

Sharpened cortical tuning and enhanced cortico-cortical communication



investigate what longer-lasting neural changes may be associated with VPL.

In our current investigation, we studied visual motion perceptual learning, with two specific aims: whether the neural modifications occurred at low- or high-level, and what neural modifications may be longer-lasting. Human subjects were trained in a motion direction discrimination task. Their behavioral performance and BOLD signals were measured before, immediately after, and two weeks after training. We examined not only how learning affected the local representation of the trained motion direction within individual visual cortical areas and IPS, a motion decision-making area and homologue of monkey LIP (lateral intraparietal area) (Kayser et al., 2010), but also how learning changed the effective connectivities between the visual areas and IPS. Law and Gold (2008, 2009) modeled the learning process as a high-level decision unit refining its connectivities to sensory neurons tuned to a specific motion direction through response reweighting (Poggio et al., 1992; Doshier and Lu, 1998; Bejjanki et al., 2011). However, there is no empirical evidence yet directly supporting this hypothesis.

Here, we report that, parallel to the long-lasting motion discrimination improvement, the neural selectivity in V3A and the effective connectivity from V3A to IPS for the trained direction exhibited a persistent increase after training, as revealed by both decoding and encoding analyses and dynamic causal modeling (DCM). We found that the behavioral learning could be well explained by a linear combination of improvements from these two sources. These findings make headways towards resolving previous controversies and demonstrate that perceptual learning should be attributed to changes both in the sensory representation of trained stimuli and the transmission of sensory signals to decision circuitry.

Materials and methods

Subjects

averaged, and then plotted as a function of training day. The learning curves were fitted with a power function (Jeter et al., 2009).

During the three test phases, psychophysical and fMRI tests were performed at four motion directions, which were 0°, 30°, 60°, and 90° deviated from the trained direction all either clockwise or counter-clockwise (hereafter referred to as 0°, 30°, 60°, and 90°). We first measured motion direction discrimination thresholds at these four directions. Ten QUEST staircases (same as above) were completed for each direction. The four directions were counterbalanced for individual subjects. Discrimination thresholds from the 10 staircases for each direction were averaged as a measure of subjects' discrimination performance. Subjects' performance improvement at a direction was calculated as $(pre\text{-}training\ threshold - post\text{-}training\ threshold) / pre\text{-}training\ threshold \times 100\%$.

After acquiring psychophysical discrimination thresholds, we measured BOLD signals responding to the four motion directions in 16 fMRI runs in two daily sessions (eight runs per session). Each run contained 10 stimulus blocks of 12 s, two blocks for one of five stimulus conditions (see below). Stimulus blocks were interleaved with 12 s fixation blocks. Each stimulus block consisted of five trials. In a trial, two RDKs were each presented for 200 ms. They were separated by a

block, resulting in 32 beta value patterns per test for each stimulus condition and ROI. For the decoding analysis, we trained linear support vector machine (SVM) classifiers (www.csie.ntu.edu.tw/~cjlin/libsvm) using these patterns per ROI and calculated mean decoding accuracies following a leave-one-run-out cross validation procedure. That is, we trained one-against-one binary classifiers (e.g., 30° vs. 90°) on 30 training patterns and tested their accuracy on the remaining two patterns per stimulus condition and ROI using a 16-fold cross-validation procedure. These binary classifiers were used to construct a four-way classifier for decoding the four motion directions (Kamitani and Tong, 2005; Preston et al., 2008; Serences et al., 2009; Zhang et al., 2010a). The chance performance for the four-way classifier was 0.25. Similar to the LMI for BOLD amplitudes, we defined the LMI for decoding accuracy as $[Acc(\text{trained direction post-training}) - Acc(\text{trained direction pre-training})] - [Acc(\text{untrained directions post-training}) - Acc(\text{untrained directions pre-training})]$, where *Acc* stands for decoding accuracy. The decoding accuracy for the untrained directions was the average accuracy for the 30°, 60°, and 90° directions.

Multivariate analysis – forward model

The decoding analysis is a sensitive tool to detect changes in spatial activation pattern, as reflected by changes in decoding accuracy.

