Neural substrates of visual perceptual learning of simple and complex stimuli

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Abstract

Objective: The two experiments described here used event-related potentials (ERPs) to investigate whether perceptual learning of different complexities of stimuli involves different levels of visual cortical processing in human adults.

Methods: Reaction times and ERPs were recorded during 3 consecutive training sessions in which subjects discriminated between simple stimuli made of line segments or complex stimuli made of compound shapes.

Results: Reaction times in both experiments were shortened across training sessions. For simple stimuli, training resulted in a decreased N1 (125–155 ms) and an increased P2 (180–240 ms) over the occipital area. For complex stimuli, however, training resulted in a decreased N1 (125–155 ms) and N2 (290–340 ms) and an increased P3 (350–550 ms) over the central/parietal areas.

Conclusions: These findings suggest that perceptual learning modifies the response at different levels of visual cortical processing related to the complexity of the stimulus.

Significance: The neuronal mechanisms involved in perceptual learning may depend on the nature (e.g. the complexity) of the stimuli used in the discrimination task.

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Keywords: Visual perceptual learning; Event-related potentials (ERPs); Simple stimuli; Complex stimuli; Discrimination; Human adults

1. Introduction

It is well known that in the developing organism, sensory functions improve with maturation during the early years of life. A dominant view in neuroscience has been that the adult cortex is hard-wired, having been shaped by early-life experience, so it provides a precise and unchanging representation of the physical environment. Over the last several decades, however, an accumulating body of

behavioral and electrophysiological studies has demonstrated that even at the earliest stage of sensory processing, neuronal properties as well as the neuronal circuitry underlying basic sensory representations are subject to modifications as a function of training in the adult brain (see Karni, 1996 for a review).

The improvement of perceptual performance as a function of training is defined as perceptual learning. In humans, the effects of learning on the visual system have thus far been mainly investigated at the behavioral level. Many psychophysical studies have shown that perceptual learning can be found for the attributes of simple stimuli, such as orientation, position and size (e.g. Ahissar and Hochstein, 1996, 1997; Crist et al., 1997). For example, the sensitivity of detecting a bar of specific orientation was improved by orientation-discrimination training (Matthews et al., 2001). On the other hand, some studies have shown that perceptual learning can also be found for the attributes

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of more complex stimuli, such as complex shapes, common objects and faces (e.g. Furmanski and Engel, 2000; Gold et al., 1999). For instance, a recent visual search study showed that the subject's ability to find a shape (a triangle) could improve dramatically after training (Sigman and Gilbert, 2000).

These behavioral results give rise to an important question: Does perceptual learning of different complexities of stimuli occur at the same level of visual processing in the human brain? Previous studies of neurons reveal that there is both anatomical and physiological evidence for hierarchical information processing in the visual system. Neurons at lower levels of the visual pathway are highly specialized for simple attributes. Neurons in higher anatomical visual areas, however, generalize over these stimulus variables and are sensitive to increasingly more complex aspects of the stimuli (e.g. Desimone et al., 1985; Felleman and Van Essen, 1991; Maunsell and Newsome, 1987). Recent studies of neurons reveal that learning has similar hierarchical effects. For instance, preliminary electrophysiological data from monkey cortices showed that after simple grating orientation-discrimination training, neurons at lower levels of the visual cortex (striate cortex) tuned to the trained orientation exhibit firing-rate reductions (Schoups et al., 1998), while after training monkeys for complex shape discrimination, learning increased the proportion of neurons in higher visual areas (inferotemporal cortex) responding to the trained shapes (Kobatake et al., 1998).

Although these neurophysiological findings suggest that perceptual learning of different complexities of stimuli may involve different levels of visual cortical processing in the brain, there has been little direct evidence for this suggestion. The current work, using the same experimental parameters, systematically examined ERPs from two groups of human adults who discriminated between simple stimuli or complex stimuli. By comparing ERP correlates for simple stimuli with those for complex stimuli, we intended to investigate whether learning involves different levels of cortical processing related to the complexity of the stimulus.

2. Experiment 1

In Experiment 1, participants were presented with stimulus arrays made of line segments. We investigated the neural substrates of learning a simple visual attribute-orientation of line segments.

