,  $p=0.4$ ,  $\eta_p^2=0.1$ ;  $2.0 \pm 0.7$ ,  $F(1,6)=6.9$ ,  $p<0.05$ ,  $\eta_p^2=0.5$ ;  $3.1 \pm 1.0$ ,  $F(1,6)=9.4$ ,  $p<0.05$ ,  $\eta_p^2=0.6$ , improvements in the 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup>, and 4<sup>th</sup> target sizes, respectively). In order to include in our analysis also the intermediate blocks (blocks 2 & 3), we defined and calculated a within-session improvement score for each day and size, as the dot product of the thresholds of the four daily blocks and a contrast vector [3 1 -1 -3], and then ran an ANOVA on the improvement scores with the factors of day (4 days) and size (4 sizes). This analysis confirmed our previous results and showed a significant within-session improvement in both groups ( $17.1 \pm 2.3$ ,  $F(1,9) = 42.7$ ,  $p<0.001$ ,  $\eta_p^2=0.8$ ;  $6.7 \pm 2.7$ ,  $F(1,6) = 11.6$ ,  $p<0.05$ ,  $\eta_p^2=0.7$ , in the 'Non-matched' group and the 'Matched' group, respectively). We also tested how these within-session improvements changed between sizes, by running separate ANOVAs for each stimulus size. The findings are compatible with our previous results by showing significant within-session improvements for all sizes in the 'Non-matched' group ( $20.6 \pm 4.2$ ,  $F(1,9)=23.9$ ,  $p<0.001$ ,  $\eta_p^2=0.7$ ;  $25.2 \pm 6.8$ ,  $F(1,9)=13.9$ ,  $p<0.01$ ,  $\eta_p^2=0.6$ ;  $13.2 \pm 2.8$ ,  $F(1,9)=22.3$ ,  $p=0.001$ ,  $\eta_p^2=0.7$ ;  $9.5 \pm 4.1$ ,  $F(1,9)=5.4$ ,  $p<0.05$ ,  $\eta_p^2=0.4$ , improvements in the 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup>, and 4<sup>th</sup> target sizes, respectively), but significant within-session improvements only for the two large target sizes (sizes  $0.84^\circ$  and  $1.3^\circ$ ) in the 'Matched' group ( $7.0 \pm 4.6$ ,  $F(1,6)=2.3$ ,  $p=0.2$ ,  $\eta_p^2=0.3$ ;  $2.9 \pm 2.5$ ,  $F(1,6)=1.4$ ,  $p=0.3$ ,  $\eta_p^2=0.2$ ;  $6.3 \pm 2.4$ ,  $F(1,6)=6.7$ ,  $p<0.05$ ,  $\eta_p^2=0.5$ ;  $10.7 \pm 2.9$ ,  $F(1,6)=13.3$ ,  $p=0.01$ ,  $\eta_p^2=0.7$ , improvements in the 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup>, and 4<sup>th</sup> target sizes, respectively).

Figure 2 shows that most of the within-session gains did not survive the time between sessions: the first measured threshold during a session was higher than the last measured threshold in a previous session. To further test the perseverance of the within-session improvements, we ran a repeated measures ANOVA with the within-observer factors of day (day 2-day 4), size (4 sizes), and block (the last block of the previous session vs the

first block of the next session). In both groups the performance significantly deteriorated from the end of the previous session to the beginning of the next session ( $3.4 \pm 0.8$ ,  $F(1,9)=17.8$ ,  $p<0.01$ ,  $\eta_p^2=0.7$ ;  $1.9 \pm 0.8$ ,  $F(1,9)=5.9$ ,  $p=0.05$ ,  $\eta_p^2=0.5$  in the ‘Non-matched’ group and the ‘Matched’ group, respectively), showing that the within-session gains were not fully retained between sessions. No significant interactions were found in this ANOVA analysis.

Next, we tested for between-session improvements by running a repeated measures ANOVA with factors of day (only the thresholds of the first daily session and the last daily session), size (4 sizes), and block (4 blocks). Both groups showed no significant change in the overall daily performance from the first session to the last session ( $1.2 \pm 1.1$ ,  $F(1,9) = 1.2$ ,  $p=0.3$ ,  $\eta_p^2=0.1$ ;  $0.7 \pm 0.5$ ,  $F(1,6) = 1.9$ ,  $p=0.2$ ,  $\eta_p^2=0.2$ , in the ‘Non-matched’ group and the ‘Matched’ group, respectively). However, in the 'Non-matched' group, there was a significant interaction between day and block (Day\*Block), indicating that learning was different for different blocks ( $F(1,9) = 6.0$ ,  $p<0.01$ ,  $\eta_p^2=0.4$ ). Testing for learning effects separately at the start (block 1) and at the end (block 4) of the session showed that significant learning occurred only at the start of the session, and only for the ‘Non-matched’ group (start:  $6.1 \pm 1.6$ ,  $F(1,9) = 14.6$ ,  $p < 0.01$ ,  $\eta_p^2=0.6$ ;  $1.4 \pm 0.9$ ,  $F(1,6) = 2.5$ ,  $p = 0.2$ ,  $\eta_p^2=0.3$ ; end:  $1.9 \pm 1.5$ ,  $F(1,9) = 1.6$ ,  $p = 0.2$ ,  $\eta_p^2=0.2$ ;  $0.8 \pm 1.2$ ,  $F(1,6) = 0.4$ ,  $p = 0.6$ ,  $\eta_p^2=0.4$ , in the ‘Non-matched’ group and the ‘Matched’ group, respectively). In order to include in our analysis also the intermediate sessions (sessions 2 & 3), we defined and calculated a between-session improvement score as the dot product of the four thresholds for the first blocks and a contrast vector [3 1 -1 -3], and then ran an ANOVA on the improvement scores with the size factor (4 sizes). This analysis confirmed our previous results and showed a significant between-session learning of the first block only in the ‘Non-matched’ group ( $24.9 \pm 6.0$ ,  $F(1,9) = 17.4$ ,  $p<0.01$ ,  $\eta_p^2=0.7$ ;  $2.0 \pm 2.8$ ,  $F(1,6) = 0.5$ ,  $p=0.5$ ,  $\eta_p^2=0.08$ ; in the ‘Non-matched’ group and the ‘Matched’ group, respectively). Next, we tested for possible interaction between the short-term within-session effects, related to adaptation, and the long-term between-sessions effects, related to perceptual learning. We found a significant correlation between the within-session improvement scores and the between-session improvement scores in the 'Non-

matched' group ( $r = 0.67$ ,  $p < 0.001$ ), but not in the 'Matched' group ( $r = 0.27$ ,  $p = 0.2$ ). This significant correlation suggests that with repetitions the short-term effects of adaptation may consolidate and result in long-term effects.

