Note

ERP evidence for distinct mechanisms of fast and slow visual perceptual learning

Zhe Qu [a,b,1], Yan Song [c,1], Yulong Ding [a,b,*]

[a] Department of Psychology, Sun Yat-Sen University, Guangzhou 510275, China
[b] State Key Laboratory of Brain and Cognitive Science, Institute of Biophysics, Chinese Academy of Sciences, 15 Datun Road, Beijing 100101, China
[c] State Key Laboratory of Cognitive Neuroscience and Learning, Beijing Normal University, Beijing 100875, China

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ABSTRACT

Perceptual learning (PL) occurs not only within the first training session but also between sessions. Once acquired, the learning effects can last for a long time. By examining the time course of learning-associated ERP changes, this study explores whether fast and slow visual PL contribute to long-term preservation. Subjects first participated in a visual task for three training sessions, and were then given one test session six months later. ERP results showed that fast learning effects, as reflected by the decrement of posterior N1 and increment of posterior P2 within session 1, were preserved in session 3 but not in the test session. However, slow learning effects, as reflected by the increment of posterior N1 and decrement of frontal P170 between sessions 1 and 3, were retained completely in the test session. This study indicates that PL induces different changes in the human adult brain during and after active training, and only the delayed changes of brain activity can be preserved for a long period of six months.

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1. Introduction

Perceptual learning (PL) represents one kind of skill learning whereby relatively permanent and consistent changes in perception take place with repeated practice or experience. PL involves consolidation of implicit memory formed by training (Squire, 2004), and its time course has drawn a great deal of attention (Alain, Snyder, He, & Reinke, 2007; Atienza, Cantero, & Dominguez-Marin, 2002; Karni & Sagi, 1993; Mednick, Arman, & Boynton, 2005; Tremblay, Kraus, & McGee, 1998; Yotsumoto, Watanabe, & Sasaki, 2008). It has been shown that a naïve subject's performance on a simple discrimination task can be significantly improved with only a few trials, a process referred to as fast learning (e.g., Poggio, Fahle, & Edelman, 1992). This fast, within-the-first-session learning is followed by relatively slow learning that accumulates across many training sessions and training days. One important finding about slow learning is that PL may even occur between sessions when no actual training is conducted (Karni & Sagi, 1993). A time period of 1 h immediately after training (Seitz et al., 2005) and various amounts of post-training sleep (Aeschbach, Cutler, & Ronda, 2008; Karni, Tanne, Rubenstein, Askenasy, & Sagi, 1994;

Matarazzo, Frankó, Maquet, & Vogels, 2008; Mednick, Nakayama, & Stickgold, 2003; Stickgold, James, & Hobson, 2000; Stickgold, Whidbee, Schirmer, Patel, & Hobson, 2000) seem to be crucial for the learning to take place and to consolidate. Once acquired, the learning effect can last for a long time, from months to even years without further training (Karni & Sagi, 1993; Polat & Sagi, 1994; Polat, Ma-Naim, Belkin, & Sagi, 2004; Roth, Kishon-Rabin, Hildesheimer, & Karni, 2005).

From these earlier findings, an interesting question arises: whether both fast and slow learning contribute to the long-term preservation of the PL effect? Although it has been proposed that slow learning may subserve the long-term retention of some perceptual skills (Karni & Sagi, 1993), direct evidence supporting this hypothesis is lacking. Because the effects of fast and slow learning may be intermixed in behavioral measures, it is difficult to address this issue using traditional behavioral measures (i.e., psychophysical threshold, reaction time, accuracy). On the other hand, the event-related potentials (ERPs) that offer high temporal resolution with reasonable spatial resolution may provide additional information to differentiate fast and slow learning contributions to PL.

In the domain of visual research, a number of studies have used ERP and other brain imaging techniques (e.g., functional magnetic resonance imaging, fMRI) to investigate the neural mechanisms of visual PL under different time scales, from tens of minutes (Ding, Song, Fan, Qu, & Chen, 2003; Itier & Taylor, 2004; Scott, Tanaka, Sheinberg, & Curran, 2006; Skrandies, Jedynak, & Fahle, 2001; Song et al., 2005, 2007; Wang, Song, Qu, Ding, in press) to a few days

* Corresponding author at: Department of Psychology, Sun Yat-Sen University, 135 West Xingang Road, Guangzhou, 510275, China. Tel.: +86 20 8411 4266; fax: +86 20 8411 4266.
E-mail address: edsdyl@mail.sysu.edu.cn (Y. Ding).
[1] These authors contributed equally to this paper.

