

# Function and Structure of Human Left Fusiform Cortex Are Closely Associated with Perceptual Learning of Faces

Taiyong Bi,<sup>1,2,9</sup> Juan Chen,<sup>3,4,5,9</sup> Tiangang Zhou,<sup>6</sup> Yong He,<sup>7,8</sup> and Fang Fang<sup>3,4,5,\*</sup>

<sup>1</sup>Key Laboratory of Cognition and Personality (SWU), Ministry of Education, Chongqing 400715, China

<sup>2</sup>Faculty of Psychology, Southwest University, Chongqing 400715, China

<sup>3</sup>Department of Psychology and Key Laboratory of Machine Perception (Ministry of Education), Peking University, Beijing 100871, China

<sup>4</sup>Peking-Tsinghua Center for Life Sciences, Peking University, Beijing 100871, China

<sup>5</sup>PKU-IDG/McGovern Institute for Brain Research, Peking University, Beijing 100871, China

<sup>6</sup>State Key Laboratory of Brain and Cognitive Science, Institute of Biophysics, Chinese Academy of Sciences, Beijing 100101, China

<sup>7</sup>State Key Laboratory of Cognitive Neuroscience and Learning and IDG/McGovern Institute for Brain Research, Beijing Normal University, Beijing 100875, China

<sup>8</sup>Center for Collaboration and Innovation in Brain and Learning Sciences, Beijing Normal University, Beijing 100875, China

## Summary

Training can lead to long-lasting improvement in our perceptual ability, which is referred to as perceptual learning. Unraveling its neural mechanisms has proved difficult. With functional and structural magnetic resonance imaging (MRI), we addressed this issue by searching for the neural correlates of perceptual learning of face views over a long time course. Human subjects were trained to perform a face view discrimination task. Their behavioral performance and MRI signals were measured before, immediately after, and 1 month after training. We found that, across individual subjects, their behavioral learning effects correlated with the stability improvement of spatial activity pattern in the left fusiform cortex immediately after and 1 month after training. We also found that the thickness of the left fusiform cortex before training could predict subjects' behavioral learning effects. These findings, for the first time, not only suggest that, remarkably, the improved pattern stability contributes to the long-term mechanisms of perceptual learning, but also provide strong and converging evidence for the pivotal role of the left fusiform cortex in adaptive face processing.

## Results and Discussion

Perceptual learning has been studied extensively both 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 [1]. Not surprisingly, visual object recognition and discrimination rely critically on learning [2]. Although behavioral characteristics of

object perceptual learning have been well recognized [3, 4], its neural mechanisms remain elusive. A popular view is that training could induce strong and focal changes in the strength and/or the selectivity of neural responses to trained stimuli. However, evidence from both functional magnetic resonance imaging (fMRI) and neurophysiology is inconclusive, even contradictory [5–10]. An alternative view is that perceptual learning introduces moderate and distributed effects that modulate a preexisting, rich, and flexible set of neural object representations [11].

Notably, two critical issues in object perceptual learning (and other kinds of visual perceptual learning) are left unaddressed. First, we know almost nothing about the mechanisms mediating long-lasting learning effects. Previous studies usually focused on neural changes immediately after training, and attempts to reveal the mechanisms did not succeed [12, 13]. For example, the learning effect with a texture segmentation task could be retained for at least 2–3 years [12]. Yotsumoto and colleagues [13] measured the dynamics of subjects' behavioral performance with the task and their V1 activation over a long time course of perceptual learning. Within the first few weeks of training, V1 activation in a subregion corresponding to the trained visual field quadrant and task performance both increased. However, while the improved performance was maintained 2 weeks after training, the V1 activation decreased to the level observed before training. Thus, the long-term mechanisms of perceptual learning are still mysterious. Second, there is no existing knowledge of neuroanatomic correlates of visual perceptual learning, although considerable progress has been made with other types of learning (e.g., music learning, language learning) [14–17]. These two issues are not only theoretically interesting, as they inform us about brain organization and limits of plasticity, but they also have significant clinical implications as they can assist the development of optimal training/rehabilitation programs [18].

To address the issues raised above, we took advantage of a behavioral paradigm developed previously [19] and performed three MRI experiments to investigate the functional and structural correlates of perceptual learning of face views (Figure 1A) over a long time course. We used this paradigm not only because perceptual learning of face views clearly exhibited two fundamental characteristics of perceptual learning—specificity and persistency—but also because face view perception is important for face recognition [20] and social perception [21].

## Psychophysical Results

Experiment 1 consisted of four phases—pretraining test (Pre), face view discrimination training, posttraining test 1 (Post1), and posttraining test 2 (Post2). Pre, Post1, and Post2 took place on the days before, immediately after, and 1 month after training (Figure 1B). During the training phase, subjects underwent eight daily training sessions (1,000 trials per session) to discriminate face views around the in-depth face orientation of 30°. In a trial, two face views with slightly different orientations were presented sequentially. Subjects were asked to make a two-alternative forced-choice (2-AFC) judgment of the orientation of the second view relative to the first (left or

<sup>9</sup>These authors contributed equally to this work.