To directly compare the groups (Figure 3), we added to the repeated measures ANOVAs the between-observer factor of group type ('Non-matched' group or 'Matched' group). At the beginning of the session (first block), the performance of the 'Matched' group was significantly better than the performance of the 'Non-matched' group ( $4.1 \pm 1.8$ ,  $F(1,15) = 5.1$ ,  $p < 0.05$ ,  $\eta_p^2 = 0.3$ ). However, during the session, the performance differences between the groups diminished, and they were no longer significant at the end of the session ( $1.2 \pm 1.0$ ,  $F(1,15) = 1.2$ ,  $p = 0.3$ ,  $\eta_p^2 = 0.08$ ). The significantly better performance of the 'Matched' group at the beginning of the session was found to depend on the day (significant interaction,  $F(3,15) = 4.2$ ,  $p = 0.01$ ,  $\eta_p^2 = 0.2$ ). Separate analyses for each day showed significant effects on all days except on day 3 ( $8.0 \pm 2.8$ ,  $F(1,15) = 8.2$ ,  $p = 0.01$ ,  $\eta_p^2 = 0.4$ ;  $4.5 \pm 2.1$ ,  $F(1,15) = 4.7$ ,  $p < 0.05$ ,  $\eta_p^2 = 0.2$ ;  $0.6 \pm 2.5$ ,  $F(1,15) = 0.1$ ,  $p = 0.8$ ,  $\eta_p^2 = 0.004$ ,  $3.2 \pm 1.3$ ,  $F(1,15) = 5.8$ ,  $p < 0.05$ ,  $\eta_p^2 = 0.3$ , performance differences at the beginning of daily sessions, the 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup>, and 4<sup>th</sup>, respectively). Apparently these differences between the groups, at the beginning of the session, decreased from day to day, probably due to the significant between day (first day vs last day) improvement of the first block only in the 'Non-matched' group (previously reported), which was significantly higher than the corresponding insignificant improvement in the 'Matched' group ( $F(1,15) = 5.5$ ,  $p < 0.05$ ,  $\eta_p^2 = 0.3$ ). In addition, the within-session improvements were significantly higher in the 'Non-matched' group ( $F(1,15) = 7.6$ ,  $p = 0.01$ ,  $\eta_p^2 = 0.3$ ), probably due to the significantly higher thresholds in the 'Non-matched' group at the beginning of the sessions, since there were no significant threshold differences at the end of the sessions. The deterioration between sessions ( $F(1,15) = 1.5$ ,  $p = 0.2$ ,  $\eta_p^2 = 0.09$ ), and the threshold differences between target sizes at the beginning of the session ( $F(3,15) = 2.1$ ,  $p = 0.1$ ,  $\eta_p^2 = 0.1$ ) and at the end of the session ( $F(3,15) = 0.5$ ,  $p = 0.7$ ,  $\eta_p^2 = 0.03$ ) were not significantly different between the groups.

One of the main objectives of the current study was to test the effect of contrast adaptation on contrast integration across space. Improved performance with increasing target size suggests that spatial integration exists in the contrast discrimination process. Figure 4 shows that at the beginning of the session the performance was significantly enhanced with target size only in the 'Non-matched' group ( $F(3,9) = 4.5, p = 0.01, \eta_p^2 = 0.3$ ;  $F(3,6) = 2.2, p = 0.1, \eta_p^2 = 0.3$ , the 'Non-matched' group, and the 'Matched' group, respectively), indicating significant spatial integration only in the 'Non-matched' group. However, at the end of the session the performance in both groups was significantly enhanced with increasing target size ( $F(3,9) = 4.1, p < 0.05, \eta_p^2 = 0.3$ ;  $F(3,6) = 5.0, p = 0.01, \eta_p^2 = 0.5$  for the 'Non-matched' group and the 'Matched' group, respectively), indicating that spatial integration also developed in the 'Matched' group. These differences between groups did not reach significance ( $F(3,15) = 2.1, p = 0.1, \eta_p^2 = 0.1$ ;  $F(3,15) = 0.5, p = 0.7, \eta_p^2 = 0.03$ , at the start of a session (1<sup>st</sup> block) and at the end of a session (4<sup>th</sup> block), respectively). To quantify the extent of the spatial integration, we calculated the summation slope of the (log) average threshold (across days and observers) as a function of the (log) squared value of the target size (see Figure 4). We then tested how the summation slope changes from the start of the session (block 1) to the end of the session (block 4). For the 'Non-matched' group the summation slopes were significantly negative at both the start and the end of the session ( $-0.23 \pm 0.07, p = 0.01, \text{Cohen's } d = 1.5$ ;  $-0.18 \pm 0.06, p = 0.01, \text{Cohen's } d = 1.3$ , paired t-test, at the start of a session and at the end of a session, respectively), indicating significant spatial integration throughout the session. For the 'Matched' group the summation slopes at the start of the session were not significantly different from zero ( $-0.05 \pm 0.07, p = 0.5, \text{Cohen's } d = 0.4$ , paired t-test), indicating the lack of spatial integration. However, the summation factor at the end of the session became significantly negative ( $-0.14 \pm 0.03, p = 0.001, \text{Cohen's } d = 2.9$ , paired t-test), indicating the development of spatial integration in the 'Matched' group.

Table 1 summarizes the statistical results.

**Table 1. Statistical results for Exp2, 'Matched' vs 'Non-matched' conditions. \*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001**

Factor	'Non-matched' group	'Matched' group	Between groups
Performance at the beginning of the session (1 <sup>st</sup> block)			*
Performance at the end of the session (4 <sup>th</sup> block)			n.s
Improvements within-session (1 <sup>st</sup> block vs 4 <sup>th</sup> block)	***	**	**
Deteriorations between the end of the previous session (4 <sup>th</sup> block) and the beginning of the next session (1 <sup>st</sup> block)	**	*	n.s
Learning between the first day and the last day (all blocks)	n.s	n.s	n.s
Learning between the beginning of the first day and the last day (1 <sup>st</sup> block)	**	n.s	*
Learning between the end of the first day and the last day (4 <sup>th</sup> block)	n.s	n.s	n.s
<b>Target's size statistics</b>			
Influence of the target's size at the beginning of the session (1 <sup>st</sup> block)	**	n.s	n.s
Influence of the target's size at the end of the session (4 <sup>th</sup> block)	**	**	n.s

