



Target-selective tilt aftereffect during texture learning



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ABSTRACT

Sensory adaptation and perceptual learning are two forms of plasticity in the visual system, with some potential overlapping neural mechanisms and functional benefits. However, they have been largely considered in isolation. Here we examined whether extensive perceptual training with oriented textures (texture discrimination task, TDT) induces adaptation tilt aftereffects (TAE). Texture elements were oriented lines at -22.5° (target) and 22.5° (background). Observers were trained in 5 daily sessions on the TDT, with 800–1000 trials/session. Thresholds increased within the daily sessions, showing within-session performance deterioration, but decreased between days, showing learning. To evaluate TAE, perceived vertical (0°) was measured prior to and after each daily session using a single line element. The results showed a TAE of $\sim 1.5^\circ$ at retinal locations consistently stimulated by the target, but none at locations consistently stimulated by the background texture. Retinal locations equally stimulated by target and background elements showed a significant TAE ($\sim 0.7^\circ$), in a direction expected by target-driven sensory adaptation. Moreover, these locations showed increasing TAE persistence with training. Additional experiments with a modified target, in order to have balanced stimulation around the vertical direction in all target locations, confirmed the locality of the task-dependent TAE. The present results support a strong link between perceptual learning and local orientation-selective adaptation leading to TAE; the latter was shown here to be task and experience dependent.

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1. Introduction

In perceptual learning, repetitively performing a perceptual task leads to long-lasting improvements in performance (Fahle & Poggio, 2002; Sagi, 2011). In visual learning, these tasks involve discriminating fine visual features such as discrimination of contrast (Adini, Sagi, & Tsodyks, 2002), orientation (Schoups, Vogels, & Orban, 1995), hyperacuity (Fahle & Edelman, 1993; Poggio, Fahle, & Edelman, 1992), motion direction (Ball & Sekuler, 1987), and texture (Karni & Sagi, 1991). The neural mechanisms underlying visual learning are not fully understood (Sagi, 2011). One body of evidence suggests low-level neural modifications during learning (Fahle, 2004; Karni & Sagi, 1991; Poggio et al., 1992; Pourtois, Rauss, Vuilleumier, & Schwartz, 2008; Schoups et al., 1995; Yotsumoto, Watanabe, & Sasaki, 2008), whereas other works demonstrated the role of the higher cortical levels in the process of learning (Ahissar & Hochstein, 2004; Doshier & Lu, 1998; Karni & Sagi, 1995; Law & Gold, 2008). It is likely that several cortical levels are essential for learning with an unknown interplay between them (Karni & Sagi, 1993).

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Another form of plasticity in the visual system is sensory adaptation. This effect is primarily driven by mere exposure to the stimulus and occurs even when the observer is not actively performing a task on the adapted stimulus (Clifford et al., 2007; Webster, 2011). Unlike the long-term increased sensitivity following perceptual learning, adaptation typically results in short-term reduced sensitivity. Changes in adaptation states may lead to a biased appearance, known as visual aftereffects. For example, adaptation to an oriented stimulus causes a tilt aftereffect (TAE), in which the perceived orientation of a test stimulus appears slightly repelled away from the direction of the adapted orientation (Gibson & Radner, 1935). Practice was shown to speed-up the transition between different adaptation states, shortening the aftereffect duration (Yehezkel, Sagi, Sterkin, Belkin, & Polat, 2010).

The typical perceptual learning training consists of many repetitions, and promotes improved sensory sensitivity. However, several studies demonstrated performance deterioration during perceptual training. For example, increasing Vernier thresholds were found following extended exposure to Vernier stimuli (Ludwig & Skrandies, 2002). In some cases the performance deterioration was suggested to result from the reduced sensitivity following sensory adaptation to the stimulus (Censor & Sagi, 2008; Ludwig & Skrandies, 2002). The link between reduced Vernier acuity and sensory adaptation was supported by decreasing visual evoked potential (VEP) with

increasing Vernier thresholds (Ludwig & Skrandies, 2002). In another work, the deteriorative effect was shown to be reduced due to learning, pointing to a link between adaptation and learning. Censor and Sagi (2008) found that a short training session, followed by efficient consolidation, enables long-term resistance to perceptual deterioration induced by intensive training.

Recent studies have directly tested aftereffects following perceptual learning. Petrov and Van Horn (2012) examined the effects of 4 days of motion direction-discrimination training on motion aftereffect (MAE) duration. Their measurements, carried out separately for learning and adaptation, showed no differences between MAE tested before and after training. Another work (Chen & Fang, 2011) measured changes in the perceived vertical following orientation discrimination learning with tilted line stimuli. They found that following training, the observers' perceived vertical shifted toward the trained orientation (to the same direction as in the adaptation induced TAE), an effect seen one day following training, but disappeared a week afterwards. Chen and Fang (2011) attributed this shift to reduced bandwidth of the trained orientation-selective neuron. Both studies evaluated perceived orientation/direction prior to a multi-day training procedure relative to its completion, without testing effects of adaptation generated during repeated stimulations within a daily training session.

