Orientation-selective adaptation improves perceptual grouping

Noga Pinchuk-Yacobi

Department of Neurobiology, Weizmann Institute of Science, Rehovot, Israel

Dov Sagi

Department of Neurobiology, Weizmann Institute of Science, Rehovot, Israel

The role of visual pattern adaptation, and learning, in spatial integration was investigated. Observers reported whether a grid of identical tilted bars was perceived as rows or columns (perceptual grouping task). Performance was measured multiple times during a session to determine effects of repeated exposure to the stimuli. To test for possible effects of learning on the within-session dynamics, observers repeated the experiment on five days. We found that repeated performance produced rapid within-day improvements, which were largely transient and were not retained on subsequent days. In addition, exposure to stimuli with equal orientation contributed to the within-session improvement, whereas stimuli having an orientation differing by 45° from the original orientation diminished the improvement previously obtained in the same session. Practice with the task over days resulted in faster improvements. The transient nature of these exposure-driven improvements and their susceptibility to interference by stimuli designed to reduce adaptation suggest that adaptation was their main cause. Finally, to investigate the effects of adaptation on internal noise and on spatial integration, we employed an external-noise paradigm, showing that internal-noise reduction resulted from adaptation. Internal noise was reduced only when spatial integration was effective, suggesting that adaptation improved perception of global stimulus properties. Overall, our results suggest that the grouping task benefits from a rapid adaptation process that adjusts the visual system to the statistics of the visual stimuli. We suggest that this effect is achieved through spatial decorrelation of neural responses. With practice, those adjustments are made faster.

Introduction

Grouping of spatially distinct elements into coherent objects, a fundamental function of the visual system, requires spatial integration, with its effectiveness depending on long-range correlations in the image. A previous report demonstrated the effectiveness of a model based on spatial correlations to successfully account for performance in a perceptual grouping task (Ben-Av & Sagi, 1995). It was shown that for a task in which observers had to report the organization of the stimuli as either horizontal rows or vertical columns, grouping occurred in the direction with higher spatial correlations. However, brain representations of the stimuli are contaminated with internal, neuronal, noise. Uncorrelated internal noise is averaged out by spatial integration, but spatially correlated internal noise may bias the grouping signal and distort perception. It was demonstrated that even weakly correlated noise substantially limits effective signal capacity, which in return can reduce psychophysical performance (Zohary, Shadlen, & Newsome, 1994).

Visual adaptation is considered here as a stimulus-driven process which continuously and quickly 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 typically short-term. Previous studies have tested the effects of visual pattern adaptation on visual sensitivity. Adaptation to intensity-modulated gratings typically shows reduced sensitivity to low-contrast gratings of similar orientation and spatial frequency (Blakemore & Campbell, 1969). Some evidence for improved contrast discrimination around the adapted contrast level has been shown, but these effects are small and inconsistent (Barlow, Macleod, & Van Meeteren, 1976; Greenlee & Heitger, 1988; Määttänen & Koenderink, 1991; Ross, Speed, & Morgan, 1993). Similarly, only mixed and weak results have been found for improved discrimination following face adaptation (Ng, Boynton, & Fine, 2008; Rhodes, Maloney, Turner, & Ewing, 2007; Yang, Shen, Chen, & Fang, 2011). Sensory adaptation has been proposed to improve coding efficiency by reducing redundancy in

sensory signals, possibly by decorrelating neuronal responses (Barlow & Földiák, 1989). Experimental support for this idea has been provided by studies showing that adaptation decorrelates neural responses in monkey V1 neurons (Gutnisky & Dragoi, 2008) and maintains decorrelation across the population of cat V1 neurons (Benucci, Saleem, & Carandini, 2013). Thus, spatial decorrelation is expected to improve performance on visual tasks involving spatial integration, such as perceptual grouping.

Here we examined the spatial aspects of visual adaptation by testing the effects of adaptation on the spatial integration of visual information. For this purpose, we tested how performance on a perceptual grouping task, which includes repeated exposure to the grouping stimulus, changes during a testing session. To test the possible effects of experience with the stimuli on the within-session dynamics (Yehezkel, Sagi, Sterkin, Belkin, & Polat, 2010), observers performed five daily sessions. We found that repeated performance of the grouping task produced a rapid within-day improvement, which was largely transient and was not fully retained when tested on subsequent days. We took the transient nature of the gains to imply that they resulted from rapid adaptation to the visual stimuli. Practice with the task over several days resulted in faster adaptation, in accordance with previous findings (Yehezkel et al., 2010). To further test our suggestion that exposure-based adaptation affects performance in the grouping task, we explicitly tested how performance on the task changed following exposure to stimuli with the same orientation as in the grouping task or to stimuli with the orientation offset by 45°. Performance in the task improved following adaptation to the same stimuli, whereas adaptation to stimuli with orientation offset by 45° (deadaptation) reduced performance. Finally, to uncover the effects of adaptation on internal noise and on noise reduction, we used an external-noise paradigm (Green & Swets, 1966; Lu & Dosher, 2008). The results showed reduced internal noise as a consequence of adaptation, with learning reducing the effect of external noise.