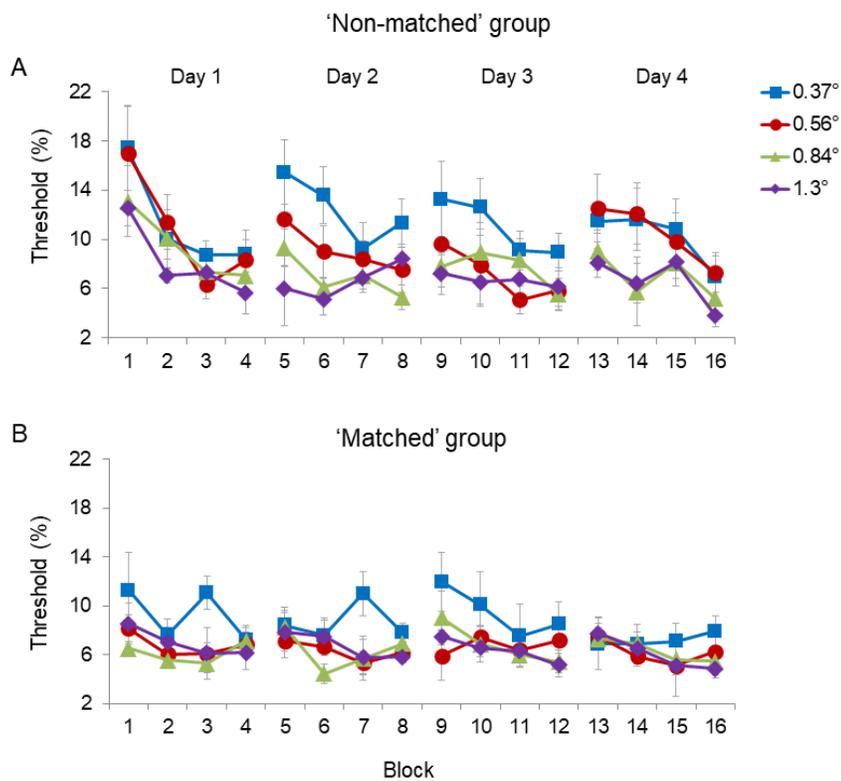


Fig. 2. Contrast discrimination thresholds for stimulus configurations in which a target Gabor pattern (with sizes:  $0.37^\circ$ ,  $0.56^\circ$ ,  $0.84^\circ$ , or  $1.3^\circ$ ) was added to a pedestal Gabor pattern that was either with a fixed maximal size (A, 'Non-matched' group), or with a size equal to the target size (B, 'Matched' group). Results show within-day improvements that are not fully retained in subsequent daily sessions. Thresholds represent averages across observers (A:  $N = 10$ , B:  $N=7$ ), with error bars corresponding to  $\pm 1$  standard error of the mean.

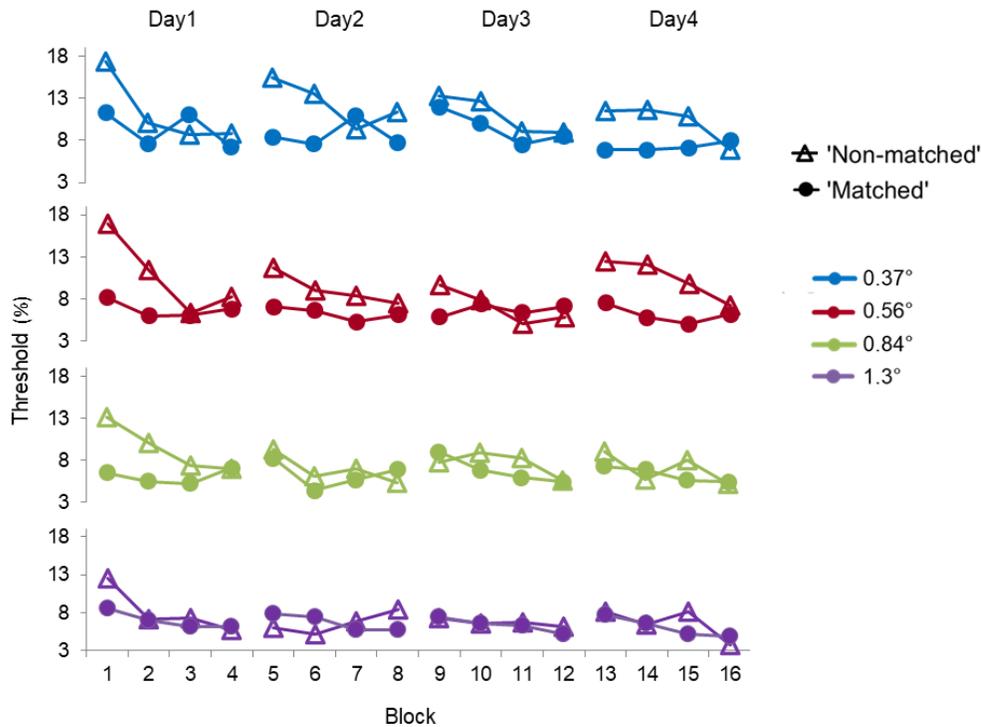


Fig. 3. Comparing discrimination thresholds in the 'Non-matched' group (triangular markers) vs the 'Matched' group (circular markers) for different target sizes. At the beginning of each daily session the thresholds in the 'Non-matched' group were generally higher than those in the 'Matched' group, especially for the smaller target sizes (red and blue markers). However, thresholds at the end of the sessions (560 or 672 trials) were equivalent in both groups. Thresholds represent averages across observers ( $N = 10$ ,  $N=7$ , for the 'Non-matched' and 'Matched' groups, respectively). Note that for the largest size ( $1.3^\circ$ ) the 'Matched' and the 'Non-matched' stimuli are identical but are presented within different mixtures of trials. Data is the same as in Fig. 2, re-formatted to allow closer comparison between the groups

## The decorrelation model

To explain our results for the contrast-discrimination threshold measurements and explain how thresholds change with the adaptation state, we constructed a simple toy model, based on the following assumptions:

1. Each stimulus (Left and Right) is processed by multiple functional units covering the stimulus area, creating two activity maps. Receptive fields of individual units are assumed to match the smallest target size (Gabor shaped,  $\sigma=0.37^\circ$ ,  $\lambda=0.53^\circ$ ).
2. Spatial integration of signal and noise:

Following Quick (1974), we defined the task relevant signal ( $S$ ) to be the integrated incremental contrast

$$(1) \quad S = (\sum_{i=1}^{M_t} |C_t(i)|^q)^{1/q},$$

where  $M_t$  is the number of functional stimulus units covering the target,  $C_t(i)$  is the local incremental contrast contributed by the target, and  $q=4$ , assuming the well-documented 4<sup>th</sup> root summation rule (Bonneh & Sagi, 1998; Graham, 1989; Meese & Summers, 2012; Usher et al., 1999). Here, following Quick (1974), we interpreted this equation as a nonlinear response pooling prior to noise application, rather than a probabilistic summation (Graham, 1989), motivated by results showing that spatial integration depends on orientation and spatial proximity (Bonneh & Sagi, 1998).