(Schiltz et al., 1999; Sigman et al., 2005; Yotsumoto et al., 2008). However, to date no published study has been able to examine both the fast and slow PL-associated neural changes in the same experiment, therefore, studies directly comparing the neural mechanisms of fast and slow visual PL are still lacking. Moreover, previous studies did not provide data demonstrating the reliability of specific brain activity after training had been discontinued for months. For these reasons, it is not clear whether neural changes associated with fast or slow PL can be preserved for a long time as the changes in perceptual ability do.

In the present study, by observing the time course of learning-associated changes in different ERP components over a period of six months, we examined whether fast and slow visual PL involves differential ERP changes as well as the roles of fast and slow learning in the long-term preservation of PL. We found that fast and slow learning were reflected by different ERP changes, and only the ERP changes associated with slow learning were retained for a long period of six months. The present study provides, to our knowledge, the first electrophysiological evidence for long-term human adult brain plasticity induced by PL. A general model for perceptual and skill learning was proposed based on these findings and the literature.

2. Materials and methods

2.1. Subjects

Ten healthy right-handed adults (21–25 years old, six male) participated in this experiment as compensated volunteers. All had normal or corrected-to-normal vision and were naïve, with no prior experience in the task. Informed consent was obtained from each subject.

2.2. Stimuli, task and procedure

A simple visual task reported in our previous studies (Ding et al., 2003; Song et al., 2005) was adopted in the present experiment. There were five stimulus patterns (Fig. 1a), each consisting of four $3.5° \times 0.2°$ lines forming a 2×2 array subtending $10.9° \times 10.9°$. There were two stimulus conditions: either all the four lines were orientated at 45°, or one of the lines was set at 60°. All lines were white on a black background. Stimulus duration was 200 ms, and the inter-stimulus intervals were randomized between 1400 and 1800 ms. In the display center a green cross $(0.3° \times 0.3°)$ was present throughout each trail as the fixation point.

Subjects were instructed to determine whether the orientations of the four lines in a stimulus were identical, and to press a button with their dominant hands when the target was presented (i.e., four line elements with identical orientation, Fig. 1a). They were told to respond as quickly and accurately as possible but not to emphasize one with the cost of another (e.g., emphasize the speed with the cost of the accuracy). Each subject participated in three training sessions (S1–S3) on different days within one week. Each session contained three blocks of 360 trials and lasted for about 1.5 h. The target and four non-targets were interspersed randomly with equal probability in a block. Prior to the first training session, the subjects were given 40–80 practice trials to ensure they understood the task. Six months later, each subject participated in a test session (S4) which was identical to the initial training session.

2.3. Electrophysiological recordings

Electroencephalogram (EEG) was recorded in S1, S3 and S4, from 27 scalp electrodes of the 10/10 system. Horizontal and vertical electro-oculograms (EOGs) were also recorded. EEG was physically referenced to the left mastoid, and then off-line re-referenced to the average of the left and right mastoids. Electrode impedance was kept below 5 kΩ. EEG was amplified with a band pass of 0.1–100 Hz, digitized online at a sampling rate of 500 Hz, and then off-line filtered with a digital low-pass of 40 Hz. Each epoch of EEG was from 200 ms of pre-stimulus to 1000 ms of post-stimulus. To minimize movement-related artifacts of finger responses, EEG for all non-target stimuli (without explicit response) within each block was averaged. Trials contaminated by eye blinks or muscle potentials at any electrode and by incorrect behavioral responses were excluded. The baseline for ERP measurements was the mean voltage of a 200 ms pre-stimulus interval.