Overall, our results suggest that the grouping task benefits from an adaptation process that rapidly adjusts the visual system to the statistics of the stimulus orientations. With practice, this adjustment can be made faster.

### Methods

#### Apparatus

The stimuli were presented on a 23.6-in. VIEWPixed/3D monitor (1,920 × 1,080, 10 bits, 120 Hz, with scanning backlight mode) viewed at a distance of 100 cm. The mean luminance of the display was 47 cd/m² in an otherwise dark environment.

#### Observers

Thirty-five observers with normal or corrected-to-normal vision participated in the experiments. All observers were unfamiliar with the perceptual grouping 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).

#### Stimuli and task

##### Perceptual grouping task

The stimulus, of 40 ms duration, consisted of a grid of identical diagonal bars (19 × 19, tilted 45° counterclockwise from the vertical, length × width: 26.4 × 2.8 arcmin, spaced 46.8 arcmin apart). The experimental variable was the difference between the horizontal spacing and the vertical spacing between the bars (dh – dv), thus controlling proximity-based grouping (Ben-Av & Sagi, 1995). The 13 differences tested were ±13.9, ±10.8, ±7.4, ±3.9, ±2.0, ±1.0, and 0 arcmin. A positive difference implies smaller spacing in the vertical direction, a columnar organization. Since the unequal spacing between the rows and the columns also affected the overall shape of the stimulus, introducing unwanted cues, a circular frame was added (radius = 366 arcmin), so that the global form of the stimulus was circular across all experiments (Figure 1A). A two-alternative forced-choice task was used, where observers reported the perceived organization of the display as one of two possible configurations: rows or columns. Response feedback was provided only during the familiarization session performed on the first day (to be consistent with previous studies using the same stimuli and task; e.g., Yehezkel et al., 2010). Each block of trials, of about 4 min duration, contained 12 or 13 dh – dv differences (depending on the inclusion of dh – dv = 0), intermixed (eight or nine trials per difference). The measured psychometric curves (the percentage of vertical responses as a function of dh – dv) were fitted with a cumulative normal distribution (Figure 2). The parameters obtained were used to estimate the point of subjective equality where the rows and columns were reported with equal probability, and the slope of the psychometric function at that point (performance sensitivity). The discrimination threshold was defined as the standard deviation of the normal distribution fitted to the produced psychometric functions (lapse...
rate: up to 0.05, separately for lambda and gamma). Fitting was performed using Psignifit 4.0 software for MATLAB (MathWorks, Natick, MA; Schütt, Harmeling, Macke, & Wichmann, 2016). In order to verify that the grid stimulus did not cause a specific bias in favor of one of the perceptual organizations (horizontal or vertical), we calculated for each observer the average point of subjective equality (across all blocks). The average point of subjective equality across observers was not significantly different from zero ($M ± SEM = 0.28 ± 0.4$, $p = 0.5$, paired t test), indicating that there was no consistent perceptual bias in favor of one of the perceptual organizations.

**Adaptation induction**

Observers were presented with trials exposing the same grid of bars as in the grouping task (40 ms duration), but without performing the task. To ensure that the observers were effectively exposed to the stimuli, they were asked to report the presence/absence of an easily detectable (>90% correct detection) wide bar, presented in the left or right stimulus quadrant with equal probability (Figure 1B). Each adaptation block contained five $dh - dv$ differences ($±2.0$, $±1.0$, and 0 arcmin), intermixed (40 trials per difference), and lasted about 4 min. There were three types of adaptation blocks: diagonal blocks, in which the orientation of the bars in the adapting stimulus was the same as in the perceptual grouping task (tilted 45° counterclockwise from the vertical); vertical blocks, in which the orientation of the adapting stimulus was vertical; and mixed blocks, in which vertical and horizontal adapting stimuli were randomly mixed during adaptation (Figure 1C). Exposure to stimuli having the same orientation as the tested grouping stimuli (diagonal stimuli) is expected to enhance adaptation to the grouping stimuli, whereas exposure to stimuli with 45° offset orientation (vertical and mixed stimuli) is expected to reduce adaptation to the previous orientation (Greenlee & Magnussen, 1988; Harris, Gliksberg, & Sagi, 2012).