From the above equation, assuming constant  $C_t(i)$  in Eq 1, the relationship between the effective signal ( $S$ ) and the target area ( $A_t$ ) is

$$S = C_t A_t^{1/q}.$$

We assume the presence of target-independent response noise integrated across the pedestal area (e.g., on the non-target side). We formalized this integration using the above Quick (1974) equation, applied to the equivalent external noise (replacing target amplitude,  $C_t$ , by equivalent external noise amplitude,  $N_p$ ). Thus, for correlated noise the integrated noise amplitude ( $N$ ) across the pedestal area ( $A_p$ ) is

$$N = N_p A_p^{1/q},$$

and for uncorrelated noise, the noise amplitude increases as the square root of the number of measurements (area), it is

$$N = N_p A_p^{1/2q} .$$

Noise correlations:

The noise is assumed to be spatially correlated before adaptation (block 1), but spatially uncorrelated after adaptation (block 4). Partial correlations, expected during the development of adaptation, are not considered here.

Based on the above assumptions, we estimated the dependence of target sensitivity ( $S/N$ ) on the stimulus area before and after adaptation. The target strength ( $S$ ) is proportional to the target\_area<sup>1/q</sup> independent of the adaptation state and the experimental condition. The noise level ( $N$ ) depends on the pedestal size and on the state of adaptation:

In the Non-Matched condition, we assume that the noise is independent of the target area, set by the fixed pedestal extent (note that the different target sizes are presented in random order within each block of trials; thus, the integration area cannot be adjusted to the target size, but see below). Thus,

$$\text{Before adaptation} \quad N \propto A_p^{1/q}$$

$$\text{After adaptation} \quad N \propto A_p^{1/2q}$$

Therefore,  $S/N \propto A_t^{1/q}$ , before and after adaptation.

In the Matched condition, the noise depends on the target area, since the pedestal area matches the target area:

$$\text{Before adaptation, } N \propto A_t^{1/q} \Rightarrow S/N = \text{constant}$$

$$\text{After adaptation, } N \propto A_t^{1/2q} \Rightarrow S/N = A_t^{1/2q}$$

### ***Predictions***

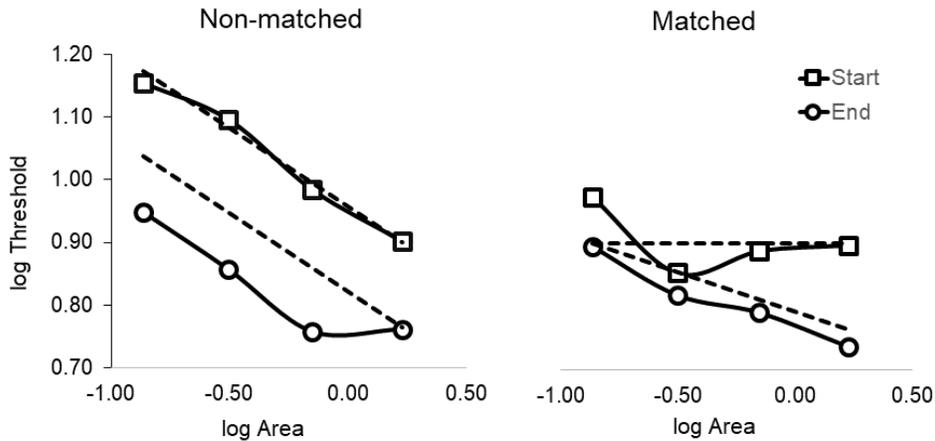
Slopes of  $\log(\text{threshold})$  vs  $\log(\text{target\_area})$  are -0.25 in the 'Non-matched' condition, before and after adaptation, and 0 and -0.125 in the 'Matched' condition, before and after adaptation, respectively (Figure 4, dashed lines).

### ***Model fitting results***

To test our model predictions, we plotted the measured thresholds as a function of the target area ( $\sigma^2$ ) using a log-log scale for both the start and the end of the sessions (Figure 4). To match the model predictions with the data, we used the 'Start' threshold of the largest target as a reference, averaging the corresponding measurements from the two conditions (these particular thresholds are available from both experimental groups and are expected to be equal at the beginning of the session, as indeed measured). Other thresholds are derived using the fourth root summation rule, assuming adaptation-dependent noise correlation (fully correlated before adaptation and limited to the receptive field size after adaptation). As shown in Figure 4, the predicted thresholds obtained from the model are very similar to the measured thresholds. At the beginning of the session, there was a significant spatial integration in the 'Non-matched' condition, with a (log-log) summation slope of -0.24, close to the predicted slope of -0.25. In the 'Matched' condition the summation slope was -0.05, compared with 0 predicted. However, at the end of the session, there was significant spatial integration in both conditions. In the 'Non-matched' condition, the value of the summation slope was -0.18 (but see below), compared with -0.25 predicted, and in the 'Matched' condition the value was -0.14, compared with -0.125 predicted.

The model overestimates the adapted thresholds. This can result from our assumption that  $S$  and  $N$  are integrated over all of the pedestal area. This assumption is motivated by the uncertainty imposed on the observer regarding the target size. However, it is possible that, during the experimental session, observers narrow down the integration area to reduce noise, thus improving sensitivity with smaller targets, while losing it with larger ones. Such a strategy is beneficial mainly in the 'Non-matched' condition where the noise source (the pedestal) is fixed and large, so that an intermediate integration area can

reduce noise without affecting target signal for smaller targets. This hypothesis is supported by the results showing no spatial integration with the largest target size after adaptation in the 'Non-matched' condition (note that without this datum point the spatial integration slope is -0.27). For the 'Matched' condition, the predictions for the adapted thresholds are close to the data, suggesting that the observers match the integration area to target area (that matches pedestal area, thus clearly marked in the stimulus). Additionally, the predicted post-adaptation thresholds depend on the assumed receptive field size, here set to the smallest target size. Smaller receptive fields will increase the decorrelation gain in both experimental conditions.



**Figure 4:** Contrast spatial integration at the start and at the end of a session for the Non-Matched and Matched conditions. ‘Start’ and ‘End’ results are from the first and the last blocks of trials in each session, respectively, averaged across all days ( $N=4$ ) and observers ( $N=10$  &  $7$  for the Non-Matched and the Matched conditions, respectively). The ‘Start’ results confirm previous results, showing that thresholds are roughly independent of stimulus area in the Matched condition; however, they improved with increasing area in the Non-Matched conditions, following the 4<sup>th</sup> root summation rule (Bonneh & Sagi, 1998). The ‘End’ results show that spatial integration was developed in the ‘Matched’ condition during the session. Dashed lines denote the predictions of the model, assuming the 4<sup>th</sup> root summation rule with spatially correlated noise at the ‘Start’ of the session and uncorrelated noise at the ‘End’ of the session (see the text for details).

