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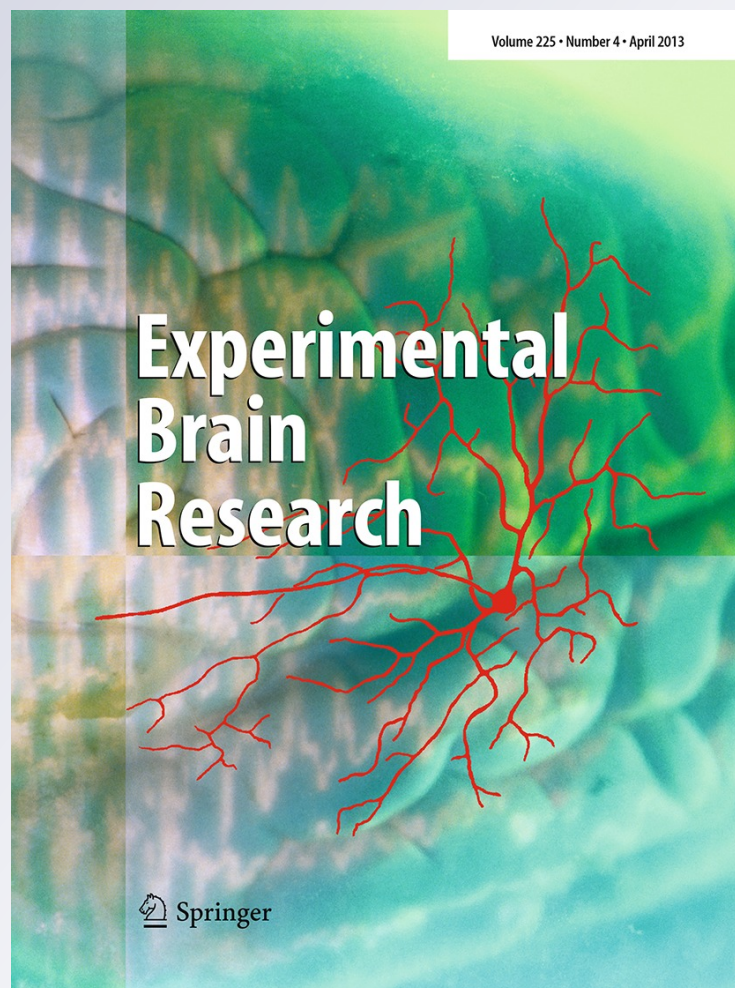
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Abstract Using combined psychophysics and event-related potentials (ERPs), we investigated the effect of perceptual learning on face gender discrimination and probe the neural correlates of the learning effect. Human subjects were trained to perform a gender discrimination task with male or female faces. Before and after training, they were tested with the trained faces and other faces with the same and opposite genders. ERPs responding to these faces were recorded. Psychophysical results showed that training significantly improved subjects' discrimination performance and the improvement was specific to the trained gender, as well as to the trained identities. The training effect indicates that learning occurs at two levels—the category level (gender) and the exemplar level (identity). ERP analyses showed that the gender and identity learning was associated with the N170 latency reduction at the left occipital-temporal area and the N170 amplitude reduction at the right occipital-temporal area, respectively. These findings provide evidence for the facilitation model and the sharpening model on neuronal plasticity from visual experience, suggesting a faster processing speed and a sparser representation of face induced by perceptual learning.

Junzhu Su and Qingleng Tan contributed equally to this work.

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Introduction

Training can improve our perceptual ability persistently, which is referred to as perceptual learning. Perceptual learning has been studied intensively in past decades because of its close links to cortical plasticity and because it reflects an inherent property of our perceptual systems and thus must be studied to understand perception (Gilbert et al. 2001; Fahle 2005; Gold and Watanabe 2010). Although the majority of perceptual learning studies concern the learning effect with simple visual features, including stereoacuity (Fendick and Westheimer 1983), spatial phase (Berardi and Fiorentini 1987), motion direction (Ball 1987), texture (Karni and Sagi 1991), hyperacuity (Fahle and Edelman 1993), orientation (Schoups et al. 1995) and contrast (Yu et al. 2004), perceptual learning also occurs with complex visual stimuli, such as objects and faces. Psychophysical studies have demonstrated that object and face perception can be significantly enhanced by training and the enhancement was usually specific to trained objects and faces (Gold et al. 1999; Furmanski and Engel 2000; Gölcü and Gilbert 2009). Bi et al. (2010) showed that face view (in-depth orientation) discrimination training could lead to a significant improvement in sensitivity to the trained face view orientation. This improved sensitivity was highly specific to the trained view and persisted up to 6 months. Hussain et al. (2009) trained subjects to identify faces in a ten-alternative forced-choice task. Subjects' identification performance

improved after training, and the improvement was specific to the trained face exemplars.

