

Tilt aftereffect from orientation discrimination learning

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Abstract Using psychophysical methods, the present study aims to investigate whether orientation discrimination learning can modify the visual cortex and how the modification is related to the development of perceptual learning (performance improvement). In Experiment 1, subjects were trained with an orientation discrimination task at the orientation of 15° right tilted from the vertical. The training not only improved subjects' orientation discrimination performance, but also shifted their perceived vertical toward the trained orientation, which resembles a well-known visual illusion—tilt aftereffect. Interestingly, the change of perceived vertical and performance improvement had different dynamics. Subjects' performance levels were maintained at a constant level, even 2 months after training. However, their perceived vertical changes reduced dramatically 1 week after training. In addition, Experiment 1 showed that there was only a weak transfer of the perceived vertical change from the trained location to the untrained location. Experiment 2 demonstrated that subjects' perceived vertical was not affected by training at 75°. These results suggest that the orientation discrimination training could modify neuronal responses in human retinotopic visual areas and the development of perceptual learning is not a single neural process.

Keywords Perceptual learning · Tilt aftereffect · Orientation · Plasticity · Psychophysics

Introduction

Perceptual learning is experience-dependent enhancement of our ability to make sense of what we see, hear, feel, taste, or smell (Gold and Watanabe 2010). In vision, learning can improve discrimination of many fine visual features, including contrast (Yu et al. 2004), orientation (Schoups et al. 1995), spatial phase (Berardi and Fiorentini 1987), stereoacuity (Fendick and Westheimer 1983), hyperacuity (Fahle and Edelman 1993), motion direction (Ball and Sekuler 1987), and texture (Karni and Sagi 1991). A hallmark feature of perceptual learning is that the improvement obtained by practicing a perceptual discrimination task is often restricted to stimuli similar to the trained stimulus. This specificity implies that the neural substrate of the learning effect might reside in the early stages of the sensory processing pathway (Gilbert et al. 2001). For instance, orientation discrimination learning (Schoups et al. 1995) was highly specific to the trained retinal location and orientation, suggesting that this form of learning engages early visual areas where both visual space and orientation are precisely represented.

This dominant view was mainly based on psychophysical data (Karni and Sagi 1991) and received only inconsistent support from neurophysiological studies. Schoups et al. (2001) found that orientation discrimination learning led to an orientation- and location-specific increase in the slope of the orientation tuning curves of V1 neurons. However, no changes in the orientation tuning of V1 or V2 neurons were observed by another group (Ghose et al. 2002; Yang and Maunsell 2004; see also Crist et al. 2001). Orientation

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discrimination learning effects were found to be more evident in V4. Both groups reported a narrowing of orientation tuning curves of neurons in this cortical area (Raiguel et al. 2006; Yang and Maunsell 2004).

Recent psychophysical studies suggest that perceptual learning effects might be associated with changes outside visual cortical areas (Xiao et al. 2008; Zhang and Li 2010; Zhang et al. 2010). Xiao et al. (2008) demonstrated that location specificity of perceptual learning could be abolished by a feature and location double training procedure. For example, location-specific contrast discrimination learning can be rendered completely transferrable to a new location if the new location is trained with an irrelevant orientation discrimination task. This finding poses a challenge to the fundamental assumption that perceptual learning is specific to the trained retinal location and supports the hypothesis that learning occurs at a central site in the brain (Mollon and Danilova 1996). Resonant with this, it has been shown that the performance improvements in discriminating motion direction were accompanied by changes in neuronal responses of a decision-making area—lateral intraparietal area (LIP), but not the key motion processing area—middle temporal area (MT; Law and Gold 2008).

Currently, there is no consensus on whether perceptual learning can modify the visual cortex and how the modification is related to the performance improvement. To infer the locus of cortical change, previous psychophysical studies focused on the specificity and transfer of perceptual improvement. In this study, we investigated this issue in a new way. Subjects were trained to do an orientation discrimination task at the orientation of 15° right tilted from the vertical (i.e., 0°). We measured subjects' perceived vertical before and after training. Note that several single-unit studies found a narrowing of orientation tuning curves of neurons in visual cortical areas after the orientation discrimination training (Raiguel et al. 2006; Schoups et al. 2001; Yang and Maunsell 2004). If human visual cortex has a similar change after training, we predict that subjects' perceived vertical would shift toward the trained orientation (see below for a detailed explanation). In other words, the perceived orientation of a test grating around 0° would be pushed away from the trained orientation, which is reminiscent of a well-known visual illusion—tilt aftereffect.