## Discussion

In the experiment described here, observers performed a contrast discrimination task with a fixed base contrast (pedestal), and a variable target size. We compared discrimination behavior between an experimental condition in which the pedestal size was fixed, equal to the largest target size ('Non-matched' condition), and a condition in which the pedestal size matched the target size and thus varied with it ('Matched' condition). Discrimination performance significantly improved during the testing sessions for both conditions. In the 'Non-matched' condition, the performance improved for all target sizes. In the 'Matched' condition performance improved only for the larger targets, indicating improvement by means of spatial integration (see Appendix for similar results in the pilot experiment). However, these within-session improvements were mostly temporary and were not fully retained between sessions (Figs. 2 and 3). The transient nature of these improvements implies that they result, at least in part, from an adaptation process that rapidly adjusts the visual system to the current statistics of the visual stimulation. Theoretical considerations suggest that these adjustments reduce input redundancy by a decorrelation process. Such a process is thought to improve coding efficiency (Barlow & Földiák, 1989). Accordingly, we suggest that adaptation improves discrimination performance as well as spatial integration by decorrelating and thus reducing the background noise generated by the high-contrast stimulus (i.e., the pedestal). A decorrelation analysis of our experiments was found to successfully predict the results (Figure 4), as described in the results section.

*Spatial integration:* At the beginning of the sessions, in agreement with previous studies (Bonneh & Sagi, 1999b), there were significant differences between the conditions, regarding the general performance level and regarding how performance changed with target size (see Figure 3 and 4 thresholds at the start of the sessions). In the 'Non-matched' condition, with fixed pedestal size, increasing the target's size reduced thresholds, indicating spatial integration. The  $\log(\text{Threshold})$  vs  $\log(\text{Area})$  summation slope was around  $-1/4$  (fourth-root summation), in agreement with previous contrast discrimination studies (Bonneh & Sagi, 1999b), and with studies of contrast detection (Robson & Graham, 1981). However, in the 'Matched' condition, in which the pedestal

size matched the target size, performance at the beginning of the session was almost equal for all the sizes (summation slope = -0.05). These results are in agreement with our pilot experiment results (see appen

ndix) as well as with previous studies showing that spatial integration (area summation) is much reduced, practically non-existent, for a suprathreshold pedestal whose size matches the target's size (Bonneh & Sagi, 1999b; Legge & Foley, 1980; Meese, 2004). Performance was significantly better in the 'Matched' condition compared with the 'Non-matched' condition. This was due to the larger pedestal in the 'Non-matched' condition, which extended beyond the target area (except for the largest target size), thus forming an extra surround that reduced the target's visibility. Such a surround suppression was previously shown (Bonneh & Sagi, 1999b; Meese, 2004; Meese et al., 2005), and is consistent with studies showing reduced contrast discrimination performance with a high-contrast pedestal in the presence of an iso-oriented surround (Adini & Sagi, 2001; Chen & Tyler, 2001; Chen & Tyler, 2008, Bonneh & Sagi, 1999a; Snowden & Hammett, 1998; Wilkinson et al., 1997; Xing & Heeger, 2000; Zenger-Landolt & Koch, 2001), especially at the periphery (Petrov et al., 2005; Wilkinson et al., 1997; Xing & Heeger, 2000), supporting the involvement of spatial lateral-inhibitory interactions (Polat & Sagi, 1993; Sagi & Hochstein, 1985).

*Dynamics of spatial integration:* In contrast with the beginning, at the end of the sessions the differences between the conditions vanished. A moderate spatial integration developed in the 'Matched' condition, in which discrimination thresholds improved only for the larger targets, resulting in a significant spatial integration in both conditions (see Figure 4, thresholds at the end of the sessions, and Appendix). In the 'Non-matched' condition, performance significantly improved during the session for all target sizes, resulting in equivalent performance levels in both conditions (see Figure 3, thresholds at the end of the sessions). These discrimination improvements were mostly not retained between sessions (but see below); thus, they are considered here to result from contrast adaptation. Within the context of the standard contrast discrimination models and assuming contrast gain control (Foley, 1994; Foley & Chen, 1999; Meese, 2004) by a

normalization process (Carandini & Heeger, 2012), our results can be implemented as dynamic normalization (Ross & Speed, 1991). According to these models, the response to each stimulus (either target+pedestal or pedestal alone) is proportional to the integrated excitatory inputs from all local units activated, divided by the activity in a ‘normalization pool’. The ‘normalization pool’ consists of a weighted sum of all units’ responses, activated by the target stimulus, the pedestal, and other contextual elements. In this type of models, adaptation can improve discrimination performance in the ‘Non-matched’ condition for all target sizes, by reducing the suppressive effects produced by the large and fixed pedestal. Weakening of surround suppression signals by adaptation is supported by electro-physiology (Patterson et al., 2013, 2014; Wissig & Kohn, 2012), especially after a prolonged adaptation time (Patterson et al., 2013). The development of spatial integration in the ‘Matched’ condition can result from asymmetric changes in the excitatory and suppressive summation weights due to adaptation. This suggestion is supported by results showing that adaptation in the barrel cortex shifts the balance between excitation to inhibition toward excitation, by adapting the inhibitory inputs more than the excitatory inputs (Heiss et al., 2008). In agreement with our results, recording from macaque V1 shows that by suppressing the neurons’ surround more than the neurons’ center, adaptation changes the balance of center and surround gains. Such a change of balance was shown to increase the neurons’ receptive field and consequently, increase the cortical summation (Cavanaugh et al., 2002). Functionally, surround suppression and normalization processes are thought to remove local correlations in neuronal activity arising from redundancy within natural images (Schwartz & Simoncelli, 2001). Barlow (1990) suggested adaptation as a process by which such inhibitory processes are strengthened to reduce correlations, an idea supported by our modeling results. Strengthening of inhibitory connections during adaptation may reduce the saliency of uniform stimuli, thus increase detection thresholds (Ross & Speed, 1991), and improve detection of texture boundaries (Sagi, 1995). Atick et al (2010) describe a formal decorrelation theory of adaptation, incorporating normalization, suggesting that the changes in the neural code induced by contrast adaptation could alter the relative contrast of different stimulus parts in ways that could either enhance or diminish their saliency.