\*Correspondence: [ffang@pku.edu.cn](mailto:ffang@pku.edu.cn)

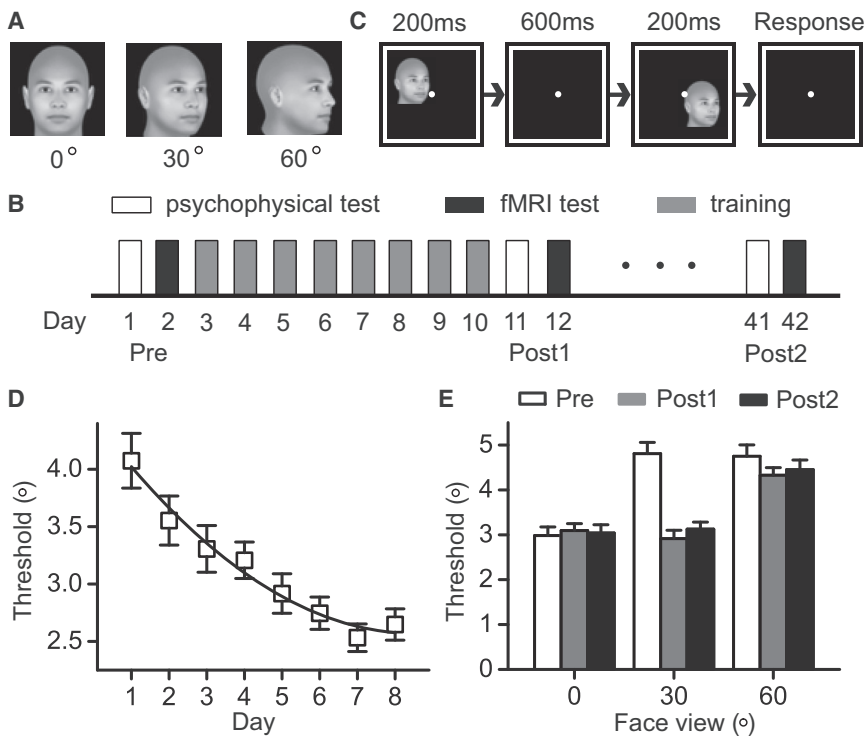


Figure 1. Stimuli, Design and Psychophysical Results of Experiment 1

(A) Exemplar face views at the orientations of 0°, 30°, and 60°.  
 (B) Schematic description of a two-alternative forced-choice (2-AFC) trial in a QUEST staircase for measuring face view discrimination thresholds.  
 (C) Experimental protocol. Subjects underwent eight daily training sessions. The pretraining test (Pre) and the posttraining test 1 (Post1) and test 2 (Post2) took place on the days before, immediately after, and 1 month after training.  
 (D) Learning curve. Face view discrimination thresholds are plotted as a function of training day.  
 (E) Face view discrimination thresholds for the 0°, 30°, and 60° face views at Pre, Post1, and Post2. Error bars indicate 1 SEM. See also Figure S1.

right) (Figure 1C). QUEST staircase [22] was used to control the orientation difference between the two views adaptively for estimating subjects' face view discrimination thresholds (75% correct). Throughout the training course, their thresholds gradually decreased and saturated after day 6 (Figure 1D).

During the three test phases, psychophysical and MRI tests were performed. We first measured face view discrimination thresholds at the orientations of 0°, 30°, and 60°, similar to the training phase. Relative to Pre, the discrimination thresholds at Post1 and Post2 were significantly lower for the trained view (i.e., the 30° view; both  $t(17) > 11.79$ ,  $p < 0.001$ ), but showed little change for the untrained views (i.e., the 0° and 60° views; all  $t(17) < 2.13$ ,  $p > 0.05$ ) (Figure 1E). This result demonstrated that training led to a significant learning effect, which was specific to the trained view and persisted up to 1 month.

**fMRI Results**

After acquiring the thresholds, we measured blood-oxygenation-level-dependent (BOLD) signals responding to the three face views in 18 fMRI runs. Each run consisted of three 12 s stimulus blocks, one for each view, interleaved with three 18 s blank intervals. Each stimulus block contained five trials. The trials and subject's task were very similar to those in the psychophysical tests except that the orientation difference of two views in a trial was the discrimination threshold measured in the preceding psychophysical test, which caused subjects to perform equally well across blocks and tests.