**Procedures**

**Experiment 1: Testing perceptual grouping**

Observers ($N = 12$) carried out the perceptual grouping task during five daily sessions (four blocks on Day 1, five blocks on Days 2 and 3, and six blocks on Days 4 and 5). The time interval between subsequent sessions was 1–4 days. Overall, observers performed 2,704 grouping trials each (26 blocks $× 13 dh - dv$ differences $× 8$ trials per difference).

**Experiment 2: Adaptation and deadaptation**

Two experiments examined the dependence of the grouping performance on the adaptation/deadaptation induction.

**Experiment 2a:** Nine of the observers that participated in Experiment 1 participated in this experiment, which included four daily sessions. In each session, observers were tested with three blocks of the perceptual grouping task, followed by three blocks of adaptation/deadaptation, and then tested again with three blocks of the perceptual grouping task. Two of the sessions contained diagonal adaptation blocks (the same orientation as in the perceptual grouping task), whereas the other two sessions contained either
vertical deadaptation blocks (six observers) or mixed deadaptation blocks (three observers). Overall, each observer performed 2,496 grouping trials (24 blocks \( \times \) 13 dh – dv differences \( \times \) 8 trials per difference) and 2,400 adaptation/deadaptation trials.

**Experiment 2b:** Ten new observers performed the grouping task in testing blocks that were interleaved with adaptation/deadaptation blocks. The experiment included two daily sessions, each containing five blocks of the perceptual grouping task and four adaptation/deadaptation blocks (diagonal or mixed, respectively). The grouping (G) blocks were interleaved with the adaptation/deadaptation (Ad/deAd) blocks to create one of two block sequences: G \( \rightarrow \) Ad \( \rightarrow \) G \( \rightarrow \) deAd \( \rightarrow \) G \( \rightarrow \) Ad \( \rightarrow \) deAd \( \rightarrow \) G or G \( \rightarrow \) deAd \( \rightarrow \) G \( \rightarrow \) Ad \( \rightarrow \) deAd \( \rightarrow \) G \( \rightarrow \) Ad \( \rightarrow \) G. Observers performed both sequences, on different days, starting with either the first sequence or the second sequence, counterbalanced between observers. Overall, each observer performed 1,040 grouping trials (10 blocks \( \times \) 13 dh – dv differences \( \times \) 8 trials per difference) and 1,600 adaptation/deadaptation trials.

**Experiment 3: External noise**

Observers performed the perceptual grouping task with external noise added to the stimuli. External noise was added as a random uniformly distributed displacement (in x and y directions), independently, to the position of each element in the display. There were two groups, differing in their levels of external noise included: lower noise \( (N = 7) \) and higher noise \( (N = 6) \). There were five daily sessions, each with two blocks of trials. Each block contained equal numbers of randomly intermixed trials that included stimuli either without external noise or with one of two noise levels. In the lower noise group, the external noise was either low or intermediate (uniformly distributed within a range of \( \pm 2.8 \) to \( \pm 5.6 \) arcmin). In the higher noise group, the external noise was either intermediate or high (uniformly distributed within a range of \( \pm 5.6 \) to \( \pm 11.2 \) arcmin). Overall, the observers performed 3,240 trials each (10 blocks \( \times \) 12 dh – dv differences \( \times \) 9 trials per difference \( \times \) 3 noise levels).

**Modeling the external noise:** Testing human sensitivity to external noise allows one to characterize the limiting properties of task performance arising from internal and external noise (Lu & Dosher, 1999; Nagaraja, 1964). We fitted the measured thresholds to a standard model assuming the additivity of external noise and equivalent internal noise, the latter representing internal variations expressed in terms of stimulus variations, limiting performance in the absence of external noise. Accordingly, we defined threshold as the displacement (dh – dv) value equal to the total noise in the stimulus—that is, the sum of variations generated by the external noise (sum of the noise variances in the x and y directions) and the equivalent internal noise. This threshold was estimated by the standard deviation of the normal distribu-
tion fitted to the produced psychometric functions (see Stimuli and task). We further assumed that the visual system integrates the spatially distributed external noise with an integration coefficient that depends on the adaptation level and experience with the task. This model is summarized by

$$\text{Threshold} = \sqrt{\frac{\alpha}{N_{\text{int}}} + \frac{N_{\text{ext}}^2}{\alpha}}$$