2.1. Methods

2.1.1. Subjects

Thirteen healthy right-handed undergraduate and graduate students (21–27 years old, 8 male) participated in this experiment as paid volunteers. All had normal or corrected-to-normal vision and were naive to the task.

Informed consent was obtained from each subject before the experiment.

2.1.2. Stimuli

Five types of stimuli, illustrated in Fig. 1, were used in this experiment. Each stimulus ($10.9° \times 10.9°$) was composed of 4 lines (each 3.5° long and 0.2° wide) in a 2×2 array. The 4 lines had either an identical orientation of 45° (Fig. 1a, top) or the orientation of one line was changed to 60° (Fig. 1b–e, top). All the stimuli were white on a black background. A fixation cross ($0.3° \times 0.3°$) was continuously visible at the center of the display. Stimulus duration was 200 ms. Interstimulus intervals were randomized between 1600 and 2000 ms.

2.1.3. Procedure

The task was to discriminate whether the 4 lines in a stimulus had an identical orientation or not. The subjects were instructed to press a button with their dominant hands when the target (i.e. 4 lines with an identical orientation, Fig. 1a, top) was presented. Accuracy and speed were emphasized equally. The target and 4 non-target stimuli were presented in a pseudo-random order and with equal probability (each 20%). Each subject was given 3 consecutive training sessions during which both reaction times and ERPs were recorded. Each session contained 9 blocks of 40 trials and lasted about 30 min. Breaks of 10–15 min between two sessions were given to subjects to maintain high concentration and prevent fatigue. At the very beginning, the subjects practiced the operation for one or two blocks to ensure that they understood the task. The whole experiment lasted about 2 h.

2.1.4. Recording and analysis

The electroencephalogram (EEG) was recorded from 18 scalp sites over the central, parietal, occipital and temporal cortices (see Fig. 5). The horizontal electro-oculogram (EOG) was recorded from two electrodes positioned at the outer canthus of each eye, and the vertical EOG was recorded from an electrode located below the left eye. All the electrodes, except for horizontal EOG, were physically referenced to left mastoid and were then off-line re-referenced to the average of the left and right mastoid.
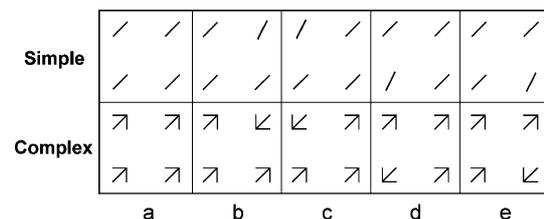

Fig. 1. The simple stimuli (top) used in Experiment 1 and the complex stimuli (bottom) used in Experiment 2. The target stimuli with a press response (a) and the 4 types of non-target stimuli without explicit response (b–e) used in equi-probability (each 20%).
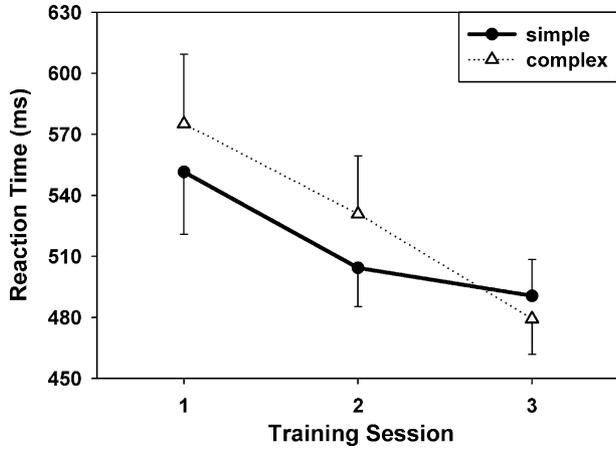
Fig. 2. Changes in reaction times in the course of learning. Closed circles, simple stimuli; open triangles, complex stimuli. Error bars indicate SEM.

Electrode impedance was kept below 5 kΩ. EEG was amplified with a bandpass of 0.1–40 Hz, digitized on-line at a sampling rate of 250 Hz and a sampling resolution of 16 bits. Each epoch of EEG was 200 ms of pre-stimulus to 1000 ms of post-stimulus. To minimize movement-related artifacts of finger response, EEG for all non-target stimuli (without explicit response) within each session was averaged. Trials contaminated by eye blinks or muscle potentials at any electrode or incorrect behavioral responses were excluded from the ERP averages. The baseline for

ERP measurements was the mean voltage of a 200 ms pre-stimulus interval.