The first purpose of experiment 1 was to investigate whether or not there was any long-term neural change associated with the persistent behavioral learning effect. We focused the data analyses on BOLD signals in several regions of interest (ROIs), which were face selective areas and early visual cortex (EVC, consisting of V1 and V2; see the Supplemental Experimental Procedures available online). Face selective areas included the left and right fusiform face areas (IFFA and rFFA), the left

and right superior temporal sulci (ISTS and rSTS), and the left and right occipital face areas (IOFA and rOFA). BOLD signals were analyzed in two ways—univariate amplitude analysis and multivariate pattern analysis (MVPA). For the univariate amplitude analysis, in each ROI, BOLD signal amplitudes for the 0°, 30°, and 60° face views were estimated with a general linear model (GLM) (Figure S1A) and were then used to calculate the learning modulation index (LMI) for BOLD amplitude as follows: [Amp (trained view posttraining) – Amp (trained view pretraining)] – [Amp (untrained views posttraining) – Amp (untrained views pretraining)] [10, 23]. The mean amplitude for the 0° and 60° views served as the amplitude for the untrained views. The LMI quantified the amplitude difference for the trained view before and after training while subtracting out the difference for the untrained views. By contrasting the differences for the trained and the untrained views, the LMI measure isolated those effects specific to the trained view and the trained task and distinguished these from general practice effects or common sources of variance (e.g., day-to-day measurement variance, stimulus repetition). An index significantly above zero indicates that training enhances the BOLD signal to the trained view. At Post1, the indices at the IFFA and rFFA were significantly greater than zero (both  $t(17) > 3.63$ ,  $p < 0.05$ ). At Post2, the IOFA and rFFA showed a significantly positive index (both  $t(17) > 3.20$ ,  $p < 0.05$ ) (Figure 2A). These results showed that training boosted cortical response at some ROIs. In particular, the boost at the rFFA lasted 1 month, which was parallel to the behavioral learning effect.

Are the BOLD signal enhancements at the IOFA, IFFA, and rFFA closely associated with the persistent learning effect? To investigate this issue, for these three areas, we calculated the correlation coefficients between the psychophysical learning index and the LMI for BOLD amplitude at Post1 and Post2 across individual subjects. Similar to the LMI for BOLD amplitude, we defined the psychophysical learning index as [Thr (trained view pretraining) – Thr (trained views posttraining)] – [Thr (untrained views pretraining) – Thr (untrained views posttraining)], where Thr is the face view discrimination threshold measured at the test phases. The larger the index, the greater the behavioral learning effect. No significant

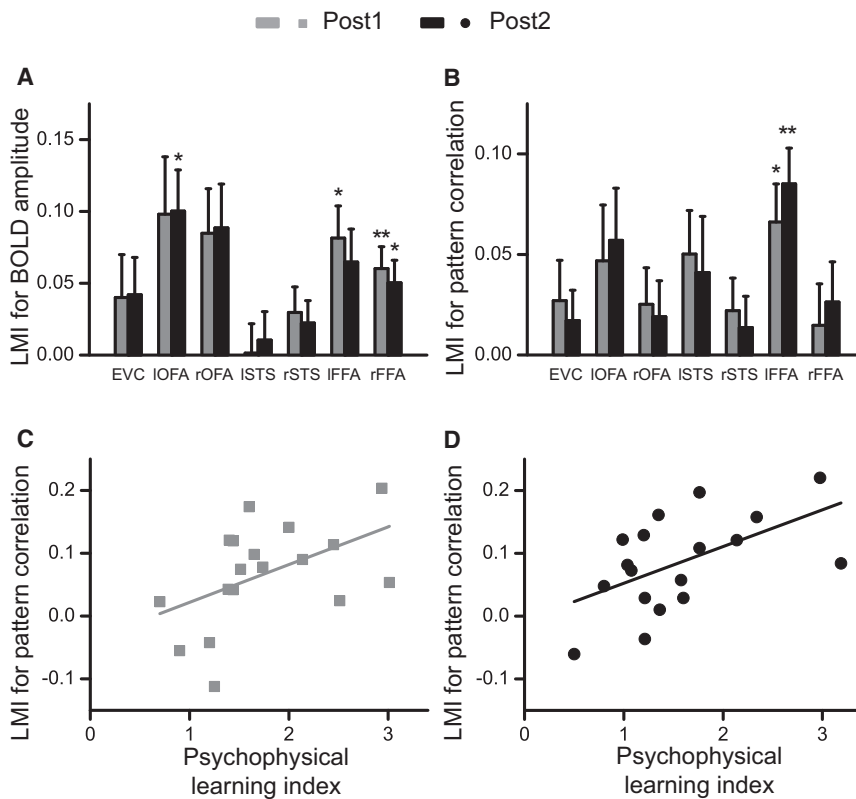


Figure 2. fMRI Results of Experiment 1

(A) LMIs for BOLD amplitude.

(B) LMIs for pattern correlation. Asterisks indicate the index significantly above zero (\* $p < 0.05$ ; \*\* $p < 0.01$ ).

(C and D) Correlations between the psychophysical learning index and the LMI for pattern correlation in the IFFA across subjects at (C) Post1 and (D) Post2.

Error bars indicate 1 SEM. See also Figure S2.

correlation was found (all  $abs(r) < 0.26$ ,  $p > 0.05$ ), suggesting that these areas might not play an important role in the face learning. These results do not support the view that focal changes in the strength of neural responses to trained stimuli are critical mechanisms for perceptual learning.

