Vision Research 93 (2013) 1–9

Contents lists available at ScienceDirect

Vision Research

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

Comparison of perceptual learning of real and virtual line orientations: An event-related potential study

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ARTICLE INFO

Article history:
Received 22 March 2013
Received in revised form 9 July 2013
Available online 15 October 2013

Keywords:
Event-related potentials
Orientation discrimination
Perceptual learning
Virtual line

ABSTRACT

When investigating perceptual learning (PL), most researchers use real figures as stimuli, but PL can occur when subjects are trained with virtual stimuli or even without any visual stimuli at all. Here, we first demonstrated that virtual lines have the same perceptual attributes as real lines by confirming that there is also an oblique effect in virtual lines (formed by a pair of circles) in an orientation discrimination task. Then, our ERP study showed that orientation discrimination learning and its transfer across real and virtual lines were associated with more negative parietal–occipital P1–N1 (reduced P1 and enhanced N1), which indicated the involvement of high-level stages of visual information processing or the involvement of top-down influences. At the same time, the specific ERP changes in the frontal ERP components were differently associated with real versus virtual line orientation learning. That is, real line learning was characterized by an early and short-lasting frontal N1 (120–140 ms) reduction, in contrast to a much later, widespread, and long-lasting P150–300 decrease in virtual line learning. These results contribute to the understanding of the neural basis of perceptual learning and the distinction between real and virtual stimulus learning.

1. Introduction

Perceptual learning (PL) refers to the relatively permanent modification of perception and behavior following a sensory experience. The orientation discrimination task is one of the most intensively studied PL tasks. In this task, subjects need to decide whether a grating or a line is tilted clockwise or anticlockwise with respect to the reference. Performance on this task dramatically improves with practice; moreover, this learning effect is specific to the position and orientation of the stimuli (Schoups, Vogels, & Orban, 1995). In typical PL models, this specificity is interpreted as an indicator of the retinotopic early visual cortical locus of learning, where different orientations are processed separately (Adini, Sagi, & Tsodyks, 2002; Freeman et al., 2003; Teich & Qian, 2003). Indeed, significant modulation of learning on V1/V2 activity have been found in single-unit recording studies of animals and functional magnetic resonance imaging (fMRI) studies in humans (Schoups et al., 2001; Yotsumoto, Watanabe, & Sasaki, 2008). However, recent studies have found that this specificity can be abolished in some situations (Aberg, Tartaglia, & Herzog, 2009; Harris, Gliksberg, & Sagi, 2012; Jeter et al., 2010; Wang et al., 2012; Xiao et al., 2008; Zhang et al., 2010). At the same time, neuroimaging studies suggest that perceptual improvements could be associated with changes in higher visual areas (Yang & Maunsell, 2004), even outside the visual cortices (Bartolucci & Smith, 2011; Kahnt et al., 2011; Lewis et al., 2009).

When investigating PL, most researchers have used real figures as stimuli, with the explicit or implicit assumption that PL is driven by real stimuli. However, visual PL can occur when subjects are trained with virtual stimuli or even without any visual stimuli at all (Shibata et al., 2011). For example, perceptual learning improved bisection discrimination when only the two outer lines of the bisection stimulus were presented, and the central line had to be imagined (Tartaglia et al., 2009). Similarly, significant learning was evident after training of an illusory line orientation discrimination task (Zhang et al., 2008). These data demonstrate the generality of perceptual learning with multiple stimuli. In addition, psychophysical observations have shown a prominent oblique effect in the orientation discrimination of virtual lines formed by a pair of blobs (Heeley & Buchanan-Smith, 1996) or dots (Westheimer, 2001) that would elicit little or no response in the oriented neurons in the visual cortex, suggesting that the perception of real and virtual line orientations might share common neural substrates at sites more central than the primary visual cortex.

Therefore, it is of interest to compare visual PL on a range of visual stimuli and to examine conclusions about the stage of visual processing at which real and virtual stimuli learning share

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http://dx.doi.org/10.1016/j.visres.2013.10.004

overlapping or distinct neural substrates. In this study, we first replicated the oblique effect with real and virtual lines in a foveal orientation discrimination task. Then, two groups of participants were trained by the same line orientation discrimination task with real or virtual lines. Except for the stimuli, all experimental paradigms for these two groups were the same. We monitored the two groups' orientation discrimination threshold changes during training and measured their EEGs before, during, and after training. Our aim was to determine which type of learning effects in the brain, i.e., early or late cortical processing changes, could transfer between real and virtual line learning. High-density event-related potentials (ERPs), which offer high temporal resolution with reasonable spatial resolution, may provide indexes for differentiating the common and specific neural substrates of visual PL.

2. Experiment 1: oblique effects of real and virtual lines

There is a strong consensus that orientation discrimination thresholds are higher in oblique orientations than in the horizontal or vertical. This orientation anisotropy, known as the oblique effect, is manifested in a wide variety of perceptual tasks (Davey & Zanker, 1998; Westheimer, 2003). In Experiment 1, we investigated whether virtual lines have similar oblique effects as real lines. The oblique effect index (OEI) is defined here as the ratio of the threshold in the oblique orientation (~36°) to that in the horizontal orientation (~0°). OEI > 1 indicates a higher threshold for the oblique orientation.

