

**NEURAL CORRELATES OF VISUAL PERCEPTUAL LEARNING IN HUMANS INDEXED
BY EVENT-RELATED POTENTIALS**

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SUMMARY

The current work investigated the neural correlates of visual perceptual learning by recording event-related potentials (ERPs) from human adults. Subjects were trained with a discrimination task of arrow orientation in three consecutive training sessions within 2 hours. While reaction times (RTs) were shortened gradually across training sessions, the amplitudes of negativities between 125-155 ms (N1) and between 290-340 ms (N2) decreased mainly over the central and parietal areas respectively. However, a broadly distributed P3 component increased along with more practice. In addition, the decrease in N1 and increase in P3 preceded the decrease in N2. The implications of these results to the neural mechanisms subserving perceptual learning are discussed.

Key words: Event-related potentials; perceptual learning; human adults; complex visual shapes; orientation

INTRODUCTION

Psychological studies of human adults have found the improvement of perceptual performance as a function of training - perceptual learning - in various visual tasks (1). For example, sensitivity of detecting a bar of specific orientation was improved by orientation-discrimination training in several days (2). The study of visual conjunction search showed that serial tasks became parallel and

reaction times decreased after a few hundred trials (3).

Neuroscience studies to explore the neural mechanisms of perceptual learning are being developed through techniques of neuroimaging, neuronal discharge, and event-related potential (ERP). Some neural localization studies of visual perceptual learning focused on striate and extrastriate cortex (4, 5). There has been no consistent conclusion yet, whether perceptual learning results in increased or decreased neural activities. As known, ERP can be recorded non-invasively with high temporal resolution (in order of milliseconds) while human subjects perform perceptual tasks, and ERP recording is a very useful method for exploring the neural correlates of perceptual learning in humans. However, so far, there are only a few ERP studies on visual perceptual learning in humans such as those by Skrandies et al. (6, 7) and Doniger et al. (8, 9). They reported larger amplitudes of negativities induced by visual perceptual learning.

The present study investigated the underlying ERP correlates of perceptual learning in a visual discrimination task using complex shapes. Based on previous research, in the present study we analyzed and discussed training-related changes of ERP amplitudes, including their scalp distribution and time course, to address neural mechanisms of visual perceptual learning.

MATERIALS AND METHODS

Twelve naive right-handed subjects (aged 18-25, six male) participated in the experiment as paid volunteers. All subjects had normal or corrected-to-normal vision. White stimuli on a black background were presented on a computer-controlled video monitor placed 70 cm from subject's eyes. A green fixation cross of $0.3^\circ \times 0.3^\circ$ was continuously visible in the center of monitor. Each stimulus consisted of four arrows that were located in four quadrants and equally distant from the fixation. The whole stimulus and each arrow subtended a visual angle of $10.9^\circ \times 10.9^\circ$ and $2.5^\circ \times 2.5^\circ$, respectively. The stimulus with identical arrow orientations was referred as a target (Fig. 1a) and those with an arrow of different orientation were referred as non-targets (Fig. 1b-e). The five types of stimuli were presented in a pseudo-random order with equal probability (20% each). Stimulus duration was 200 ms and interstimulus interval (ISI) was randomized between 1600 and 2000 ms. Subjects were instructed to both accurately and speedily detect the present of target by pressing a button with the right thumb. Each subject was trained with three sessions. Each session contained nine 40-trial blocks. Before the experiment, the subjects practiced the operation for one or two blocks to reduce the effect of task familiarization. The electroencephalogram (EEG) was recorded from electrodes at F3, F4, T3, T4, C3, C4, P3, P4, O1 and O2 according to the International 10–20 System, and the right mastoid. The physical

reference located at the left mastoid. Electro-oculogram (EOG) of two channels (Horizontal and vertical) was also recorded. Electrode impedance was kept below 5 k Ω . EEG was amplified with a band pass of 0.1 to 40 Hz, digitized on-line at a sampling rate of 250 Hz and a resolution of 16-bit. The ERPs to all non-target stimuli in each session were averaged off-line and re-referenced to the algebraic mean of the left and right mastoids. Trials contaminated by eye blinks, muscle potentials and other artifacts at any electrode, and trials with incorrect responses were excluded from averaging. The baseline for amplitude measurement was defined as the mean voltage of 200-ms pre-stimulus period. Reaction times (for target) and ERP mean amplitudes (for non-targets) were analyzed with repeated measure analysis of variances (ANOVAs). Bonferroni correction was used in the analysis.