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models. We fitted each of these three models for each subject. Using a hierarchical Bayesian approach (Friston, 2006), we compared the three models by computing the exceedance probability of each model, i.e., the probability to which a given model is more likely than the other two models to have generated data from a randomly selected subject. In the best model, we examined changes in the modulatory effects by the trained and untrained directions at Post1 and Post2, relative to Pre. In the psychophysical and fMRI data analyses, Bonferroni correction was applied with t-tests and ANOVAs involving multiple comparisons.

Results

Psychophysical results

Subjects underwent eight daily training sessions (1000 trials per session) to discriminate motion directions around a pre-specified, but randomly selected direction (hereafter the direction is referred to as 0°). In a trial, two random-dot kinematograms (RDKs) with slightly different directions were presented sequentially. Subjects were asked to make a two-alternative forced-choice (2-AFC) judgment of the direction of the second RDK relative to the first one (clockwise or counter-clockwise) (Fig. 1A). The QUEST staircase was used to control the direction difference between the two RDKs adaptively to estimate subjects' motion direction discrimination thresholds at 75% correct. Throughout the training, subjects' discrimination thresholds gradually decreased and saturated after day 6 (Fig. 2A). The thresholds on days 7 and 8 were not significantly different from that on day 6 (both $t(16) < 1.39, p > 0.05$). Note that, in our psychophysical and fMRI data analyses, Bonferroni correction was applied with t-tests and ANOVAs involving multiple comparisons.

Psychophysical and fMRI tests were performed on the days before (Pre), immediately after (Post1), and two weeks after training (Post2) (Fig. 1B). We first measured motion direction discrimination thresholds at the trained direction, as well as at the untrained directions

that were 30°, 60°, and 90° away from the trained direction. The discrimination thresholds were submitted to a repeated-measures ANOVA with test (Pre, Post1, and Post2) and direction (0°, 30°, 60°, and 90°) as within-subject factors. We found a significant main effect of test ($F(2,32) = 16.73, p < 0.01$) and a significant interaction between test and direction ($F(6,96) = 16.78, p < 0.01$) (Fig. 2B). To compare the learning effects at the trained and untrained directions, we calculated the percent improvements in discrimination performance after training. The improvement for the trained direction at Post1 and Post2 were 41% and 33%, respectively, which were significantly higher than those for the untrained directions (<15%) (all $t(16) > 3.4, p < 0.01$) (Fig. 2C). These results demonstrated that training led to a significant learning effect, which was specific to the trained direction and persisted for at least two weeks.

Univariate analysis of fMRI data

After acquiring the discrimination thresholds, we measured BOLD signals responding to the trained and untrained directions in 16 fMRI runs, in which stimulus blocks were interleaved with blank intervals. Each stimulus block contained five trials. The trials and subjects' task were very similar to those in the psychophysical tests except that the direction difference of two stimuli in a trial was the discrimination threshold obtained from the preceding psychophysical test. This ensured that subjects performed equally well at 75% accuracy and therefore hold attention constant across blocks and tests, which was confirmed by subjects' behavioral responses during fMRI data acquisition for the 0°, 30°, 60°, and 90° directions (Pre: $78 \pm 2\%, 72 \pm 2\%, 75 \pm 2\%, 78 \pm 2\%$; Post1: $79 \pm 2\%, 75 \pm 2\%, 77 \pm 2\%, 79 \pm 1\%$; Post2: $78 \pm 2\%, 73 \pm 2\%, 74 \pm 2\%, 77 \pm 2\%$). Subjects' response accuracies were not significantly different among the three test phases and the four directions (all $t(16) < 1.31, p > 0.05$).

We focused fMRI data analyses on BOLD signals in seven ROIs, including V1, V2, V3, V3A, V4, MT+, and IPS. Eighty most responsive voxels were selected per ROI. Since the behavioral learning effect