The multivariate pattern analysis was a standard correlation analysis of spatial activity pattern [24]. For each ROI, we computed the correlation coefficient between the spatial activity patterns evoked by the same face view in different runs (Figure S1B). We defined the LMI for pattern correlation as [Coef (trained view posttraining) – Coef (trained view pretraining)] – [Coef (untrained views posttraining) – Coef (untrained views pretraining)]. An index significantly above zero indicates that training improves the stability of the spatial activity pattern evoked by the trained view. We found that only the IFFA exhibited a significantly positive index at both Post1 and Post2 (both  $t(17) > 3.16$ ,  $p < 0.05$ ) (Figure 2B), demonstrating that the improved stability of the spatial activity pattern in the IFFA persisted over the long time course of perceptual learning.

The MVPA performed above used a single statistical threshold to define the ROIs, which usually had different numbers of voxels. It is likely that the correlation coefficient in an ROI was affected by its voxel number. To rule out this explanation, for each subject, we adjusted the thresholds for the rFFA, rSTS, ISTS, rOFA, IOFA, and EVC individually to ensure that they had the same voxel numbers as the IFFA (the mean voxel number in the IFFA across subjects was 73). With these redefined ROIs, we performed the same analysis. None of these areas exhibited a significantly positive LMI at Post1 and Post2 after ROI resizing (Figure S2A).

To further evaluate the role of the improved IFFA pattern stability in the learning, we calculated the correlation coefficients between the psychophysical learning index and the LMI for

pattern correlation at Post1 and Post2 across individual subjects. Both the coefficients were significant, demonstrating a close relationship between the behavioral learning effect and the improved IFFA stability (both  $r > 0.56$ ,  $p < 0.05$ ) (Figure 2C and 2D). No other ROIs showed significant correlations at both Post1 and Post2 (all  $r < 0.40$ ,  $p > 0.05$ ) (Figure S3A). The persistent stabilization of the IFFA activation pattern suggests that the long-lasting neural mechanism of perceptual learning is to make the neural representation (e.g., spatial activation pattern) of trained stimuli more precise and reliable, even in the absence of an increase in overall neural response. Doshier and Lu [25] suggested that the perceptual learning

mechanism reflects a combination of external noise exclusion and internal noise reduction, which was mainly supported by psychophysical studies. Since we did not add noise to the face stimuli, we were not able to test the idea of external noise exclusion. Nevertheless, the observation that the spatial activation pattern became less variable after training may provide evidence for the internal noise reduction idea. Consistent with our result, recent research shows that more-stable neural activation patterns were associated with more-conscious cognitive processing [26], better episodic memory encoding [27], and better orientation perception [28], suggesting that consistency of pattern engagement may be a general marker of effective cognitive processing.

Several studies [10, 29, 30] on object perceptual learning might be conceptually related to the current study. In these studies, the relationship between fMRI activation pattern and perceptual learning was explored. However, none of these studies examined the pattern stability issue. Furthermore, none of them investigated the long-term neural mechanisms of perceptual learning, which might be distinctive from the short-term mechanisms (see our description on Yotsumoto et al.'s study in the Introduction).

We believe that the close association between the learning effect and the improved pattern stability cannot be explained by other factors (e.g., task difficulty, attention, or eye movement). During scanning, subjects performed the same discrimination task in the magnet as that during training. There was no significant difference in subject performance among the three test phases (all were about 75% correct), suggesting no difference in task difficulty and (presumably) attention. Eye movement data show that subjects' eye movements were small and that their eye position distributions were not systematically different across face views and tests

