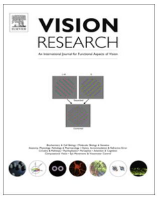
Vision Research 105 (2014) 166–176

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres



Brain mechanisms underlying behavioral specificity and generalization of short-term texture discrimination learning

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ARTICLE INFO

Article history:
Received 3 November 2013
Received in revised form 14 October 2014
Available online 27 October 2014

Keywords:
Perceptual learning
Event-related potential (ERP)
Specificity
Generalization
Compensation
Attention

ABSTRACT

In this study, we used high-density event-related potentials (ERPs) to investigate the brain mechanisms underlying behavioral specificity and generalization of short-term learning of texture discrimination task (TDT). Human adults were trained with TDT for a single session of 1.5 h and their ERPs were measured on the following day. Behavioral performance showed that, after a same amount of exposure of the trained and untrained conditions during EEG session, learning effects were specific to the trained background orientation but generalized across target locations. ERP data, however, revealed both target-location and background-orientation specific changes. While the behavioral background-orientation specificity mainly involved amplitude enhancement of early N2pc over occipital cortex, behavioral target-location generalization was associated with modulation of tempo-spatial configurations of the N2pc component (early-occipital vs. late-parietal/temporal pattern) and decrease of frontal P2 amplitudes for the trained relative to the untrained condition. The earliest visual component C1 did not show specific effects for either background orientation or target location. These results indicated different brain mechanisms underlying the behavioral specificity and generalization of TDT learning. Based on the present findings and literatures, we propose that perceptual learning may induce not only enhancement of relatively early visual selection of the trained target among distractors but also decreases of top-down attention originating from high-level brain center. The reactivation of top-down attention control in some conditions (e.g., the untrained target-location condition) may compensate for the specific effect induced by the early visual selective attention mechanism, leading to generalization or less specificity of perceptual learning in behavioral performance.

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1. Introduction

Perceptual learning (PL) refers to relatively permanent and consistent changes in the perception of a stimulus array following practice or experience with this array. Specificity and generalization of visual PL and their brain mechanisms are hot debated issues during recent years. Many behavioral studies reported that PL is specific to simple stimulus attributes, such as stimulus location and orientation (e.g., Ball & Sekuler, 1982; Crist et al., 1997; Fiorentini & Berardi, 1980; Karni & Sagi, 1991; Poggio, Fahle, & Edelman, 1992; Schoups, Vogels, & Orban, 1995; for reviews see Fahle, 2005; Gilbert, Sigman, & Crist, 2001). In many PL models, the stimulus-specificity of PL is attributed to the primary visual cortex (i.e., area V1) where neurons are highly selective for stimulus location and orientation (e.g., Adini, Sagi, & Tsodyks, 2002; Teich & Qian, 2010; Zhaoping, Herzog, & Dayan, 2003). However, some studies found such behavioral stimulus specificity can be eliminated under certain conditions, showing strong transfer of PL effects (Aberg, Tartaglia, & Herzog, 2009; Ahissar & Hochstein, 1997; Harris, Gliksberg, & Sagi, 2012; Hussain, Bennett, & Sekuler, 2012; Liu & Weinshall, 2000; Tartaglia et al., 2009; Xiao et al., 2008). Moreover, some behavioral studies showed task-specificity of PL in which the PL effect cannot transfer from the trained task to another task involving the same or similar stimuli (Ahissar & Hochstein, 1993; Huang et al., 2007; Shiu & Pashler, 1992), though others found successful transfer of learning across tasks (Chung, Legge, & Cheung, 2004; Green & Bavelier, 2003; Leonards et al., 2002; Nazir et al., 2004; Yu, Klein, & Levi, 2004). Based on the stimulus-generalization and/or task-specificity effects in behavioral performance, some PL models proposed that high-level brain areas related with attentional control or decision making

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http://dx.doi.org/10.1016/j.visres.2014.10.017
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play an important role in PL (e.g., Ahissar & Hochstein, 2004; Dosher & Lu, 1998; Zhang et al., 2010). It is even proposed that the higher central mechanism, rather than the early visual processing itself, may account for the stimulus-specificity of PL (Mollon & Danilova, 1996; Petrov, Dosher, & Lu, 2005). In addition, some behavioral studies found that visual PL depends on perceptual constancy (Garrigan & Kellman, 2008) and is diagonal mirror-transferable (Chen et al., 2008). Accordingly, it was also proposed that visual PL occurs at the middle visual stages, such as the extrastriate cortex including V2–V4, where neurons are characterized by both orientation/location selectivity and more complex properties (Chen et al., 2008), and involves feature-based selective attention (Su et al., 2014).

Several brain imaging studies have directly investigated the brain mechanisms of specificity and generalization of human visual PL (e.g., Ding et al., 2003; Schiltz et al., 1999; Song et al., 2007). Specifically, although some behavioral studies showed both target-location and background-orientation specificities in the learning of a texture discrimination task (TDT, e.g., Karni & Sagi, 1991), only the brain mechanism of target-location specificity has been investigated by brain imaging methods, such as functional magnetic resonance imaging (fMRI) and event-related potential (ERP) techniques (Pourtois et al., 2008; Yotsumoto, Watanabe, & Sasaki, 2008). These fMRI and ERP studies mainly concerned the learning-associated changes of activities in the primary visual cortex (area V1). It is not clear yet whether higher brain activities are also important for the target-location specificity of TDT learning. In addition, some recent behavioral studies showed that TDT learning sometimes could completely transfer to a new target-location condition (e.g., Harris, Gliksberg, & Sagi, 2012). However, the brain mechanism underlying the behavioral generalization across target locations have not been investigated yet. Moreover, background orientation is a feature very different from target location. Whether background-orientation specificity and target-location specificity share similar brain mechanisms or not is still an open question.

