



## Target-selective tilt aftereffect during texture learning



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### ARTICLE INFO

#### Article history:

Received 17 February 2016

Received in revised form 12 May 2016

Accepted 7 June 2016

Available online 6 July 2016

#### Keywords:

Perceptual learning

Sensory adaptation

Tilt aftereffect (TAE)

Texture-discrimination

### 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  $-22.5^\circ$  (target) and  $22.5^\circ$  (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 ( $0^\circ$ ) 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/m<sup>2</sup> 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)

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