


Neural Mechanisms of Motion Perceptual Learning in Noise

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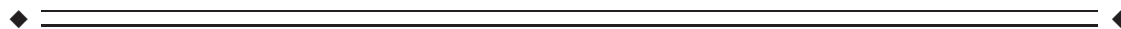
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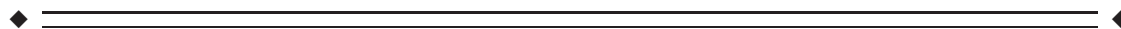
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Abstract: Practice improves our perceptual ability. However, the neural mechanisms underlying this experience-dependent plasticity in adult brain remain unclear. Here, we studied the long-term neural correlates of motion perceptual learning. Subjects' behavioral performance and BOLD signals were tracked before, immediately after, and 2 weeks after practicing a motion direction discrimination task in noise over six daily sessions. Parallel to the specificity and persistency of the behavioral learning effect, we found that training sharpened the cortical tuning in MT, and enhanced the connectivity strength from MT to the intraparietal sulcus (IPS, a motion decision-making area). In addition, the decoding accuracy for the trained motion direction was improved in IPS 2 weeks after training. The dual changes in the sensory and the high-level cortical areas suggest that learning refines the neural representation of the trained stimulus and facilitates the information transmission in the decision process. Our findings are consistent with the functional specialization in the visual cortex, and provide empirical evidence to the reweighting theory of perceptual learning at a large spatial scale. *Hum Brain Mapp* 38:6029–6042, 2017. © 2017 Wiley Periodicals, Inc.

Key words: perceptual learning; functional magnetic resonance imaging; multivariate pattern analysis; dynamic causal modeling; visual cortex



Contract grant sponsor: National Natural Science Foundation of China; Contract grant numbers: 31230029, 31421003, 61621136008, 61527804, and 31671168; Contract grant sponsor: Ministry of Science and Technology of the People's Republic of China; Contract grant number: 2015CB351800

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Received for publication 25 July 2017; Revised 31 August 2017; Accepted 1 September 2017.

DOI: 10.1002/hbm.23808

Published online 12 September 2017 in Wiley Online Library (wileyonlinelibrary.com).

INTRODUCTION

Our ability to discriminate or detect sensory stimuli can be enhanced by practice. This phenomenon, known as *perceptual learning*, is widely used as a model to study experience-dependent cortical plasticity in adults [Fahle and Poggio, 2002; Sagi, 2011; Watanabe and Sasaki, 2015]. One characteristic of perceptual learning is that the acquired behavioral improvement is usually restricted to the physical properties of the trained stimulus. Such specificity implies that learning is mediated by changes in the early visual processing stage, among neurons with a relative small receptive field and feature-selective tuning [Poggio et al., 1992]. Electrophysiological and brain imaging studies have revealed learning-related changes at multiple stages in the visual cortex, from the primary visual cortex V1 [Hua et al., 2010; Jehee et al., 2012; Schoups et al., 2001], extrastriate cortex such as V4 [Adab and Vogels, 2011], to object selective areas in the inferior temporal cortex [Bi et al., 2014; Lim et al., 2015]. An alternative hypothesis, however, assumes that perceptual learning engages the high-level decision stage. Instead of changes in the tuning properties of sensory encoding neurons, learning can be modeled via adjusting the weights between the early and late areas, so as to optimize the processing of task-relevant information [Bejjanki et al., 2011; Doshier and Lu, 1999; Law and Gold, 2009].

Compared to the “early” theory regarding the neural locus of perceptual learning, the “late” theory has received limited support from empirical evidence. A closely related issue is how learning-induced changes in the sensory and decision processes are implemented at a larger spatial scale beyond local visual circuits. When multiple visual areas participate in the information processing for a task, would perceptual learning trigger reweighting at the regional level? Take motion processing for example, MT and V3A are recognized as two key areas in the human brain [Bartels et al., 2008; Orban et al., 2003; Tootell et al., 1997], and their involvement in motion perceptual learning has been demonstrated in several brain imaging studies [Chen et al., 2015, 2016; Shibata et al., 2012, 2016; Tompson et al., 2013; Vaina et al., 1998]. Previously, we found motion direction discrimination training sharpened the cortical tuning for the trained motion direction in area V3A, and enhanced the connectivity from V3A to the motion-decision making area IPS (intraparietal sulcus) [Chen et al., 2015]. While these results indicate that learning induces *retuning* in the visual cortex, and *reweighting* in the high-level decision process, it remains unclear why there was a lack of learning effect in area MT.

We hypothesized that the neural correlates of perceptual learning are based on the functional specialization of visual cortex. Neuropsychological findings suggest that V3A dominates in local motion processing, whereas MT+ dominates in global motion processing [Cai et al., 2014; Vaina et al., 2003, 2005]. This specialization is consistent with the learning-related changes in V3A when subjects practiced

motion direction discrimination at 100% coherence [Chen et al., 2015, 2016]—as all dots move in the same direction, subjects’ ability to discriminate motion directions relied on the improvement in processing the local motion information. Conversely, motion discrimination learning may be mediated by MT/MST when global integration of motion direction is necessary. To test this hypothesis, we introduced external noise in the motion direction discrimination task by reducing the coherence level of the moving dots.

In the present study, we studied the neural mechanisms of motion perceptual learning in noise over a long-time course. Human subjects were trained to discriminate the global direction of moving dots at 35% coherence over six daily sessions. Subjects’ behavioral performance and BOLD signals were measured before, immediately after, and 2 weeks after training. We examined how learning affected the activation pattern of the trained motion direction in V1-V4, MT, MST, and IPS, using multi-voxel pattern analysis. In addition, we examined whether learning changed the effective connectivity between the visual motion areas and IPS using dynamic causal modeling (DCM).

MATERIALS AND METHODS

Subjects

Fourteen subjects (nine females) participated in the study. 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 29 years. They were naïve to the purpose of the study and had never participated in any perceptual learning experiment before. They gave written, informed consent in accordance with the procedures and protocols approved by the human subject review committee of the Center for Cognition and Brain Disorders, Hangzhou Normal University.

Stimuli and Apparatus

Subjects were viewing random dot kinematograms (RDKs) consisting of 400 dark dots (luminance: 3.76 cd/m²; diameter: 0.1°), with a gray background (luminance: 27.5 cd/m²). The dots moved at a velocity of 37°/s within a virtual circular area subtending 9° in diameter (Fig. 1A).