In particular, in texture learning, it has been shown that an intense training (consisting of many trials within each daily session) with the texture-discrimination task (TDT) leads to performance decrements within training sessions, and reduces learning relative to training, with shorter sessions showing no within-session deterioration (Censor, Karni, & Sagi, 2006; Mednick et al., 2002; Ofen, Moran, & Sagi, 2007). The possibility that these decrements are the outcome of general fatigue was ruled out due to the location specificity of these decrements, and their independence of monetary reward (Mednick, Drummond, Arman, & Boynton, 2008). It has been suggested that these effects reflect adaptation to the trained visual stimulus (Censor & Sagi, 2008). However, no direct behavioral link between the declined TDT performance and sensory adaptation such as adaptation aftereffects has been found. More specifically, we consider here the hypothesis that the observed within session deterioration in TDT is a result of orientation selective adaptation.

Recent studies (Harris, Gliksberg, & Sagi, 2012; Harris & Sagi, 2015) showed that the within-day deterioration in TDT exists (although to a lesser extent) even when a shorter training session is applied. This deterioration was shown to be eliminated by inserting dummy trials containing bars that deviated 45° relative to the targets' local orientations. Since the elimination of within-day decrements by the dummy trials is determined by their local orientation, as in contrast adaptation experiments (Greenlee & Magnussen, 1988), it was suggested that they reduce sensory adaptation.

Here we tested whether TDT training produces adaptation tilt aftereffects (TAE) resulting from the trained stimuli. Importantly, no additional exposure was provided during training; thus, here, the role of TDT training as an adaptor was evaluated. We hypothesized that although the task consists of multiple discrete trials, each followed by a noisy mask, adaptation would be induced. Additionally, we tested whether TDT-induced TAE changes with learning.

2. Methods

2.1. Apparatus

The stimuli were presented on a 19" Mitsubishi Diamond Pro 930SB color monitor, using a PC with an Intel processor. The monitor refresh rate was 100 Hz. The luminance of the texture lines was 63–65 cd/m² in an otherwise dark environment.

2.2. Observers

Eleven observers with normal or corrected-to-normal vision participated in this experiment. All observers were naïve to the texture 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).

2.3. Stimuli and task

2.3.1. Texture discrimination task (TDT)

The standard texture discrimination task was used (Karni & Sagi, 1991) consisting of a 40 ms target frame followed by a 100 ms mask frame. The target frame contained a peripheral target (an array of 3 bars tilted 22.5° counterclockwise from the vertical), embedded in a background texture (19 × 19 array of identical bars tilted 22.5° clockwise from the vertical). The target always appeared in the lower-left visual quadrant (Fig. 1A). The mask frame contained an array (19 × 19) of randomly oriented 'V'-shaped patterns. Target and mask presentations were separated by a time interval (stimulus-to-mask onset asynchrony, SOA) with a range 80–340 ms. Observers were asked to report whether the arrangement of the target texture is vertical or horizontal. Fixation was enforced by a forced-choice letter-discrimination task, between a "T" and an "L", at the center of the display. Each daily session consisted of four consecutive sub-sessions (A, B, C, and D). In each sub-session, the SOA started at the highest value (340 ms) and gradually decreased (340, 300, 260, 220, 200, 180, 160, 140, 120, 100, and 80), with 24 trials per SOA (a total of ~800–1000 trials/day). Sub-sessions were terminated at the SOA for which the performance level was <65% correct. The psychometric curves obtained were fitted with the Weibull function, in order to estimate the discrimination threshold

$$P(\text{SOA}) = \frac{1}{2} \left[1 + (1 - fe) \left(1 - e^{-\left(\frac{\text{SOA}}{T}\right)^\beta} \right) \right],$$

where P(SOA) is the measured probability of a correct response per SOA, T is the estimated discrimination threshold for each sub-session, β describes the psychometric function's estimated slope, and fe is the estimated "finger error" parameter (0 ≤ fe ≤ 1).

2.3.2. Perceived vertical (PV) test

Each perceived vertical measurement consisted of two consecutive test sessions. On each trial, observers were asked to make a 2-AFC judgment of whether a test bar (orientations 0°, ±3, ±6, or ±9 relative to vertical; duration = 40 ms, appeared at one out of four locations) is tilted clockwise or counterclockwise from the vertical. Each test session contained 12 trials per orientation, for a total of 84 trials per test location. The test bar could appear at one out of four locations, corresponding to four TDT locations: target central element (TC), target lateral element (TL); two background locations, near (BN, right next to a target lateral location) and far from the target (BF, at a different quadrant, Fig. 1A). The test trials were randomly and equally intermixed across locations and orientations. A cumulative normal function was fitted to the measured psychometric curve and interpolated at the 50% point to determine the perceived vertical.