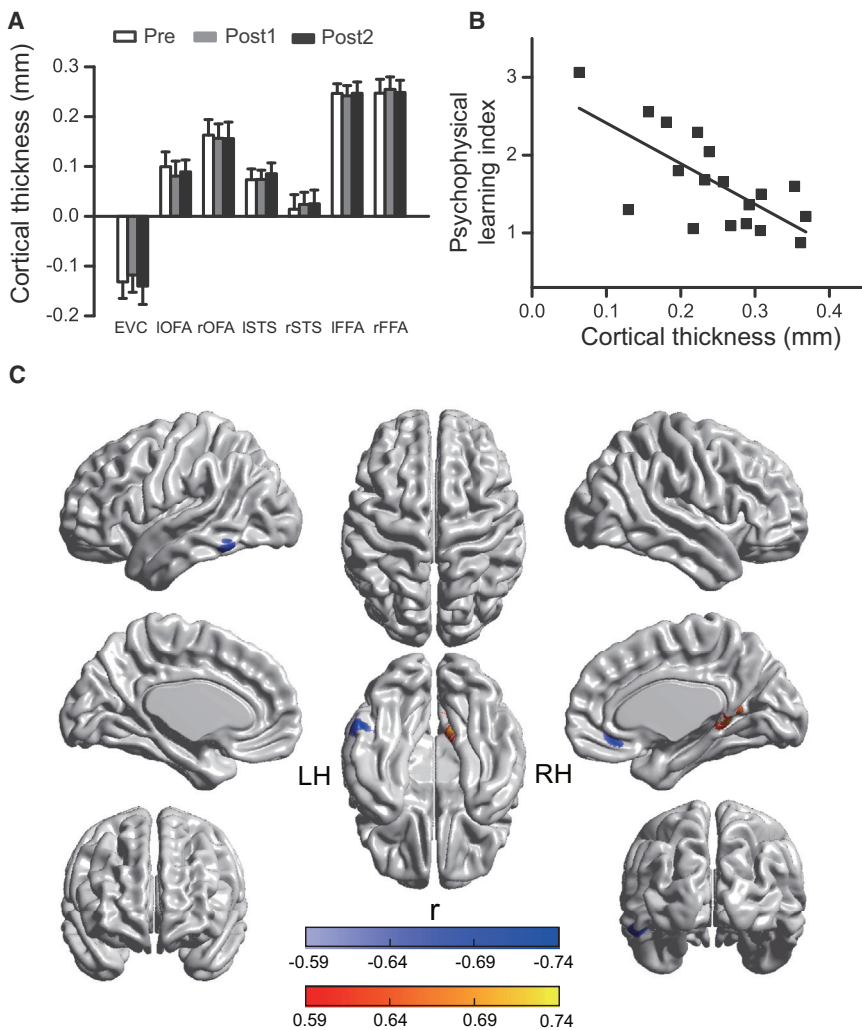


Figure 3. Cortical Thickness Results of Experiment 1

(A) Cortical thickness of the ROIs at Pre, Post1, and Post2. Cortical thickness analyses were performed with the relative cortical thickness (i.e., the original thickness of each vertex minus the average thickness of the whole cortex). A positive or negative value of a ROI thickness means that the ROI is thicker or thinner than the average thickness of the whole cortex. Error bars indicate 1 SEM.

(B) Correlation between the cortical thickness of the IFFA and the average psychophysical learning index of Post1 and Post2 across subjects.

(C) Regions with a significant correlation between cortical thickness and the average psychophysical learning index across subjects. Positive correlations are shown in hot colors, and negative correlations in cool colors. Images were thresholded at  $p < 0.01$  (uncorrected) and cluster size  $> 100$  vertices.

See also Figure S3.

(Figure S2B). The null result in EVC also excludes the possibility that the observed learning effect here could be due to some kind of feature learning, which is consistent with our previous psychophysical findings [19].

### Cortical Thickness Results

The second purpose of experiment 1 was to explore the structural correlates of the face view discrimination learning. Because of the close relationship between brain structure and brain function, it is natural to ask whether or not, after training, there was any structural change accompanying the functional change in the IFFA, as well as in the other ROIs. In each test phase, subjects' structural images were acquired before the fMRI runs. We measured the thickness of the cortex before and after training, as cortical thickness is a sensitive index of brain plasticity [31, 32]. To remove the fluctuation in the average thickness of the whole cortex among different scanning sessions, we subtracted the average thickness in each session for each subject from the original thickness of each vertex. All the subsequent analyses were based on the relative cortical thickness. We found that the average cortical thickness for each ROI did not change after training (all  $t(17) < 1.40$ ,  $p > 0.05$ ) (Figure 3A). We then searched the whole cortical surface and still found no reliable change in cortical thickness. This result was in sharp contrast with previous learning studies

in other functional domains, in which regional increases in cortical thickness were detected after memory, music, language, or navigation training [14–17].

Although there was little cortical thickness change after training, a surprising finding in our analysis was that the cortical thickness of the IFFA before training (at Pre) was predictive of the behavioral learning effect across individual subjects. Figure 3B shows an inverse correlation between the cortical thickness of the IFFA and the average psychophysical learning index of Post1 and Post2 ( $r = -0.70$ ,  $p < 0.01$ ). In other words, the thinner the cortex of the

IFFA, the greater the behavioral learning effect. Other ROIs did not show a significant correlation (all  $abs(r) < 0.49$ ,  $p > 0.05$ ) (Figure S3B). It is important to note that, before training, the cortical thickness of the IFFA did not correlate with the discrimination threshold for the trained view ( $r = -0.15$ ,  $p = 0.565$ ). This observation ruled out a possible explanation that the thinner IFFA cortex caused a lower performance before training and therefore allowed more room for improvement. We further searched the entire cortical surface and computed correlations between the cortical thickness of each vertex and the average psychophysical learning index. Figure 3C shows vertex-based, correlational maps across the entire cortical surface depicting the topography of significant correlations at a statistical threshold of  $p < 0.01$  (uncorrected). The area showing the strongest correlation was in the left fusiform cortex (peak vertex:  $r = -0.73$ ,  $p < 0.001$ ; Talairach coordinates:  $-50, -48, -17$ ), which was strikingly overlapped with the IFFA defined by the functional localizer (Talairach coordinates:  $-41, -46, -14$ ). Two additional regions were detected by this analysis, the right parahippocampal gyrus (peak vertex:  $r = 0.71$ ,  $p < 0.001$ ; Talairach coordinates:  $13, -49, 4$ ) and the right anterior cingulate cortex (peak vertex:  $r = -0.70$ ,  $p < 0.01$ ; Talairach coordinates:  $6, 31, -5$ ). Thus, this unbiased, post hoc approach supported the specificity of our ROI findings to the IFFA.