where $\alpha$ denotes the (inverse) efficiency of external-noise integration, estimating the capacity of the grouping process to reduce the impact of external noise by spatial integration, and $N_{\text{int}}$ and $N_{\text{ext}}$ correspond to the standard deviations of the equivalent internal and external noises, respectively, both expressed in stimulus units. Note that we do not assume that the efficiency parameter controls the effective internal noise, an assumption that would require the internal noise to be spatially uncorrelated. We tested the dependence of the two free parameters $\alpha$ and $N_{\text{int}}$ on experience within and between sessions by fitting the equation to the threshold versus external-noise data at each session start and end, for each observer separately. In each such fit, there were three external-noise levels (zero, low, and intermediate levels in the lower noise group; zero, intermediate, and high in the higher noise group) and three threshold measurements. A least-square fitting method was used. Note that $\alpha$ and $N_{\text{int}}$ may display similar dependencies on time, since $N_{\text{int}}$ may improve with spatial integration, depending on spatial correlations within the visual system.

Results

Experiment 1: Repeated performance on the perceptual grouping task

The observer’s performance on the perceptual grouping task was measured by the percentage of vertical reports as a function of $dh - dv$ (psychometric function, Figure 2). The discrimination threshold was defined as the standard deviation of the normal distribution fitted to the produced psychometric functions (see Methods). Figure 3 displays the average discrimination threshold (across observers) for each testing block and daily session. Results show significant within-session improvements, indicated by a significant decrease in the threshold from the first training block to the last training block: $M \pm SEM = 2.5 \pm 0.6, p < 0.01; 3.1 \pm 0.9, p < 0.01; 3.0 \pm 0.8, p < 0.01; 1.1 \pm 0.6, p = 0.09; \text{and } 2.0 \pm 0.6, p < 0.01$ (paired $t$ test; improvements within Sessions 1, 2, 3, 4, and 5, respectively). In addition, the first threshold measured on each day was significantly higher than the threshold of the last training block of the previous day—$M \pm SEM = 2.5 \pm 0.6, p < 0.01; 2.3 \pm 0.6, p < 0.01; 0.9 \pm 0.4, p < 0.05; \text{and } 1.7 \pm 0.3, p < 0.01$ (paired $t$ test; threshold increase between Sessions 1 and 2, 2 and 3, 3 and 4, and 4 and 5, respectively)—showing that the within-day performance gains were not fully retained in subsequent daily sessions. The transient nature of these gains suggests the involvement of visual adaptation as their main cause.
Next we investigated whether the dynamics of performance changed between days. The results show that there were no significant changes between the threshold reductions within the first day and those within subsequent days (vs. second day: \( p = 0.5 \); vs. third day: \( p = 0.6 \); vs. fourth day: \( p = 0.2 \); vs. fifth day: \( p = 0.5 \); paired \( t \) test). However, as shown in Figure 3, practice with the task resulted in faster within-session threshold reductions. On Day 1 the threshold was sharply reduced already in the second block. And whereas the threshold of the first block on Days 2 and 3 was similar to that on Day 1 \((M \pm SEM)_{\text{Day 1}}: 7.9 \pm 0.7; \text{Day 2}: 7.9 \pm 0.8, p = 1.0; \text{Day 3}: 7.0 \pm 0.9, p = 0.5; \text{paired } t \) test), the threshold of the second block on these days was significantly reduced as compared to that on the first day \((M \pm SEM)_{\text{Day 4}}: 4.9 \pm 0.4, p < 0.01; \text{Day 5}: 5.6 \pm 0.6, p < 0.05; \text{paired } t \) test). To quantify the speedup of the within-session threshold decrease, we fitted the daily thresholds (averaged across observers) to an exponential-decay model, assuming that the initial and final thresholds are fixed across days. The model was successful in accounting for 86\% \((R^2)\) of the variance in the data (Figure 3: 26 data points, seven free parameters). We found that the time constant gradually decreased during the five testing days, showing \( \sim 4 \) times faster within-session threshold reduction at Day 5 as compared with Day 1 (see inset, Figure 3). These faster within-session improvements with practice could possibly result from faster readaptation (Yehezkel et al., 2010).

**Experiment 2: Adaptation/deadaptation**

Here we set out to test the hypothesis that the transient within-day improvement obtained in the grouping task was due to task-independent, exposure-based sensory adaptation.