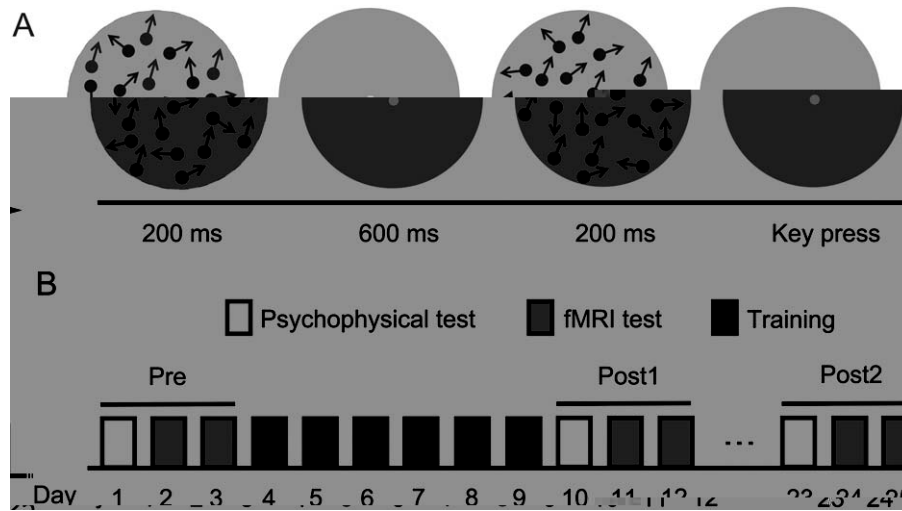


Figure 1.

Stimuli and experimental protocol. **(A)** Schematic description of a two-alternative forced-choice (2-AFC) trial in a QUEST staircase for measuring motion direction discrimination thresholds. **(B)** Experimental protocol. Subjects underwent eight daily training sessions. The pre-training test (Pre) and the post-training test 1 (Post1) and test 2 (Post2) took place on the days before, immediately after, and 2 weeks after training.

before, after, and 2 weeks after training, they performed pre-training test (Pre), post-training test 1 (Post1), and post-training test 2 (Post2) (Fig. 1B).

Two RDKs were presented successively per trial, with motion directions of θ and $\theta \pm \Delta\theta$ for 200 ms each and were separated by a 600 ms blank interval (Fig. 1A). The temporal order of these two RDKs was randomized. Subjects judged whether the direction of the second RDK was clockwise or counter-clockwise relative to the first one via a right-hand finger press on the response key. After each response, feedback was provided to the subject by brightening (correct response) or dimming (incorrect response) the fixation point. The next trial began 1 s after feedback. $\Delta\theta$ was estimated adaptively from trial to trial with the QUEST staircase, to quantify subjects' discrimination threshold at 75% correct [Watson and Pelli, 1983]. For each subject, the trained direction (θ) was chosen randomly from eight non-cardinal directions (22.5° , 67.5° , 112.5° , ..., and 337.5°), and was fixed for all the training sessions. A daily session (about 1 hour) consisted of 25 QUEST staircases of 40 trials. The discrimination thresholds from these staircases were averaged, and then plotted as a function of training day. The learning curves were fitted with a power function [Jeter et al., 2009].

During each test phase, subject' motion direction discrimination thresholds were measured at four motion directions, 0° , 30° , 60° , and 90° deviated from the trained direction (hereafter referred to as 0° , 30° , 60° , and 90°) in both psychophysical and fMRI tests. Discrimination thresholds from 10 Quest staircases for each direction were averaged as a measure of subjects' discrimination performance. Subjects' performance improvement at each

motion direction was calculated as $(pre\text{-}training\ threshold - post\text{-}training\ threshold) / pre\text{-}training\ threshold \times 100\%$. The learning effect specific to the trained direction was quantified as $Imp(trained) - Imp(untrained)$, where the improvement for the untrained directions was the average improvement for the 30° , 60° , and 90° directions.

After psychophysical measurements, subjects' BOLD signals responding to the four motion directions in 16 fMRI runs were acquired in two daily sessions (eight runs per session). Similar to the task in psychophysical tests, subjects performed motion direction discrimination during scan. In a trial, two RDKs were each presented for 200 ms and were separated by a 600 ms blank interval, followed by a 1,400 ms blank interval between trials. For the directions of the two RDKs, one was fixed in a block and could be 0° , 30° , 60° , or 90° . The other deviated from the fixed one by $\pm \Delta\theta$, which was the discrimination threshold measured in the corresponding psychophysical test, to make subjects perform equally well at 75% correct across the stimulus conditions and tests. At Pre, we had a fifth condition, in which the RDKs of 0° and $0.5 \times \Delta\theta$ were presented. Each stimulus block consisted of five trials. Each run contained 10 stimulus blocks of 12 s, two blocks for one of five stimulus conditions. Stimulus blocks were interleaved with 12 s fixation blocks. Prior to the experiment, subjects practiced 10 staircases for each direction to get familiar with the experimental procedure.

Defining Regions of Interest

Retinotopic mapping of visual areas was performed using standard phase-encoded methods developed by

Sereno et al. [1995] and Engel et al. [1997], in which subjects viewed a rotating wedge or an expanding ring that created traveling waves of neural activity in visual cortex. An independent run was performed to define the regions of interest (ROIs) in areas V1, V2, V3, V3A, V4, MT, MST, and IPS. The run contained eight moving dot blocks of 12 s, interleaved with stationary dot blocks of 12 s. The