2.4. Data analysis

For behavioral data, response accuracy and reaction time (RT) were analyzed. For ERP data, the effects of training were studied by examining changes in amplitudes of posterior N1, P2 and frontal P170. The former two were chosen because they were found to be related to fast learning in previous studies (Ding et al., 2003; Song et al., 2005), and these components showed significant differences within S1 in the present study. Frontal P170 was chosen because it showed significant difference between S1 and S3. Posterior N1 and P2 were measured and averaged across from six posterior electrodes (O1/O2, P3/P4 and P7/P8); frontal P170 was measured and averaged across from three frontal electrodes (F3, F4, and Fz). For each subject, the N1 amplitude was measured as the mean value of a 20-ms window centered at the average peak latency of the six posterior electrodes. The amplitudes of posterior P2 and frontal P170 were measured as the mean values of 200–240 ms and 150–200 ms, respectively.

Repeated measure ANOVAs and two tailed t-tests were used to analyze the fast and slow learning effects, as well as their preservations. Significance levels of the F ratios were adjusted with the Greenhouse–Geisser correction.

3. Results

3.1. Behavioral results

Response accuracy was high (averaged 98%) and stable throughout the training and test sessions. After three consecutive training sessions, RT decreased from 558 ms in S1B1 (i.e., Block 1 in session 1) to 423 ms in S3B3 (Fig. 2a; one-way ANOVA, $F(8,72) = 10.20$, $p = 0.001$). Significant decreases in RT were observed not only between the first two blocks in session 1 (S1B1 vs S1B2: decrement 56 ± 25 ms, mean $\pm$ S.E.; $t(9) = 2.28$, $p = 0.04$), but also across two adjacent training sessions (S1B3 vs S2B1: decrement 15 ± 5 ms, $t(9) = 2.93$, $p = 0.02$; S2B3 vs S3B1: decrement 31 ± 12 ms, $t(9) = 2.48$, $p = 0.03$). These results suggested two stages of visual PL, specifically, a fast learning effect occurred at the beginning of training, followed by slow learning effects occurring after each training session.

When tested six months later, RT was 455 ms (S4B1), which was longer than the RT in S3B3 (increment: 31 ± 10 ms; $t(9) = 3.17$, $p = 0.01$), but much shorter than the RT in S1B1 (decrement: 104 ± 31 ms; $t(9) = 3.33$, $p = 0.01$), indicating that the improvement in behavioral response was largely preserved even after six months.

3.2. ERP results

ERP peak latencies did not show obvious changes throughout the training stage, both within and between training sessions. However, training induced significant differences in ERP amplitudes. As shown in Figs. 2b and 3, there was a significant within-
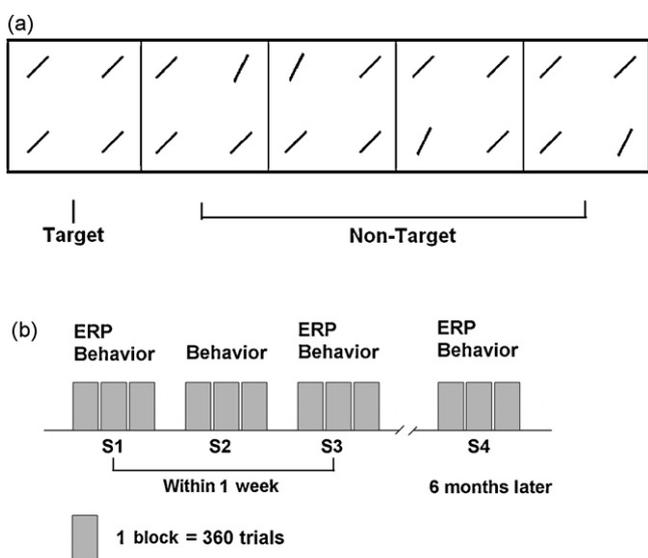