The narrowing of orientation tuning curves was reported to manifest in two ways. Yang and Maunsell (2004) showed a two-side, symmetric narrowing, which was most prominent for neurons that preferred orientations close to the trained orientation (Fig. 1a). Schoups et al. (2001) and Raiguel et al. (2006) found that training resulted in a one-side, local increase in the slope of the tuning curve, leading to an increase in discriminability around the trained orientation. The increases in slope and discriminability were restricted to the most informative neurons, those with

preferred orientations offset by some degrees from the trained orientation (Fig. 2a). Following the two ways of narrowing, Figs. 1b, 2b show the changes of tuning curves of orientation-selective model neurons after the orientation discrimination training at 15° . It is generally thought that perception of local orientation is based on the distribution of activity among many orientation-selective neurons in visual cortex. After training, the distribution of neuronal activity representing the vertical is shifted away from the trained orientation. As a result, the vertical should appear to be left tilted. The perceived orientation of the vertical before and after training can be modeled quantitatively by a method proposed by Pouget et al. (2003) (see also Clifford et al. 2000; Vogels 1990). It is determined by the response of the model neuronal population, the vector sum of individual neuronal responses. To compute the vector sum, each model neuron contributes a vector in the direction representing its preferred orientation with a length proportional to its response (Figs. 1c, 2c). The method confirms that the vertical should appear to be left tilted after training (Figs. 1d, 2d).

The current study aims to test our prediction. In Experiment 1, subjects were trained to perform an orientation discrimination task at 15° in the upper visual field. We measured the change of perceived vertical and performance improvement 1 day, 1 week, and 2 months after training. Previous studies (Karni and Sagi 1991; Bi et al. 2010) have demonstrated that performance improvements from training were long lasting. It is interesting to examine the persistence of the perceived vertical change based on the measurements at multiple time points. We also examined whether the change of perceived vertical could transfer to the lower visual field. In Experiment 2, subjects were trained with a similar task at 75° , and the change of perceived vertical was measured. If there is any perceived vertical change and if the change is dependent on the trained location and orientation, then it is reasonable to infer that perceptual learning can modify the visual cortex. Meanwhile, examining the similarity of the dynamics of the perceived vertical change and performance improvement will be able to inform us how the modification is related to the performance improvement.

Methods

Subjects

A total of sixteen naive subjects (8 men and 8 women) participated in the study. They were randomly split into two groups of eight subjects for Experiments 1 and 2, respectively. They were right-handed with reported normal or corrected-to-normal vision and had no known neurological