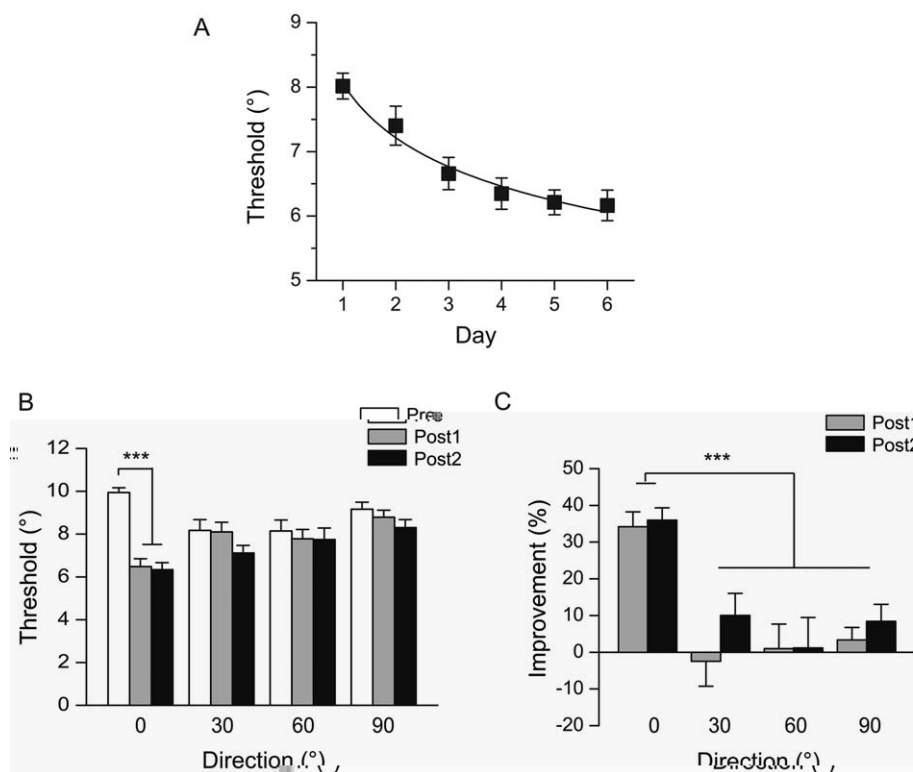


Figure 2.

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 (** $p < 0.001$). Error bars denote 1 SEM across subjects.

parameter, σ is the standard deviation, and C is the baseline.

Dynamic Causal Modeling

DCM, an approach for estimating effective strength of synaptic connections among neuronal populations and their context-dependent modulation, was performed to examine whether there was any connectivity change between sensory areas and decision-making areas after training. We estimated the effective connectivities between IPS and two visual areas MT and V3A using DCM in SPM10 [Friston, 2007]. For each area, time series from voxels within a 5-mm-radius sphere centered on the most responsive voxel in the localizer run were extracted for the DCM analysis in both hemispheres. The estimated DCM parameters were later averaged using the Bayesian model averaging method [Friston, 2007]. The mean MNI coordinates of these voxels and the SEs across subjects in MT, V3A, and IPS were $(41.08 \pm 1.1, -71.33 \pm 1.7, 4.25 \pm 1.2)$, $(24.2 \pm 4.1, -86.9 \pm 1.2,$

$16.17 \pm 2.0)$, and $(23.6 \pm 4.0, -61.2 \pm 2.5, 47.5 \pm 1.5)$ for the right hemisphere; $(-43.26 \pm 1.1, -69.54 \pm 2.0, 6.03 \pm 1.4)$, $(-25.1 \pm 4.6, -87.4 \pm 1.0, 12.5 \pm 2.2)$ and $(-21.6 \pm 4.1, -63.5 \pm 2.9, 47.7 \pm 1.9)$ for the left hemisphere.

DCM models neural population dynamics using a bilinear model and a hemodynamic model [Friston et al., 2003]. The model consists of three sets of parameters: extrinsic inputs into one or more regions, intrinsic connectivity among the modeled regions, and parameters encoding the modulation of the specified intrinsic connections by experimental manipulations. fMRI data were modeled with a GLM procedure, including regressors for the trained or the untrained motion direction as the modulatory input from MT/V3A to IPS, as well as a condition comprising all the directions as the extrinsic input to MT/V3A (Fig. 7A). Bidirectional intrinsic connections were hypothesized to exist between IPS and MT/V3A, and the strengths of these connections were modulated by either the trained or the untrained directions. For each subject, we examined the modulatory effects in recurrent, feedforward, and feedback models. Using a hierarchical Bayesian approach, we

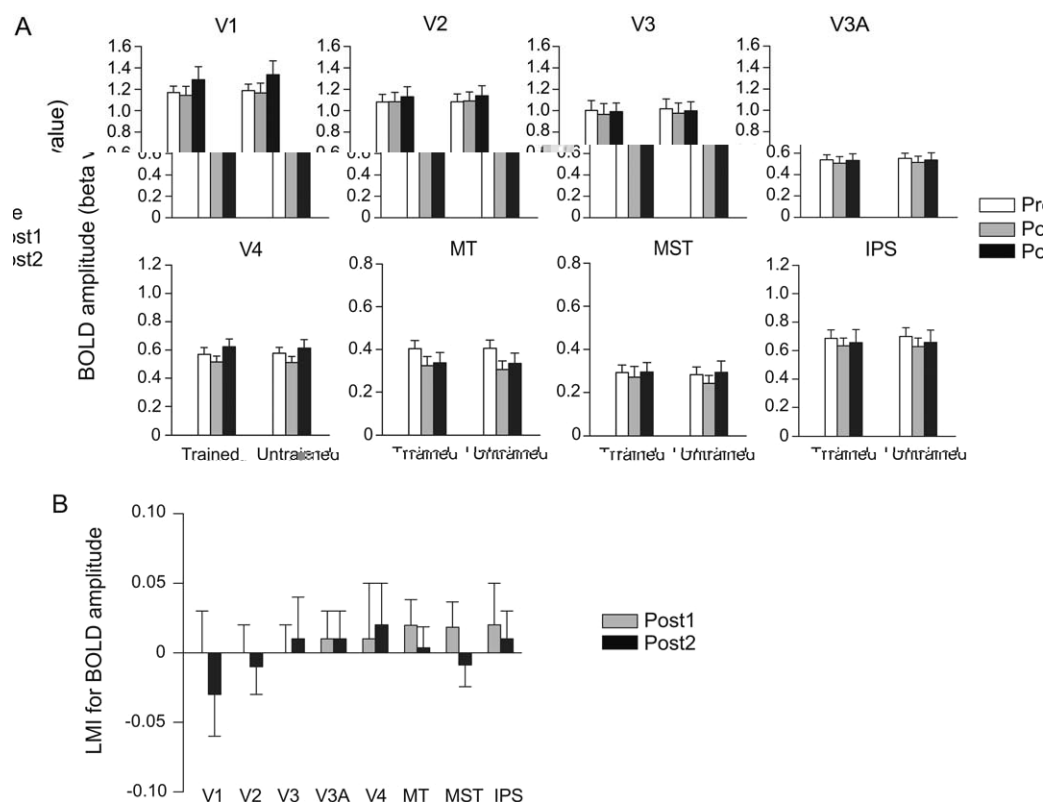


Figure 3. Results of the univariate analysis of fMRI data. **(A)** BOLD amplitudes for the trained and untrained directions. **(B)** LMIs for BOLD amplitude. Error bars denote 1 SEM across subjects.

computed the exceedance probability for each model, that is, 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 model with the highest exceedance probability, we examined changes in the modulatory effects for either the trained or the untrained directions at Post1 and Post2, relative to Pre.