Fig. 1. Stimuli (a) and training paradigm (b) used in the experiment. (a) All the stimuli were white on a uniform black background. (b) Each subject was first given three consecutive training sessions (S1–S3) within a week, and at least one night was between two adjacent sessions. Six months later, each subject was given a test session (S4).
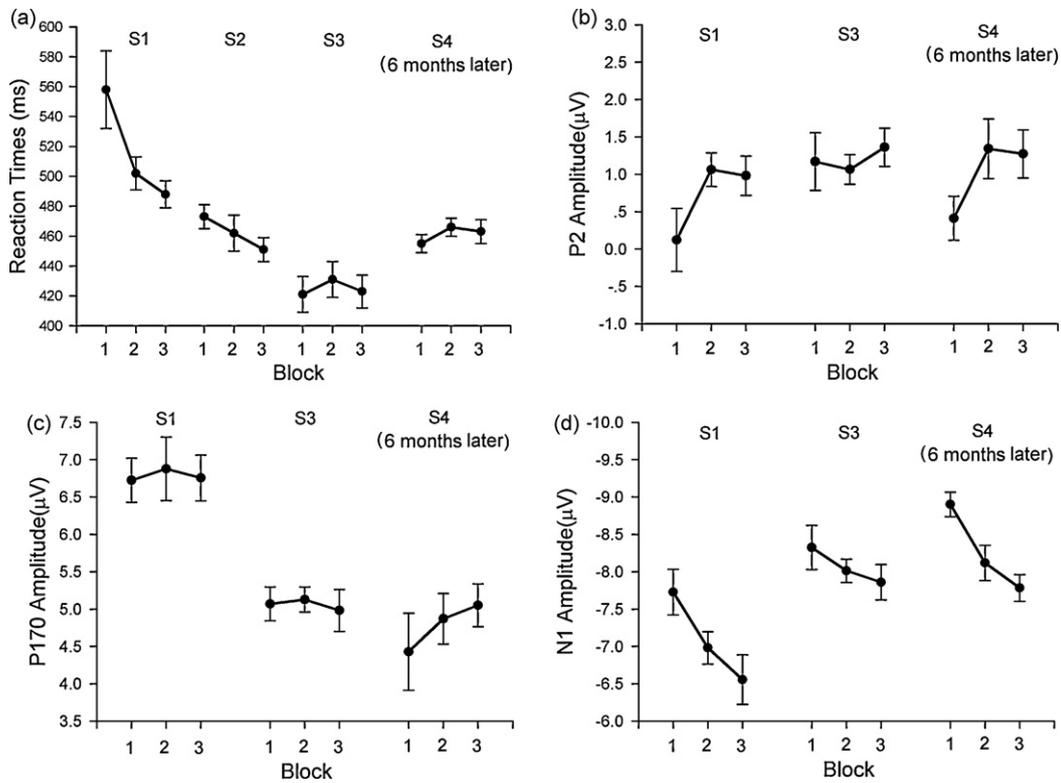
Fig. 2. Time courses of RT (a) and ERP amplitudes (b–d) along training and test sessions. The mean values (S.E.) of 10 subjects are presented. N1 and P2 were measured from six posterior electrodes (O1/O2, P3/P4, and P7/P8); P170 was measured from three frontal electrodes (F3, FZ, and F4). (a) RT decreased both within S1 and between training sessions, and such improvement of performance was largely preserved in S4. (b–d) While posterior N1 decreased and posterior P2 increased within S1, posterior N1 increased and anterior P170 decreased between S1 and S3. Fast learning effects (N1 decrement and P2 increment) were preserved in S3, but not in S4. However, slow learning effects (N1 increment and P170 decrement) were retained completely in S4.

session effect on the posterior P2 amplitude and this effect was different among S1, S3 and S4 (3×3 ANOVA, main effect of block: $F(2,18) = 6.01$, $p = 0.02$; main effect of session: $F(2,18) = 0.56$, $p = 0.57$; session $\times$ block: $F(4,36) = 2.38$, $p = 0.07$). Specifically, the P2 increased after a single block of trials in S1 (S1B1 vs S1B2: increment $0.94 \pm 0.30\,\mu$V, mean $\pm$ S.E.; $t(9) = 3.13$, $p = 0.01$). Subsequently, no significant differences were found among S1B2, S1B3, S3B1, S3B2