*Contrast discrimination and adaptation:* Previous psychophysical studies that tested how adaptation affects contrast discrimination found only weak and inconsistent evidence of improved discriminability for stimuli similar to the adapter (Abbonizio et al., 2003; Barlow et al., 1976; Foley & Chen, 1997; Greenlee & Heitger, 1988; Määtänen & Koenderink, 1991a; Wilson & Humanski, 1993). The adaptation effects observed here were larger in the 'Non-matched' condition using stimuli that are quite different from those used in traditional contrast discrimination studies. Previous studies used different methods, but all had the target and the pedestal of an equal area, as in our 'Matched' condition. We note that the 'Matched' effects are relatively small and are significant only with the larger stimuli. Indeed, Greenlee & Heitger (1988), who used high-contrast (0.8) gratings, found that adaptation improved the discriminability of high-contrast targets. In contrast, Foley & Boynton (1993), Määtänen & Koenderink (1991b), and Wilson & Humanski (1993), who used narrowly localized Gabor stimuli, found that adaptation either did not affect the discrimination of high base contrast (Foley & Boynton, 1993), or only slightly improved discrimination in the highest base contrasts, but not for all observers (Wilson & Humanski, 1993). Interestingly, for the observer who initially did not improve in the Wilson & Humanski (1993) experiment, increasing the stimulus spatial frequency, which allowed for more spatial integration, resulted in some discrimination enhancement with a high base contrast. Barlow et al. (1976), using grating stimuli, found that adaptation had no effect on contrast discrimination at high base contrasts. However, Barlow measured discrimination either by using vertically split-field contrasts, which required only local discrimination around the vertical central line, or by detecting the point in time when a change in contrast occurred, which can be viewed as a change-detection task. Importantly, stimuli presented in the fovea benefit less from spatial integration due to the large sensitivity drop around the fovea. In our experiments, stimuli were presented in the near periphery, activating areas of relatively uniform sensitivity. Notably, unlike other studies using passive adaptation, in our experiments the adapted stimuli were task related, and the observers were asked to make an explicit judgment regarding each of them. Previous studies showed that passive adaptation is sufficient to cause adaptation-dependent sensitivity improvements (Greenlee & Heitger, 1988; Pinchuk-Yacobi & Sagi, 2019). However, top-down influences such as task

relevance and attention can enhance the effects for some types of adaptation but not for others (Festman & Ahissar, 2004; Pinchuk-Yacobi, Harris, et al., 2016).

*Dynamics of contrast discrimination:* Comparing the within-session dynamics in our study to other contrast discrimination studies is difficult, since nearly none reported performance changes within sessions, only the session means. The only study we found that did report within-session dynamics in contrast-discrimination is a study by Yu et al. (2004), showing performance gains within sessions that were not retained between sessions, as found in the present study. Dynamics of rapid within-session improvements that are later forgotten between the sessions were reported in only a few other perceptual tasks, such as a perceptual grouping task (Pinchuk-Yacobi & Sagi, 2019) and a vernier acuity task (Beard et al., 1995; Levi et al., 1997). We suggest that in these tasks, the fast and temporal within-session gains result from an adaptation process that improves the spatial integration of the stimuli. Thus, the effects of adaptation depend on the specific stimulus and task probed. Adaptation may improve performance on tasks that benefit from spatial integration, but not on all tasks (Ng et al., 2008). An interesting case is the search task where a small texture target is embedded in a larger textured background. Results with orientation (Censor et al., 2006; Censor & Sagi, 2008; Mednick et al., 2008; Ofen et al., 2007; Pinchuk-Yacobi, Harris, et al., 2016) and with color (McDermott et al., 2010) textures show decremental and incremental effects of adaptation.

*Learning and adaptation:* Examining changes in performance across days showed a significant decrease between the first day and the last day in the threshold measured at the beginning of the session (1<sup>st</sup> block) in the 'Non-matched' group, but not in the 'Matched' group (see Figure 3 for main experiment results, and Figures 1A and 2A in the Appendix for similar results in the pilot experiment). The dependence of the between-days improvements on stimulus configuration is similar to the learning found in contrast discrimination when flankers were added (Adini et al., 2002, 2004). The large pedestal in the 'Non-matched' condition, extending beyond the target area, possibly activates a context-induced learning-mechanism similar to that of the added flankers. The lack of long-term improvement across days in the 'Matched' condition is compatible with some

previous studies (Dorais & Sagi, 1997), but not with all (Yu et al., 2004). Learning in the contrast discrimination task is usually stronger with longer training periods and is diminished with roving stimuli (Adini et al., 2004; Yu et al., 2004). Within the context of the current proposal, reduced learning in roving conditions is explained by linking short-term adaptation effects with long-term learning effects. Accordingly, performance on the task is improved by adaptation adjusting gain control mechanisms or noise mechanisms that are dependent on contrast. Roving between multiple base contrasts and sizes interferes with these contrast-dependent adjustments, leading eventually to diminished across-days learning. In agreement, we found that the between-session improvement scores in the 'Non-matched' group correlated significantly with the within-session improvement scores. Thus, observers with larger within-session improvements also tended to manifest larger between-session improvements. Similar results were shown in a parafoveal vernier acuity task when observers showing significant within-session improvements, which were mainly forgotten between days, were more likely to experience significant between-session overall improvement (Beard et al., 1995). A link between adaptation effects and learning was also suggested by a recurrent model of V1 orientation selectivity, according to which orientation adaptation is a short-term form of orientation learning that gradually become permanent with experience (Teich & Qian, 2003). The significant improved performance at the start of the session in the 'Non-matched' group can result from faster readaptation with practice, as was shown following adaptation to a prism distortion (Habtegiorgis et al., 2018; Yehezkel et al., 2010), or following repeated adaptation to visual patterns in a perceptual grouping task (Pinchuk-Yacobi & Sagi, 2019) or a vernier acuity task (Beard et al., 1995). Our results also resemble some findings in the motor domain, such as faster relearning of a motor adaptation task following repetitive practice over time (“savings”), and the “forgetting” of motor improvements on delayed reexposure to the same motor adaptation task (Krakauer, 2009; Krakauer et al., 2005; Mawase et al., 2014). These results of long-term effects of adaptation, which are found in several modalities including motor and vision, call for a reevaluation of the traditional distinction between visual adaptation and perceptual learning. We suggest that both phenomena are forms of experience-dependent plasticity on varying time-scales, ranging from short-term adjustments driven by mere

exposure to stimuli to the complex adjustments needed when learning a task over longer timescales like in perceptual learning. Other phenomena that support this view include contingent adaptation (e.g., McCollough effect, Howard & Webster, 2011) which involved more complex adaptation of two paired features, adaptation to second order stimulus-statistics (e.g., temporal contingencies between orientations, Pinchuk-Yacobi, Dekel, et al., 2016), prism adaptations (Yehezkel et al., 2010), and task-irrelevant learning (Seitz & Watanabe, 2009; Shibata et al., 2014). This suggestion is consistent with theories indicating that adaptation involves temporary plasticity of inhibitory synapses (Dealy & Tolhurst, 1974; Wilson, 1975). With repeated adaptation in a specific context (such as in the context of a perceptual task), such temporary plasticity can be made long-term.