RESULTS

Psychophysical Results

Subjects underwent six daily training sessions (1,000 trials per session) to perform motion direction discrimination around a non-cardinal direction (Fig. 1A). Throughout the training, subjects' discrimination thresholds gradually decreased and saturated after day 4 (Fig. 2A).

We compared their discrimination thresholds on the days before (Pre), immediately after (Post1), and 2 weeks after training (Post2) (Fig. 1B). Repeated-measures ANOVA revealed a significant main effect of test ($F(2, 26) = 18.97, P < 0.01$) and a significant interaction between test and direction ($F(6, 78) = 9.74, P < 0.01$) (Fig. 2B). The percent improvements for the trained direction were 34% at Post1

and 36% at Post2, which were significantly higher than those for the untrained directions (<11%) (all $t(13) > 4.20, P < 0.01$) (Fig. 2C). These results demonstrate that training induced specific and persistent behavioral improvement for the trained motion direction.

Univariate Amplitude Analysis of fMRI Data

fMRI data analyses were focused in eight ROIs, including V1, V2, V3, V3A, V4, MT, MST, and IPS. With the univariate amplitude analysis, we examined whether training could lead to changes in the averaged BOLD amplitude for the trained direction, compared with the untrained directions. We found no significant main effect of test (all $F(2, 26) < 1.73, P > 0.19$), and no significant interaction between test and direction (all $F(2, 26) < 1.08, P > 0.35$) in any of the eight ROIs (Fig. 3A).

The LMI (see Materials and Methods) was defined to isolate the BOLD amplitude change specific to the trained direction. An index significantly above/below zero indicates that training increased/decreased the BOLD signal to the trained direction. Consistent with the ANOVA results above, no significant index was found in any ROI (Fig. 3B). Thus, no learning-specific effect was observed on the

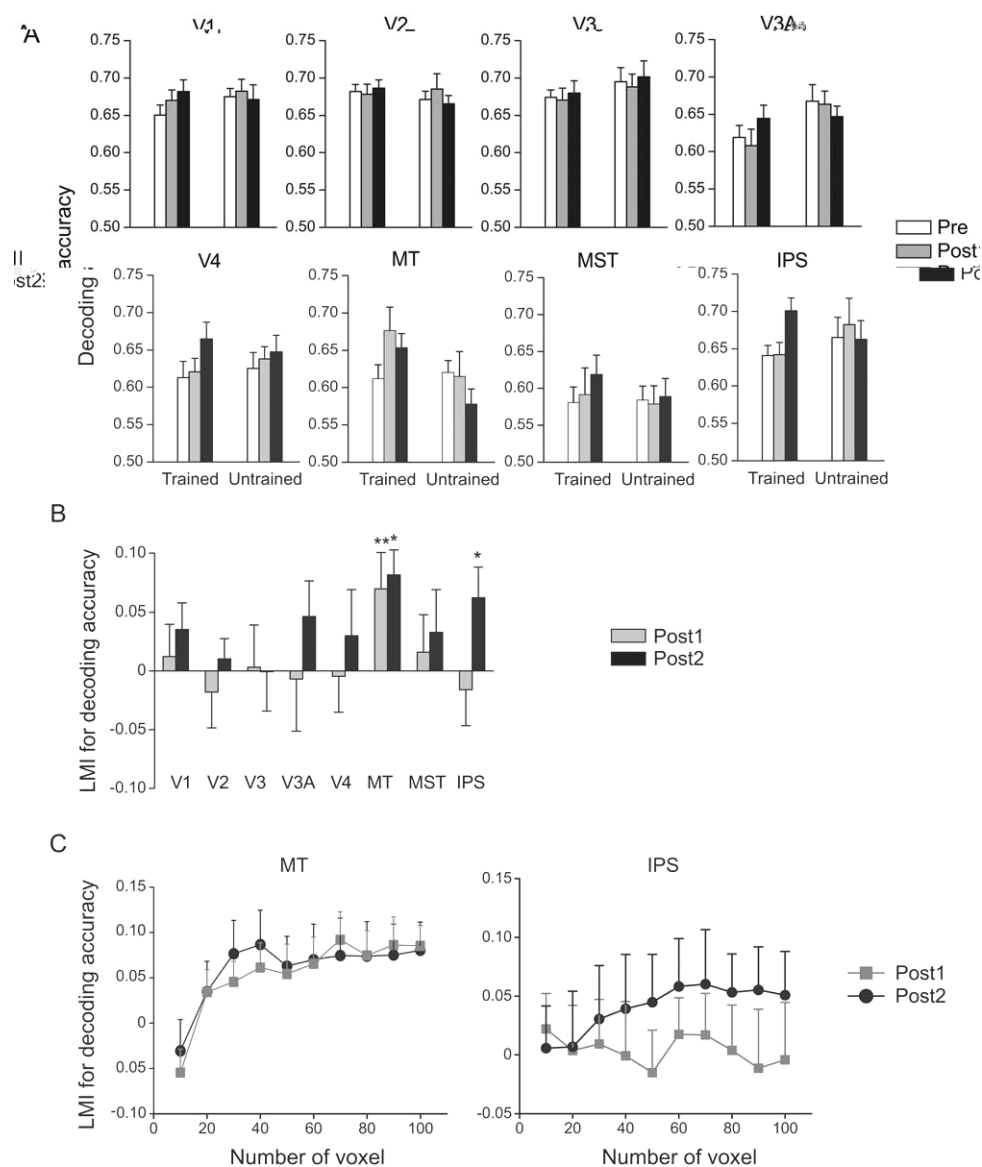


Figure 4.

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 ($*P < 0.05$, $**P < 0.01$). **(C)** LMIs for decoding accuracy as a function of voxel number in MT and IPS. Error bars denote 1 SEM across subjects.

average BOLD amplitudes evoked by the trained and untrained motion directions.

Multivariate Pattern Analysis of fMRI Data

We examined whether training led to specific improvement in the decoding accuracy of the trained condition. Decoding accuracies for 0° versus 30° (trained condition) and 60° versus 90° (untrained condition) were submitted

to a repeated-measures ANOVA. While there was no significant main effect of test in any ROI (all $F(2, 26) < 0.79$, $P > 0.46$), we found a significant interaction between test and direction in MT ($F(2, 26) = 6.07$, $P < 0.01$) and IPS ($F(2, 26) = 4.70$, $P = 0.02$), suggesting specific learning effect on the decoding accuracies for the trained compared to the untrained conditions (Fig. 4A). MT exhibited a significantly positive LMI at both Post1 ($t(13) = 2.25$, $P = 0.04$) and Post2 ($t(13) = 3.81$, $P < 0.01$) (Fig. 4B), demonstrating that the improved decoding accuracy in MT persisted over

the long time course of the perceptual learning. Meanwhile, a higher-level cortical area IPS, has a significantly positive index at Post2 ($t(13) = 2.38$, $P = 0.03$), indicating an improved decoding accuracy in the decision-related area in the late stage of perpetual learning.