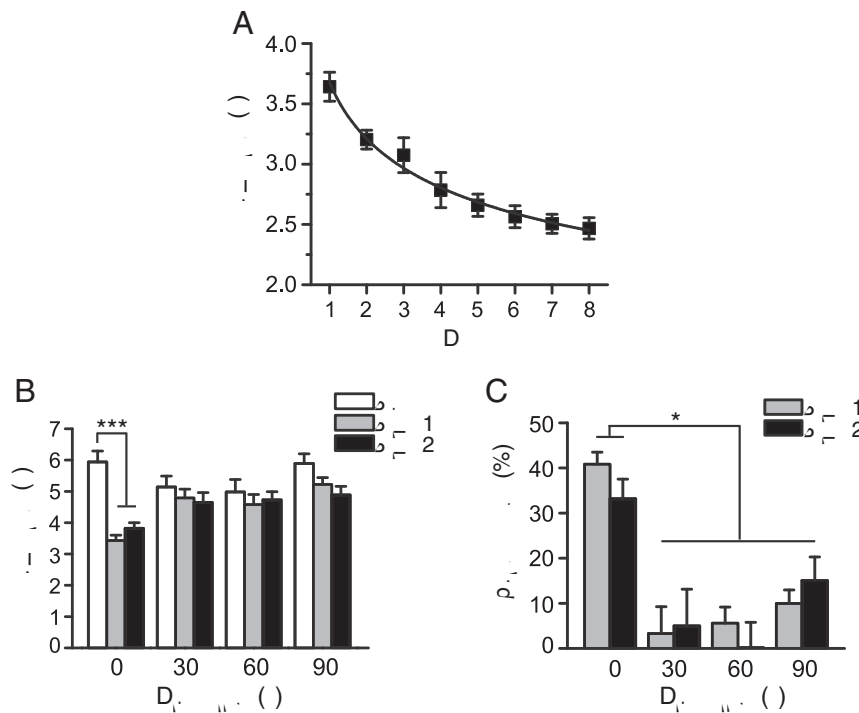


Fig. 2. Psychophysical results. (A) Learning curve. Motion direction discrimination thresholds are plotted as a function of training day. (B) Motion direction discrimination thresholds for the trained direction (0°) and the untrained directions (30°, 60°, and 90°) at Pre, Post1, and Post2. Asterisks indicate significant difference between Pre and Post1, Post2 (*** $p < 0.001$). (C) Percent improvement in motion direction discrimination performance for the trained and untrained directions at Post1 and Post2, relative to Pre. The asterisk indicates significant difference between the trained and the untrained directions (* $p < 0.05$). Error bars denote 1 SEM across subjects.

persisted for at least two weeks after training, if any training-induced neural change is considered to constitute the neural mechanisms of the learning, the change should manifest at both Post1 and Post2. Note that subjects showed a similar behavioral learning effect for the three untrained directions, suggesting that training-induced neural changes (if there were any) associated with these three directions might be similar. For all the fMRI data analyses (including the univariate analysis, the multivariate analyses, and the DCM analysis), we not only compared the data between the trained direction and each of the untrained directions, but also compared the data for the trained direction with the averaged data for the untrained directions. Since the results of the comparisons were very similar, for the sake of simplicity, we chose to present the comparison between the trained direction and the average of the untrained directions.