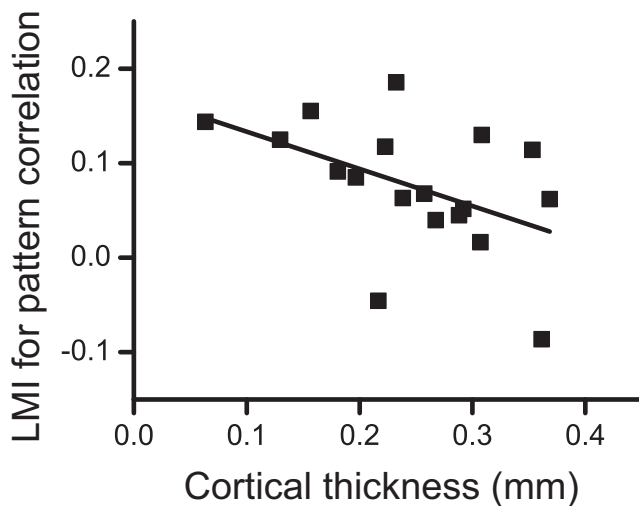


Figure 4. Correlation between the Cortical Thickness and the Average LMI for Pattern Correlation of Post1 and Post2 at the IFFA across Subjects. See also [Figure S4](#).

The inverse relationship between the cortical thickness of the IFFA and the behavioral learning effect is counterintuitive. It challenges a common assumption that a greater cortical thickness is associated with better processing efficacy of that region [18]. Shaw et al. [31] found a negative correlation between IQ and cortical thickness in early childhood. In agreement with our study, children who had thinner cortex in frontal regions gained more in an intelligence measure. Although the microstructure and cellular events contributing to cortical thickness are largely unknown, a compelling explanation of our finding is cortical pruning. Cortical pruning is a process of removing inefficient synapses and neurons, especially during adolescence [33]. It is conceivable that thinner cortex as a consequence of cortical pruning leads to more efficient processing, as well as strong learning ability. We further speculate that the thinner IFFA cortex, after training, could become more functionally stable because of fewer inefficient synapses and neurons, consequently leading to a greater behavioral learning effect. The significant correlation between the cortical thickness and the average LMI for pattern correlation of Post1 and Post2 at the IFFA ( $r = -0.49$ ,  $p < 0.05$ ) (Figure 4) provides tentative evidence for this idea and suggests a close correspondence between cortical thickness and increased brain function.

### Control Experiments

Experiments 2 and 3 were designed to investigate whether the neural changes found in experiment 1 depend on subjects' attention to the face stimuli and the face view discrimination task. These two experiments were identical to experiment 1 except that subjects performed a luminance discrimination task at fixation (instead of the face view discrimination task) in the fMRI tests (experiment 2) or during training (experiment 3). In an fMRI test trial of experiment 2, fixation point was presented at two different luminances during the presentation intervals of two face views. Subjects needed to judge which interval contained a brighter fixation point. In a training trial of experiment 3, subjects performed the same task.

In experiment 2, the face view discrimination training led to a similar behavioral learning effect as that in experiment 1. Relative to Pre, the discrimination thresholds at Post1 and Post2

were significantly lower for the 30° view (both  $t(14) > 7.43$ ,  $p < 0.001$ ), but showed little change for the 0° and 60° views (all  $t(14) < 3.06$ ,  $p > 0.05$ ) (Figure S2C). In experiment 3, because subjects were trained with the luminance discrimination task, after training, subjects' face view discrimination performance showed little improvement for all the three face views (all  $t(11) < 1.58$ ,  $p > 0.05$ ) (Figure S2D). In both experiments, LMIs for BOLD amplitude and pattern correlation were not significantly greater than zero in any ROI at Post1 and Post2 (experiment 2: all  $t(14) < 2.36$ ,  $p > 0.05$ , Figure S2C; experiment 3: all  $t(11) < 3.28$ ,  $p > 0.05$ , Figure S2D). These results demonstrated that only exposure to the trained view (without performing the face view discrimination task) during training and test was not able to induce the neural changes observed in experiment 1.

We also performed the cortical thickness analysis with the anatomical data in experiments 2 and 3. In experiment 2, a significant correlation between the cortical thickness and the average psychophysical learning index of Post1 and Post2 was found only in the IFFA, but not other ROIs (Figure S4A). Before training, the cortical thickness of the IFFA did not correlate with the discrimination threshold for the trained view in both experiment 2 ( $r = -0.11$ ,  $p = 0.685$ ) and experiment 3 ( $r = -0.10$ ,  $p = 0.753$ ). The cortical thickness analyses above were performed with the relative cortical thickness data. It should be noted that these findings can be replicated with the raw cortical thickness data (Figures S4B and S4C). Taken together, these results strengthen the cortical thickness conclusion in experiment 1.

### The Role of the Left Fusiform Cortex in Face Processing

Our finding that both the function and structure of the left fusiform cortex are closely associated with the long-lasting effect of face view discrimination learning has important implications on face processing and its plasticity. Using fMRI adaptation and MVPA methods, previous studies [34, 35] have demonstrated that face views are represented in the FFA and STS. But it was unknown whether and how the neural representation of face views can be shaped by visual experience. The current study provides strong and converging evidence that the face view representation is plastic even in the adult brain and suggests that the IFFA plays a pivotal role in adaptive face view processing.