To examine whether the finding depended on the number of selected voxels, the decoding performance was tested on the most responsive voxels with a range from 10

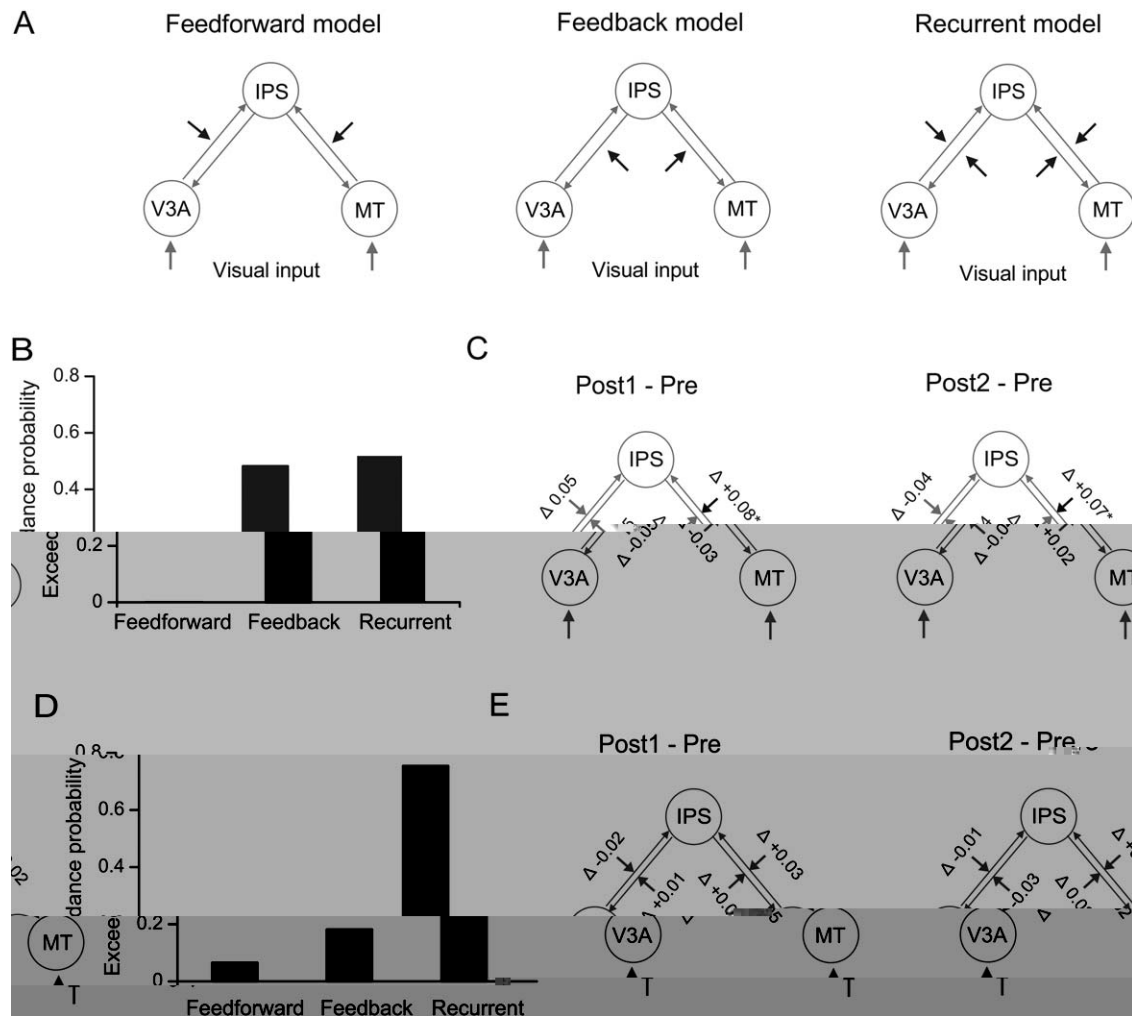


Figure 6.

Dynamic causal modeling of connectivities between V3A and IPS and between MT and IPS. **(A)** Recurrent, feedforward, and feedback models for modeling the modulatory effect by the trained or the untrained directions. **(B)** Exceedance probabilities for the three models with the trained direction as the modulatory

input. **(C)** Changes in the modulatory effect by the trained direction at Post1 and Post2, relative to Pre. **(D)** Exceedance probabilities for the three models with the untrained directions as the modulatory input. **(E)** Changes in the modulatory effect by the untrained directions at Post1 and Post2, relative to Pre.

6.5%, 18.1%, and 75.4%, respectively, suggesting that the modulatory effect by the untrained directions could also be best explained by the recurrent model (Fig. 6D). However, little change was found in the modulatory effect of the connections between MT/V3A and IPS (all $t(13) < 1.55$, $P > 0.14$) (Fig. 6E).

Links Between the Behavioral Improvement and Neural Changes

To evaluate the role of the neural changes revealed in noisy motion perceptual learning, we calculated the correlation coefficients between the behavioral improvement

and the neural changes (i.e., changes in the bandwidth of pattern-based tuning in MT/IPS, and in connectivity strength from MT to IPS) specific to the trained direction across individual subjects. Significant correlations were found between the performance change and the bandwidth change in MT at both Post1 ($r = 0.73$, $P < 0.01$) and Post2 ($r = 0.60$, $P = 0.02$) (Fig. 7A,B). No significant correlations were found between the performance change and bandwidth change in IPS (Fig. 7C,D), or between the performance change and connectivity change (Fig. 7E,F). These results suggest the sharpening of the pattern-based tuning functions in MT as the critical neural substrate underlying the behavioral learning effect.