By recording ERPs from healthy human adults after a single training session of 1.5 h, this study aimed to investigate the brain mechanisms associated with behavioral specificity and/or generalization of target-location and background-orientation in short-term TDT learning. We focused on three ERP components: C1, N2pc and frontal/anterior P2. C1 is the earliest visual evoked component with its peak normally observed in the 60–100 ms range post-stimulus onset and is deemed to represent the initial visual cortical processing in area V1 (Di Russo, Martínez, & Hillyard, 2003; Ding et al., 2014; Jeffreys & Axford, 1972). N2pc is a negative deflection usually observed at the posterior scalp sites contra-lateral to the attended location during 180–300 ms after stimulus onset. It is closely related to attentional selection of a potential target in a visual search array and is considered to be generated in the extrastriate visual areas including occipital, temporal and parietal cortex (Eimer, 1996; Hopf et al., 2000, 2006; Luck, 2011; Luck & Hillyard, 1994). The frontal or anterior P2 component, with peak latencies typically during 150–280 ms and scalp distribution over frontal scalp sites, is thought to involve activations in the frontal cortex and to be related with the goal-directed attentional control (Potts, 2004; Potts & Tucker, 2001). These three components therefore can be used as indices to investigate the contributions of different levels of mental and cortical processing in PL. These components have been respectively reported to be associated with PL in different studies using various tasks and paradigms (C1: Bao et al., 2010; Pourtois et al., 2008; N2pc: An et al., 2012; Hamamé et al., 2011; anterior P2: Qu, Song, & Ding, 2010; Wang et al., 2010). The present study investigated all these three components in a short-term TDT learning paradigm with high-density ERPs, which offer high temporal resolution with reasonable spatial resolution and may provide indices for differentiating the neural substrates underlying specificity and generalization of visual PL.

2. Methods

2.1. Subjects

Twenty-four healthy young adults (6 males, ages 18–31 years) participated in this study as volunteers. Half of the subjects (Background-Orientation Specificity Group; BOS Group) were tested with the trained and the untrained background orientation, and the other half (Target-Location Specificity Group; TLS Group) were tested with the trained and untrained target location. All subjects were right-handed, with normal or corrected-to-normal vision. All were compensated for their participation, either with payment or with credit hours fulfilling a course requirement. The research was conducted in accord with the Code of Ethics of the World Medical Association (Declaration of Helsinki) and informed consent was obtained from each subject before the beginning of experiment.

2.2. Stimuli and tasks

We used the same task and similar stimulus parameters as described in a previous study (Pourtois et al., 2008). A small target texture (three 45°-clockwise bars, forming either a horizontal or a vertical orientation) embedded within a background of horizontal (or vertical) bars (see Fig. 1A). The display ($21^\circ \times 41^\circ$) was composed of white line segments ($1.0^\circ \times 0.16^\circ$, spaced 1.64° apart) slightly “jittered” (0–0.14°) on a black background within a 13×25 lattice. A randomly rotated ‘L’ or ‘T’ was presented at the center of the bottom edge of the display in order to impose fixation. Target location was varied randomly from trial to trial but always within a specific quadrant and within 13–19° visual angle from fixation. The mask display was made of randomly oriented V-shaped micropatterns and a central letter ‘F’.

At the beginning of each trial, a small central cross was presented for 600 ms to help with the fixation. After a blank interval (400 ms), the stimulus was briefly flashed (17 ms), followed by a blank interval (stimulus-to-mask onset asynchrony, SOA), a mask (100 ms), and a blank screen until response. On each trial, subjects first reported the central letter at fixation (‘T’ or ‘L’) and then judged the orientation of the target texture (horizontal or vertical), using four predefined keys (two for each task). The next trial was initiated by the response to the target texture of the current trial.

2.3. Procedure

A behavioral training session was given on the first day (see Fig. 1B). The training session contained 20 blocks of 64 trials, with decreasing SOA from 477 to 117 ms to establish learning. For the first five blocks, SOAs were 477, 377, 277, 237 and 217 ms respectively. For the next fifteen blocks, five SOAs (197, 177, 157, 137 and 117 ms) were used, each for three consecutive blocks. For the BOS Group, the target texture of the trained stimuli was always presented in the upper-right quadrant; and the background bars were always in the same orientation during training (either horizontal or vertical, counterbalanced across subjects). For the TLS Group, the background bars of the trained stimuli were always horizontally oriented, and the target texture was always presented in the same quadrant during training (either in upper-left or upper-right quadrant, counterbalanced across subjects). The training session lasted for about 1.5 h.

During the ERP recording session on the following test day, SOA was constant at 517 ms to avoid any contamination of early ERPs evoked by the mask. For the BOS Group, the location of target

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