2.4. Procedures

Observers were trained on the texture discrimination task (TDT) for five daily sessions. Each daily session consisted of four consecutive sub-sessions (A, B, C, and D). The observers' perceived vertical was measured prior to ('pre-TDT') and immediately after ('post-TDT') training the TDT. One group of observers ('Standard', n = 6)

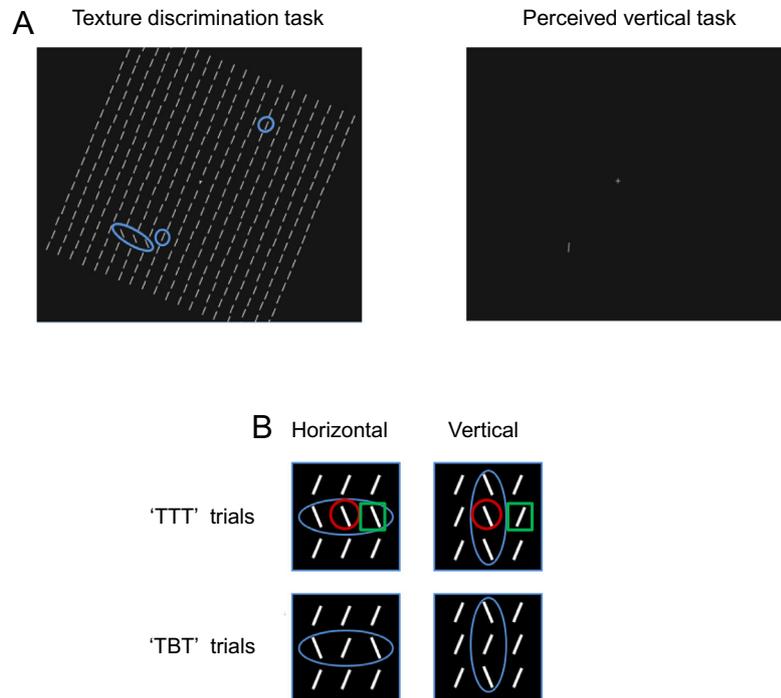


Fig. 1. Stimuli and task. (A) The target stimulus for the perceived vertical task (PV, left, measured prior to and immediately after training the TDT) and the texture discrimination task (TDT, right, mask not shown). In the PV task the observers were asked to respond whether a test bar (40 ms) is tilted clockwise or counterclockwise relative to vertical (orientations 0° , $\pm 3^\circ$, $\pm 6^\circ$, or $\pm 9^\circ$). In the TDT task the observers were asked to report whether the arrangement of the target's texture (3 bars-arrays) is vertical or horizontal. The 3 bars differed from the background in their orientation (target: -22.5° , background: $+22.5^\circ$). Circled in blue are the retinal locations in which the PV task was performed: the target's central element (TC), the target's lateral element (TL); the background nearby (BN, marked by the separate circle near the target) and far from the target (marked by the circle at the upper right quadrant of the display). (B) The 3-bar array could be either vertical or horizontal. The standard training session consisted of only 'TTT' trials, whereas the balanced training consisted of interleaved presentations of 'TTT' and 'TBT' trials. In the 'TBT' trials, the central target's element was oriented 22.5° clockwise from the vertical (the same as the background orientation). The observers were requested to respond in all trials. By design, the lateral target location (TL, denoted by a green rectangle) had a net orientation of 0° , since half of the trials contained a -22.5° orientation (horizontal target) and the other half contained a $+22.5^\circ$ orientation stimulus (corresponding to the background orientation when the vertical target appears). Regarding the location TC (denoted by a red circle), during the standard training it persistently had the same -22.5° orientation from the vertical, whereas during the balanced training this location had a net orientation of 0° owing to the interleaved 'TBT' trials. (For interpretation of the references to colours in this figure legend, the reader is referred to the web version of this paper.)

performed the standard texture discrimination task. This training consisted of standard trials, which are denoted as 'TTT' trials (each 'T' marks the target's orientation of a target bar). By designing the TDT task, different locations presented the target and background orientations with a different probability:

TC: This location contained the -22.5° (target) orientation in all the trials.

TL: This location presented the target and the background orientations with equal probability, depending on whether a horizontal or vertical target is shown. When the TL element is part of the target (as in Fig. 1A, illustrating the horizontal arrangement possibility), it displayed the -22.5° (target) orientation. However, for the vertical arrangement the same TL location presented a $+22.5^\circ$ (background) orientation. Thus, the net orientation presented at the TL location was 0° .

BN and BF: These locations presented the background's orientation in all the trials.

In the second group ('balanced', $n = 5$) half of the trials were 'TBT' trials, in which the central target element was oriented as the background orientation ('B' – background). The observers were instructed to respond to these trials the same way that they responded to the 'TTT' trials. In the 'balanced' group, the 'TBT' trials were randomly intermixed with the 'TTT' trials, and the total number of trials matched the total number of trials in the 'standard' group (24 trials/SOA). The term 'balanced' refers to the balanced presentation across the target's central and lateral elements. In this

'balanced' group, all target locations presented the target and the background orientations with equal probability; thus their net orientation was zero degrees. The magnitude of the Tilt-aftereffect was calculated for each block and location separately as the shift in the observers' perceived vertical from the 'pre-TDT' measurement to the 'post-TDT' measurement. On 'day 0' the observers performed the perceived vertical task (~ 900 trials) to introduce them to the task prior to the TDT training on the subsequent days.