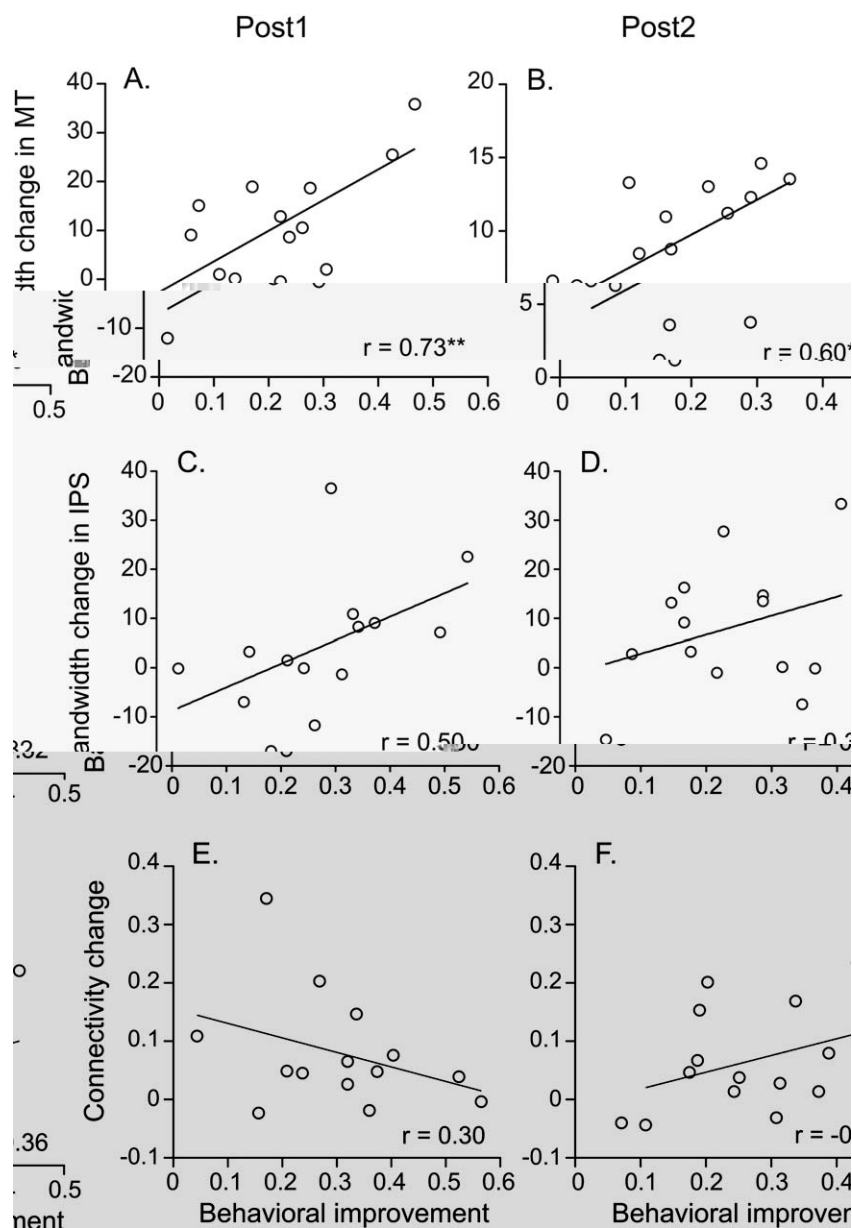


Figure 7.

Correlations between the behavioral improvement and neural changes specific to the trained motion direction at Post1 (**A**, **C**, **E**) and Post2 (**B**, **D**, **F**). (A, B) Correlations between the behavioral improvement and the bandwidth change in MT. (C, D) Correlations between the behavioral improvement and the

bandwidth change in IPS. (E, F) Correlations between the behavioral improvement and the connectivity change. The asterisk indicates the significance level of the correlation coefficient at Post1 (* $P < 0.05$, ** $P < 0.01$).

DISCUSSION

We studied the neural mechanisms of perceptual learning, using motion direction discrimination training paradigm with noisy stimuli. Behaviorally, training led to a specific improvement in the trained direction and was well preserved after 2 weeks. We found that motion

perceptual learning in noise (1) increased decoding accuracies in MT, (2) sharpened pattern-based tuning functions in MT, which correlated with subjects' behavioral improvement, and (3) enhanced feedforward connectivity from MT to IPS. In addition, there was an emergence of increased neural decoding accuracy in IPS 2 weeks after training.

Our results lend strong support for the long-term involvement of MT in motion perceptual learning in noise. Learning-related changes had been observed in MT/MST in previous electrophysiological and imaging studies

fundamental limit, noise exclusion is suggested to be the major mechanism of perceptual learning [Doshier and Lu, 2005]. The specialization of MT in noisy motion processing can be based on its large receptive field size [Albright, 1984]. During the spatial pooling of local motion, neurons in MT operate to average out motion noise to extract the global motion direction. In line with this hypothesis, a recent electrophysiological study showed that motion learning in noise enhanced subjects' spatial integration ability, with a critical contribution of MT [Liu and Pack, 2017]. Compared to learning in a clear display, learning in noise often induces neural changes in a higher-level cortical area, subserved by its larger receptive field size and broader tuning width. A similar effect has also been observed in orientation learning—while training without noise altered neural activities in V1 [Schoups et al., 2001], training in noise led to changes in V4 [Adab and Vogels, 2011].

The current study used motion stimuli at a high speed, which may not be optimal for psychophysical performance or MT neurons [Lagae et al., 1993; Orban et al., 1985; Pilly and Seitz, 2009; Seitz et al., 2008]. However, it is still within the effective range of parameters to activate MT [Liu and Newsome, 2003; van Essen and Maunsell, 1983; Rodman and Albright, 1987]. One advantage of using non-optimal stimuli is that the effect of learning could be more pronounced with non-optimal stimuli—direction/orientation discrimination learning leads to greater improvement in non-cardinal than in cardinal directions/orientations [Ball and Sekuler, 1987; Vogels and Orban, 1985]. In addition, motion learning occurred even without motion perception with sub-threshold motion stimuli [Watanabe et al., 2001]. These results suggest that learning can be triggered by non-optimal stimuli, at both behavioral and cortical levels.

As the sensory signal of learned motion direction became better represented in MT, the way in which sensory signals were relayed to and weighted by decision-making areas was also changed. DCM analysis demonstrated an increase in the feedforward connectivity from MT to IPS. Previously, we found that motion direction discrimination training at 100% coherence enhanced feedforward connectivity from V3A to IPS [Chen et al., 2015]. Together with the electrophysiological findings showing the involvement of macaque LIP in motion discrimination training [Law and Gold, 2008], our results support the idea that the learning process could be modeled as a high-level decision unit refining its pooling from the most relevant sensory neurons through response reweighting [Doshier et al., 2013; Law and Gold, 2009].