Behavioral data were analyzed with repeated measures analysis of variances (ANOVAs) with the factor being Session (sessions 1, 2 or 3). For ERP analysis, the waves were measured at the C3/C4, P3/P4, and O1/O2 electrodes sites where learning effects were evident. The ANOVAs of mean ERP amplitudes were computed with factors being Session and Hemisphere (left or right hemisphere) for each pair of symmetrically placed electrodes. Significance levels of the F ratios were adjusted with the Greenhouse-Geisser correction. To clarify the source of the significant Session effect in different time courses, further pairwise comparisons were performed to compare the difference between each pair of training sessions.

2.2. Results

2.2.1. Behavioral measures

The mean reaction times for the 3 training sessions are shown in Fig. 2. Mean reaction times decreased significantly across training sessions (551, 504, 491 ms in sessions 1, 2 and 3, respectively; $F(2, 24) = 8.316$, $P < 0.009$, $\varepsilon = 0.620$), suggesting that the performance of discrimination was improved by training. Further pairwise comparisons revealed that the improvement reach significance only between the first two sessions ($P < 0.034$). A significant quadratic trend further indicates that the difference between
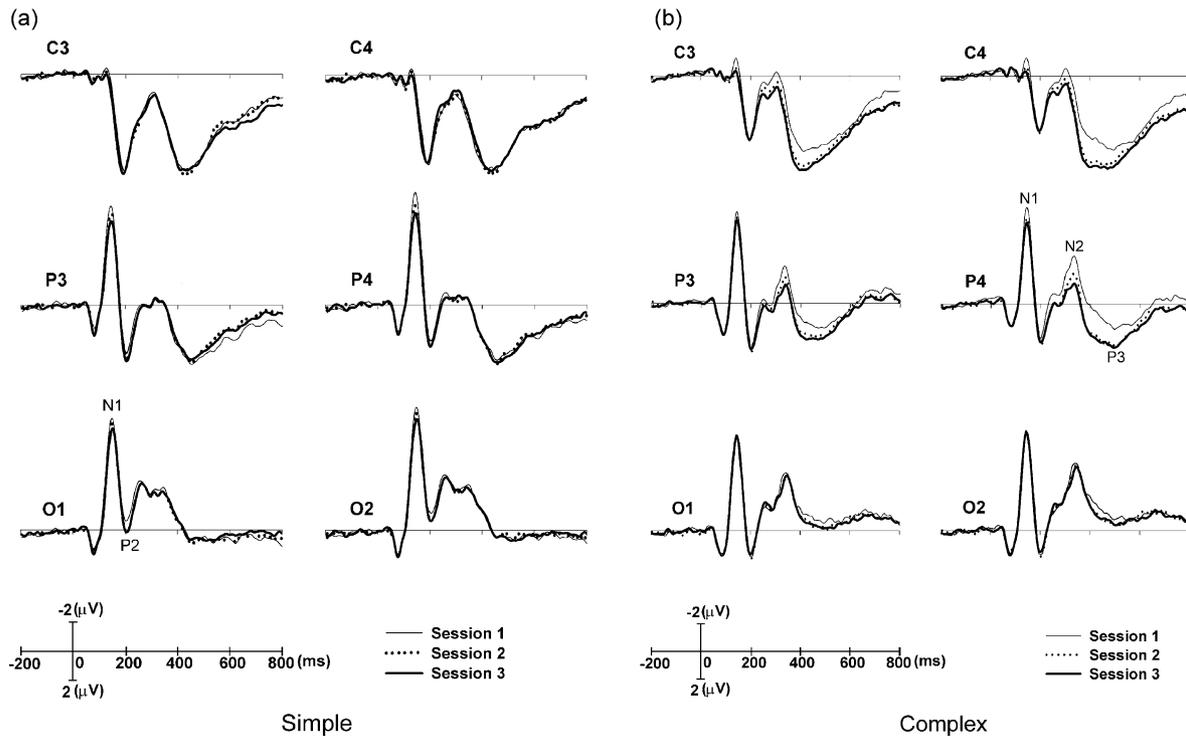