**Experiment 2a**

Nine observers from Experiment 1 completed trials presenting the grouping stimuli, but they performed a detection task instead of the grouping task (see Methods). Figure 4 displays the average grouping performance in daily sessions that contained diagonal adaptation blocks and in daily sessions that contained vertical or mixed deadaptation blocks. The results show that following exposure to stimuli with the same orientation as the grouping stimuli (diagonal), the within-session improved grouping performance was preserved and somewhat improved, as expected from sensory adaptation. However, with the vertical and mixed blocks, the grouping thresholds significantly increased, in agreement with the deadaptation hypothesis. In order to investigate whether these trends were statistically significant, we quantified for each observer the pre- and postexposure performance. The pre-exposure performance was calculated as the average threshold of the two perceptual grouping blocks before exposure, and the postadaptation performance was calculated as the average threshold of the two blocks after exposure. The differences between pre- and postexposure performance were statistically significant for the different adaptation/deadaptation types (diagonal adaptation: \(-0.8 \pm 0.2\), vertical and mixed de-adaptation: \(0.7 \pm 0.2\); pairwise \( t \) test between conditions showing \( p < 0.01 \); Figure 4). The threshold was significantly reduced following exposure to diagonal blocks (preadaptation: \(4.3 \pm 0.4\); postadaptation: \(3.5 \pm 0.4\); \( p < 0.05 \); paired \( t \) test; Figure 4) and significantly increased following exposure to vertical and mixed blocks (preadaptation: \(3.98 \pm 0.3\); postadaptation: \(4.64 \pm 0.4\); \( p < 0.05 \); paired \( t \) test; Figure 4).

**Experiment 2b**

Ten new observers performed grouping blocks that were interleaved with exposure blocks. Figure 5 displays the average grouping performance (across observers) for the two interleaved block sequences. The average threshold (across blocks) following a diagonal exposure (adaptation: \(4.8 \pm 0.5\), \( SEM \)) was signifi-
importantly, exposure to stimuli with 45° offset orientation is thought to be task specific (Ahissar & Hochstein, 1993; Fahle & Morgan, 1996). Most importantly, exposure to stimuli with the same orientation is suggested to arise from adaptation, since perceptual learning is thought to be task specific (Ahissar & Hochstein, 1993; Fahle & Morgan, 1996). Most importantly, exposure to stimuli with 45° offset orientation, as in the vertical and mixed blocks, resulted in a significant deterioration of performance rather than improvement. This result is in accordance with the adaptation literature showing deadaptation for stimuli offset by 45° (Greenlee & Magnussen, 1988; Harris et al., 2012; Pinchuk-Yacobi, Harris, & Sagi, 2016).

### Experiment 3: Effects of external noise

Here we tested performance in the task while adding different levels of external noise to the stimuli. Figure 6A and 6B displays the average discrimination threshold (across observers) for each testing block and noise level, for the lower noise and higher noise groups, respectively.

The effects of experimental manipulations on threshold were evaluated using a repeated-measures analysis of variance (ANOVA) with within-subject factors of noise (two levels: no noise and mid noise levels), day (five days), and time (start and end of session), performed separately for the two groups. We used only the data obtained from trials with no noise and mid noise levels, since only those noise levels were used in both groups (see the Appendix for statistical analysis performed on the whole data). For both groups, threshold increased significantly when external noise was added to the stimuli—lower noise: $F(1, 6) = 130.3, p < 0.001$; higher noise: $F(1, 5) = 10.3, p < 0.05$. Improvement within session, as indicated by the threshold reduction from the start to the end of the session, was significant only for the lower noise group—lower noise: $F(1, 6) = 93.6, p < 0.01$; higher noise: $F(1, 5) = 3.7, p = 0.1$.

In order to test the effect of learning in the task, we ran an ANOVA with only the thresholds of the first day (Day 1) and the last day (Day 5), separately for the thresholds at the start and at the end of the session. Learning between the first day and the last day was significant only for the higher noise group, and only at the start of the session—lower noise, start: $F(1, 6) = 3.7, p = 0.1$; lower noise, end: $F(1, 6) = 0.06, p = 0.8$; higher noise, start: $F(1, 5) = 10.3, p < 0.05$; higher noise, end: $F(1, 5) = 5.9, p = 0.06$.

Next we investigated whether the within-session gains obtained in a training session were retained in the following session, or whether performance deteriorated from the end of the session to the beginning of the next session. For that purpose, we ran another repeated-measures ANOVA, with within-subject factors of noise (no noise and mid noise levels), day (Day 2 through Day 5), and time (end of the previous session or the start of the next session). Performance significantly deteriorated from the end of the previous session to the beginning of the next session only for the lower noise group—lower noise: $F(1, 6) = 31.1, p = 0.001$; higher noise: $F(1, 5) = 0.03, p = 0.9$. This was clearly seen on the second day (Figure 6A), where noise levels 0 and 1 at the start of Day 2 are back to the starting level of the first day.