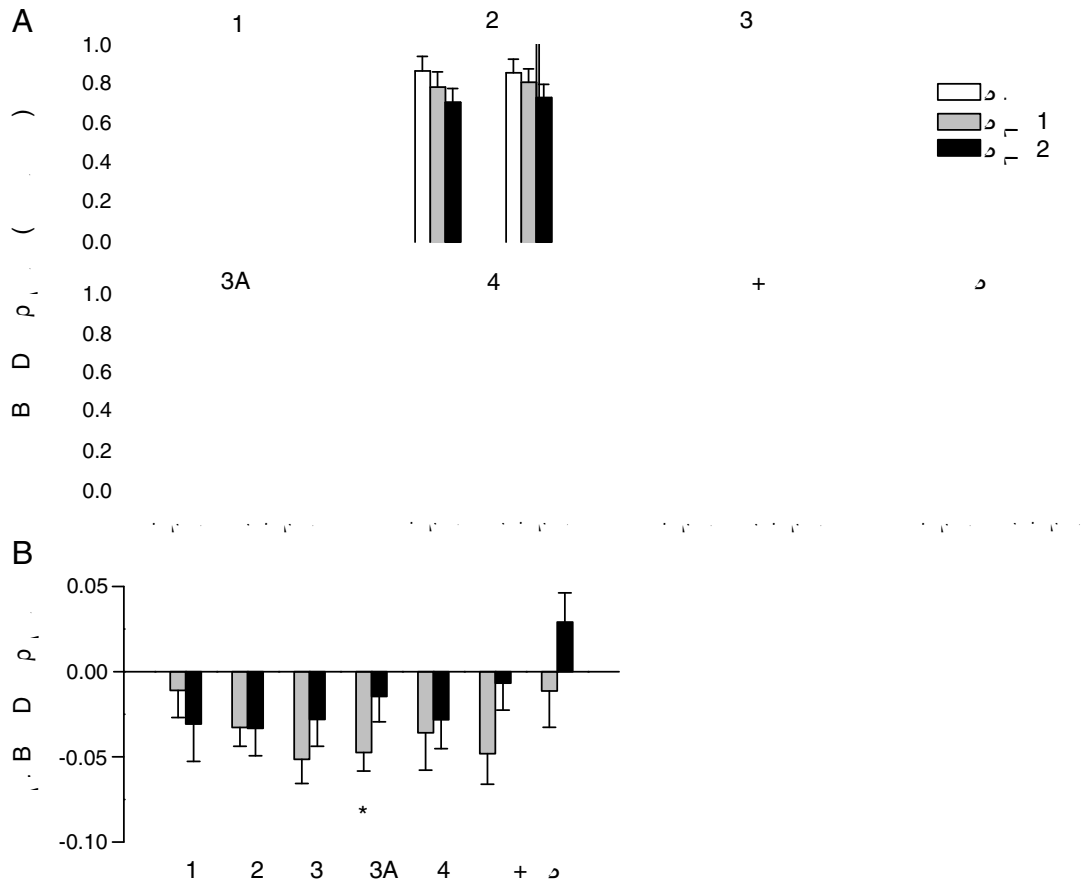
With the univariate analysis, we examined whether training could change the mean BOLD amplitude for the trained direction when compared with the untrained directions. For each ROI, BOLD amplitudes (i.e., beta values) for the trained and untrained directions were estimated with a general linear model (GLM). Beta values were submitted to a repeated-measures ANOVA with test (Pre, Post1, and Post2) and direction (trained and untrained) as within-subject factors. A significant interaction between test and direction was found only in V3A ($F(2,32) = 6.57, p < 0.05$), suggesting that training had different effects on the mean BOLD amplitudes evoked by the trained and untrained directions in this area (Fig. 3A).

To isolate the BOLD amplitude change that was specific to the trained direction and to distinguish it from general practice effects or common sources of variance, we defined the learning modulation index (LMI) for BOLD amplitude as $[Amp(\text{trained direction post-training}) - Amp(\text{trained direction pre-training})] - [Amp(\text{untrained directions post-training}) - Amp$

$(\text{untrained directions pre-training})]$. The LMI quantified the amplitude difference for the trained direction before and after training while subtracting out the difference for the untrained directions. An index significantly above/below zero indicates that training increased/decreased the BOLD signal to the trained direction. We calculated the LMI for BOLD amplitude in V3A because only this area showed a significant interaction effect in the ANOVA above. At Post1, the index, though very small, was significantly lower than zero ($t(16) = 4.35, p < 0.01$). However, relative to Post1, the magnitude of the index decreased at Post2 ($t(16) = 2.35, p < 0.05$), and was not significantly different from zero (Fig. 3B). These results demonstrated that training decreased the cortical response in V3A to the trained direction immediately after training, but the decrease vanished two weeks later even though the improved behavioral performance was largely maintained. This finding suggests that changes in mean BOLD amplitude might not play a critical role in the long-term neural mechanisms of the motion perceptual learning.

Decoding analysis of fMRI data

Since the univariate analysis failed to detect long-term neural changes associated with the persistent behavioral learning effect, we then performed the more sensitive multivariate analysis to examine whether perceptual learning could modify the spatially distributed activation pattern evoked by the trained direction across all voxels within an ROI. More specifically, we used the decoding analysis to examine whether training could improve the decoding accuracy for the trained direction when compared with the untrained directions. For each ROI, we trained the SVM classifiers using the spatial pattern of BOLD signals