Although the effect of perceptual learning is robust with a variety of object and face stimuli, it still remains illusive how perceptual learning affects the processing and representation of trained objects and faces in the brain. Both functional magnetic resonance imaging (fMRI) and single-unit studies to date have generated inconclusive, even contradictory results. A popular view on the neural mechanism of perceptual learning is that training could induce changes in the strength and/or the selectivity of neuronal responses to trained stimuli, which has received support from recent researches. Several fMRI studies showed that object recognition or discrimination training generally increased the neural response strength to trained stimuli in ventral object-selective areas (e.g. fusiform cortex and lateral occipital cortex) (Gauthier et al. 1999; Grill-Spector et al. 2000; Jiang et al. 2007). Two neurophysiological studies showed that neuronal selectivity for trained objects was remarkably enhanced after object discrimination training (Logothetis et al. 1995; Baker et al. 2002). Consistent with these findings, fMRI adaptation studies also suggested that training could narrow neuronal tuning in the lateral occipital cortex (Yue et al. 2006; Jiang et al. 2007). However, there has been some evidence against this view. Some researchers found that neural responses in ventral object-selective areas decreased or did not change after object training (Gauthier et al. 2000; Op de Beeck et al. 2006; Yue et al. 2006; Harley et al. 2009). Other neurophysiological studies failed to find evidence of enhanced selectivity for trained objects (Vogels and Orban 1994; Erickson et al. 2000).

Object learning occurs not only at the exemplar level as described above, but also at the category level. Category perception is a fundamental property of the human brain since, ecologically, if every stimulus was perceived as a unique event, we would be rapidly inundated with pointless information. On the contrary, if we organize our perception into categories, it would allow us to describe the world in a much simpler manner and to generalize better to novel situations. Categorical face perception (e.g. race, gender, age) has been well demonstrated (Johnston et al. 1997; Campanella et al. 2001), and they can be mediated by learning. A good example is 'own-race bias', which means that humans remember own-race faces more accurately than other-race faces due to more exposure to instances of own-race faces in their life, and thus, this effect can be reduced by expertise with other-race faces (Rhodes et al. 2006; Stahl et al. 2008). Gender is another important face category. It is a very salient characteristic for face perception and is an important dimension for face representation. Psychophysical, fMRI and single-unit studies have found neuronal selectivity for face gender, especially in the ventral visual pathway (Fried et al. 2002; Webster et al. 2004; Ng et al. 2006). Yang et al. (2011) found

that visual psychophysical adaptation (i.e. tens of seconds of visual experience) to a male/female face could selectively enhance discrimination for male/female faces. However, it still remains unknown how longer visual experience (e.g. perceptual learning) affects face gender discrimination.

Su et al. (2012) used the event-related potential (ERP) technique to study the neural mechanism of face view discrimination learning (Bi et al. 2010, also see above). They investigated how the amplitude and latency of early ERP components (P100 and N170) were modulated by learning. Note that the occipito-temporal N170 component is an established neural correlate of face processing, whose amplitude and latency can be significantly modulated by face representation strength and processing speed, respectively (Rossion and Jacques 2008). They found that face view discrimination training led to a larger reduction in N170 latency at the left occipital-temporal area with the trained face view, compared with the untrained ones. However, no significant N170 amplitude change specific to the trained face view was found after training. These findings do not provide evidence that perceptual learning can alter the strength of neuronal responses at population level to those trained objects. Instead, they support the facilitation model on neuronal plasticity from visual experience, which predicts that visual experience causes faster processing of stimuli, that is, shorter latencies or shorter durations of neural firing (Friston 2005; Grill-Spector et al. 2006).

In this study, we carried out psychophysical and ERP experiments to measure the effect of perceptual learning on face gender discrimination and probe the neural correlates of the learning effect. Subjects were trained to perform a gender discrimination task with male or female faces. Before and after training, they were tested with the trained faces and other faces with the same and opposite genders. ERPs responding to these faces were recorded. We attempted to address two issues. First, what are the properties (e.g. specificity and transfer) of the face gender discrimination learning? Second, does the gender discrimination learning share the same neural mechanism (e.g. the N170 latency reduction) as the face view discrimination learning? Or are there other neural changes associated with this kind of learning?

Methods

Subjects

A total of eighteen naïve human subjects (9 male and 9 female) participated in the study. They were right-handed with reported normal or corrected-to-normal vision and had no known neurological or visual disorders. Their ages ranged from 20 to 25. They gave written, informed consent in

accordance with the procedures and protocols approved by the human subjects review committee of Peking University.