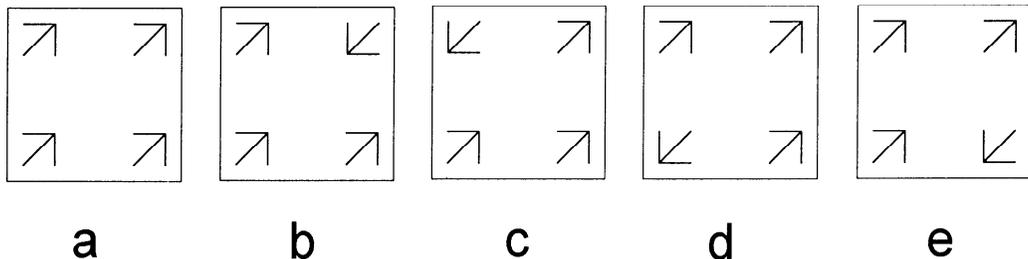


Figure 1. The target stimuli with a press response (a) and four types of non-target stimuli without explicit response (b-e) used in equi-probability.

RESULTS

The reaction times (RTs) were analyzed with ANOVAs with factor being training (session 1, 2 or 3). The results showed that the RTs decreased as a function of training factor (598 ms, 554 ms, 494 ms in session 1, 2 and 3 respectively, $F(2, 22) = 20.624$, $P < 0.001$). Further pairwise comparisons confirmed that the RTs decreased gradually across the three training sessions (session 1 vs. session 2, session 2 vs. session 3: both $P_s < 0.007$; session 1 vs. session 3: $P_s < 0.005$). Response accuracy (averaged 98.5% for targets and 99.5% for non-targets) was high and stable throughout training sessions.

ERPs for the three sessions were all characterized by P1, N1 and N2 with maximum over the posterior area, P2 with maximum over the frontal-central area, and a broadly distributed P3 (Fig. 2). Peak latencies were similar for the three sessions. However, the amplitudes of the N1, N2 and P3 showed difference among sessions. To get steady data, the amplitudes of N1, N2 and P3 were measured as the mean voltages within the intervals 125-155, 290-340 and 380-500 ms respectively

(Table 1) based on the grand average ERPs. Mean amplitudes over the temporal, central, parietal and occipital areas for N1, and over the frontal, temporal, central, parietal and occipital areas for N2 and P3 were subjected to ANOVAs with factors being training, area and hemisphere (left or right).