Fig. 3. The grand averaged ERPs elicited by simple and complex stimuli during the 3 training sessions. The thin continuous, dotted, and thick continuous lines referred to sessions 1, 2 and 3, respectively. (a) For simple stimuli, N1 decreased and P2 increased across training sessions at the posterior electrodes. (b) For complex stimuli, N1, N2 decreased and P3 increased across training sessions at the central/parietal electrodes.
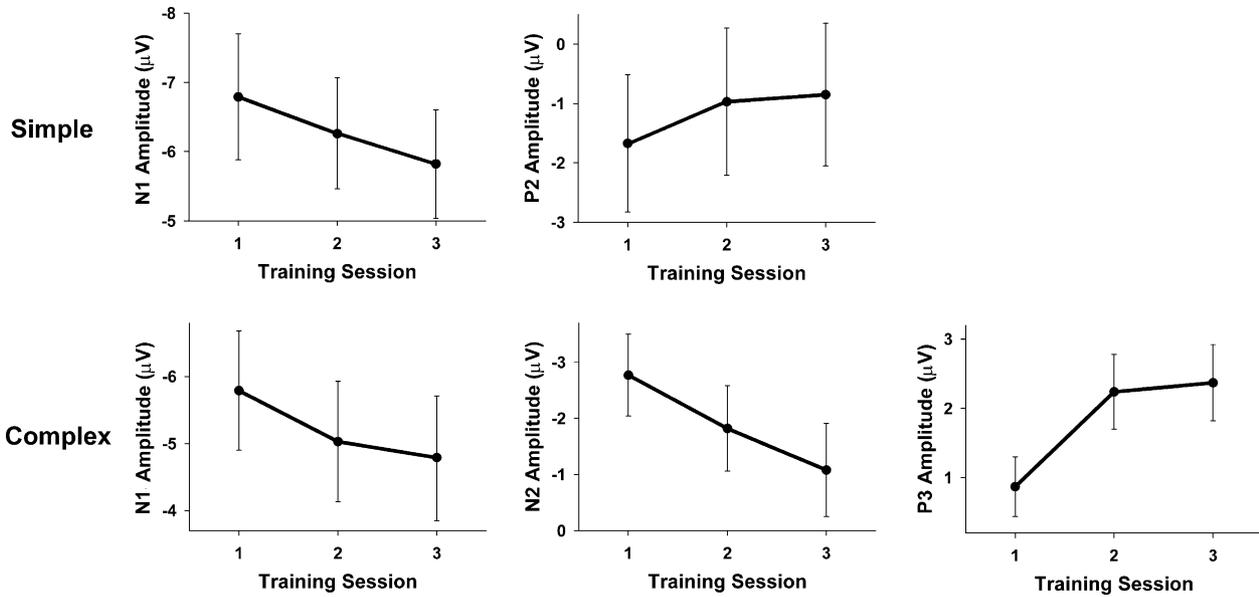
Fig. 4. Change in mean ERP amplitudes in the course of learning. Top, changes of N1 and P2 amplitudes (at O1 site) for simple stimuli; bottom, changes of N1, N2 and P3 amplitudes (at P4 site) for complex stimuli.

sessions 1 and 2 is greater than the non-significant difference between sessions 2 and 3 ($F(1, 12) = 5.012$, $P < 0.046$). Response accuracy was high (averaged 99%) and stable throughout the experiment.

2.2.2. ERP measures

Fig. 3a displays grand average ERP waveforms elicited by simple stimuli. The ERPs of the 3 training sessions were characterized by P1 (60–110 ms), N1 (110–170 ms), and N2 (240–360 ms) with maxima over the posterior areas, and P2 (170–240 ms) and P3 (360–550 ms) with maxima over the central/parietal areas. We measured and analyzed the P1 component at parietal and occipital electrode sites, and the N1, P2, N2, and P3 component at central, parietal and occipital electrode sites. We found that peak latencies of

each component were similar for the 3 training sessions. There were, however, differences of ERP amplitude on two important components, i.e. N1 and P2. Their amplitudes were analyzed as the mean voltages within the intervals 125–155, 180–240 ms, respectively.