and S3B3 (all $t(9)s < 1.25$; $ps > 0.24$). These results indicate that the enhancement of P2 amplitude is related to fast learning that occurs only at the beginning of S1 and is preserved throughout the following consecutive training sessions. Six months later, however, the P2 amplitude in S4 showed similar changes as that in S1, both in terms of the mean value ($p = 0.58$) and in terms of the time course (S4B1 vs S4B2: increment $0.93 \pm 0.39\,\mu$V, $t(9) = 2.36$, $p = 0.04$; S4B2
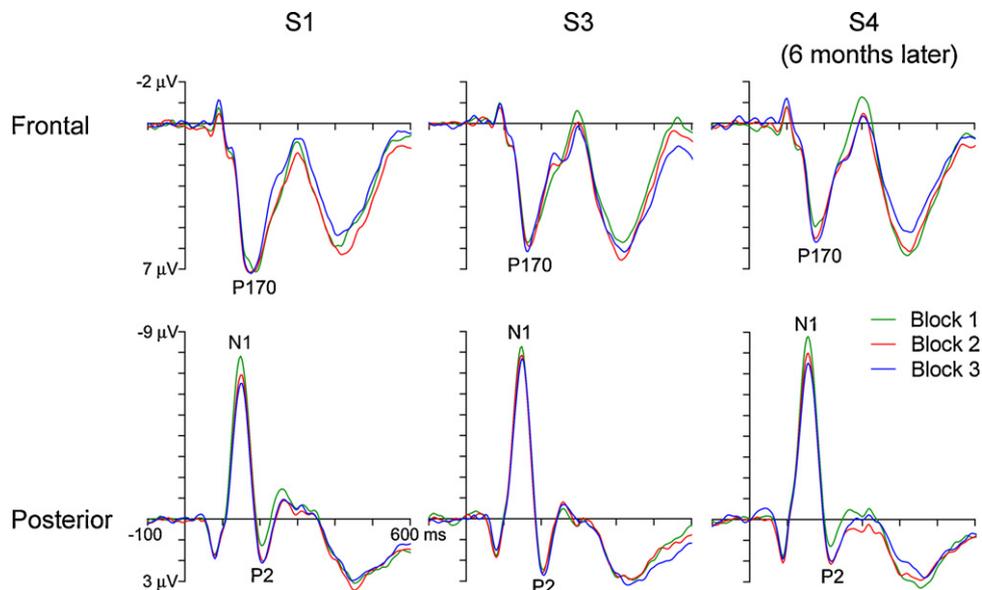

Fig. 3. Grand average ($n = 10$) ERP waveforms. Top: average waveforms of three frontal electrodes (F3, FZ, F4); bottom: average waveforms of six posterior electrodes (O1/O2, P3/P4, P7/P8).

vs S4B3: $t(9) = 0.43$, $p = 0.68$). These results indicate that the fast learning effect associated with P2 changes is not preserved after six months.

In contrast to the posterior P2, the frontal P170 amplitude showed a significant between-session effect, but no within-session effect (3×3 ANOVA, main effect of session: $F(2,18) = 10.00$, $p = 0.006$, main effect of block: $F(2,18) = 0.86$, $p = 0.42$; session × block: $F(4,36) = 0.81$, $p = 0.49$; Figs. 2c and 3). Specifically, the P170 significantly decreased from S1 to S3 (decrement: $1.73 \pm 0.34 \mu V$; $p = 0.0006$), but no changes were observed within S1 (S1B1, S1B2 vs S1B3, all $t(9)s < 0.63$, $ps > 0.54$) or S3 (S3B1, S3B2 vs S3B3, all $t(9)s < 0.52$, $ps > 0.61$). These findings suggested that such between-session frontal P170 amplitude decreases may be related to slow learning. Moreover, the P170 amplitude in S4 ($4.78 \mu V$, mean across three blocks) was significantly smaller than that in S1 ($6.79 \mu V$; $p = 0.01$), but showed no significant difference when comparing to that in S3 ($5.06 \mu V$; $p = 0.54$), indicating that the slow learning effect associated with P170 change is preserved even after six months.