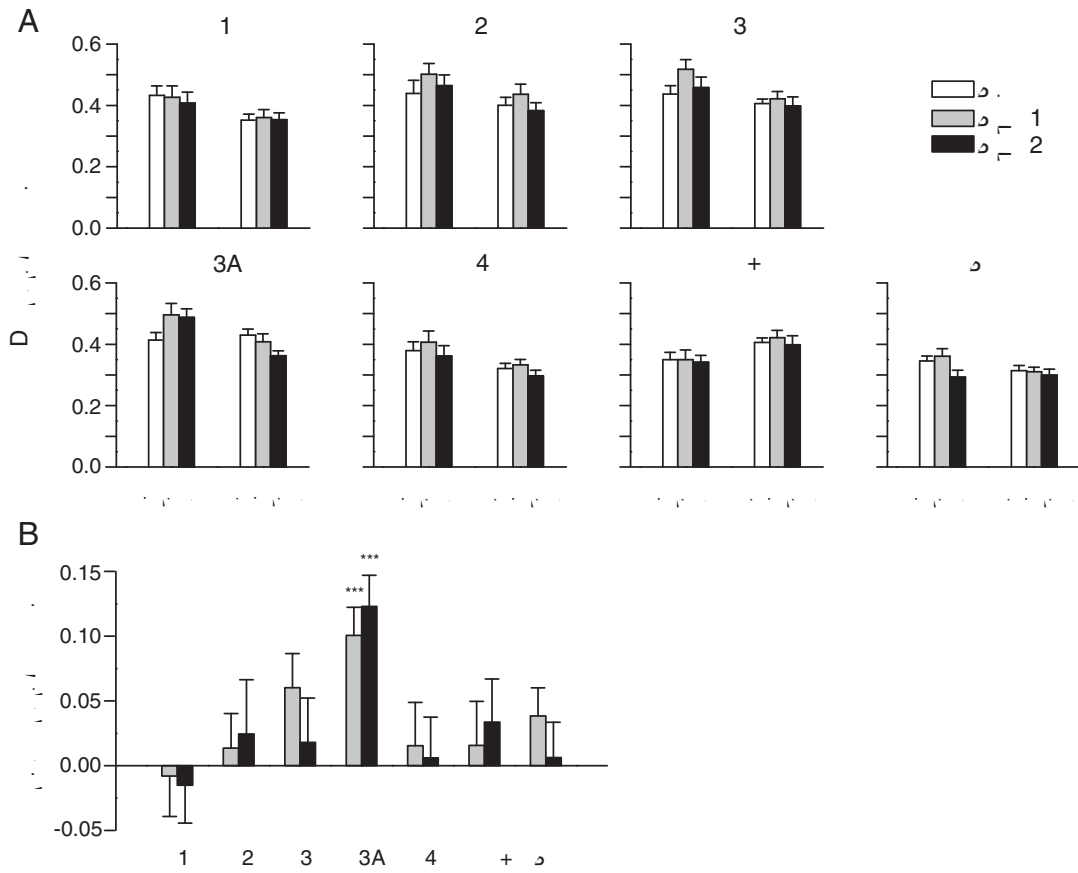


Fig. 4. Results of the multivariate pattern analysis of fMRI data. (A) Decoding accuracies for the trained and untrained directions. (B) LMIs for decoding accuracy. Asterisks indicate the index significantly above zero (** $p < 0.001$). Error bars denote 1 SEM across subjects.

and calculated the decoding accuracy following a leave-one-run-out cross validation procedure.

Decoding accuracies were submitted to a repeated-measures ANOVA with test (Pre, Post1, and Post2) and direction (trained and

untrained) as within-subject factors. A significant interaction between test and direction was found in V3A ($F(2,32) = 19.07, p < 0.001$), suggesting that training may have different effects on the decoding accuracies for the trained and untrained directions in this area