2.1. Materials and methods

2.1.1. Subjects

Eleven right-handed observers (five males and six females, undergraduate and graduate students, aged 20–28 years) with normal or corrected-to-normal vision participated in this study as paid volunteers. All were new to psychophysical experiments and were unaware of the purpose of the study. This research was approved by the Beijing Normal University Institutional Review Board, and informed consent was obtained from all subjects.

2.1.2. Stimuli and apparatus

Two types of lines (real and virtual lines, Fig. 1A) were used in the experiment. All the stimuli were white (full luminance) on a uniform black background and were presented in the center of the screen. The real line was a single straight white line (2 pixels, 0.8 arcmin wide; 750 pixels, subtending 5°). There was no explicit line for the virtual line whose orientation was demarcated by a pair of circles at each end (3 arcmin outer diameters and 2 arcmin inner diameters each; the distance between the two circles was 750 pixels, subtending 5°).

All the stimuli were generated by a MATLAB program and presented on a 21-in. CRT gamma-linearized color monitor (1600 × 1200 pixels; 0.25 × 0.25 mm per pixel; 75 Hz frame rate). To prevent subjects from using external references, such as monitor edges, to determine the orientations of the stimuli, the stimuli were viewed at a distance of 85 cm through a circular opening (29 cm diameter) of a black piece of cardboard that covered the entire monitor screen. All experiments were conducted in a dimly lit room. Viewing was binocular.

2.1.3. Trial sequence and procedure

We measured the orientation discrimination thresholds for each of two orientations (~0° or ~36°) for both real and virtual lines by using a standard two-alternative forced choice (2-AFC). Each trial began with the presentation of a central green fixation dot (400 ms), followed by a blank interval (300 ms), then the reference and test lines (both were real lines or virtual lines) were separately presented for 200 ms with an inter-stimulus interval of 600 ms. Subjects were asked to judge whether the test line, compared to the reference line (~0° or ~36°), had a more clockwise or anti-clockwise orientation by pressing one of the two buttons with their right hand. Auditory feedback was given for incorrect responses. The orientation of the reference line was varied slightly on every trial (randomized at 0 ± 5° or 36 ± 5°) to ensure that the stimulus presented during each interval were actively compared to each other, rather than to remembered information about the average reference orientation. An additional position jitter was added separately to both the reference and test lines on each trial (vertically and horizontally randomized in the center of the screen by −0.75° to 0.75°) to prevent the subjects from using the relative positions of dots or line terminals/endpoints to perform the task.

The staircase followed a 3-down–1-up rule, which resulted in a 79.4% convergence rate. The step size of the staircase was 0.05 log units. Each staircase (approximately 60 trials) consisted of 4 preliminary reversals and 6 experimental reversals. The geometric mean of the experimental reversals was taken as the threshold for each staircase. There were 5 staircases for each orientation. The reference orientation (~0° or ~36°) and line type (real or virtual) was presented in a counterbalanced order between subjects. At the beginning of the experiment, the subjects practiced the operation for several trials of each condition to ensure that they understood how to perform the task.

2.2. Results

The mean orientation discrimination thresholds of the real lines were 1.59 ± 0.09 (mean ± standard error) for 0° and 2.71 ± 0.22 for 36°. For the virtual lines, the mean thresholds were 2.46 ± 0.25 for 0° and 3.70 ± 0.32 for 36° (Fig. 1B). The statistical results suggest that there is an oblique effect in virtual lines, and it is as prominent as that of real lines (2 × 2 ANOVA, main effect of stimulus type (real or virtual): $F(1,10) = 14.262$, $p < 0.005$; main effect of orientation (~0° and ~36°): $F(1,10) = 31.456$, $p < 0.001$; stimuli type × orientation: $F(1,10) = 0.130$, $p = 0.726$). This suggestion was confirmed by the insignificant difference [$t(10) = -0.611$, $p = 0.555$] between the mean OEIs of the real lines (36°/0° threshold ratio = 1.74 ± 0.15) and virtual lines (1.61 ± 0.17).

2.3. Discussion

There was, notably, a prominent oblique effect for both real and virtual lines. These results should be interpreted in association with earlier ones demonstrating a powerful oblique effect for the orientation of more complex configurations (Li & Westheimer, 1997; Westheimer, 2001, 2003). In addition, this experiment confirmed that virtual lines have the same perceptual attributes as real lines and excluded the possibility that the subjects performed the task by comparing the relative positions of two circles or line terminals because position discrimination exhibited no oblique effect (Westheimer, 2001).

3. Experiment 2

In Experiment 2, we used ERPs to compare the neural substrates underlying PL in real lines with those underlying PL in virtual lines. Because PL could not change the thresholds in vertical or horizontal orientations, even after 5000 practice trials (Vogels & Orban, 1985), only the oblique orientation (~36°) was used for training in this experiment.