For N1, there was a marked decrease across training sessions over the occipital area (O1/O2: $F(2, 24) = 6.773$, $P < 0.017$, $\varepsilon = 0.613$; Figs. 4 and 5), and this decrement became weaker over the parietal (P3/P4: $F(2, 24) = 4.023$, $P = 0.058$, $\varepsilon = 0.599$) and central areas (C3/C4: $F(2, 24) = 2.920$, $P = 0.093$, $\varepsilon = 0.857$).

On the other hand, the amplitudes of P2 increased across training sessions over the occipital area (O1/O2: $F(2, 24) = 5.664$, $P < 0.016$, $\varepsilon = 0.831$; Figs. 4 and 5), and this increment of P2 amplitude was not significant over
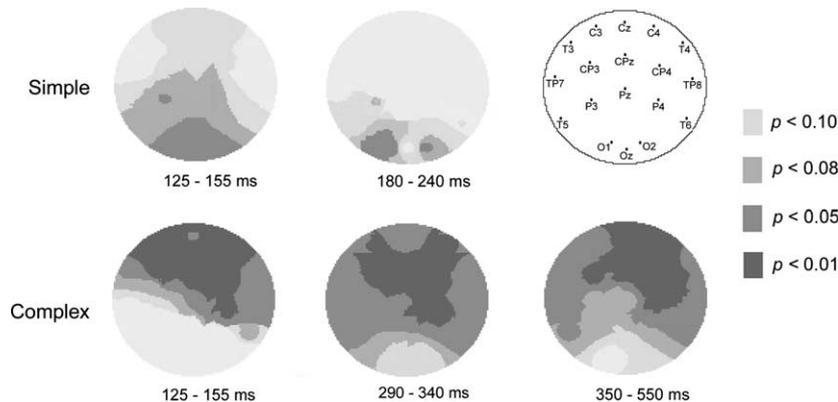

Fig. 5. Significance probability maps displaying the results of paired t tests between ERPs of sessions 1 and 3. The degrees of luminance indicated two-tailed significant levels. Note that for simple stimuli, the effects of learning in the N1 (125–155 ms) and P2 (180–240 ms) time windows focused on the occipital area. For complex stimuli, however, the effects of learning in the N1 (125–155 ms), N2 (290–340 ms) and P3 (350–550 ms) time windows focused on the central/parietal areas. In addition, there was a right hemispheric predominance for complex stimuli. The distribution of 18 scalp electrodes used for EEG recording is shown on the upper-right-hand corner.

the parietal (P3/P4: $F(2, 24) = 1.857$, $P = 0.188$, $\varepsilon = 0.779$) or central area (C3/C4: $F(2, 24) = 0.574$, $P = 0.496$, $\varepsilon = 0.620$). Further pairwise comparisons showed that the occipital N1 decrement appeared not only between sessions 1 and 2 ($P < 0.047$), but also between sessions 2 and 3 ($P < 0.026$). However, the occipital P2 increment reached significance only between sessions 1 and 2 ($P < 0.031$), but not between sessions 2 and 3 ($P = 0.491$). In addition, the significant difference between sessions 2 and 3 for N1 is greater that the non-significant differences for P2 over the occipital area ($P < 0.034$).

For both N1 and P2 components, there were not significant Session×Hemisphere interactions ($F_s < 1$), suggesting that the Session effects were not different at electrodes over the left and right hemispheres (Fig. 5).

3. Experiment 2

In Experiment 2, another group of participants were presented with more complex stimuli made of compound arrow-shapes. Each arrow was composed of 3 line segments. We investigated the neural substrates of learning a complex visual attribute-direction of compound shapes.

3.1. Methods

3.1.1. Subjects

Fifteen healthy right-handed undergraduate and graduate students (18–25 years old, 8 male) participated in this experiment as paid volunteers. All had normal or corrected-to-normal vision and were naive to the task. None of them took part in Experiment 1. Informed consent was obtained from each subject before the experiment.

3.1.2. Stimuli

Each of the stimuli ($10.9° \times 10.9°$), as illustrated in Fig. 1, consisted of 4 arrows (each $2.5° \times 2.5°$) on 4 quadrants, respectively. Each arrow was made up of 3 line segments, i.e. the horizontal ($0°$), vertical ($90°$) and diagonal ($45°$) line (the diagonal line was identical to the line of $45°$ used in the simple stimuli in Experiment 1). All 4 arrows pointed to the upper-right (Fig. 1a, bottom) or the direction of one arrow was changed to the lower-left (Fig. 1b–e, bottom). Other parameters were identical to those in Experiment 1.