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## **Appendix**

### **Practicing CD with the target subtracted from the pedestal**

#### **Stimuli and procedure**

This pilot experiment was very similar to the main experiment. The major differences were: (1) the target here was subtracted from, instead of added to, the pedestal. Thus, observers reported which of the Gabor patterns (left or right) appeared to have a lower contrast. (2) the target contrast was determined by a staircase method, instead of using a constant stimuli method. The contrast of the target decreased by 0.1 log units after three consecutive correct responses and increased by 0.1 log units after each mistake. This staircase converges at a level of 79.3% correct (Levitt, 1971). In addition, there were some minor differences between the experiments in the stimuli used. The pedestal Gabor had a phase of  $90^\circ$  and a constant base contrast of 63%, and the target Gabor had a phase of  $270^\circ$ . Eleven observers participated in this experiment. Five of them participated in the 'Non-matched' condition, and six participated in the 'Matched' condition. The pilot included five daily sessions, with three blocks in each session. A block consisted of four parallel randomly interleaved staircases, one for each target size. For each staircase run, the threshold was calculated as the geometrical mean of all reversals except for the first three reversals, which were ignored. All staircases started with a high target contrast that enabled error-free detection or discrimination. In the 'Non-matched' condition the initial contrast was 31% for target sizes  $0.37^\circ$  and  $0.56^\circ$ , and 24% for target sizes  $0.84^\circ$  and  $1.3^\circ$ . In the 'Matched' condition the contrast was 24% for all target sizes.

#### **Results**

Results for the average contrast discrimination thresholds (across observers) for the 'Non-matched' group and the 'Matched' group are displayed in Figures A1 and A2, respectively. To test for within-session improvements, we ran a repeated measures ANOVA with the within-observer factors including day (5 days), size (4 sizes), and block (first block vs last block), performed separately for the two groups. Performance within-session improved significantly in both groups, as indicated by a significant decrease in

the threshold from the first block to the last block ( $11.8 \pm 1.9$ ,  $F(1,4) = 39.8$ ,  $p < 0.01$ ;  $1.3 \pm 0.5$ ,  $F(1,5) = 7.7$ ,  $p < 0.05$ ,  $\text{mean} \pm \text{SEM}$  in the 'Non-matched' group and the 'Matched' group, respectively). In the 'Non-matched' group, there was also a significant interaction between the block threshold and size ( $F(3,4) = 4.8$ ,  $p < 0.05$ ). To determine how the within-session improvements changed between sizes, we ran separate ANOVAs for each size. Results for the 'Non-matched' group show significant within-session improvements for every target size ( $16.3 \pm 1.7$ ,  $F(1,4) = 92.3$ ,  $p = 0.001$ ,  $15.6 \pm 4.4$ ,  $F(1,4) = 12.8$ ,  $p < 0.05$ ,  $8.0 \pm 2.2$ ,  $F(1,4) = 13.4$ ,  $p < 0.05$ ,  $7.1 \pm 1.5$ ,  $F(1,4) = 23.7$ ,  $p < 0.01$ , improvements in the 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup>, and 4<sup>th</sup> target sizes, respectively). However, in the 'Matched' group, only the two largest target sizes ( $0.84^\circ$  and  $1.3^\circ$ ) reached a significant within-session improvement ( $0.6 \pm 1.0$ ,  $F(1,5) = 0.4$ ,  $p = 0.6$ ;  $1.7 \pm 0.9$ ,  $F(1,5) = 3.4$ ,  $p = 0.1$ ;  $1.1 \pm 0.3$ ,  $F(1,5) = 13.7$ ,  $p < 0.05$ ;  $1.8 \pm 0.4$ ,  $F(1,5) = 18.6$ ,  $p < 0.01$ , improvements in the 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup>, and 4<sup>th</sup> target sizes, respectively).

Figure A suggests that many of the within-session gains, especially in the 'Non-matched' group, did not survive the time between sessions: the first measured threshold during a session was higher than the last measured threshold in a previous session. To further test the perseverance of the within-session improvements, we ran a repeated measures ANOVA with the within-observer factors of day (day 2-day 5), size (4 sizes), and block (the last block of the previous session vs the first block of the next session). Performance significantly deteriorated from the end of the previous session to the beginning of the next session only in the 'Non-matched' group ( $9.7 \pm 0.7$ ,  $F(1,4) = 213.6$ ,  $p < 0.001$ ;  $0.7 \pm 0.6$ ,  $F(1,5) = 1.2$ ,  $p = 0.3$  for the 'Non-matched' group and the 'Matched' group, respectively), showing that the within-session gains were not fully retained between sessions. In the 'Non-matched' group, there was also a significant interaction between block threshold and size ( $F(3,4) = 3.9$ ,  $p < 0.05$ ). To determine how the between-session deterioration changed between sizes, we ran separate ANOVAs for each size. Results for the 'Non-matched' group show a significant between-session deterioration for every target size ( $13.4 \pm 2.6$ ,  $F(1,4) = 25.8$ ,  $p = 0.01$ ,  $14.1 \pm 3.0$ ,  $F(1,4) = 21.9$ ,  $p < 0.01$ ,  $6.3 \pm 1.7$ ,  $F(1,4) = 13.9$ ,  $p < 0.05$ ,  $5.0 \pm 0.4$ ,  $F(1,4) = 173.0$ ,  $p < 0.001$  for deterioration in the 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup>, and 4<sup>th</sup> target sizes, respectively). In the 'Matched' group, none of the target sizes reached significant between-session deterioration ( $0.6 \pm 1.2$ ,  $F(1,5) = 0.28$ ,  $p = 0.6$ ;  $0.6 \pm 0.9$ ,  $F(1,5) = 0.4$ ,  $p = 0.5$ ;

0.9±0.5,  $F(1,5)=4.2$ ,  $p=0.1$ ; 1.4±0.7,  $F(1,5)=3.9$ ,  $p=0.1$  for deterioration in the 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup>, and 4<sup>th</sup> target sizes, respectively). In addition, in both groups, performance was significantly enhanced when the size of the target increased ( $F(3,4) = 252.5$ ,  $p<0.0001$ ,  $F(3,5) = 3.4$ ,  $p<0.05$  in the 'Non-matched' group and the 'Matched' group, respectively).

Next, we tested for between-session improvements by running a repeated measures ANOVA with only the thresholds of the first day (day1) and the last day (day 5). The change in the overall daily performance (including all blocks of trials in a daily session) from the first session to the last session was significant only in the 'Non-matched' group (8.5±3.1,  $F(1,4) = 7.3$ ,  $p=0.05$ , 2.2±1.3,  $F(1,5) = 2.9$ ,  $p=0.2$  in the 'Non-matched' group and the 'Matched' group, respectively). When testing for learning effects separately for the thresholds at the start (block 1) and at the end (block 3), there were no significant effects (start: 14.6±8.2,  $F(1,4) = 3.1$ ,  $p = 0.1$ , 3.2±1.8,  $F(1,5) = 3.3$ ,  $p = 0.1$ ; end: 2.6±1.7,  $F(1,4) = 2.3$ ,  $p = 0.2$ , 1.3±0.9,  $F(1,5) = 2.5$ ,  $p = 0.2$  in the 'Non-matched' group and the 'Matched' group, respectively).