Stimuli and apparatus

Four pairs of faces were generated by FaceGen Modeller 3.1 (http://www.facegen.com/). In each pair, one face was fully female, and the other, fully male. Fully female/male faces were determined by setting the gender slider position to 100 % female/male in FaceGen Modeller 3.1. We then morphed between faces in each pair using Morpher 3.1 (http://www.asahi-net.or.jp) to generate a symmetrical continuum of 201 images (morphs) that represented a gradual transition from a fully female face to a fully male face in steps of 0.5 (gender strength ranged from 0 to 100, see also Rotshtein et al. 2005). Four morph continua used in this study are showed in Fig. 1a. For each continuum, the mean luminance and the root-mean-square (RMS) contrast of all morphs were equalized. The stimuli extended $4.5° \times 5.5°$ of visual angle.

The stimuli were presented on an IIYAMA HM204DT 22 inch monitor, with a spatial resolution of $1,024 \times 768$ and a refresh rate of 100 Hz. Subjects viewed the stimuli from a distance of 60 cm. Their head position was stabilized using a chinrest and a headrest. Throughout the experiment, subjects were asked to fixate a small white dot presented at the center of the monitor.

Designs

The study consisted of three phases—pre-training psychophysical and EEG tests, face gender discrimination training, and post-training psychophysical and EEG tests. We used QUEST staircases to measure face gender discrimination thresholds, not only in psychophysical tests, but also in training (see below).

During the training phase, each subject underwent six daily training sessions to perform a gender discrimination task at a gender strength in two randomly selected morph continua. Nine subjects were randomly selected and trained at the gender strength of 20 (female face), and the remaining nine subjects, at the gender strength of 80 (male face). A daily session (about 1 h) consisted of 28 QUEST staircases of 40 trials (Watson and Pelli 1983) (14 staircases for one continuum). In a trial, two faces with gender strengths of 20 and $20 \pm \theta$ (or 80 and $80 \pm \theta$) were each displayed for 200 ms and separated by a 600-ms blank interval (Fig. 1b). The two faces were from the same continuum. Their temporal order was randomized. Their spatial positions were randomly distributed within an $8.5° \times 8.5°$ area whose center was coincident with the fixation point, with a constraint that the two faces were separated by at least $1.5°$ of visual angle. Subjects were asked to make a two-alternative forced-choice
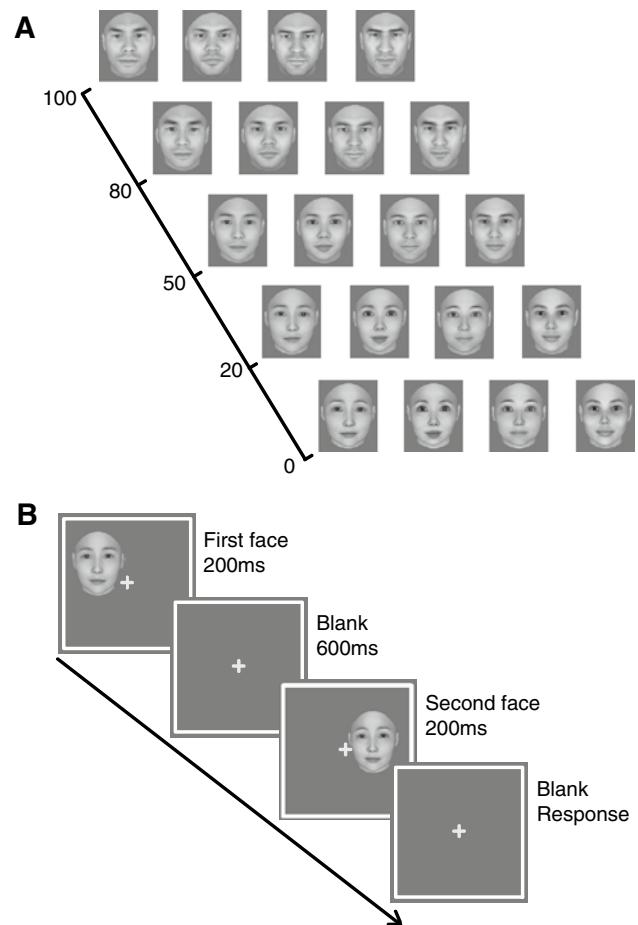

Fig. 1 Face stimuli and experimental procedure. **a** Four gender morph continua from fully female (0) to fully male (100). Each *column* represents a morph continuum. **b** Schematic description of a 2-AFC trial for measuring face gender discrimination thresholds. Two faces with a slight gender difference were presented successively. Subjects were asked to judge whether the second face was more male or more female, relative to the first face

(2-AFC) judgment, indicating whether the second face was more male or more female, relative to the first face. A high-pitched tone was provided after a wrong response and the next trial began one second after response. θ was the gender strength difference between two faces in a trial, and it varied trial by trial and was controlled by the QUEST staircase to estimate subjects' face gender discrimination threshold (75 % correct).