3.1.3. Procedure

Subjects were instructed to press a button with their dominant hands when the target (i.e. all 4 arrows pointing in the same direction, Fig. 1a, bottom) was presented. Others were identical to those in Experiment 1.

3.1.4. Recording and analysis

The recording and analysis were identical to those in Experiment 1.

3.2. Results

3.2.1. Behavioral measures

As in Experiment 1, response accuracy in Experiment 2 was high (averaged 99%) and stable throughout the experiment, and mean reaction times decreased as a function of training sessions (575, 531, 479 ms in sessions 1, 2 and 3, respectively; $F(2, 28) = 23.446$, $P < 0.001$, $\varepsilon = 0.607$), suggesting that the behavioral performance was also improved by training (Fig. 2). Different from Experiment 1, further pairwise comparisons showed that the decrement of reaction times was ongoing throughout the 3 training sessions (session 1 vs. session 2: $P < 0.001$; session 2 vs. session 3: $P < 0.002$). A further t test showed that the significant improvement in RT between sessions 2 and 3 for complex stimuli is greater than that for simple stimuli ($P < 0.020$).

3.2.2. ERP measures

Fig. 3b displays grand average ERP waveforms elicited by complex stimuli. The scalp distributions and time windows of the main ERP components were similar to those elicited by simple stimuli in Experiment 1: P1 (60–120 ms), N1 (120–170 ms), and N2 (240–350 ms) with maxima over the posterior areas, and P2 (170–240 ms) and P3 (350–550 ms) with maxima over the central/parietal areas. We measured and analyzed the P1 component at parietal and occipital electrode sites, and the N1, P2, N2, and P3 component at central, parietal and occipital electrode sites. We found that peak latencies of each component were also similar for the 3 training sessions. There were, however, differences of ERP amplitude on 3 manifest components, i.e. N1, N2, and P3. Their amplitudes were analyzed as the mean voltages within the intervals 125–155, 290–340, 350–550 ms, respectively.

The N1 amplitudes decreased across training sessions over the central/parietal areas (C3/C4: $F(2, 28) = 8.968$, $P < 0.002$, $\varepsilon = 0.787$; P3/P4: $F(2, 28) = 4.405$, $P < 0.030$, $\varepsilon = 0.750$; Figs. 4 and 5), but this decrement of N1 amplitudes was not significant over the occipital area (O1/O2: $F(2, 28) = 0.060$, $P = 0.911$, $\varepsilon = 0.716$). Similar to N1, N2 also decreased over the central/parietal areas (C3/C4: $F(2, 28) = 6.984$, $P < 0.008$, $\varepsilon = 0.798$; P3/P4: $F(2, 28) = 13.170$, $P < 0.001$, $\varepsilon = 0.734$; Figs. 4 and 5), and there was no reliable decline for the occipital area (O1/O2: $F(2, 28) = 2.727$, $P = 0.093$, $\varepsilon = 0.733$). However, the P3 amplitudes were enhanced by training over the central/ parietal areas (C3/C4: $F(2, 28) = 8.872$, $P < 0.005$, $\varepsilon = 0.615$; P3/P4: $F(2, 28) = 9.620$, $P < 0.003$, $\varepsilon = 0.714$; Figs. 4 and 5), and no significant P3 change was found over the occipital area (O1/O2: $F(2, 28) = 1.864$, $P = 0.179$, $\varepsilon = 0.747$). In addition, the Session×Hemisphere interactions were all significant at parietal sites for the N1, N2, and P3 components ($P_s < 0.039$), indicating the right-hemisphere predominance during learning complex stimuli (Fig. 5).

Further pairwise comparisons showed that training affected the 3 components in different time courses.

The changes in N1 and P3 were significant only between sessions 1 and 2 ($P_s < 0.029$), whereas the change in N2 appeared not only between sessions 1 and 2 ($P_s < 0.026$), but also between sessions 2 and 3 ($P_s < 0.046$). In addition, the significant difference between sessions 2 and 3 for N2 is greater than the non-significant differences for N1 and P3 ($P_s < 0.036$).