To compare the performances of the groups, we added to the repeated-measures ANOVAs the between-subjects factor of group type (lower noise or higher noise). The only significant differences between the
groups were the improvements within sessions, $F(1, 11) = 16.3, p < 0.01$, and the deterioration between sessions, $F(1, 11) = 11.1, p < 0.01$, which were significantly lower for the higher noise group. These results suggest that mixing trials with high external noise, as with the higher noise group, reduces the adaptation effect. The learning effects—start: $F(1, 11) = 1.0, p = 0.4$; end: $F(1, 11) = 0.7, p = 0.4$—and the noise effect, $F(1, 11) = 3.1, p = 0.1$, were not significantly different between the groups. No significant interactions were found in any ANOVA analysis.

Table 1 summarizes the statistical results for the analysis performed on data only from trials with no noise and mid noise levels.

In order to better explore the factors that could contribute to the changes between the groups’ thresholds, we fitted the thresholds (using data from both lower and higher noise groups) to the external-noise model that includes the parameters of an integration coefficient $\alpha$ as well as internal and external noise levels (see Methods). Fitting the integration coefficient resulted in inconsistent and minor changes (either a slight increase or a slight decrease) between subsequent

---

**Table 1. Statistical results for the external-noise experiment.** Analysis was performed only on data from trials with no noise and intermediate noise. Notes: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; n.s. = not significant.

---

Figure 6. Performance in the perceptual grouping task with external noise. The experiment included five daily sessions, with two blocks per day (start and end). Each block contained equal numbers of randomly intermixed trials with stimuli either without external noise (noise level = 0) or with one of two noise levels. Overall, there were three external-noise levels: low (1, jitter of 2.8 arcmin), intermediate (2, jitter of 5.6 arcmin), and high (4, jitter of 11.2 arcmin). (A) Performance of the lower noise group ($N = 7$), low and intermediate noise levels. (B) Performance of the higher noise group ($N = 6$), intermediate and high noise levels. Thresholds are averages across observers, with error bars corresponding to $\pm$1 standard error of the mean.
sessions—that is, between a session end and the start of the following session. Therefore, we fixed the value of the integration coefficient between subsequent sessions (value at the start of the session equals the value at the end of the previous sessions) to reduce the degrees of freedom. Results for the fitted parameters of the integration coefficient and the internal noise, averaged across observers, are displayed in Figure 7A and 7B, respectively. The two parameters display different dependencies in the two tested groups. When only low and intermediate levels of external noise were added to the stimuli, as in the lower noise group, observers quickly learned to integrate the bars, as indicated by a significant reduction of the integration coefficient apparent already on the first training day (1.9 ± 0.6, p < 0.05, paired t test). This fast improvement in integration, already on the first day, seemed to enable a significant within-session reduction in the internal noise—F(1, 6) = 14.6, p < 0.01 (two-way ANOVA with within-observer factors of day and time in the session)—and there was no correlation between the values of the internal noise and the of the integration coefficient (r = 0.0, p = 1.0, n = 60). Comparing the two groups shows significantly lower internal noise at the end of the sessions in the lower noise group compared with the higher noise group (1.1 ± 0.2, p < 0.01, two-sample t test). Given that the internal noise was significantly reduced only when spatial integration was present (as in the lower noise group), this suggests that adaptation improves performance not by uniform reduction of local internal noise but by global decorrelation of internal noise across the whole stimulus.

**Discussion**

Our results show that repeated performance on the perceptual grouping task produced within-session improvements, especially at the beginning of each daily session (Figure 3). These improvements were largely dependent on exposure (Figures 4 and 5), not task, and were not fully retained in subsequent daily sessions (Figure 3). In addition, exposure to stimuli with an orientation differing by 45° from the orientation used in the grouping task diminished the improvement previously obtained in the same session (Figures 4 and 5). The transient nature of these exposure-driven im-

---

**Figure 7.** Fitted values of (A) the integration coefficient α (lower value indicates improved spatial integration) and (B) the internal noise, shown for each training day and time within a session (start or end) for (left) the lower noise group (N = 7) and (right) the higher noise group (N = 6). Results show that spatial integration is essential for obtaining lower internal noise. Error bars represent ±1 standard error of the mean.
improvements and their susceptibility to interference by deadadaptation stimuli suggest that they result from an adaptation process that rapidly adjusts the visual system to the orientation statistics of the stimuli.