To compare the performances of the groups, we added to the repeated measures ANOVAs the between-observer factor of group type ('Non-matched' group or the 'Matched' group). At the beginning of the session (first block), the performance of the 'Matched' group was significantly better than the performance of the 'Non-matched' group (20.9±1.8,  $F(1,9) = 137.4$ ,  $p < 0.001$ ). During the session, the performance difference between the groups was reduced by half, but performance was still significantly better in the 'Matched' group (10.5±1.3,  $F(1,9) = 63.4$ ,  $p < 0.001$ ). The improvements within-session ( $F(1,9) = 37.4$ ,  $p < 0.001$ ), the learning between days (first day vs last day, including all blocks in a session) ( $F(1,9) = 5.8$ ,  $p < 0.05$ ), and the deterioration between sessions ( $F(1,9) = 85.2$ ,  $p < 0.0001$ ) were significantly higher for the 'Non-matched' group. There was also a significant interaction between block threshold and size, indicating that the difference between groups in the within-session improvement depended on the size of the target ( $F(3,9) = 5.9$ ,  $p < 0.01$ ). Running separate ANOVAs for each size showed that for each size the within-session improvement was significantly higher for the 'Non-matched' group ( $F(1,9)=69.8$ ,  $p<0.001$ ;  $F(1,9)=27.1$ ,  $p=0.001$ ;  $F(1,9)=11.6$ ,  $p<0.01$ ;  $F(1,9)=17.6$ ,  $p<0.01$ , improvements in the 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup>, and 4<sup>th</sup> target

sizes, respectively). The difference between thresholds for different target sizes was also significantly lower for the 'Matched' group ( $F(3,9) = 195.5, p < 0.0001$ ).

The effect of contrast adaptation on spatial integration was tested. At the beginning of the session the performance was significantly enhanced with target size only in the 'Non-matched' group ( $F(3,4) = 90.3, p < 0.001, F(3,5) = 1.2, p = 0.3$ , the 'Non-matched' group, and the 'Matched' group, respectively), indicating significant spatial integration only in the 'Non-matched' group. However, at the end of the session the performance in both groups was significantly enhanced with increasing target size ( $F(3,4) = 226.1, p < 0.001, F(3,5) = 3.4, p < 0.05$ , for the 'Non-matched' group and the 'Matched' group, respectively), indicating that spatial integration also developed in the 'Matched' group. The effect of target size on performance was significantly higher in the 'Non-matched' group compared with the 'Matched' group ( $F(3,9) = 86.2, p < 0.001, F(3,9) = 140, p < 0.001$ , at the start of a session (1<sup>st</sup> block) and at the end of a session (4<sup>th</sup> block), respectively).

Table A summarizes the statistical results.

**Table A. Statistical results for Exp1, 'Matched' vs 'Non-matched' conditions. \*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001**

Factor	'Non-matched' group	'Matched' group	Between groups
Performance at the beginning of the session (1 <sup>st</sup> block)			***
Performance at the end of the session (3 <sup>th</sup> block)			***
Improvements within-session (1 <sup>st</sup> block vs 3 <sup>th</sup> block)	**	*	***
Deteriorations between the end of the previous session (3 <sup>th</sup> block) and the beginning of the next session (1 <sup>st</sup> block)	***	n.s	***
Learning between the first day and the last day (all blocks)	*	n.s	*
Learning between the first day and the last day (the first block)	n.s	n.s	n.s

Learning between the first day and the last day (the last block)	n.s	n.s	n.s
<b>Target's size statistics</b>			
Influence of the target's size at the beginning of the session (1 <sup>st</sup> block)	***	n.s	***
Influence of the target's size at the end of the session (3 <sup>th</sup> block)	***	*	***

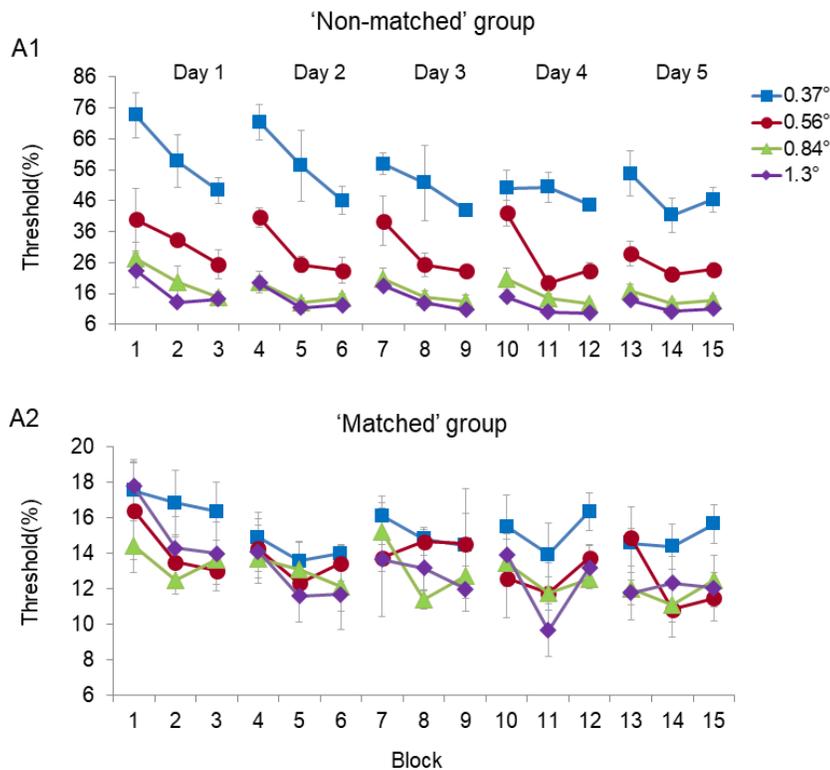


Fig. A. Contrast discrimination thresholds for stimulus configurations in which a target Gabor pattern (with sizes: 0.37°, 0.56°, 0.84°, or 1.3°) was subtracted from a pedestal Gabor pattern that was either fixed at a maximal size (1, 'Non-matched' group), or it had a size equal to the target size (2, 'Matched' group). Results show within-day improvements that are not fully retained in subsequent daily sessions. Thresholds are averages across observers (1: N = 5, 2: N=6), with error bars corresponding to  $\pm 1$  standard error of the mean.