More interestingly, the posterior N1 amplitude showed both significant within-session and between-session effects and these two effects showed opposite change directions (3×3 ANOVA, main effect of session: $F(2,18) = 10.44$, $p = 0.001$; main effect of block: $F(2,18) = 7.96$, $p = 0.02$; session × block: $F(4,36) = 1.18$, $p = 0.33$; Figs. 2d and 3). Specifically, N1 amplitude significantly decreased within S1 (S1B1: $-7.73 \mu V$, S1B2: $-6.98 \mu V$, S1B3: $-6.56 \mu V$; S1B1 vs S1B3, $t(9) = 2.21$, $p = 0.05$), but increased from S1 to S3 (increment: $0.98 \pm 0.28 \mu V$; $p = 0.006$). Similar to the effects observed in the P2, the within-session changes of N1 amplitude did not occur in S3 (S3B1: $-8.33 \mu V$, S3B2: $-8.01 \mu V$, S3B3: $-7.86 \mu V$; all $t(9)s < 1.14$, $ps > 0.28$), but recurred in S4 (S4B1: $-8.90 \mu V$, S4B2: $-8.11 \mu V$, S4B3: $-7.78 \mu V$; S4B1 vs S4B3, $t(9) = -5.71$, $p = 0.0003$). These findings suggested that the profound within-session decrement of N1 associated with fast learning is not preserved after six months. In addition, similar to the effects observed in the frontal P170, the mean N1 amplitude in S4 ($-8.27 \mu V$) was significantly different from that in S1 ($-7.09 \mu V$, $p = 0.004$), but showed no difference when comparing to that in S3 ($-8.07 \mu V$, $p = 0.41$), indicating that the elevation of N1 across sessions was preserved even after six months.

4. Discussion

The present study showed that, using RT as an index, visual skill training induced an improvement in behavioral performance not only during training, but also after training. The learning effect was largely preserved even after six months. These results are consistent with previous studies using threshold or accuracy as a measure, supporting the prevailing notion that skill learning is a multistep process continuing beyond the actual training experience (Karni & Bertini, 1997; Stickgold, 2005). Although RTs decreased significantly along training, reliable ERP effects were observed only on the amplitudes but not on the peak latencies, which were consistent with previous studies (e.g., Atienza et al., 2002; Alain et al., 2007; Ding et al., 2003; Song et al., 2005, 2007; Sterkin, Yehezkel, Bonneh, Norcia, & Polat, 2008; Sterkin, Yehezkel, Bonneh, Norcia, & Polat, 2009; Wang et al., in press), and suggested that the ERP amplitudes are more sensitive to training than the ERP latencies.

Most importantly, using ERP as a measure, the present study provides compelling evidence for PL-induced adult brain plasticity, which can persist over many months. Our results not only show that fast and slow visual PL are associated with different ERP changes, but also clarify the differential time courses of the fast and slow PL over a long period of memory consolidation. While fast learning effects which consisted of within-session decrement of posterior N1 and increment of posterior P2 were preserved only throughout

consecutive training sessions, slow learning effects which consisted of between-session increment of posterior N1 and decrement of frontal P170 were retained completely over a period of six months during which time no training occurred.

Fast learning associated with changes in posterior N1 and P2 amplitudes may be related to priming, adaptation or habituation process (Fahle, 2002), which involves a rapid establishing of a processing routine for the perceptual task (Karni & Bertini, 1997). This routine can be maintained only if training is not interrupted for a long period of time. Once the training is discontinued, it will fade away, and retraining is needed to rebuild the routine. Our previous studies (Ding et al., 2003; Song et al., 2005) have used a similar experimental paradigm and shown that fast learning associated with N1 changes is related to PL of both simple and complex stimuli, and can be generalized across stimuli with different spatial orientations. However, fast learning associated with P2 changes is only observed with simple stimuli and is specific to stimulus orientation. Taken together, these findings suggest that fast learning effects associated with N1 and P2 changes reflect changes of neuronal populations at different processing stages, both of which are important in establishing proper routines for processing the task stimuli.