To examine the topographical distribution difference between the learning of simple and complex stimuli, we did additional between-subject ANOVAs for the N1 component, which was related to both learning processes. The factors of ANOVAs were Group (simple or complex), Area (central, parietal or occipital area), Session and Hemisphere. As suggested by McCarthy and Wood (1985), the voltage for each electrode and training session was scaled by dividing by the square root of the sum of the squares of the voltage values at all electrodes. The results showed a significant Group × Area × Session interaction ($F(4, 104) = 2.713$, $P < 0.046$, $\varepsilon = 0.716$), supporting the hypothesis that different brain regions were involved in the learning of simple and complex stimuli.

4. Discussion

The two present experiments investigated learning-induced changes of event-related potentials in human adults, focusing on making a comparison between perceptual learning of simple and complex stimuli. We found that the two learning processes have many common characteristics, which were especially manifested in the early stage of visual processing. For instance, the earliest stage modulated by learning was about 125–155 ms (N1 component) in both experiments. The two learning processes both changed the amplitudes, but not the latencies of the ERP components. This kind of change was only partial, and was not observed for all of the electrodes. These common characteristics suggest that the same neural mechanism underlies the two learning processes. On the other hand, there were several differences between the two learning processes, which were manifested in time course, brain region, ERP components and hemisphere predominance. The existence of these differences indicates that the two learning processes might occur at different levels of the brain.

4.1. Time course of learning

Behavioral performance showed that the participants responded faster after training in both experiments, indicating that their performance was improved by training. In addition, behavioral results supported the proposal that there are different time courses of learning during training for discrimination of different stimuli (Gilbert, 1994): the reaction times decreased significantly only during the first two sessions for simple stimuli, while the significant decrement of reaction times was ongoing throughout all

3 training sessions for complex stimuli, suggesting that before a stable level of behavioral performance was attained, more training was need for learning the discrimination of a more complex attribute.

The ERPs showed significant changes during perceptual learning in both experiments, indicating that the cortex can dynamically modify the processing of visual information according to immediate behavioral requirements (Gilbert et al., 2001). Compared with the reaction times, the ERP data provided more details about the time course of learning. Different ERP components showed different time courses of learning. For simple stimuli, the time course of learning reflected in the P2 amplitudes was in line with the changes of reaction times and showed the stable level in the later training, whereas for complex stimuli, the time course of learning reflected in the N2 amplitudes was in line with the changes of reaction times and showed some need for more training. Previous studies proposed that P2 was sensitive to stimulus orientation (O'Donnell et al., 1997), and N2 might reflect stimulus identification and selection based on stimulus features, such as orientation (Harter and Aine, 1984; Hillyard and Munte, 1984; Mulder, 1986; Renault et al., 1982). Therefore, it is not strange to find the time course of P2 or N2 was in line with the behavioral data in our study. These results were consistent with two recent studies (Ding et al., 2003; Song et al., 2002). Compared with simple stimuli, the change of a later component was consistent with the behavior for complex stimuli. Therefore, these ERP differences between the two learning processes may not only be related to the time course of learning, but also related to the time course of processing of simple and complex stimuli.

We found that the two learning processes both changed the amplitudes, but not the latencies of the ERP components. It was consistent with auditory perceptual learning studies in humans (Atienza et al., 2002) and in animals (Takeuchi et al., 2000). This result was, however, different from the ERP study by Skrandies et al. (1996), who found visual perceptual learning shortened the latency of a negative peak. The difference between these findings might be accounted by different stimuli and paradigms used in these experiments. We suggest that the change of ERP latencies might need more time (or sleep) to be observed. For example, Atienza and Cantero (2001) found the mismatch negativity (MMN) latency was not changed after training during wakefulness, but this latency was significantly shortened during succedent REM sleep.

4.2. Brain regions

The main ERP components elicited by simple and complex stimuli were similar in both time windows and distributions; however, the two learning processes modulated different ERP components over different brain regions. For simple stimuli, learning effects were focused over

the occipital cortex. For complex stimuli, however, learning effects were focused over the central/parietal regions.