During the pre- and post-training test phases, psychophysical and EEG tests were performed in three face conditions—two trained faces (TF), two untrained faces that had the same gender as the trained faces but were in different continua (untrained faces with the same gender, UFS), two untrained faces that were in the same continua as the trained faces but had the opposite gender (untrained faces with the opposite gender, UFO). For example, if a subject was trained with two faces with a gender strength of 20 in continua 1

and 2, he/she was tested not only with the two trained faces, but also with the two faces with a gender strength of 80 in continua 1 and 2 and the two faces with a gender strength of 20 in continua 3 and 4. We first measured face gender discrimination thresholds in the three face conditions (always at gender strengths of 20 and 80). Eight QUEST staircases (same as above) were completed for each condition—four staircases for one face. The three conditions were counterbalanced within subjects. Discrimination thresholds from the eight staircases in a condition were averaged as a measure of subjects' discrimination performance. Subjects' performance improvement in a condition was calculated as (pre-training threshold−post-training threshold)/pre-training threshold × 100 %. To measure the time course of the training effect (learning curve), discrimination thresholds from 28 QUEST staircases in a daily training session were averaged and then plotted as a function of training day. Learning curves were fitted with a power function (Jeter et al. 2009).

After acquiring psychophysical discrimination thresholds, we recorded EEG signals in the three face conditions. The EEG test consisted of 20 blocks of 36 trials. A block included twelve trials for each condition. There were totally 240 trials for each condition (120 trials for one of two faces). In a trial, two faces were each presented for 200 ms and separated by a 600 ms blank interval. Similar to the psychophysical test, subjects were asked to make a 2-AFC judgment of the gender strength of the second face relative to the first face (more female or male) by pressing one of two buttons with their left and right index fingers. The first face always had the gender strength of 20 or 80 to make sure that, in the pre-training and the post-training tests, ERPs were evoked by the same stimuli (see EEG recoding and analysis). The gender difference (increment or decrement) between the first and the second faces was the discrimination threshold (75 % correct) for the first face measured in the psychophysical test. Note the stimulus order in the EEG trials was different from that in the psychophysical trials, but the difference did not change the nature of the task because subjects performed equally well in the psychophysical and the EEG tests. In a block, the order of the three conditions was randomized. Subjects were asked to refrain from blinking and they took a short break between blocks.

Prior to the experiment, subjects practiced four QUEST staircases (160 trials) for each condition to get familiar with the stimuli and the experimental procedure.

EEG recording and analysis

EEG was continuously recorded from 28 scalp electrodes that were mounted on an elastic cap according to the 10–20 system, including F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, T7, C3, Cz, C4, T8, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, O1, Oz and O2. The electrode at the right mastoid was used as on-line reference. Electrode impedance was kept below 5 kΩ. Eye blinks and vertical eye movement were monitored with electrodes located above and below the left eye. Horizontal electro-oculogram (EOG) was recorded from electrodes placed 1.5 cm lateral to the left and right external canthi. EEG was amplified with a gain of 500 K, bandpass filtered at 0.05–100 Hz and digitized at a sampling rate of 1,000 Hz. EEG epochs were made (see below) and referenced off-line to a common average reference (Rossion et al. 2000). Those epochs contaminated by eye blinks, eye movements or muscle potentials exceeding ±50 µV at any electrode were excluded from further analysis.

EEG epochs beginning 200 ms before the onset of the first face in a trial and continuing for 600 ms were made. They were selectively averaged according to three face conditions. The average waveforms were low-pass filtered at 30 Hz and baseline corrected with respect to the mean voltage of the 200 ms pre-stimulus interval. Our analysis focused on the peak amplitude and latency (relative to stimulus onset) of N170 and P100 at the occipito-temporal electrodes.

Results

Psychophysical results

We first measured subjects' face gender discrimination thresholds in three face conditions—trained faces (TF), untrained faces with the same gender (UFS), untrained faces with the opposite gender (UFO). Then, subjects practiced for 6,720 trials during six daily training sessions on face gender discrimination at the gender strength of 20 or 80. Throughout the training course, their discrimination thresholds gradually decreased (Fig. 2a). After training, we measured thresholds in the three conditions again.