3. Results

3.1. 'Standard' group

3.1.1. TDT performance following intensive training

In the 'standard' group, significant across-day improvements were obtained for the average daily performance. Daily thresholds, calculated by averaging the 4 subsessions' thresholds, improved from 169 ± 7 ms (mean \pm SEM) at day 1 to 137 ± 7 ms at day 5 (paired t -test, $t(5) = 3.7$, $p = 0.01$). Fig. 2 displays the daily performance for each subsession (A, B, C, and D). Learning was obtained during the early subsessions (As). On day 1 the initial threshold (1A) was 164 ± 10 ms, whereas on day 5 the initial threshold (5A) significantly dropped to 122 ± 6 ms (paired t -test, $t(5) = 3.6$, $p = 0.02$), indicating learning across days. Examination of learning during the late subsessions (from 1D to 5D) showed a smaller improvement, not statistically significant, across days (from 170 ± 7 ms to 151 ± 10 ms, $t(5) = 1.6$, $p = 0.1$). Within session

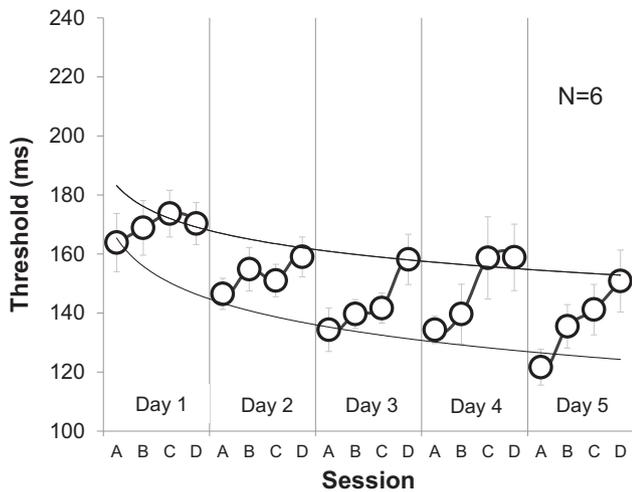


Fig. 2. Within-day deterioration and between-day learning during TDT training. Learning curves for the ‘standard’ ($n = 6$) group. Each daily session consisted of four consecutive sub-sessions (A, B, C, and D), a total of ~800–1000 trials/day. Black lines represent the logarithmic fit to thresholds for either sub-session A (lower) or sub-session D (upper). Error bars represent SEM.

deterioration is evident, ranging between 7 and 29 ms (day1: 7 ± 6 ; day2: 13 ± 5 ; day3: 24 ± 7 ; day4: 25 ± 7 ; day5: 29 ± 5), with values comparable to those previously observed with similar stimuli (Censor & Sagi, 2008).

3.1.2. Target-selective TAE following TDT training

The mean TAE was found to be stable across days (neither the locations nor the test blocks showed a significant trend, i.e. neither showed $p < 0.05$ across days, for exceptions, see Fig. 3B and text below). Thus, Fig. 3A shows the TAE averaged across days, for the ‘standard’ group. TAE was tested at four locations, corresponding to four TDT locations: the target’s central element (TC), the target’s lateral element (TL), and two background locations, near (BN) and far from the target (BF). In addition, TAE was tested at two consecutive blocks: the first (Fig. 3A, white bars) and the second (Fig. 3A, black bars). The duration of each TAE test was ~8 min.

A significant repulsive TAE was obtained immediately following TDT training (the first test, white bars) at both targets’ locations, at TC ($-1.7^\circ \pm 0.2$; one-sample t -test, $t(5) = -7.1$, $p < 0.001$) and, more surprisingly, at TL ($-0.8^\circ \pm 0.2$; $t(5) = -3.8$, $p = 0.01$). This is surprising since the net presented orientation at the target-lateral location is 0° . Thus, if the TAE depends only on the low-level statistics of the stimulus, we would not expect to see TAE at this TL location. However, the results show a clear repulsive TAE relative to the target’s orientation. Notably, although the background locations were consistently stimulated by the background’s orientation, no significant TAE was found at any of the background locations (BN: $0.2^\circ \pm 0.2$, $t(5) = 0.9$, $p = 0.4$, BF: $0.4^\circ \pm 0.3$, $t(5) = 1.6$, $p = 0.2$). These findings show that the adaptation following training is not only location- and orientation-specific, in accordance with classic adaptation reports (Blakemore & Nachmias, 1971; Kohn & Movshon, 2003)—but is also task dependent.

At both target locations the averaged TAE was significantly reduced in the second test relative to the initial test (Fig. 3A, black bars, TC: -0.6° , $t(5) = -2.8$, $p = 0.03$, TL: -0.1° , $t(5) = -2.9$, $p = 0.03$). At the TC location the TAE remained significant even in test 2 ($t(5) = -3.1$, $p = 0.03$).