As for the locus where the learning-induced changes occur, our results suggest that learning simple visual attributes may be related to changes at lower levels of visual processing, while learning complex visual attributes may be related to changes at higher levels of visual processing in human adults. This suggestion is in line with several previous neuroscience studies, which have individually investigated the possible cortical substrates for learning simple or complex attributes. For instance, an ERP study found that after human subjects were trained with simple stimuli (vertical or horizontal lines) in a vernier task, the ERP amplitudes and latencies over the occipital brain areas were changed (Skrandies et al., 1996). On the other hand, a PET study showed that perceptual learning of complex stimuli (common objects or faces) enhanced the activity of inferior temporal regions (Dolan et al., 1997).

As mentioned in Section 1, many previous studies have suggested the existence of hierarchical information processing in the visual system. Neurons at lower levels of the visual pathway are highly specialized for simple visual attributes, while neurons in higher anatomical visual areas are sensitive to increasingly more complex aspects of the stimuli. Our present results on brain regions involved in learning were also in line with hierarchical information processing. Certainly, due to the relatively low spatial resolution provided by the ERP, further research should combine the high-temporal-resolution ERP with the high-spatial-resolution neuroimaging methods (such as fMRI, PET) which can more accurately discern the cortical areas involved in learning.

4.3. ERP components

In addition to the time course and brain regions involved in learning, the ERP components modulated by learning simple and complex stimuli were also different. Two early ERP components were modulated by learning simple stimuli (N1 was decreased, P2 was increased). However, learning complex stimuli modulated not only an early component (N1 was decreased) but also two late components (N2 was decreased, P3 was increased). These results suggest that different stages of visual processing are involved in learning different visual attributes. Compared with simple stimuli, later stages of visual processing are involved in learning complex stimuli. Note that the earliest component modulated by learning was the N1 wave in both experiments. Similar results were also found in other visual or auditory perceptual learning (Doniger et al., 2000; Takeuchi et al., 2000), indicating early involvement of neural mechanisms in perceptual learning.

Previous studies have found that there is strong interaction between perceptual learning and attention: perceptual learning is under top-down control, and attentional effects are subject to learning (please see

Gilbert et al., 2001 for a review; see also Ahissar and Hochstein, 1993; Crist et al., 1997; Desimone, 1996; Ito et al., 1998). According to the finding of behavioral and ERP studies, it has been proposed that 'attention is essential for learning even simple tasks' (Ahissar and Hochstein, 2002) and 'attention is critical for establishment of perceptual learning' (Atienza and Cantero, 2001). According to the findings of brain image studies, it has even been proposed that 'one of the consequences of learning is to release the dependence of performance from attentional control' (Gilbert et al., 2001) and 'diminished attentional modulation is a component of the learning process' (Schiltz et al., 1999). In our study, we found that training affected the amplitudes of several ERP components in both experiments. Many studies found that the ERP amplitudes could be modulated by attention (e.g. Mangun, 1995). The possibility that some effects might correspond to a reduction of attentional modulation during perceptual learning could not be excluded in the present study. Further studies are required to give an accurate assessment of the relationship between attention and these ERP learning effects. The changes of ERP components in our study had a common character: a positive trend; that is, the negative waves were decreased while the positive waves were increased across training sessions. Accurate explanations for this positive effect should also be sought in further studies.

4.4. Hemispheric predominance

Many previous studies have suggested that hemispheric asymmetry is more likely to occur at the higher rather than at the early cortical levels of visual processing (see Christman, 1989 for a review). Our results showed that the effects of learning are also similar: the lower brain region, where learning simple stimuli were focused, did not show hemispheric asymmetry. The higher brain region, where learning complex stimuli were focused, showed a right hemispheric predominance.

4.5. Conclusion

The present two experiments trained the subjects to discriminate between different complexities of the stimuli within brief time periods. We found that training could induce significant effects not only in behavioral performance, but also in brain activity. For both simple and complex stimuli, along with the reduction of reaction times, the amplitudes of several early and late ERP components were changed with training. Compared with simple stimuli, the higher visual cortex, later ERP components and more hemispheric lateralization were involved in learning complex stimuli, suggesting that learning of complex visual attributes may occur at relatively higher levels of information processing. Our findings further indicate that learning may involve different levels of visual cortical processing related to the complexity of the stimulus.

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