After training, subjects' gender discrimination thresholds decreased significantly in the TF ($t(17) = 8.616$, $p < 0.001$) and UFS ($t(17) = 4.271$, $p = 0.001$) conditions, but remained about the same in the UFO condition ($t(17) = -2.047$, $p = 0.056$) (Fig. 2b). We calculated percent improvements in discrimination performance after training. The improvements were 30.9, 9.3 and −7.4 % in the TF, UFS and UFO conditions, respectively. Their differences were significant (TF vs. UFS: $t(17) = 4.510$, $p < 0.001$; UFS vs. UFO: $t(17) = 2.642$, $p = 0.017$; TF vs. UFO: $t(17) = 7.070$, $p < 0.001$) (Fig. 2c). These results demonstrated that the face learning effect was largely specific to the trained faces. The effect could be partially transferred to the untrained faces with the same gender as the trained face, which suggests that the effect was not only identity specific, but also gender specific.
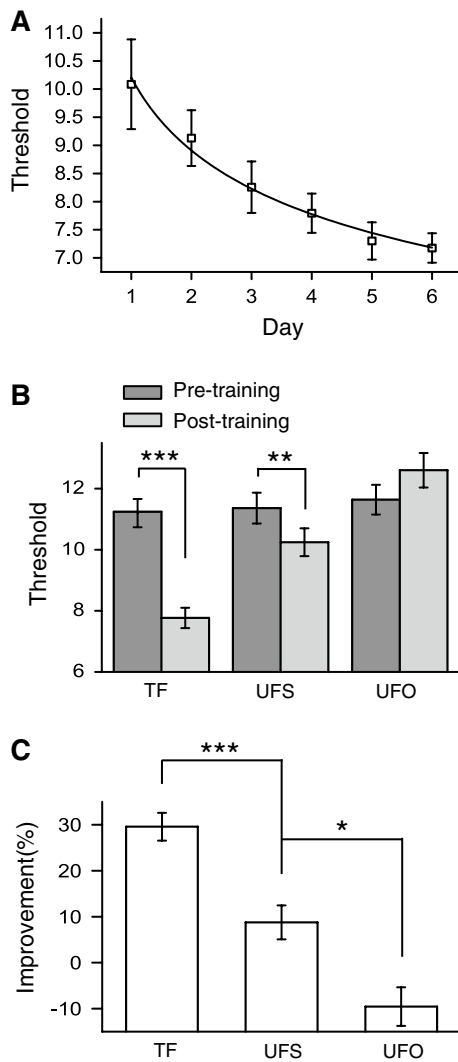
Fig. 2 Psychophysical results. **a** Learning curve with the trained faces. Face gender discrimination thresholds are plotted as a function of training day. **b** Face gender discrimination thresholds before and after training in the three face conditions—the trained faces (TF), the untrained faces with the same gender as the trained faces (UFS), the untrained faces with the opposite gender to the trained faces (UFO). *Asterisks* indicate a statistically significant difference between the pre-training and post-training tests (****$p < 0.01$; ***$p < 0.001$**). **c** Percent improvement in face gender discrimination performance after training. *Asterisks* indicate a statistically significant difference between the face conditions (*$p < 0.05$; ***$p < 0.001$). *Error bars* denote 1 SEM calculated across subjects

Fig. 3 ERP results. **a** Mean voltage topographies between 160 and 180 ms after the onset of the trained faces (TF) before and after training. *Black dots* indicate electrode locations. **b** Grand averaged ERPs at P7 and P8 evoked by the trained faces before and after training

ERP results

Since the occipito-temporal N170 component is an established neural correlate of face processing, our ERP analysis focused on N170 latency and amplitude. Figure 3a shows the mean voltage topographies between 160 and 180 ms after the onset of the trained faces before and after training. Consistent with previous studies (Rossion and
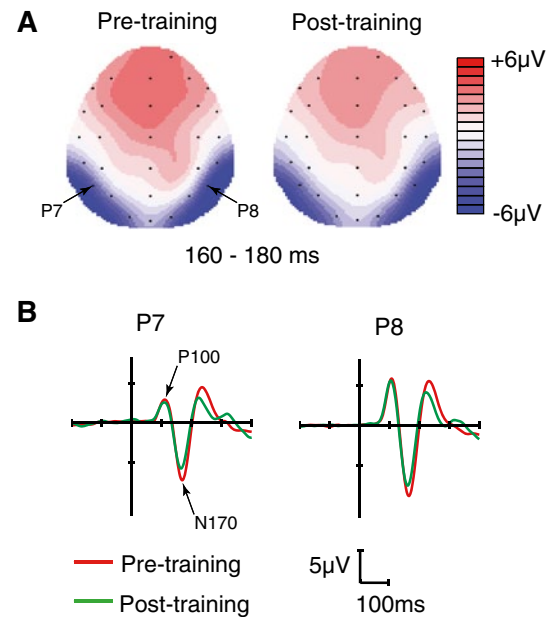
Jacques 2008; Chen et al. 2009), the left and right occipito-temporal areas (i.e. P7 and P8, respectively, see Fig. 3b) exhibited the largest N170 responses to faces (only one subject did not show an identifiable N170 at P7). Thus, ERP data analyses were performed with the peak amplitude and latency (relative to stimulus onset) of N170 at P7 and P8. Inspection of Fig. 3b revealed that, relative to the pre-training test, the N170 amplitude reduced in the post-training test. However, it was unclear if the reduction was due to the discrimination learning itself or some other factors (i.e. day-to-day measurement variance and stimulus repetition in the pre- and post-training tests). To resolve this issue, we performed the following analyses to search for changes in peak amplitude and latency that were specifically related to the face gender discrimination learning. For both electrodes, a repeated-measures analysis of variance (ANOVA) of peak amplitude and latency was performed with test (pre- and post-training tests) and face condition (TF, UFS and UFO) as within-subject factors. A main effect of test means a significant amplitude/latency difference between the pre- and post-training tests. An interaction effect between test and face condition means that the difference varies significantly across face conditions. Since there was no significant performance change after training in the UFO condition, the amplitude/latency difference in this condition can be used to quantify the effects of day-to-day measurement variance and stimulus

