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Souza et al. 2005; Desimone et al. 1984; Perrett et al. 1985,

was randomized. Their spatial positions were randomly distributed within a  $6.2 \times 6.2^\circ$  area whose center was coincident with the fixation point, with a constraint that these two face views were separated by  $\geq 1.5^\circ$  of visual angle. Subjects were asked to make a two-alternative-forced-choice (2-AFC) judgment of the orientation of the second face relative to the first face (left or right). A high-pitched tone was provided after a wrong response, and the next trial began 1 s after response. The  $\theta$  varied trial by trial and was controlled by the QUEST staircase to estimate subjects' face view discrimination threshold (75% correct).

Before and after the 8-day training, we tested subjects' discrimination performance. Their face view discrimination thresholds were measured at the face orientations of  $-90^\circ$ ,  $-60^\circ$ ,  $-30^\circ$ ,  $0^\circ$ ,  $30^\circ$ ,  $60^\circ$ , and  $90^\circ$  (Fig. 1). Eight QUEST staircases (same as above) were completed for each orientation and each subject within 2 days. These seven orientation conditions were counterbalanced within individual subjects. Before the experiments, subjects practiced two staircases (80 trials) for each orientation to get familiar with the stimuli and the experiment procedure.

In *Part 1* (Fig. 1, *Panel A*), we examined the orientation

averaged as a measure of subjects' discrimination performance and plotted as a function of orientation. Note that subjects were randomly selected to be trained at either  $-30^\circ$  or  $+30^\circ$ . Because training at the two orientations induced a similar learning effect, for the sake of presentation simplicity, the discrimination performance functions for subjects trained at  $-30^\circ$  were flipped horizontally and averaged together with the functions for subjects trained at  $+30^\circ$ . Subjects' performance improvement at an orientation was calculated as  $(\text{pre-training threshold} - \text{posttraining threshold}) / \text{pretraining threshold} \times 100\%$ . To measure the time course of the training effect (learning curve), discrimination thresholds from 25 QUEST staircases in a daily training session were averaged and plotted as a function of training day. Learning curves were fitted with a power function (Jeter et al. 2009).

To quantify the transfer of training between the trained and the test stimuli, transfer index was defined as the ratio of performance improvement with the test stimulus and that with the trained stimulus. Performance improvement with the trained stimulus over eight daily training sessions was calculated as  $(1\text{st day threshold} - 8\text{th day threshold}) / 1\text{st day threshold} \times 100\%$ . The test stimulus here had the same orientation as the trained stimulus. Paired  $t$ -test and independent-samples  $t$ -test were carried out for within-subject comparisons and between-subject comparisons, respectively.

## RESULTS

In *Experiment 1*, we first measured subjects' face view discrimination thresholds at seven orientations of  $-90^\circ$ ,  $-60^\circ$ ,  $-30^\circ$ ,  $0^\circ$ ,  $30^\circ$ ,  $60^\circ$ , and  $90^\circ$  (Fig. 1, and ). Subjects practiced for 8,000 trials during eight daily training sessions on face view discrimination at the orientation of  $30^\circ$ . Throughout the training course, their discrimination thresholds gradually decreased, which resulted in a 36% performance improvement (Fig. 1 ). After training,  $90^\circ$  (Fig. 1,

orientation specific because the improvement with the test stimulus at 30° was 41%, significantly higher than those at the untrained orientations [all (6) > 2.5, < 0.05].

In Experiment 1 and 2, the test stimulus was a face and the trained stimuli were an inverted face (Fig. 2) and an M-like paperclip (Fig. 2). Here we examined how face inversion and object category change affected the learning transfer. Similar to the training effect with an upright face, training with the inverted face and the paperclip at the orientation of 30° also improved subjects' discrimination performance by 36 and 45%, respectively. However, compared with Experiment 2, the performance improvements with the test face at 30° were weak (13 and 22%). These improvements were not orientation-specific because there was no significant difference between the trained orientation and the untrained orientations [inverted face: all (6) < 1.9, > 0.12; paperclip: all (7) < 2.3; > 0.07].