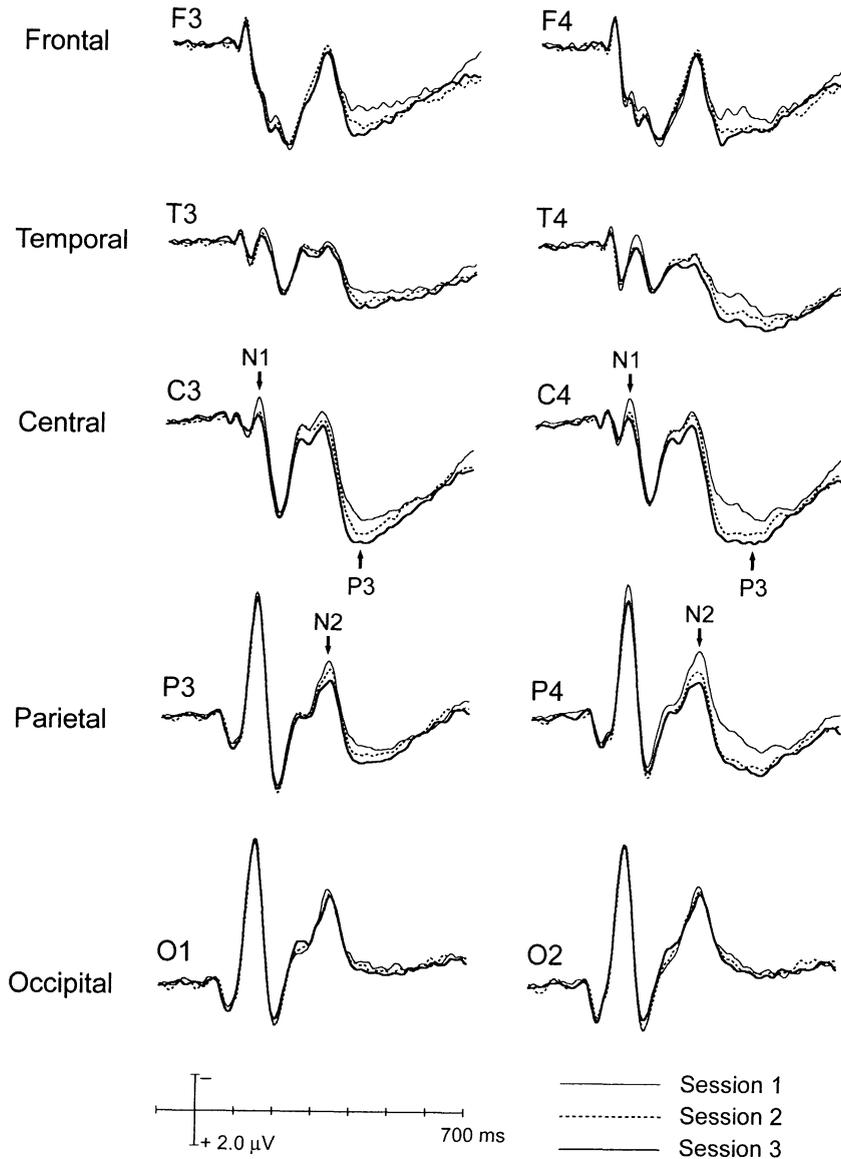


Figure 2. Grand averaged ERPs (12 subjects) to non-target stimuli during the three training sessions. Note that the thin continuous, dotted, and thick continuous waveform referred to session 1, 2, and 3 respectively. Across the three training sessions, the N1 and N2 decreased whereas the P3 increased.

Table 1. The mean amplitudes (mean \pm S.E. μ V) of ERPs in three time windows for each training session.

Time window	Electrode	Session 1	Session 2	Session 3
N1 (125-155ms)	T3	-0.62 \pm 0.82	-0.25 \pm 0.88	-0.22 \pm 0.79
	T4	-0.24 \pm 0.75	0.25 \pm 0.80	0.36 \pm 0.73
	C3	-0.84 \pm 1.00	-0.08 \pm 1.10	-0.01 \pm 1.00
	C4	-1.14 \pm 1.01	-0.40 \pm 1.13	-0.20 \pm 1.06
	P3	-6.04 \pm 0.78	-5.69 \pm 0.80	-5.71 \pm 0.79
	P4	-6.63 \pm 0.93	-5.78 \pm 0.94	-5.77 \pm 0.96
	O1	-6.96 \pm 0.82	-6.98 \pm 0.77	-7.09 \pm 0.79
	O2	-6.80 \pm 0.96	-6.73 \pm 0.81	-6.89 \pm 0.77
N2 (290-340 ms)	F3	1.22 \pm 0.71	1.30 \pm 0.84	1.59 \pm 0.83
	F4	1.57 \pm 0.59	1.43 \pm 0.72	1.82 \pm 0.71
	T3	0.13 \pm 0.73	0.29 \pm 0.68	0.48 \pm 0.68
	T4	0.84 \pm 0.35	0.86 \pm 0.30	1.45 \pm 0.49
	C3	0.01 \pm 0.79	0.50 \pm 0.83	1.01 \pm 0.85
	C4	-0.21 \pm 0.71	0.25 \pm 0.66	0.86 \pm 0.80
	P3	-2.54 \pm 0.98	-2.14 \pm 0.99	-1.67 \pm 0.87
	P4	-3.39 \pm 0.76	-2.51 \pm 0.66	-1.97 \pm 0.73
P3 (380-500 ms)	O1	-4.18 \pm 0.81	-3.95 \pm 0.86	-3.79 \pm 0.81
	O2	-4.47 \pm 0.82	-4.35 \pm 0.86	-4.13 \pm 0.87
	F3	3.16 \pm 0.66	3.92 \pm 0.60	4.13 \pm 0.66
	F4	3.51 \pm 0.68	4.25 \pm 0.67	4.39 \pm 0.67
	T3	2.52 \pm 0.71	2.96 \pm 0.67	3.19 \pm 0.64
	T4	2.93 \pm 0.52	3.63 \pm 0.50	4.09 \pm 0.60
	C3	4.79 \pm 0.87	5.40 \pm 0.93	5.91 \pm 0.86
	C4	4.35 \pm 0.85	5.51 \pm 0.84	5.95 \pm 0.88
P3	1.45 \pm 0.76	1.84 \pm 0.85	2.23 \pm 0.76	
P4	0.86 \pm 0.53	2.20 \pm 0.54	2.46 \pm 0.54	
O1	-1.24 \pm 0.46	-1.05 \pm 0.52	-0.89 \pm 0.45	
O2	-1.54 \pm 0.50	-1.32 \pm 0.48	-1.17 \pm 0.41	

For N1, the main effect of training was not significant ($F(2,22)=2.545, P>0.1$). However, there was a significant interaction of training \times area ($F(6,66)=2.845, P<0.02$). Separate ANOVAs revealed a marked decrease across training sessions over the central area ($F(2,22)=7.724, P<0.004$), a

somewhat weaker effect over the temporal area ($F(2,22)=3.639, P<0.05$), and no reliable decline for the parietal ($F(2,22)=2.168, P>0.1$) and occipital ($F(2,22)=0.09, P>0.9$) areas. Further pairwise comparisons showed that the training-induced N1 decrement was mainly occurred during the first two sessions (central area: session 1 vs. session 2, $P<0.05$; session 2 vs. session 3: $P>0.9$).