repetition. Planned paired *t* tests were run to compare amplitude/latency differences between the TF, UFS and UFO conditions. If the difference in the TF and/or UFS conditions is significantly larger than that in the UFO condition, the difference should be specifically related to the discrimination learning.

Figure 4 shows N170 amplitudes and latencies at P7 and P8 in the pre- and post-training tests and their differences between the two tests. At P7, there was a significant main effect of test on the latency ($F(1,32) = 12.714$, $p = 0.003$),

but not on the amplitude ($F(1,32) = 1.948$, $p = 0.182$). The latency reduced in the post-training test relative to the pre-training test. For the latency, P7 also showed a significant interaction between test and face condition ($F(2,32) = 4.461$, $p = 0.020$). Further planned paired *t* tests showed that the latency reduction in the UFO condition was significantly smaller than those in the TF ($t(16) = 2.126$, $p = 0.049$) and UFS ($t(16) = 2.849$, $p = 0.012$) conditions. But there was no significant difference between the TF and UFS conditions ($t(16) = 0.233$, $p = 0.819$). These results suggest that

Fig. 4 N170 amplitudes and latencies in the pre- and post-training tests and their differences between the two tests at P7 (**a**) and P8 (**b**). *Asterisk* indicates a statistically significant difference between the face conditions (*$p < 0.05$). *Error bars* denote 1 SEM calculated across subjects
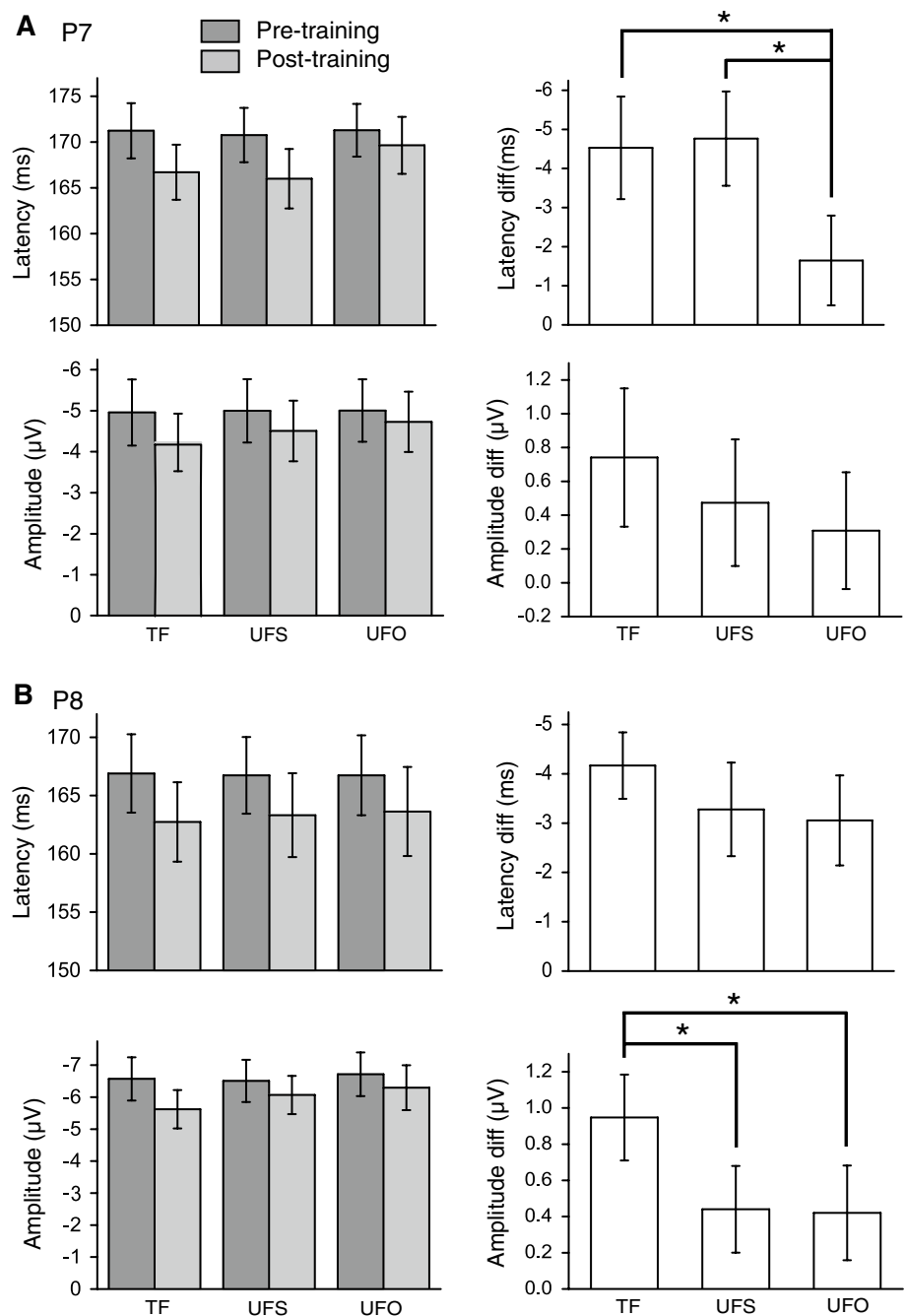
the face gender discrimination training led to a larger reduction in N170 latency at P7 with the trained gender, compared with the untrained gender. The effect manifested not only with the trained faces, but also with the untrained faces that had the same gender as the trained faces.