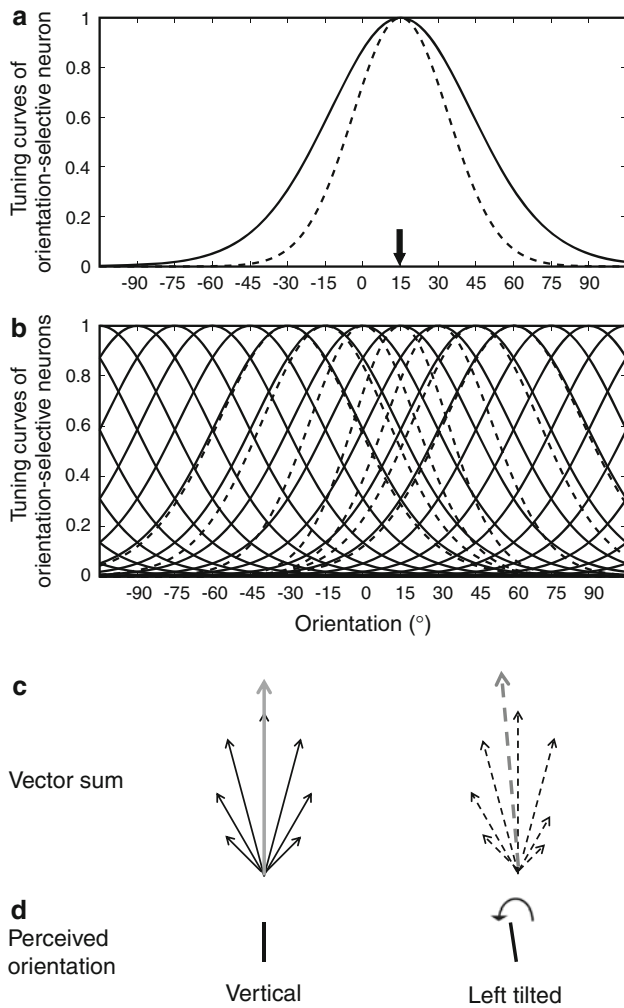


Fig. 1 **a** Tuning curves of an orientation-selective model neuron peaking at 15° before (*solid line*) and after (*dashed line*) orientation discrimination training at 15°. The effect of orientation discrimination training has been shown to narrow orientation tuning curves around the trained orientation (Yang and Maunsell 2004). **b** Tuning curves of orientation-selective model neurons before (*solid line*) and after (*dashed line*) orientation discrimination training at 15°. **c** The percept of orientation is determined by the vector sum of the individual neuronal responses. Each model neuron contributes a vector in the direction representing its preferred orientation with a length proportional to its response (*solid arrows* for pre-training and *dashed arrows* for post-training). **d** After training, the perceived orientation of the physical vertical is predicted to be left tilted in terms of Yang and Maunsell’s physiological finding

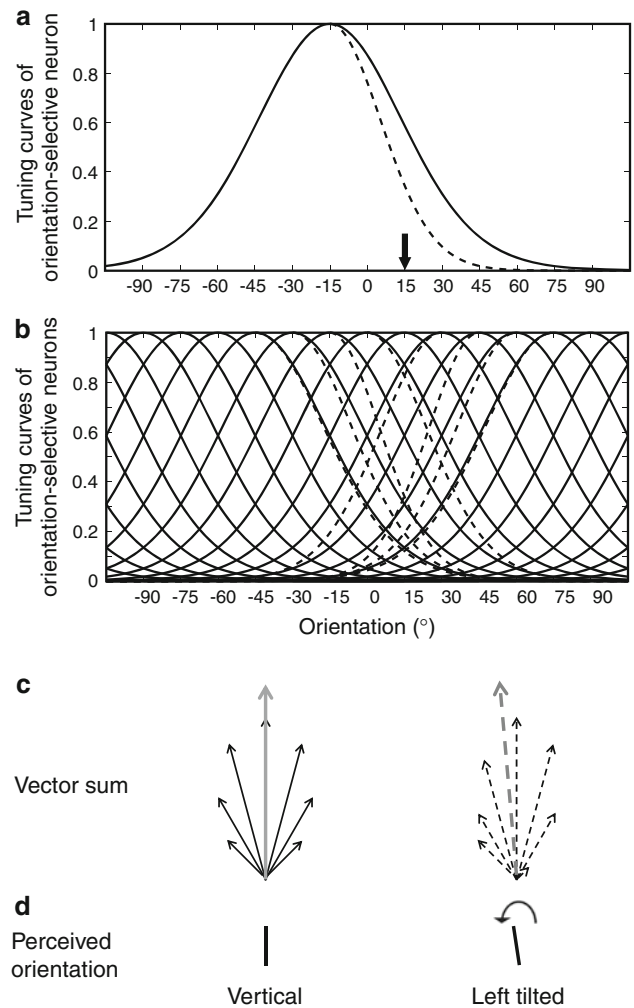


Fig. 2 **a** Tuning curves of an orientation-selective model neuron peaking at −15° before (*solid line*) and after (*dashed line*) orientation discrimination training at 15°. Orientation discrimination training leads to a single-side, local increase in the slope of the tuning curve, which is restricted to the informative neurons (e.g., the one peaking at −15°) with preferred orientations offset by some degrees from the trained orientation (Schoups et al. 2001). **b** Tuning curves of orientation-selective model neurons before (*solid line*) and after (*dashed line*) orientation discrimination training at 15°. **c** The percept of orientation is determined by the vector sum of the individual neuronal responses. Each model neuron contributes a vector in the direction representing its preferred orientation with a length proportional to its response (*solid arrows* for pre-training and *dashed arrows* for post-training). **d** After training, the perceived orientation of the physical vertical is predicted to be left tilted in terms of Schoups et al.’s physiological finding

or visual disorders. Their ages ranged from 18 to 24. They gave written, informed consent in accordance with the procedures and protocols approved by the human subjects review committee of Peking University.