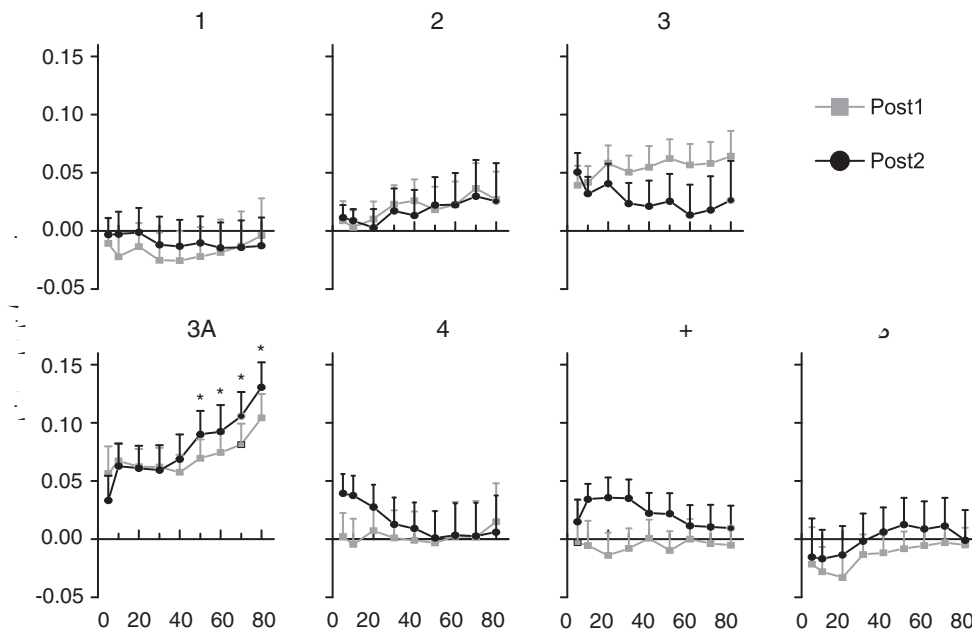
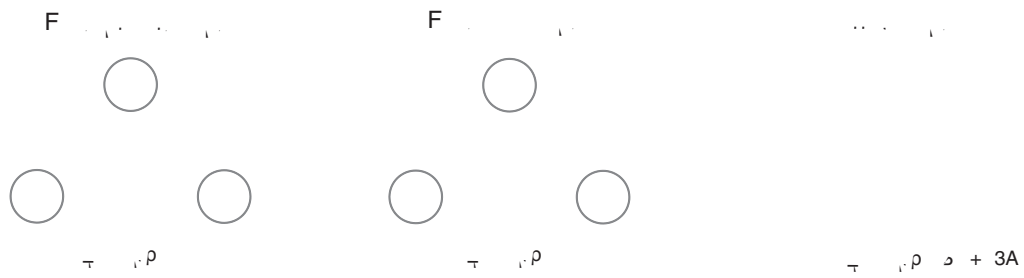


Fig. 5. LMIs for decoding accuracy as a function of voxel number. Asterisks indicate the indexes that are significantly above zero ($*p < 0.05$). Error bars denote 1 SEM across subjects.

(Fig. 4A). Similar to the LMI for BOLD amplitude, we defined the LMI for decoding accuracy as $[Acc(\text{trained direction post-training}) - Acc(\text{trained direction pre-training})] - [Acc(\text{untrained directions post-training}) - Acc(\text{untrained directions pre-training})]$. We found that V3A exhibited a significantly positive LMI for decoding accuracy at both Post1 and Post2 (both $t(16) > 4.64$, $p < 0.001$) (Fig. 4B), demonstrating that the improved decoding accuracy in V3A persisted over the entire time course of the measurement.

We further examined if this finding depended on the number of selected voxels. For each ROI, we randomly sampled selected 5–80 responsive voxels and performed the decoding analysis. When at least 50 voxels were selected, the LMI for decoding accuracy in V3A was significantly above zero at Post1 and Post2 (all $t(16) > 4.05$, $p < 0.05$) (Fig. 5). Other ROIs did not show a significant positive index within this voxel number range. This result demonstrated that the V3A finding was robust across the selected voxel numbers.

Recall that, in the blocks containing the trained direction, the stimuli were slightly different across Pre, Post1, and Post2. In a trial, the RDKs of 0° and $\pm \Delta\theta$ were presented. $\Delta\theta$ was the discrimination threshold measured in the preceding psychophysical test. Although the 0° RDK was always presented in the three tests, $\Delta\theta$ decreased after training. It is possible therefore that the observed fMRI effects were due to the stimulus difference. To rule out this explanation, at Post1 and Post2,



Having shown that training increased the forward connectivity from V3A to IPS, it is natural to ask whether training could induce any connectivity change at lower levels in the visual motion processing hierarchy. Accordingly, we built another DCM model containing the connections between V1 and V3A and between V1 and MT+. We did not find any significant change with the connections after training.

Correlation and regression analyses between psychophysical and fMRI measures

To further evaluate the role of the neural changes revealed in the motion perceptual learning, we calculated the correlation coefficients between the behavioral measure (i.e., improvement in percentage) and the fMRI measures (i.e., the bandwidth change in V3A and the connectivity change from V3A to IPS) across individual subjects. No significant correlation was found between the performance change and the bandwidth change at Post1 and Post2 (Figs. 8A and B). Only at Post1 was the performance change significantly correlated with the connectivity change (Fig. 8C), but not at Post2 (Fig. 8D). These results showed that the performance change could not be well predicted by any of the neural changes alone.