Our findings shed new light on the hemispheric asymmetry in face processing. Although the essential role of the rFFA in face recognition has been extensively documented in literature over the past few decades [36], we still know little about the exact function of the IFFA and the functional difference between these two areas. Recently, Meng and colleagues [37] proposed that the IFFA performs the graded analyses of faces, while the rFFA performs the categorical analyses. They also found that the IFFA is more susceptible to contextual information than the rFFA. Based on the findings of the current study, we argue that the IFFA is more susceptible to perceptual learning and is more plastic than the rFFA. Our view is in line with two recent event-related potential studies. First, Rossion et al. [38] found that training with novel objects (i.e., Greebles) led to a left-lateralized facelike N170 response. Second, Su et al. [39] showed that perceptual learning could shorten the N170 latency only at the left occipital-temporal area. Why is the IFFA more plastic than the rFFA? A possible explanation is that the rFFA in the adult brain has fully developed and its function is fixed after maturation [40], while the IFFA is still open to changes for adapting to the dynamic visual world.

It should be noted that, although we emphasize the importance of the IFFA in perceptual learning of faces, we cannot deny potential contributions from other cortical areas (e.g., rFFA). In future research, it would be interesting to examine whether there is any brain network serving for the face perceptual learning. It is possible that the IFFA is a part of this network and the observed neural effect is most prominent in this area. Also, other kinds of face learning (e.g., identity learning) should be investigated to further clarify the plasticity of the IFFA and other related areas, as well as the brain network for face learning.

#### Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and four figures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2013.12.028>.

#### Acknowledgments

We thank Ren Na and Junshi Lu for their assistance in data collection, Alan Evans and Gaolang Gong for making the CIVET pipeline, and Bin Gu for his support in cortical thickness analysis. This work was supported by the Ministry of Science and Technology of China (2011CBA00400, 2010CB833903, and 2012CB825500) and the National Natural Science Foundation of China (30925014, 31230029, 91132302, 90820307, 91224008, 31221003, and 81225012).