The long-term neural substrate of perceptual learning is another important, yet less addressed issue. Perceptual learning is characterized by its persistency in the behavioral improvement. Once learned, the visual performance can be well maintained over months or years without additional training [Bi et al., 2010; Karni and Sagi, 1993]. In this study, parallel to the behavioral improvement, we found cortical changes immediately after training, in the

neural representation in MT and the connectivity from MT to IPS. Two weeks after training, in addition to the existing changes, we discovered an emergence of enhanced decoding accuracy in IPS. This result suggests that the related cortical network may undergo adjustment over a long-time course, even after training ended. These findings extend our understanding of the learning-induced temporal dynamics within the sensory cortex [Chen and Fang, 2011; Molina-Luna et al., 2008; Yotsumoto et al., 2008], indicating that the plasticity in sensory and high-level stages might be triggered at successive time points during the development of perceptual learning.

In comparison with motion learning in a clear display [Chen et al., 2015], we found that motion perceptual learning in noise led to changes in a different cortical locus along the visual dorsal pathway. These results suggest that learning induces changes in the sensory area based on the functional specialization. Meanwhile, our findings revealed a common neural mechanism underlying motion perceptual learning. First, motion discrimination training with both clear and noisy stimuli induced a refined neural representation in the visual cortex. Second, training enhanced cortico-cortical communication between the sensory area with a better representation for the trained visual feature and the high-level decision unit. Third, the neural changes accurately captured the specificity and persistency observed in the behavioral learning effect. These findings indicate that low-level and high-level processes work in cohort to optimize the learned visual signal in a long-time course.

REFERENCES

- Abdollahi RO, Kolster H, Glasser MF, Robinson EC, Coalson TS, Dierker D, Jenkinson M, Van Essen DC, Orban GA (2014): Correspondences between retinotopic areas and myelin maps in human visual cortex. *Neuroimage* 99:509–524.
- Adab HZ, Vogels R (2011): Practicing coarse orientation discrimination improves orientation signals in macaque cortical area V4. *Curr Biol* 21:1661–1666.
- Albright TD (1984): Direction and orientation selectivity of neurons in visual area MT of the macaque. *J Neurophysiol* 52:1106–1130.
- Ball K, Sekuler R (1987): Direction-specific improvement in motion discrimination. *Vis Res* 27:953–965.
- Bartels A, Zeki S, Logothetis NK (2008): Natural vision reveals regional specialization to local motion and to contrast-invariant, global flow in the human brain. *Cereb Cortex* 18:705–717.
- Bejjanki VR, Beck JM, Lu ZL, Pouget A (2011): Perceptual learning as improved probabilistic inference in early sensory areas. *Nat Neurosci* 14:642–648.
- Bi T, Chen N, Weng Q, He D, Fang F (2010): Learning to discriminate face views. *J Neurophysiol* 104:3305–3311.
- Bi T, Chen J, Zhou T, He Y, Fang F (2014): Function and structure of human left fusiform cortex are closely associated with perceptual learning of faces. *Curr Biol* 24:222–227.
- Cai P, Chen N, Zhou T, Thompson B, Fang F (2014): Global versus local: double dissociation between MT+ and V3A in motion

- processing revealed using continuous theta burst transcranial magnetic stimulation. *Exp Brain Res* 232:4035–4041.
- Chen N, Fang F (2011): Tilt aftereffect from orientation discrimination learning. *Exp Brain Res* 215:227–234.
- Chen N, Bi T, Zhou T, Li S, Liu Z, Fang F (2015): Sharpened cortical tuning and enhanced cortico-cortical communication contribute to the long-term neural mechanisms of visual motion perceptual learning. *NeuroImage* 115:17–29.
- Chen N, Cai P, Zhou T, Thompson B, Fang F (2016): Perceptual learning modifies the functional specializations of visual cortical areas. *Proc Natl Acad Sci USA* 113:5724–5729.
- Dosher BA, Lu ZL (1999): Mechanisms of perceptual learning. *Vision Res* 39:3197–3221.
- Dosher BA, Lu ZL (2005): Perceptual learning in clear displays optimizes perceptual expertise: Learning the limiting process. *Proc Natl Acad Sci USA* 102:5286–5290.
- Dosher BA, Jeter P, Liu J, Lu ZL (2013): An integrated reweighting theory of perceptual learning. *Proc Natl Acad Sci USA* 110:13678–13683.
- Engel SA, Glover GH, Wandell BA (1997): Retinotopic organization in human visual cortex and the spatial precision of functional MRI. *Cereb Cortex* 7:181–192.
- Fahle M, Poggio T (2002). *Perceptual Learning*. MIT Press.
- Friston KJ (2006): Dynamic causal models for fMRI. In: *Statistical parametric mapping: the analysis of functional brain images*. Amsterdam: Elsevier.
- Friston K (2007): Dynamic causal models for fMRI. In: *Statistical Parametric Mapping*. London: Academic Press. pp 541–560.
- Friston KJ, Harrison L, Penny W (2003): Dynamic causal modeling. *Neuroimage* 19:1273–1302.
- Gu Y, Liu S, Fetsch CR, Yang Y, Fok S, Sunkara A, DeAngelis GC, Angelaki DE (2011): Perceptual learning reduces interneuronal correlations in macaque visual cortex. *Neuron* 71:750–761.
- Heekeren HR, Marrett S, Ungerleider LG (2008): The neural systems that mediate human perceptual decision making. *Nat Rev Neurosci* 9:467–479.
- Hua T, Bao P, Huang CB, Wang Z, Xu J, Zhou Y, Lu ZL (2010): Perceptual learning improves contrast sensitivity of V1 neurons in cats. *Curr Biol* 20:887–894.
- Jehee JF, Ling S, Swisher JD, van Bergen RS, Tong F (2012): Perceptual learning selectively refines orientation representations in early visual cortex. *J Neurosci* 32:16747–16753a.
- Jeter PE, Dosher BA, Petrov A, Lu ZL (2009): Task precision at transfer determines specificity of perceptual learning. *J Vis* 9:1–13.
- Karni A, Sagi D (1993): The time course of learning a visual skill. *Nature* 365:250–252.
- Kayser AS, Buchsbaum BR, Erickson DT, D’Esposito M (2010): The functional anatomy of a perceptual decision in the human brain. *J Neurophysiol* 103:1179–1194.
- Lagae L, Raiguel S, Orban GA (1993): Speed and direction selectivity of macaque middle temporal neurons. *J Neurophysiol* 69:19–39.
- Law CT, Gold JI (2008): Neural correlates of perceptual learning in a sensory-motor, but not a sensory, cortical area. *Nat Neurosci* 11:505–513.
- Law CT, Gold JI (2009): Reinforcement learning can account for associative and perceptual learning on a visual-decision task. *Nat Neurosci* 12:655–663.
- Lee HA, Lee SH (2012): Hierarchy of direction-tuned motion adaptation in human visual cortex. *J Neurophysiol* 107:2163–2184.
- Lim S, McKee JL, Woloszyn L, Amit Y, Freedman DJ, Sheinberg DL, Brunel N (2015): Inferring learning rules from distributions of firing rates in cortical neurons. *Nat Neurosci* 18:1804–1810.
- Liu J, Newsome WT (2003): Functional organization of speed tuned neurons in visual area MT. *J Neurophysiol* 89:246–256.
- Liu LD, Pack CC (2017): The contribution of area MT to visual motion perception depends on training. *Neuron* 95:436–446.
- Molina-Luna K, Hertler B, Buitrago MM, Luft AR (2008): Motor learning transiently changes cortical somatotopy. *Neuroimage* 40:1748–1754.
- Mukai I, Kim D, Fukunaga M, Japee S, Marrett S, Ungerleider LG (2007): Activations in visual and attention-related areas predict and correlate with the degree of perceptual learning. *J Neurosci* 27:11401–11411.
- Op de Beeck HP, Baker CI, DiCarlo JJ, Kanwisher NG (2006): Discrimination training alters object representations in human extrastriate cortex. *J Neurosci* 26:13025–13036.
- Orban GA (2016): Functional definitions of parietal areas in human and non-human primates. *Proc R Soc B* 283:20160118.
- Orban GA, Van Calenbergh F, De Bruyn B, Maes H (1985): Velocity discrimination in central and peripheral visual field. *J Opt Soc Am A* 2:1836–1847.
- Orban GA, Fize D, Peuskens H, Denys K, Nelissen K, Sunaert S, Todd J, Vanduffel W (2003): Similarities and differences in motion processing between the human and macaque brain: evidence from fMRI. *Neuropsychologia* 41:1757–1768.
- Pilly PK, Seitz AR (2009): What a difference a parameter makes: A psychophysical comparison of random dot motion algorithms. *Vis Res* 49:1599–1612.
- Poggio T, Fahle M, Edelman S (1992): Fast perceptual learning in visual hyperacuity. *Science* 256:1018–1021.
- Rodman HR, Albright TD (1987): Coding of visual stimulus velocity in area MT of the macaque. *Vis Res* 27:2035–2048.
- Sagi D (2011): Perceptual learning in vision research. *Vision Res* 51:1552–1566.
- Schoups A, Vogels R, Qian N, Orban GA (2001): Practising orientation identification improves orientation coding in V1 neurons. *Nature* 412:549–553.
- Schwartz S, Maquet P, Frith C (2002): Neural correlates of perceptual learning: a functional MRI study of visual texture discrimination. *Proc Natl Acad Sci USA* 99:17137–17142.
- Seitz AR, Pilly PK, Pack CC (2008): Interactions between contrast and spatial displacement in visual motion processing. *Curr Biol* 18:R904–R906.
- Sereno MI, Dale AM, Reppas JB, Kwong KK, Belliveau JW, Brady TJ, Rosen BR, Tootell RB (1995): Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science* 268:889–893.
- Sereno MI, Pitzalis S, Martinez A (2001): Mapping of contralateral space in retinotopic coordinates by a parietal cortical area in humans. *Science* 294:1350–1354.
- Shibata K, Chang LH, Kim D, Nájuez JE, Kamitani Y, Watanabe T, Sasaki Y (2012): Decoding reveals plasticity in V3A as a result of motion perceptual learning. *PLoS One* 7:e44003.
- Shibata K, Sasaki Y, Kawato M, Watanabe T (2016): Neuroimaging evidence for 2 types of plasticity in association with visual perceptual learning. *Cereb Cortex* 26:3681–3689.