Examining the TAE across days (Fig. 3B) showed effects of the day on TAE only at the target’s lateral location (no differences were obtained at the target’s central location, first: $R^2 = 0.002$, $p = 1.0$, second: $R^2 = 0.45$, $p = 0.2$). Whereas the first test showed no trend

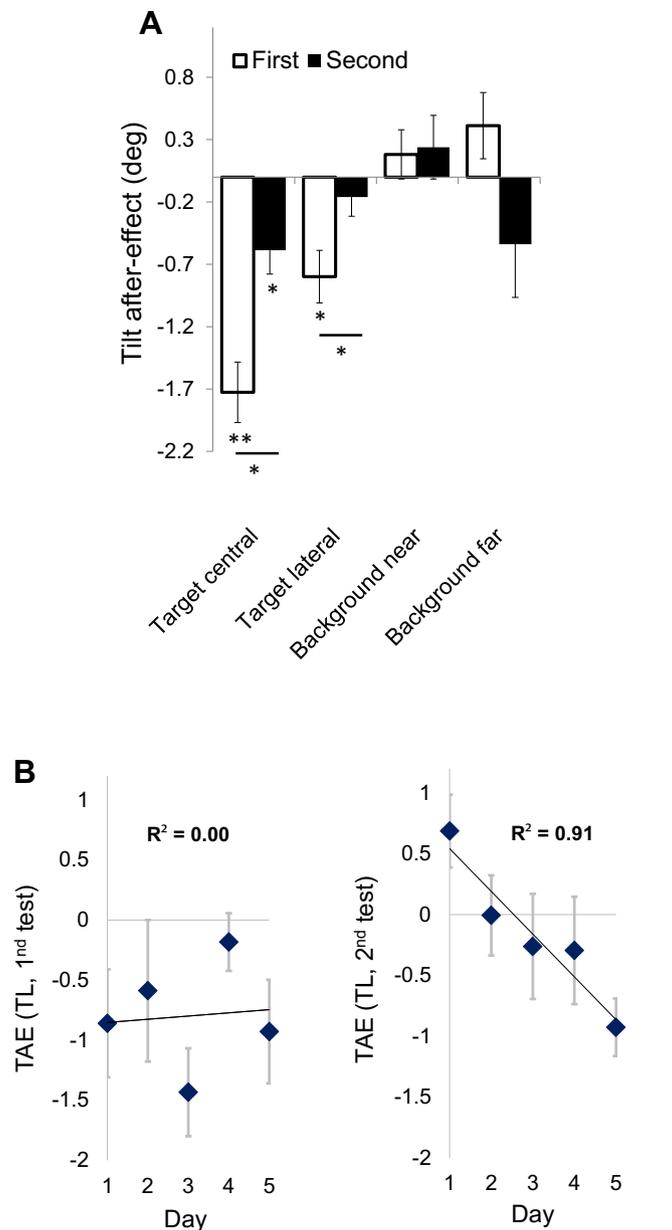


Fig. 3. Location-dependent TAE following the standard TDT training. (A) Each bar represents the TAE averaged across days and observers. The white bars represent the TAE during the 1st test block and the black bars represent the TAE during the 2nd test block. TAE was tested at four locations, corresponding to four texture locations: the target’s central element, the target’s lateral element, and two background locations, near and far from the target. (B) The TAE at the target’s lateral location across days during the first test (left) and the second test (right). Error bars represent SEM. * $p < 0.05$; ** $p < 0.01$.

($R^2 = 0.0$, $p = 0.9$), the 2nd test showed a significant trend ($R^2 = 0.9$, $p = 0.01$). The TAE in the 2nd test on day 1 was $0.7^\circ \pm 0.3$ ($t(5) = 2.3$, $p = 0.07$), whereas on day 5 the TAE was significantly repulsive ($-0.9^\circ \pm 0.2$, $t(5) = -3.9$, $p = 0.01$, Bonferroni corrected). Thus, the persistence of the TAE increases across days.

In order to test interactions between the different test times and different test locations, we performed a two-way repeated measure ANOVA. A significant interaction was found between the test time (first TAE test vs second TAE test in the target’s lateral location) and days ($F(4) = 2.9$, $p = 0.05$). Thus, the effect of days on the first test was significantly different from the effect of days on the second test. In addition a significant interaction was found between the location (target’s lateral location vs target’s central

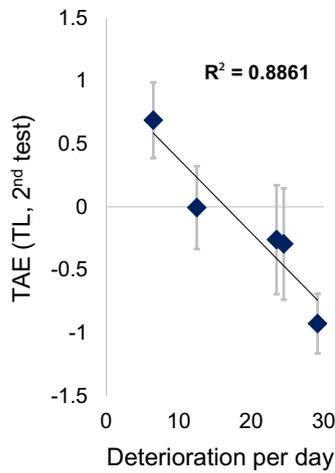


Fig. 4. Correlation between TAE in the 2nd test at the target’s lateral location and the daily TDT deterioration. Error bars represent SEM.

location) and days ($F(4) = 4.2, p = 0.01$). Thus, the effect of days on the lateral location was significantly different from the effect of days on the central location.