To quantify the transfer of training between the trained and the test stimuli, the transfer index was calculated as the ratio of performance improvement with the test stimulus and that with the trained stimulus (Fig. 3). A large index means that a large amount of the training effect has been transferred to the test stimulus; in other words, the performance improvement with the test stimulus can be largely attributed to the training effect. The transfer indices in Experiments 1-5 were 1.23, 1.12, 1.06, 1.27, and 1.18. There was no significant difference among them [F(6,50) = 1.176, p = 0.336]. Note that, in Experiment 1, the test and the trained stimuli were the same. These results suggest a complete transfer from the trained stimulus to the test stimulus in Experiments 2-5. Why are the indices larger than 1? This is because the threshold measurement before training also led to some learning effect. The transfer indices in Experiments 1 and 2 were 0.37 and 0.54, respectively. There was no significant difference between them (F = 0.85, p = 0.41). However, they were significantly lower than the indices in

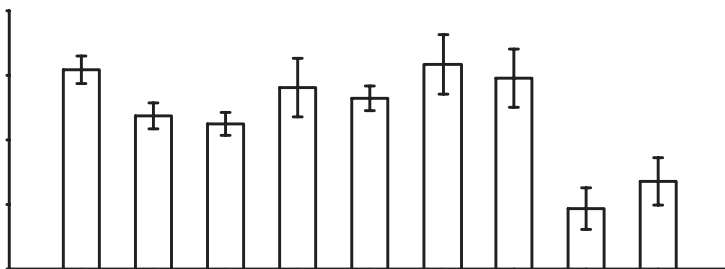
Experiment 5 [F(8,65) = 5.616, p < 0.001], which suggests a partial or weak transfer in Experiments 1 and 2.

## DISCUSSION

We see faces from various viewing angles every day. Face view perception informs us not only about a person's identity but also about his/her social attention. Even from a small face view change, we could infer changes in their current goals and intentions (Nummenmaa and Calder 2009). Can our ability of face view perception (discrimination) be improved with training? In this study, a series of seven experiments was conducted to address this question and to investigate the characteristics of perceptual learning of face view discrimination.

Experiment 1 showed that training led to a significant improvement in sensitivity to face view orientation. The improvement was highly specific to the trained orientation and lasted up to 6 mo. In Experiment 2, we found that the orientation-specific learning effect completely transferred across changes in face size, visual field, and face identity. A complete transfer also occurred between two partial face images that were mutually exclusive but constituted a complete face. However, the transfers were weak between an upright face and an inverted face and between a paperclip object and a face, as shown in Experiments 1 and 2. It should be noted that, in most experiments, only one face stimulus was used. These conclusions can be further strengthened if more face stimuli were used.

Face view learning exhibited two important characteristics of perceptual learning: specificity and persistence (Liu 1999; Sasaki et al. 2010). Training at 30° had a very weak effect on the discrimination performance at other orientations, even at 0° and 60°. It could be argued that subjects' view sensitivity at 0° (cardinal orientation) was already very high, leaving little room for improvement. To rule out the explanation, we trained two subjects using the same procedure as that for 30°. The training



resulted in a 48% performance improvement at  $0^\circ$ , comparable to the training effect at  $30^\circ$ . It has been reported that some face neurons in STS responded symmetrically to left and right views (De Souza et al. 2005). This would predict that training at  $30^\circ$  should also lead to a higher performance improvement at  $-30^\circ$  than at  $0, \pm 60$ , and  $\pm 90^\circ$ . However, we did not find such an effect, which indicates that training might have a very weak or little influence on these STS neurons. The benefits of perceptual learning with visual features are usually long-lasting, persisting for up to 2 yr (Karni and Sagi 1993). In high-level vision, training effects with a shape/object identification task could last 1 mo (Furmanski and Engel 2000; Sigman and Gilbert 2000). Here, we expanded these results by showing that the orientation-specific face view learning could last  $\leq 6$  mo.

Using a visual search or identification task, past studies indicated that face/shape recognition is subject to perceptual learning (Furmanski and Engel 2000; Golcu and Gilbert 2009; Hussain et al. 2009; Sigman and Gilbert 2000). However, few of them studied the characteristics of high-level visual perceptual learning as comprehensively as this study. There are two similar findings in previous studies and ours. One is the complete transfer across a change in face size, in agreement with the finding that object learning was insensitive to image size (Furmanski and Engel 2000). The other is the weak transfer from an upright face to its vertical inversion. Hussain et al. (2009) also found that face

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