Received: March 25, 2013

Revised: November 28, 2013

Accepted: December 13, 2013

Published: January 9, 2014

#### References

1. Gold, J.I., and Watanabe, T. (2010). Perceptual learning. *Curr. Biol.* 20, R46–R48.
2. Goldstone, R.L. (1998). Perceptual learning. *Annu. Rev. Psychol.* 49, 585–612.
3. Furmanski, C.S., and Engel, S.A. (2000). Perceptual learning in object recognition: object specificity and size invariance. *Vision Res.* 40, 473–484.
4. Gölcü, D., and Gilbert, C.D. (2009). Perceptual learning of object shape. *J. Neurosci.* 29, 13621–13629.
5. Baker, C.I., Behrmann, M., and Olson, C.R. (2002). Impact of learning on representation of parts and wholes in monkey inferotemporal cortex. *Nat. Neurosci.* 5, 1210–1216.
6. Gauthier, I., Skudlarski, P., Gore, J.C., and Anderson, A.W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nat. Neurosci.* 3, 191–197.
7. Harley, E.M., Pope, W.B., Villablanca, J.P., Mumford, J., Suh, R., Mazziotta, J.C., Enzmann, D., and Engel, S.A. (2009). Engagement of fusiform cortex and disengagement of lateral occipital cortex in the acquisition of radiological expertise. *Cereb. Cortex* 19, 2746–2754.
8. Jiang, X., Bradley, E., Rini, R.A., Zeffiro, T., Vanmeter, J., and Riesenhuber, M. (2007). Categorization training results in shape- and category-selective human neural plasticity. *Neuron* 53, 891–903.
9. Op de Beeck, H.P., and Baker, C.I. (2010). The neural basis of visual object learning. *Trends Cogn. Sci.* 14, 22–30.
10. Op de Beeck, H.P., Baker, C.I., DiCarlo, J.J., and Kanwisher, N.G. (2006). Discrimination training alters object representations in human extrastriate cortex. *J. Neurosci.* 26, 13025–13036.
11. Kourtzi, Z., Betts, L.R., Sarkheil, P., and Welchman, A.E. (2005). Distributed neural plasticity for shape learning in the human visual cortex. *PLoS Biol.* 3, e204.
12. Karni, A., and Sagi, D. (1993). The time course of learning a visual skill. *Nature* 365, 250–252.
13. Yotsumoto, Y., Watanabe, T., and Sasaki, Y. (2008). Different dynamics of performance and brain activation in the time course of perceptual learning. *Neuron* 57, 827–833.
14. Bermudez, P., Lerch, J.P., Evans, A.C., and Zatorre, R.J. (2009). Neuroanatomical correlates of musicianship as revealed by cortical thickness and voxel-based morphometry. *Cereb. Cortex* 19, 1583–1596.
15. Engvig, A., Fjell, A.M., Westlye, L.T., Moberget, T., Sundseth, O., Larsen, V.A., and Walhovd, K.B. (2010). Effects of memory training on cortical thickness in the elderly. *Neuroimage* 52, 1667–1676.
16. Mårtensson, J., Eriksson, J., Bodammer, N.C., Lindgren, M., Johansson, M., Nyberg, L., and Lövdén, M. (2012). Growth of language-related brain areas after foreign language learning. *Neuroimage* 63, 240–244.
17. Wenger, E., Schaefer, S., Noack, H., Kühn, S., Mårtensson, J., Heinze, H.J., Düzel, E., Bäckman, L., Lindenberger, U., and Lövdén, M. (2012). Cortical thickness changes following spatial navigation training in adulthood and aging. *Neuroimage* 59, 3389–3397.
18. Kanai, R., and Rees, G. (2011). The structural basis of inter-individual differences in human behaviour and cognition. *Nat. Rev. Neurosci.* 12, 231–242.
19. Bi, T.Y., Chen, N.H., Weng, Q.J., He, D.J., and Fang, F. (2010). Learning to discriminate face views. *J. Neurophysiol.* 104, 3305–3311.
20. Fang, F., and He, S. (2005). Viewer-centered object representation in the human visual system revealed by viewpoint aftereffects. *Neuron* 45, 793–800.
21. Nummenmaa, L., and Calder, A.J. (2009). Neural mechanisms of social attention. *Trends Cogn. Sci.* 13, 135–143.
22. Watson, A.B., and Pelli, D.G. (1983). QUEST: a Bayesian adaptive psychometric method. *Percept. Psychophys.* 33, 113–120.
23. Jehes, J.F.M., Ling, S., Swisher, J.D., van Bergen, R.S., and Tong, F. (2012). Perceptual learning selectively refines orientation representations in early visual cortex. *J. Neurosci.* 32, 16747–53a.
24. Haxby, J.V., Gobbini, M.I., Furey, M.L., Ishai, A., Schouten, J.L., and Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science* 293, 2425–2430.
25. Doshier, B.A., and Lu, Z.L. (1998). Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proc. Natl. Acad. Sci. USA* 95, 13988–13993.
26. Schurger, A., Pereira, F., Treisman, A., and Cohen, J.D. (2010). Reproducibility distinguishes conscious from nonconscious neural representations. *Science* 327, 97–99.
27. Xue, G., Dong, Q., Chen, C.S., Lu, Z.L., Mumford, J.A., and Poldrack, R.A. (2010). Greater neural pattern similarity across repetitions is associated with better memory. *Science* 330, 97–101.
28. Adab, H.Z., and Vogels, R. (2011). Practicing coarse orientation discrimination improves orientation signals in macaque cortical area v4. *Curr. Biol.* 21, 1661–1666.
29. Zhang, J., Meeson, A., Welchman, A.E., and Kourtzi, Z. (2010). Learning alters the tuning of functional magnetic resonance imaging patterns for visual forms. *J. Neurosci.* 30, 14127–14133.
30. Kuai, S.-G., Levi, D., and Kourtzi, Z. (2013). Learning optimizes decision templates in the human visual cortex. *Curr. Biol.* 23, 1799–1804.
31. Shaw, P., Greenstein, D., Lerch, J., Clasen, L., Lenroot, R., Gogtay, N., Evans, A., Rapoport, J., and Giedd, J. (2006). Intellectual ability and cortical development in children and adolescents. *Nature* 440, 676–679.
32. Zatorre, R.J., Fields, R.D., and Johansen-Berg, H. (2012). Plasticity in gray and white: neuroimaging changes in brain structure during learning. *Nat. Neurosci.* 15, 528–536.
33. Huttenlocher, P.R., and Dabholkar, A.S. (1997). Regional differences in synaptogenesis in human cerebral cortex. *J. Comp. Neurol.* 387, 167–178.
34. Axelrod, V., and Yovel, G. (2012). Hierarchical processing of face viewpoint in human visual cortex. *J. Neurosci.* 32, 2442–2452.
35. Fang, F., Murray, S.O., and He, S. (2007). Duration-dependent fMRI adaptation and distributed viewer-centered face representation in human visual cortex. *Cereb. Cortex* 17, 1402–1411.
36. Kanwisher, N., McDermott, J., and Chun, M.M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17, 4302–4311.
37. Meng, M., Cherian, T., Singal, G., and Sinha, P. (2012). Lateralization of face processing in the human brain. *Proc. Biol. Sci.* 279, 2052–2061.
38. Rossion, B., Gauthier, I., Goffaux, V., Tarr, M.J., and Crommelinck, M. (2002). Expertise training with novel objects leads to left-lateralized facelike electrophysiological responses. *Psychol. Sci.* 13, 250–257.
39. Su, J.Z., Chen, C., He, D.J., and Fang, F. (2012). Effects of face view discrimination learning on N170 latency and amplitude. *Vision Res.* 61, 125–131.
40. Golarai, G., Ghahremani, D.G., Whitfield-Gabrieli, S., Reiss, A., Eberhardt, J.L., Gabrieli, J.D.E., and Grill-Spector, K. (2007). Differential development of high-level visual cortex correlates with category-specific recognition memory. *Nat. Neurosci.* 10, 512–522.