Next we tested whether the change we found in the TAE across days is related to the daily performance deterioration (Fig. 4). We found that indeed the TAE in the 2nd test at the target’s lateral location was significantly correlated with the daily TDT deterioration ($R^2 = 0.9, p = 0.02$).

3.2. ‘Balanced’ group

Here we tested the relationship between local stimulus statistics and task significance in producing TDT-dependent TAE. In the standard training, by design, different target locations (central and lateral) presented the texture target’s orientation with different probabilities. The target’s central location displays the target’s orientation in all the trials, whereas the target’s lateral location displays the target’s orientation in 50% of the trials, depending if vertical or horizontal target was presented (balanced statistics between the target and background orientations displays, no TAE is expected). We suspect that the effect of the biased statistics introduced during training at the target’s central location may

“propagate” to the target’s lateral location, resulting in the TAE shown in the lateral target’s location in the ‘standard’ group.

In order to determine whether the task’s significance or the stimulus statistics produced the TAE, a new group of observers underwent a ‘balanced’ training in which both target locations (the target’s central and the target’s lateral) presented the texture target’s orientation with equal probability. Therefore, here no TAE is expected, at all target locations, if the TAE depends only on low-level stimulus statistics.

3.2.1. TDT performance following intensive training

In the ‘balanced’ group there were two types of trials (‘TTT’ and ‘TBT’). A comparison of the thresholds for the different trial types showed that only on day 4 was there a significant difference between them (day1: paired t -test, $t(4) = -0.6, p = 0.6$; day2: $t(4) = -2.3, p = 0.08$; day3: $t(4) = -0.6, p = 0.6$; day4: $t(4) = -4.7, p = 0.01$; day5: $t(4) = -1.5, p = 0.2$). Since the thresholds were largely similar, only the ‘TTT’ trials’ thresholds were analyzed.

The results show a significant improvement in the average daily performance. The average daily threshold, estimated by averaging the thresholds of the four daily subsessions, improved from 202 ± 11 ms on day 1 to 147 ± 11 ms on day 5 (paired t -test, $t(4) = 7.6, p < 0.01$). Although numerically across-day improvements were obtained for the early sessions (Fig. 5, from 189 ± 12 ms to 148 ± 14 ms), the learning was not significant ($t(4) = 2.4, p = 0.8$). However, the late sessions showed significant improvements from 216 ± 11 ms to 137 ± 15 ms ($t(4) = 6.3, p < 0.01$). Within session deterioration is evident in the first four days ranging between 5 and 30 ms (day1: 27 ± 17 ; day2: 6 ± 16 ; day3: 30 ± 9 ; day4: 27 ± 5 ; day5: 29 ± 5). On the fifth day there was no deterioration (-10 ± 9).

In comparing the standard training (Fig. 2) and the balanced training, the balanced training resulted in higher thresholds (worse performance) relative to the standard training, particularly on day 1 in which the average threshold for the ‘standard’ group was significantly lower than the threshold for the ‘balanced’ group (‘standard’: 169 ± 7 ms, ‘balanced’: 202 ± 12 ms, $t(9) = -2.5, p = 0.03$). The worse performance suggests that the balanced task was more difficult than the standard task due to the replacement of the central bar’s orientation in 50% of the trials. From an ideal observer’s perspective (utilizing the full available information presented in the stimuli for resolving the task), the central bar’s orientation does not carry any added information about resolving the fixed-location

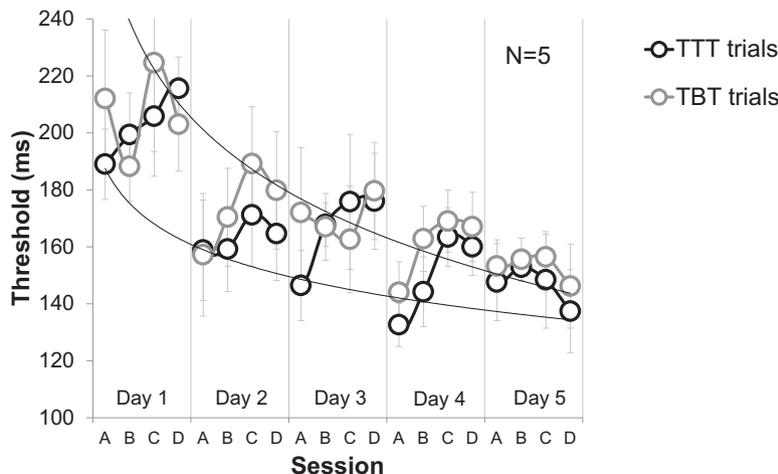


Fig. 5. Performance of the ‘balanced’ group ($n = 5$). A. TDT learning curves (format the same as in Fig. 2). In the ‘TTT’ trials, all target bars had the same oblique orientation, whereas in the ‘TBT’ trials the central target bar had a background orientation. These two types of trials were randomly intermixed. The black line represents the logarithmic fit to the ‘TTT’ trials.

texture discrimination task and therefore, the balanced stimulation should not affect the performance. However, the reduced performance in the ‘balanced’ group indicates the importance of the central bar’s orientation. Its orientation should be consistent with the orientation of the two target lateral bars so that the texture task will be performed better.