Training also elicited a reliable decrease in N2 ($F(2,22)=4.861, P<0.02$). In addition, the N2 decrement was different among areas (Table 1; training \times area: $F(8,88)=1.941, P<0.07$). Separate ANOVAs confirmed that the N2 decrement was marked over the parietal sites ($F(2,22)=7.058, P<0.005$), somewhat weaker over the central sites ($F(2,22)=4.845, P<0.03$), and not significant over the frontal ($F(2,22)=1.051, P>0.3$), temporal ($F(2,22)=2.071, P>0.1$) and occipital ($F(2,22)=0.907, P>0.4$) areas. Different from the N1, the decrease of N2 amplitude reached significance only between session 1 and session 3 (parietal area: $P<0.03$). Such decrement was not significant both between session 1 and session 2 ($P>0.20$) and between session 2 and session 3 ($P>0.17$). These results suggested that the N2 amplitudes decreased gradually over the three training sessions.

The P3 amplitude, however, was enhanced during the training ($F(2,22)=11.915, P<0.001$). The significant interaction of training \times area ($F(8,88)=2.779, P<0.04$) indicated that the training effect was different among areas. Separate ANOVAs revealed that the enhancement of P3 was highly significant over the central ($F(2,22)=12.076, P<0.001$), temporal ($F(2,22)=9.837, P<0.002$), frontal ($F(2,22)=9.710, P<0.002$) and parietal areas ($F(2,22)=7.844, P<0.004$), but not significant over the occipital area ($F(2,22)=1.406, P>0.2$). Similar to the N1, the training effect on P3 was mainly occurred during the first two sessions (frontal, temporal, central and parietal areas: session 1 vs. session 2, all $P_s<0.05$; session 2 vs. session 3: all $P_s>0.3$).

DISCUSSION

In the present study, the RTs decreased gradually across training sessions while training modulated ERPs significantly. These results suggest that the ERP effects observed here might reflect the improvement of detection ability rather than the effect of fatigue. The training-induced increment of the P3, which appeared lately and broadly, might reflect a consequence of perceptual learning such as enhanced confidence (10). Moreover, since habituation in visual tasks usually elicits smaller P3

(11), the result of enhanced P3 suggests that the ERP effects reported here might not be accounted by habituation. The oddball paradigm in present study is also of benefit to minimizing movement-related artifact since ERPs were averaged from those trials without explicit responses. In our recent ERP study in which all the experimental parameters were same with the current experiment except that the stimuli were simpler, we found different ERP training effects over the posterior areas (12). These facts indicate that ERP effects reported here might relate to perceptual learning of the present task than other possible factors.

We found that the negativities in both early and late stage (N1 and N2) were reduced across training sessions. It was consistent with brain imaging studies in humans (4) and single unit studies in animals (5), which showed reductions of neural activity after training. This result was, however, different from the ERP studies by Skrandies et al. (6) and Doniger et al. (8, 9), who found visual perceptual learning induced enhancement of negative peaks. The difference between these findings might be accounted by different stimuli and paradigms used in these experiments. Whether the modulation of ERP amplitudes induced by learning is related to stimulus and paradigm is still an open question.

The training-induced N1 decrement perhaps reflects learning at a low level of processing, which might be related to repetition suppression (i.e. decrease of neural activities over repeated exposure to identical stimulus during learning tasks). In previous studies, the repetition suppression was thought to reflect a progressive optimization of neural response (13). At the same time, modulation of top-down attention might also contribute to the training effects on ERPs. A previous single unit study (14) showed that decreased attention resulted in decreased neuronal responses. As a consequence of learning, the dependence of performance might be released from attentional control (15).

Different from the previous studies recording ERPs (6) or regional cerebral blood flow (rCBF) (4), which usually showed learning effects over occipital area, the training effect on the N1 in the present study was located over the central and temporal areas. Comparing the complex visual stimuli used here to the simple visual stimuli such as parallel lines and gratings used in previous experiments, we suggest that higher brain areas might be involved in the processing of complex shapes, and consequently, the related activities at these higher areas are also modulated by training.

Although the training effect on the later negativity (N2) was similar to the effect on N1, the

decrease of N1 preceded that of N2. Actually, while the N1 decrement appeared mainly between session 1 and session 2, the amplitude of N2 decreased gradually during the three training sessions. This result suggests that the N2 decrement is a relatively slow or long-lasting learning effect. Similar results have been observed in behavioral studies, showing that fast learning is followed by slow learning (1). There was some consistency between the time course of N2 effect and that of RTs (i.e. both appeared gradually across the three training sessions). Since the N2 is generally considered as reflecting on-line perceptual processing, stimulus identification (16) and selection of stimulus features (17), the observed effect on N2 might be partially due to the electrophysiological substrates underlying the learning effect observed in RTs.

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