Although the posterior N1 amplitude decreased within the initial training session, it increased strikingly between training sessions. Such opposite N1 changes may reflect differential training-induced neural changes in the same visual cortical areas, such as repetition suppression vs enhancement of neural activity to the trained stimulus in the ventral pathway (Desimone, 1996; Peissig, Singer, Kawasaki, & Sheinberg, 2007). While the observed fast or within-session effect may be related to a dynamic modification of receptive visual field properties (Kapadia, Gilbert, & Westheimer, 1994; Nowak, Sanchez-Vives, & McCormick, 2005) that occurs within several minutes and can be preserved only if training is continued, the slow or between-session effect may reflect plastic changes in synaptic connectivity (Dudai, 2004) that occurs after training and can be preserved over a long period of time without any further training. The opposite N1 effects may also account for perceptual adaptation and learning processes respectively, which were considered to have strong interactions but different time courses along training procedure (Censor & Sagi, 2008; Censor, Karni, & Sagi, 2006; Mednick et al., 2005). Different from previous studies (Censor, Bonneh, Arieli, & Sagi, 2009; Fahrenfort, Scholte, & Lamme, 2008), however, the present study did not observe reliable correlation between the N1 amplitude and behavioral performance during initial training stage. This may be due to different task paradigms and measures of behavior or due to the opposite effects of within- and between-session learning shown in the present study.

In addition to changes over the posterior visual cortex, slow learning also involves a decrease of frontal P170 distributed over the frontal cortex. Previous studies have shown that the frontal regions are involved in attentional control (Hopfinger, Woldorff, Fletcher, & Mangun, 2001). The decrease of P170 might reflect a reduction of top-down attentional modulation, which parallels the enhancement of stimulus representation in lower sensory cortex during PL. This hypothesis is supported by previous fMRI studies about visual PL of motion (Vaina, Belliveau, des Roziers, & Zeffiro, 1998) and shape (Sigman et al., 2005) the former study showed that the middle temporal visual cortex became more active while the anterior cingulate became less active after learning (Vaina et al., 1998); and the latter study found that learning induced an increased level of neural activity in retinotopic cortex and a decreased neural activity in the dorsal attentional network (Sigman et al., 2005).

In light of the converging evidence from the present findings and the literature, we propose the following model for visual PL.

PL involves at least two-phase processes: fast and slow learning phases. A fast learning phase is important for establishing and maintaining neural processing routines for the perceptual task. This processing usually occurs at the beginning of training and involves adaptive neural changes to the task stimuli. Consecutive training sessions are essential for short-term preservation of the adaptive routine. Once the neural routine has faded away due to an interruption of practice, retraining is needed to establish it again. Post-training and slow phases are important for the formation and consolidation of the long-term memory, which involves both increased stimulus representation in lower sensory cortex and decreased attentional modulation in higher level brain areas. These changes, which reflect long-term plastic changes in the brain induced by PL, develop over days and can be preserved for at least several months or even longer.

This model may reconcile a controversial issue in ERP studies of visual learning. While a number of studies have reported decreases in N1/N170 after repeated stimulus presentation (Ding et al., 2003; Heisz, Watter, & Shedden, 2006; Itier & Taylor, 2004; Song et al., 2005, 2007; Wang et al., in press), other studies have shown increased N1/N170 after extensive training (Curran, Tanaka, & Weiskopf, 2002; Scott et al., 2006). This controversy may actually reflect changes at different phases of PL. Decreases and increases of N1/N170 reported in previous studies may reflect fast and slow learning effects respectively, as indicated by the opposite within- and between-session N1 effects in the present study.

This model is also congruent with findings from other learning paradigms, including auditory PL and motor skill learning. It has been reported that fast and slow auditory PL were also associated with different ERP changes (Atienza et al., 2002), and that ERP changes associated with fast auditory PL could be preserved for days only if training was continued (Alain et al., 2007). Additionally, slow motor skill learning induced expanding of representation of trained motor sequence in M1, and such effect persisted for several months (Karni et al., 1995).

While previous studies of visual PL measured the changes of brain activities either within a single training session (e.g., Ding et al., 2003; Itier & Taylor, 2004; Skrandies et al., 2001; Song et al., 2005, 2007; Wang et al., in press), or between the first/pre and the last/post training sessions (e.g., Schiltz et al., 1999; Sigman et al., 2005; Scott et al., 2006), the present study measured both effects in a single experiment with the same subjects to directly compare the neural mechanisms of fast and slow visual PL. However, since substantial improvement may occur between the first and the second day, further studies which record the ERPs in the second training session as well are needed to discover the time course of perceptual learning and its brain mechanisms more thoroughly.

Acknowledgments

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