3.2.2. Target-selective TAE following TDT training

In the ‘balanced’ group there was a repulsive TAE (relative to the target’s orientation) immediately following TDT training (Fig. 6A, first test, white bars) only at the central location (TC: $-0.8^\circ \pm 0.1$, $t(4) = -2.8$, $p = 0.05$). In all other tested locations the TAE was not significant (TL: $-0.6^\circ \pm 0.2$, $t(4) = -2.5$, $p = 0.07$, BN: $-0.2^\circ \pm 0.2$, $t(4) = -0.4$, $p = 0.7$, BF: $-0.7^\circ \pm 0.4$, $t(4) = 2.4$, $p = 0.07$).

Notably, the TAE at the target’s lateral location was numerically similar to the TAE at the central location but was marginally insignificant. In the second test there was no significant TAE in any of the locations. Similar to the ‘standard’ group, in the ‘balanced’ group, both target locations showed a significant reduction

in TAE in the second test relative to the initial test (black bars, TC: $t(4) = -3.5$, $p = 0.02$, TL: $t(4) = -4.9$, $p = 0.008$). Examination of the TAE in the ‘balanced’ group over days (as shown in Fig. 6B) did not show changes following learning (first test: $R^2 = 0.2$, $p = 0.5$, second test: $R^2 = 0.1$, $p = 0.6$).

The repulsive TAE found in the target’s central location in the ‘balanced’ group is similar in size and direction to the TAE found in the target’s lateral location in the ‘standard’ group. Overall, the findings showed TAE that is in accordance with adaptation to the target’s orientation, despite the balanced stimulus statistics, suggesting that the TAEs received in both groups are a result of task significance.

4. Discussion

Here we showed that texture training induces a localized target-selective TAE, which also has a training-dependent component. The absence of a TAE at background locations, and the target biased TAE at the balanced location (repulsive relative to the targets’ orientation) indicate that aftereffects are not determined exclusively by stimulus statistics, but rather by experience-dependent task relevance. This supports interactions between sensory adaptation and perceptual learning. In addition, we observed increased persistence of the TAE following TDT learning across days.

Perceptual learning and sensory adaptation are two forms of plasticity in the visual system. Traditionally, perceptual learning is obtained following training with rapid, discrete visual presentation, whereas sensory adaptation takes place during extended exposure to a constant stimulus parameter (but see also Glasser, Tsui, Pack, & Tadin, 2011). However, it is not clear to what extent sensory adaptation aftereffects are induced during perceptual training. We found that TDT training, consisting of a series of rapid, discrete visual presentations (40 ms) of texture bars, induced significant tilt-aftereffects (TAE). These TAEs were obtained despite the fact that each target presentation was followed by a mask (100 ms) composed of randomly orientated V-shaped bars. Furthermore, as implicated by the present results and discussed below, the processes leading to the TAE are enhanced by the task’s relevance.

A significant finding here was that the training-induced TAE was generated only by the target’s texture. Both groups showed significant TAE only at the target locations and not at the background locations. Even at the background’s near location, which is adjacent to the target’s elements, no significant TAE was found. In addition, when long-term effects were noted (Fig. 3B), they were evident only at the target’s location and not at the background’s location. Most interestingly, we found target-biased TAE (repulsive relative to the target’s orientation) in neutral (balanced) locations that were equally stimulated by the target and background orientations. This finding reveals that TAE is not determined only by the local stimulus statistics (Wark, Lundstrom, & Fairhall, 2007)—it is also modulated by the task. This modulation may be implemented by enhanced target representation over the background representation, which results in effects that are repulsive relative to the target. One task-related component that may have contributed to the selective aftereffect is attention. It was shown that feature-based attention can selectively enhance TAE to one orientation in a plaid (Liu, Larsson, & Carrasco, 2007). In addition, it has been shown that spatial attention increases the duration of motion after-effect across a range of stimulus contrasts (Rezec, Kregelberg, & Dobkins, 2004). Taken together, it is possible that the training dependent increase in TAE duration we find in target-lateral location (see below) is a result of improved feature based attention with training.