We then built a multiple linear regression model to examine whether the performance change (P) could be predicted jointly by

the bandwidth change (B) and the connectivity change (C) in the following linear equation:

$$P = k_0 + k_b B + k_c C.$$

The interaction between B and C was not included in the regression model to avoid the multicollinearity problem ($B \times C$ and C were significantly correlated). Note also that there was no significant correlation between B and C (Figs. 8E and F). This model provided a good fit for the inter-individual performance change (Post1: $R^2 = 0.51$, $F(2, 16) = 7.2$, $p < 0.01$; Post2: $R^2 = 0.57$, $F(2, 16) = 9.4$, $p < 0.01$). The standardized regression coefficients for B and C were significant at both Post1 and Post2 (Post1: $k_b = 0.50$, $k_c = 0.53$, both $p < 0.05$; Post2: $k_b = 0.67$, $k_c = 0.74$, both $p < 0.01$). These results demonstrated that the performance change could be well predicted by a linear combination of the bandwidth change and the connectivity change.

Discussion

Our study provides the following psychophysical and neuroimaging findings. (1) Motion direction discrimination training improved behavioral performance, which was specific to the trained direction and persisted for at least two weeks. This finding replicated the work by Ball and Sekuler (1987). (2) Immediately after training, the mean BOLD signal in V3A responding to the trained direction decreased,



investigated here is in regard to specificity of learning with respect to motion directions. That is to say, in the perceptual learning literature, specificity usually refers to specificity of learning to a stimulus attribute, which in our case is motion direction. We considered learning-related changes with the trained direction, after subtracting learning-related changes (if any) with the untrained directions. In this sense, those untrained directions served as controls. In other words, we used within-subjects controls, rather than between-subjects controls.

It has been extensively investigated whether perceptual learning could modulate the mean neural activity in a cortical area. After subjects were trained with a visual detection task, the mean neural activity usually increased (Furmanski et al., 2004; Bao et al., 2010; Hua et al., 2010; Goldhacker et al., 2014), which can be explained by the increased number or improved sensitivity of relevant neural detectors. For studies in which subjects practiced a near-threshold discrimination task, the findings so far are mixed – the mean neural activity was found to increase (Schwartz et al., 2002), decrease (Schiltz et al., 1999; Mukai et al., 2007), or have little change (Op de Beeck et al., 2006; Jehee et al., 2012). We found a mean signal decrease in V3A immediately after the motion direction discrimination training. The interpretation of these learning-related decreases has been that they reflect improved efficiency of processing, manifested as a shift in neural firing from a large population of neurons to a smaller, more specialized subset (Mukai et al., 2007). However, two recent studies on the long-term neural mechanisms of perceptual learning (Yotsumoto et al., 2008; Bi et al., 2014) challenge the view that changes in the mean neural activity are directly related to perceptual learning. Although both studies found an increase in the mean BOLD signal immediately after training, two weeks or one month later, the increase either faded out or did not correlate with the persistent behavioral learning effect. Consistent with these two studies, the absence of the BOLD signal decrease two weeks after training in our study suggests that changes in the mean neural activity to trained stimuli might not be the critical mechanism of perceptual learning.

In contrast to the transient decrease of the mean neural activity in V3A, V3A exhibited a persistent increase in decoding accuracy, suggesting that the long-term neural mechanism of perceptual learning is to make the neural representation of trained stimuli more stable and precise, even in the absence of a change in the mean neural activity. This idea is consistent with other perceptual learning studies on form discrimination (Zhang et al., 2010a), orientation discrimination (Jehee et al., 2012), and motion detection (Shibata et al., 2012). However, it should be noted that these studies only measured the neural changes immediately after training, but not longer-term changes. A more recent study by Bi et al. (2014) identified the long-term neural mechanisms of face discrimination learning as the stability improvement of spatial activity pattern (i.e., higher correlation across multiple measures after training) in left fusiform cortex. This stability improvement finding is in line with our finding here. The improved decoding accuracy in V3A may reflect the sharpening of direction-tuned responses at the population level, as suggested by neurophysiological and modeling works (Schoups et al., 2001; Bejjanki et al., 2011). This is exactly what we found with the forward modeling analysis.