- Smith AM, Lewis BK, Ruttimann UE, Ye FQ, Sinnwell TM, Yang YH, Duyn JH, Frank JA (1999): Investigation of low frequency drift in fMRI signal. *Neuroimage* 9:526–533.
- Talairach J, Tournoux P (1988): Co-planar stereotaxic atlas of the human brain. New York: Thieme.
- Thompson B, Tjan BS, Liu Z (2013): Perceptual learning of motion direction discrimination with suppressed and unsuppressed MT in humans: an fMRI study. *PLoS ONE* 8:e53458.
- Tootell RB, Mendola JD, Hadjikhani NK, Ledden PJ, Liu AK, Reppas JB, Sereno MI, Dale AM (1997): Functional analysis of V3A and related areas in human visual cortex. *J Neurosci* 17:7060–7078.
- Tosoni A, Galati G, Romani GL, Corbetta M (2008): Sensory-motor mechanisms in human parietal cortex underlie arbitrary visual decisions. *Nat Neurosci* 11:1446–1453.
- Vaina LM, Belliveau JW, des Roziers EB, Zeffiro TA (1998): Neural systems underlying learning and representation of global motion. *Proc Natl Acad Sci USA* 95:12657–12662.
- Vaina LM, Cowey A, Jakab M, Kikinis R (2005): Deficits of motion integration and segregation in patients with unilateral extrastriate lesions. *Brain* 128:2134–2145.
- Vaina LM, Gryzwacz NM, Saiviroonporn P, LeMay M, Bienfang DC, Cowey A (2003): Can spatial and temporal motion integration compensate for deficits in local motion mechanisms? *Neuropsychologia* 41:1817–1836.
- Van Essen DC, Maunsell JH (1983): Hierarchical organization and functional streams in the visual cortex. *Trends Cogn Sci* 6:370–375.
- Vogels R, Orban GA (1985): The effect of practice on the oblique effect in line orientation judgments. *Vis Res* 25:1679–1687.
- Wandell BA, Winawer J (2015): Computational neuroimaging and population receptive fields. *Trends Cogn Sci* 19:349–357.
- Watanabe T, Náñez JE, Sasaki Y (2001): Perceptual learning without perception. *Nature* 413:844–848.
- Watanabe T, Sasaki Y (2015): Perceptual learning: toward a comprehensive theory. *Annu Rev Psychol* 66:197–221.
- Watson AB, Pelli DG (1983): QUEST: A Bayesian adaptive psychometric method. *Atten Percept Psychophys* 33:113–120.
- Yotsumoto Y, Watanabe T, Sasaki Y (2008): Different dynamics of performance and brain activation in the time course of perceptual learning. *Neuron* 57:827–833.
- Zhang J, Meeson A, Welchman AE, Kourtzi Z (2010): Learning alters the tuning of functional magnetic resonance imaging patterns for visual forms. *J Neurosci* 30:14127–14133.
- Zohary E, Celebrini S, Britten K, Newsome WT (1994): Neural plasticity that underlies improvement in perceptual performance. *Science* 263:1289–1292.