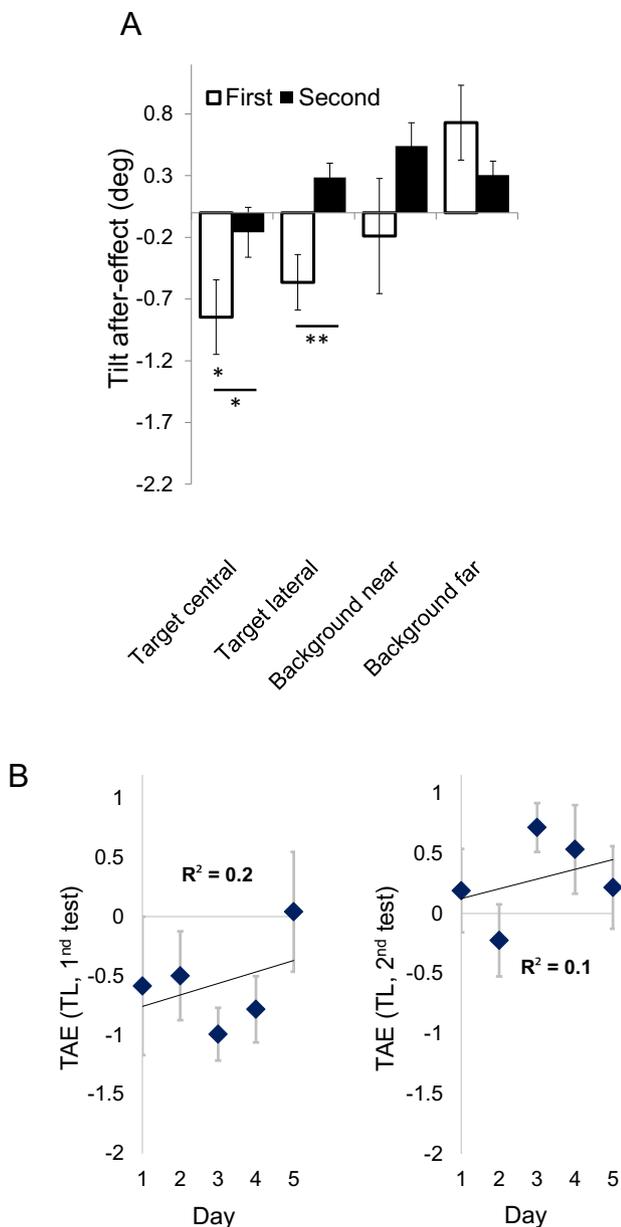


Fig. 6. Task-selective TAE following TDT training (format the same as in Fig. 3).

The finding of target-selective TAE can be used to shed light on what is actually being learned during TDT training. Currently, it is not fully known. Specifically, it is not known whether the representations of the target, background, or both are modified during learning. Previous work suggested that the improved performance is attributed to increased iso-orientation suppression between the neurons responding to the background bars (Karni & Sagi, 1991; Sagi, 1995; Zhaoping, 2009). This was motivated by a theory of texture segmentation (Sagi, 1995) and findings showing that learning was more specific for the background orientation than for the target orientation (Karni & Sagi, 1991, 1993). Recent findings (Harris & Sagi, 2015; Harris et al., 2012) further suggest that the target's orientation is also crucial for TDT. By adding dummy trials, whose effectiveness depends on their local orientation relative to the target, enhanced performance was obtained. Here our finding of target-selective TAE supports the key role of the target's representation.

Our results show that training the TDT induces a change in TAE across days (Fig. 3B). The TAE at the lateral target's location of the 'standard' group persisted longer following learning. On day 1 the repulsive TAE disappeared quickly and even reversed its direction in the second test (to be attractive, but this was insignificant). However, an across-days dependency was revealed; thus, following learning, the effect on day 5 persisted much longer, and was still high and significant in the second test. It is possible that with training, the selection of task-related features is made more efficient, possibly because the target's orientation is selected earlier over the background's orientation. The earlier selection onset may induce earlier adaptation onset and thus could explain the increase in the TAE persistence. It was previously shown that after-effects last longer for longer adaptation times (Greenlee, Georgeson, Magnussen, & Harris, 1991; Magnussen & Johnsen, 1986). Indeed, we found that the increased TAE over days was significantly correlated with the increased deterioration with more training days (Fig. 4). It also appears that with training, the deterioration starts earlier. Training in the 'balanced' group, on the other hand, did not result in extended persistence of the TAE (Fig. 3). This may occur because none of the target locations was consistently stimulated by the target's orientation, so the overall adaptation to the target's orientation was reduced in this group. Indeed, we observed reduced deterioration in this group following learning (Fig. 5).

This result offers some insights regarding the mechanism that is modified during perceptual learning. Perceptual learning is usually attributed to one of several hypotheses: low-level representation modification (Bao, Yang, Rios, He, & Engel, 2010; Pourtois et al., 2008; Schoups et al., 1995), readout modification (Law & Gold, 2008), or reweighting (Petrov, Doshier, & Lu, 2005). The change in the TAE persistence suggests that the representation of the target during TDT performance was enhanced following learning. Since the readout is typically task-restricted, it is reasonable to assume that different readouts correspond to the two different tasks: TDT and TAE. Each of these readouts uses the lower-level inputs/representations (with or without adjusting the weights). In our experiments, the lower-level representation was common for both tasks. Therefore, any interaction across these tasks may be attributed to differences in representations or differences in the corresponding weights during training (the top down connection). This challenges the notion of the readout as the sole learning unit, because the change in the readout should not have affected the target's orientation representation.

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