One of the main controversies regarding visual pattern adaptation concerns its potential benefit. At the single-neuron level, adaptation has been suggested to improve information transfer by adjusting the limited dynamic range of the neuron to the current input statistics (Wainwright, 1999). At the population level, adaptation has been suggested to remove redundancies across neurons by decorrelating their neural responses (Barlow & Foldiak, 1989). However, previous studies that tested how adaptation affects contrast discrimination have found only weak evidence for improved discriminability for stimuli similar to the adapter, predicted by dynamic-range adjustment (Barlow et al., 1976; Greenlee & Heitger, 1988; Maattanen & Koenederink, 1991; Ross et al., 1993). Here we report large improvements in grouping discrimination following adaptation. The difference between our results and those of previous perceptual adaptation experiments might arise from the different task we used. Perceptual grouping has been suggested to rely highly on spatial correlations and spatial integration (Ben-Av, Sagi, & Braun, 1992), and therefore it should be most affected by adaptation-induced changes in spatial correlation. Contrast discrimination, on the other hand, shows no improvements from spatial integration when the base and increment contrasts are over an equal spatial extent, possibly due to balanced excitation and inhibition interactions (Bonneh & Sagi, 1999). Ben-Av and Sagi (1995) suggest that perceptual grouping involves a process that compares horizontal and vertical intensity correlations, and that grouping occurs in the direction with the higher degree of correlation. Given the high reliance of grouping on spatial correlations and integration, we argue that adaptation improves performance in the task by spatial decorrelation. Consequently, we propose two possible mechanisms for such improvements: removal of the average spatial correlation between all signals, assisting the comparison process in distinguishing between small differences in correlation values, or removal of correlations between the internal noises of neighboring neurons, increasing the efficiency of spatial integration and improving signal-to-noise ratio. An alternative explanation might have been that adaptation improves performance on the task by local means, such as reduction of internal noise at all locations, or local improvements in spatial or orientation resolutions. However, our results in the external-noise experiment indicate that spatial integration is essential for obtaining the benefits of adaptation. Challenging spatial integration, by randomly mixing trials with high external noise as in the higher noise group, resulted in reduced spatial integration and a significantly higher internal noise at the end of the sessions (Figure 7). In accordance, the adaptation effects of within-session improvements and between-sessions deteriorations were significantly reduced in the higher noise group (Figure 6).

Comparing performance in the perceptual grouping task in our experiments to that in other perceptual tasks shows compatible within-session improvements (Aberg, Tartaglia, & Herzog, 2009; Fahle, Edelman, & Poggio, 1995; Hussain, Sekuler, & Bennett, 2008; Karni & Sagi, 1993). However, contrary to other perceptual tasks—in which the initial performance in each session is usually equivalent to (or even better than) that obtained at the end of the previous session (Harris & Sagi, 2015; Karni & Sagi, 1993)—performance in the grouping task was largely reduced in the first block of subsequent sessions. This reduced initial performance indicates that the within-session gains obtained in the preceding training session were not retained in the next session (Figure 3, the first three sessions) or were only partially retained (the fourth and fifth sessions). Failure to retain the within-session gains was also apparent in the repeated reemergence of significant within-session improvements in all daily sessions. This behavior is inconsistent with typical within-session improvements obtained in other perceptual learning tasks, which mostly appear during the first training session and tend to diminish in subsequent sessions (Harris et al., 2012; Karni & Sagi, 1993). In addition to diminished performance at the beginning of each session, which can be related to passive decay due to the passage of time between sessions, within-session performance was also reduced after explicit exposure to deadadaptation stimuli. Performance was diminished only following adaptation to stimuli that were offset by 45° from the orientation of the original grouping stimuli (vertical or mixed orientation), and enhanced following adaptation to stimuli with the same orientation as in the grouping task (diagonal orientation). Thus, the deterioration effect was specific to the orientation of the stimuli. These results can be related to studies that have tested the effects of adaptation on orientation mixtures. Greenlee and Magnussen (1988) found reduced contrast adaptation when vertical and diagonal gratings were interleaved during the adaptation period. Harris and Sagi (2015), using a texture discrimination task, found slower within-session learning when using a fixed texture orientation compared with conditions where two orientations differing by 45° were interleaved, attributing the effect to differences in orientation-specific adaptation.

