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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

Seventeen subjects (nine female) participated in the study. They were naïve to the purpose of the study and had never participated in any perceptual learning experiment before. All subjects 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 years. They gave written, informed consent in accordance



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](http://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  $[\text{Acc}(\text{trained direction post-training}) - \text{Acc}(\text{trained direction pre-training})] - [\text{Acc}(\text{untrained directions post-training}) - \text{Acc}(\text{untrained directions pre-training})]$ , 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.

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,

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 signi







Having shown that training increased the forward connectivity

but this decrease mostly vanished two weeks later. (3) The decoding accuracy and neural selectivity for the trained direction in V3A increased immediately after training and persisted for at least two weeks. (4) The forward connectivity from V3A to IPS also increased immediately after training and persisted for at least two weeks. (5) The behavioral learning effects could be well explained by a linear

combination of the selectivity and connectivity increases. These findings

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

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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