At P8, there was a significant main effect of test on both the latency ($F(1,34) = 20.590$, $p < 0.001$) and amplitude ($F(1,34) = 7.256$, $p = 0.015$). Both the latency and amplitude reduced in the post-training test relative to the pre-training test. However, a significant interaction between test and face condition was found only with the amplitude ($F(2,34) = 5.526$, $p = 0.008$). Further planned paired t tests showed that the amplitude reduction in the TF condition was significantly larger than those in the UFS ($t(17) = 2.726$, $p = 0.014$) and UFO conditions ($t(17) = 2.866$, $p = 0.011$). But there was no significant difference between the UFS and UFO conditions ($t(17) = 0.118$, $p = 0.908$). These results suggest that the training led to a larger reduction in N170 amplitude at P8 with the trained faces, compared with the untrained faces (even when the untrained faces had the same gender as the trained faces). In other words, this effect was specific not only to the trained gender, but also to the trained identities.

The P100 is an earlier component than the N170, peaking at around 100 ms after stimulus onset. It is thought to originate from striate and extrastriate visual areas (Di Russo et al. 2002). Previous studies (Goffaux et al. 2003; Itier and Taylor 2004a) have reported a larger P100 in response to faces than to objects, which might imply a face-selective characteristic of this component. Thus, we performed similar statistical analyses with the P100 amplitude and latency. We did not find any effect specific to the trained faces.

Discussion

Subjects were trained intensively with a fine gender discrimination task. After training, their gender discrimination performance was significantly improved and the improvement was largely specific to the trained faces. The learning effect was found to be partially transferred to the untrained faces with the same gender as the trained faces. However, no learning effect was found with the untrained faces with the opposite gender to the trained faces. The specificity of the learning effect to the trained gender and identities suggests that the learning occurs at two levels—the category level (gender) and the exemplar level (identity).

From the ERP measurements, we found that the gender discrimination learning could modify the N170 amplitude and latency. Relative to the untrained faces with the opposite gender of the trained faces, the untrained faces with the same gender as the trained faces had a larger N170 latency reduction at the left occipital-temporal area. The trained

faces also had a larger N170 latency reduction at the left occipital-temporal area, as well as a greater N170 amplitude reduction at the right occipital-temporal area. Since the amplitude reduction and the latency reduction were specific to the trained gender and identities, respectively, it is very likely that they were associated with the gender learning and the identity learning correspondingly.

The occipito-temporal N170 enjoys an important and unique status in face studies and is considered a neural correlate of face perception. This face-specificity view of the N170 is mainly supported by two findings. One is that the amplitude of the N170 is systematically larger to faces than to other object categories (Bentin et al. 1996; Itier and Taylor 2004a). The other is that the N170 is enhanced and delayed specifically by face inversion (Rossion et al. 2000), a manipulation that impairs face identification probably by disrupting configural processing (face inversion effect, Yin 1969).

In this study, we found that the gender learning effect was associated with the N170 latency reduction at the left occipital-temporal area. Many studies have demonstrated that the N170 latency is closely correlated with face processing speed (McCarthy et al. 1999; Itier and Taylor 2004b; Jacques and Rossion 2007). On one hand, face inversion and face contrast reversal are well known to impair face perception by disrupting configural information at the encoding stage of face processing. It has been shown that both of them led to a delayed behavioral response and N170 (Itier and Taylor 2004b; Jacques and Rossion 2007). On the other hand, face repetition priming could speed up behavioral response and shorten the N170 latency (Itier and Taylor 2004b). Thus, our ERP results suggest that the gender discrimination learning induced a faster speed of face processing, which is consistent with the study on face view discrimination learning (Su et al. 2012). The finding of the N170 latency reduction after training provides evidence for the facilitation model, which predicts that visual experience causes faster processing of stimuli, that is, shorter latencies or shorter durations of neural firing (Friston 2005; Grill-Spector et al. 2006). The model assumes that the cause of this faster processing is synaptic potentiation between neurons following visual experience and that this potentiation can occur at many levels in the processing stream. Consequently, information flows through the stream more rapidly, and hence, identification of a trained stimulus occurs faster (Grill-Spector et al. 2006).