We demonstrated that motion direction discrimination training could refine the neural representation of the trained direction in V3A, but not in MT+. Shibata et al. (2012) also found that motion detection training only affected V3A. These findings seem to contradict the long-standing belief that MT+ is the neural substrate of motion perceptual learning as demonstrated by earlier studies (Zohary et al., 1994; Vaina et al., 1998). Note that, in the earlier studies, human or monkey subjects were trained with only hundreds of trials (as compared to 9600 trials in our study) and the learning effects were short-term. There have been studies suggesting that neural changes in MT are not necessary for motion perceptual learning. Law and Gold (2008) found that motion perceptual learning did not induce changes

in motion-driven responses of neurons in monkey MT (see also Thompson et al., 2013). In a psychophysical study, Lu et al. (2004) found that motion direction discrimination learning was possible with the ‘paired-dots’ motion stimulus that was designed to suppress MT activity (Qian and Andersen, 1994). Although the importance of V3A in motion processing has been well recognized (Tootell et al., 1997; Orban et al., 2003; Bartels et al., 2008; Wall and Smith, 2008), the functional difference between V3A and MT+ is still not clear. Vaina and colleagues (Vaina et al., 2003; Vaina et al., 2005) provided neuropsychological evidence that V3A and MT+ are dominant in local and global motion processing, respectively. In our study, since all dots in the stimuli moved in one direction (100% coherence), subjects’ behavioral learning effect relied on the improvement of their local motion processing ability, which might be reflected as the decoding accuracy improvement in V3A. This hypothesis can be further tested in future research. For example, when subjects are trained with the same task as here, but using noisy motion stimuli, they need to integrate local motion directions to acquire the global direction. In such a case, would MT+ be affected by training?

In addition to the refined neural representation of the trained direction at the sensory area V3A, we also found that VPL could enhance the forward connection from V3A to IPS. To the best of our knowledge, this finding provided the first empirical evidence for the VPL reweighting models (Poggio et al., 1992; Doshier and Lu, 1998; Bejjanki et al., 2011). The reweighting models hypothesize that visual training improves perceptual sensitivity by selectively strengthening the connections from the most sensitive neurons in sensory area(s) to decision units. Although the models are theoretically appealing, they have never been empirically evaluated with connectivity analyses. In our study, V3A became more sensitive to the trained direction after learning. To form an optimal decision or to better read out sensory information, the decision units in IPS need to increase the pooling weight for the output of V3A neurons selective for the trained direction. The weight increase might be reflected as an increase in the forward connectivity from V3A to IPS specific to the trained direction.

It is notable that the representation of the trained direction in IPS, as quantified by the LMIs, did not change after training, which seems to contradict the finding by Law and Gold (2008). Though many differences in stimuli, experimental procedures, and subject species may explain the discrepancy, our view is that, if IPS is simply a decision-making area, its representation of motion direction does not have to be changed by perceptual learning. As suggested by the reweighting models, IPS just gives different weights to different motion channels for making a better decision after training. It seems unnecessary for training to modify the decision-making process implemented in IPS *per se*.

In the DCM analysis, we also measured the effective connectivity between MT+ and IPS, but failed to find any change after training. This finding demonstrated that the increased forward connectivity was not a general phenomenon taking place between low- and high-level cortical areas. It suggests that the connectivity increase is specific to the functional pathway starting from a cortical area (e.g., V3A) that could provide a better representation of the trained stimulus after learning. In MT+, we did not find that motion direction discrimination training altered the neural representation of the trained direction. According to the reweighting model theories, it is not necessary to change the pooling weight or the connectivity strength for the outputs from MT+.

Recently, Beste et al. (2011) discovered a new kind of exposure-based visual learning. They adapted a LTP (long-term potentiation)-like protocol to visual stimulation to alter human visual behavior. Subjects were exposed to passive visual high-frequency stimulation, which induced a long-lasting sensitivity improvement with the exposed stimulus. This finding, as well as other kinds of exposure-based learning (Beste and Dinse, 2013), demonstrated that, unlike our findings here, intensive training may not be necessary for skill learning. However, researchers still know little about the underlying mechanisms of

exposure-based learning. It is worthwhile to explore them for fully understanding the brain plasticity.

Taken together, our results suggest that the neural plasticity mediating perceptual learning occurs not only at the sensory processing stage, but also at the stage of perceptual readout by decision networks. These results help to reconcile discrepancies in the earlier literature on VPL.

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