Previous studies have used external noise to explore the factors that contribute to the learning of a perceptual task (Lu & Dosher, 2008). Most relevant to our study is a study by Li, Levi, and Klein (2004) that
used position noise to explore the neural mechanisms underlying learning of a visual position discrimination task. This research showed that with learning, observers improved performance by using more efficient and broader stimulus samples in their position judgments. These results are consistent with our findings of between-sessions learning of the integration coefficient. The within-session dynamics cannot be compared, since performance results were reported only as within-session means. Furthermore, Li et al. assumed internal noise to be spatially uncorrelated, thus predicting reduced effective internal noise with increasing sampling efficiency, while we suggest these correlations to be adaptation dependent. Interestingly, they noted that, unlike with high external noise, in the low external noise condition (which was dominated by the internal noise) the measured human thresholds were much lower than the thresholds predicted by an ideal observer. This result can be explained by assuming that the internal noise contained correlations that limited the benefit obtained from more efficient and broader stimulus sampling.

The dynamics of the within-session and between-sessions gains in our experiment can also be related to studies of motor adaptation learning (Krakauer, 2009; Krakauer, Ghez, & Ghilardi, 2005). The return to the baseline performance level at the beginning of the second and third sessions resembles the “forgetting” of motor improvements when subjects are reexposed to the same motor adaptation task later in time. In addition, the faster within-session threshold reduction with more daily sessions can be explained by a faster rate of readaptation, similar to faster relearning of a motor adaptation task following repetitive practice over time. Such faster readaptation has also been shown recently following repeated adaptation to a prism distortion (Habtegiorgis, Rifai, Lappe, & Wahl, 2018; Yehezkel et al., 2010). These results of long-term effects of adaptation, which are found in several modalities including motor and vision, are consistent with theories suggesting that adaptation involves temporary plasticity of inhibitory synapses (Dealy & Tolhurst, 1974; Wilson, 1975). Perhaps when a substantial amount of adaptation is provided in a specific context (such as in the context of a perceptual task), the temporary plasticity can be made long-term.

Keywords: sensory adaptation, decorrelation, perceptual grouping

Acknowledgments

This work was supported by the Basic Research Foundation administered by the Israel Academy of Sciences and Humanities (DS).

Commercial relationships: none.
Corresponding author: Dov Sagi.
Email: Dov.Sagi@Weizmann.ac.il.
Address: Department of Neurobiology, Weizmann Institute of Science, Rehovot, Israel.

References


Fahle, M., & Morgan, M. (1996). No transfer of perceptual learning between similar stimuli in the
same retinal position. Current Biology, 6(3), 292–297.


Appendix

Here we performed the same ANOVA analyzes as described in the Results section for Experiment 3, but...
on the whole data (including all noise levels). For both
groups, thresholds increased significantly when external
noise was added to the stimuli—lower noise: $F(2, 12) = 40.3, p < 0.001$; higher noise: $F(2, 10) = 23.1, p < 0.001$—and thresholds decreased significantly from the
start of the session to the end of the session,
demonstrating within-session improvements—lower
noise: $F(1, 6) = 72.8, p < 0.001$; higher noise: $F(1, 5) = 7.3, p < 0.05$. Learning between the first day and the
last day was only significant for the higher noise
group—lower noise, start: $F(1, 6) = 3.2, p = 0.12$; lower
noise, end: $F(1, 6) = 0.007, p = 0.9$; higher noise, start:
$F(1, 5) = 18.2, p < 0.01$; higher noise, end: $F(1, 5) = 22.6, p < 0.01$. Deterioration in performance from the
end of the previous session to the beginning of the next
session was only significant for the lower noise group—
lower noise: $F(1, 6) = 45.7, p < 0.001$; higher noise: $F(1, 5) = 0.4, p = 0.6$.

Appendix Table A1 summarizes the statistical
results for the external-noise experiment (analysis on
the whole data).

<table>
<thead>
<tr>
<th>Factor</th>
<th>Lower noise group</th>
<th>Higher noise group</th>
</tr>
</thead>
<tbody>
<tr>
<td>External noise</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Improvements within session</td>
<td>***</td>
<td>*</td>
</tr>
<tr>
<td>Learning between the first day and the last day (start of the session)</td>
<td>n.s.</td>
<td>**</td>
</tr>
<tr>
<td>Learning between the first day and the last day (end of the session)</td>
<td>n.s.</td>
<td>**</td>
</tr>
<tr>
<td>Deterioration between the end of the previous session and the beginning of the next session</td>
<td>***</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

Table A1. Statistical results for the external-noise experiment. Analysis was performed on the whole data. Notes: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; n.s. = not significant.