We also found that the identity learning effect was associated with the N170 amplitude reduction at the right occipital-temporal area. In previous studies, there is no consensus on how learning modulates the magnitude of neural response. Some fMRI studies showed that object recognition or discrimination training generally increased the neural response strength to trained stimuli in ventral object-selective areas

(Gauthier et al. 1999; Grill-Spector et al. 2000; Jiang et al. 2007). But others found that neural responses in these areas decreased or did not change after object training (Gauthier et al. 2000; Op de Beeck et al. 2006; Yue et al. 2006; Harley et al. 2009). Because ERPs reflect neuronal responses at population level, the N170 amplitude reduction finding can be well explained by the sharpening model proposed by Desimone (1996) and Wiggs and Martin (1998), which has been used to explain another kind of plasticity—priming. According to the model, neuronal tuning curves become narrower ('sharpened') after training. Neurons that initially respond to the trained stimuli and code features irrelevant to the discrimination task will show a response reduction. As a consequence, representation of the trained stimuli becomes sparser, resulting in fewer responsive neurons in total, which likely manifests as the N170 amplitude reduction. Because the representation becomes sharper, the neurons become more sensitive to change, thereby contributing to the behavioral performance improvement.

It is well established that face priming could lead to the reduction in the N170 amplitude and latency (Itier and Taylor 2004b). We observed similar reductions in the current perceptual learning study. Indeed, Posner et al. (1997) has suggested that priming and perceptual learning are two possible versions of the same process of automaticity, which share underlying neuronal mechanisms.

An interesting phenomenon in this study is that the N170 latency and amplitude reductions occurred in the left and right hemispheres, respectively. The right hemisphere dominance in face processing has been documented in the literature for a long time (Gazzaniga and Smylie 1983). N170 is also well known for its right lateralized topographical distribution on occipital-temporal sites (Rossion and Caharel 2011). It is typically larger at P8 than at P7 (see Fig. 2). However, Grill-Spector et al. (2004) showed that both left and right FFA (fusiform face area) activities were correlated with face recognition. To date, we still do not know much about the functional difference between the two hemispheres in face processing. Nevertheless, there is converging evidence suggesting that the left hemisphere (e.g. left FFA) is more susceptible to perceptual learning and more plastic. First, Rossion et al. (2002) found that training with novel objects (i.e. Greebles) led to a left-lateralized face-like N170 response. Second, Su et al. (2012) showed that face view discrimination training led to a larger reduction in N170 latency only at the left occipital-temporal area with the trained face view, compared with the untrained ones. Third, fMRI studies on the other-race effect in face perception have demonstrated that effects of long-term visual experience on face recognition were correlated with the activity in left FFA (Golby et al. 2001; Feng et al. 2011). Our study not only provides further evidence on the plasticity of the left hemisphere, but also shows that the right hemisphere is also adaptive in face processing. We have suggested that the neural changes in the left and right hemispheres are associated with learning at two levels—the category level (gender) and the exemplar level (identity), respectively. This is consistent with an influential theory on hemispheric asymmetry in visual processing—left hemisphere pathways may mediate categorical visual processes that maximize similarities among examples in a category, whereas right hemisphere pathways may mediate coordinate visual processes that maximize individuation between examples in a category (Kosslyn et al. 1989).

We believe that our results cannot be explained by other factors (e.g. attention, task difficulty, eye movement). During the pre- and post-training EEG recording periods, subjects performed the same discrimination task as that during training. There was no significant difference in subjects' discrimination performance between the pre- and post-training tests (both were about 75 % correct), suggesting no difference in task difficulty and (presumably) attention. In our study, subjects were asked to fixate a small white dot throughout the experiment. The latency of miniature saccade is usually larger than 200 ms (Yuval-Greenberg et al. 2008). Our data analysis focused on the ERP components whose latencies are shorter than 200 ms, thereby avoiding possible contamination from miniature saccade.

In summary, perceptual learning of face gender discrimination led to the N170 latency reduction at the left occipital-temporal area and the N170 amplitude reduction at the right occipital-temporal area, which were associated with the gender and identity learning, respectively. These findings provide evidence for the facilitation model and the sharpening model on neuronal plasticity from visual experience, suggesting a faster processing speed and a sparser representation of face induced by perceptual learning.

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