Stimuli and designs

Visual stimuli were circular patches of sinusoidal gratings with a randomize phase (diameter: 2.5°; contrast: 0.9; spatial

frequency: 2 cycles/°; Fig. 3). They were centered at 2.5° retinal eccentricity in either the lower or the upper visual field. The stimuli were presented on a uniform gray field with their mean luminance (59.96 cd/m²) at a viewing distance of 60 cm. The display was an IYAMA color graphic monitor (model: MM906UT; refresh rate: 100 Hz; resolution: 1,024 × 768; size: 19 inch). Subjects’ head position was stabilized using a chin and head rest. During

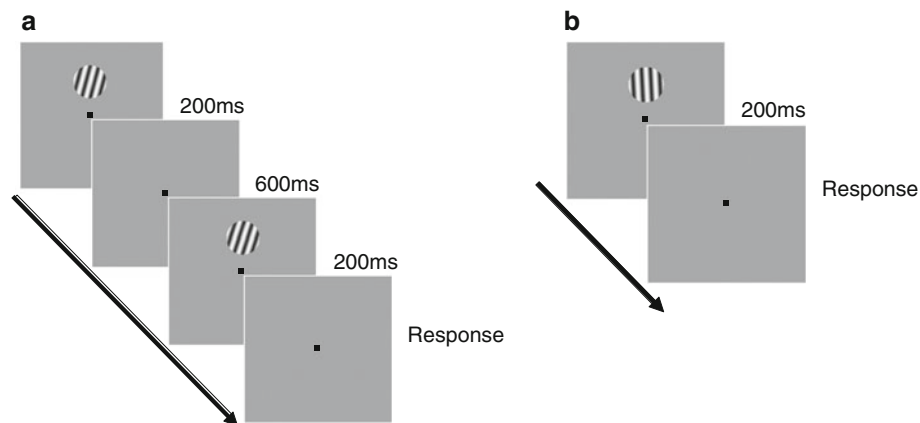


Fig. 3 **a** Schematic description of a 2-AFC trial in a QUEST staircase for measuring orientation discrimination threshold. Two gratings with a slight orientation difference were presented successively. Subjects were asked to make a 2-AFC judgment of the rotation direction (clock-

wise or counter-clockwise) from the first grating to the second one. **b** Schematic description of a 2-AFC trial for measuring subjects' perceived vertical. They were asked to make a 2-AFC judgment of whether a test grating was *left* or *right* tilted

the experimental period, a fixation point was placed in the center of the monitor and subjects were required to maintain fixation.

Experiment 1 consisted of a pre-training test (day 0), orientation discrimination training (days 1–6), and three post-training tests (Post 1 on day 7, Post 2 on day 14, Post 3 on day 68). During the training phase, each subject underwent six daily training sessions to perform an orientation discrimination task at the orientation of 15° right tilted from the vertical (i.e., 0°). A daily session (about 1.5 h) consisted of 34 QUEST staircases of 40 trials (Watson and Pelli 1983). In a trial, 15° and $15^\circ \pm \theta^\circ$ tilted gratings were each presented for 200 ms in the upper visual field and were separated by a 600 ms blank interval (Fig. 3a). Their temporal order was randomized. Subjects were asked to make a 2-alternative-forced-choice (2-AFC) judgment of the rotation direction (clockwise or counter-clockwise) from the first grating to the second one. A high-pitched tone was provided after a wrong response and the next trial began one second after response. The θ varied trial by trial and was controlled by the QUEST staircase to estimate subjects' orientation discrimination threshold (75% correct). To measure the time course of the training effect (learning curve), discrimination thresholds from 34 QUEST staircases in a daily training session were averaged and then plotted as a function of training day. Learning curves were fitted with a power function (Jeter et al. 2009).

During the pre- and post-training tests, we first measured subjects' perceived vertical with the method of constant stimuli. The measurement consisted of 9 blocks of 50 trials. In a block, each of five test gratings with the orientations of 0° , $\pm 3^\circ$, and $\pm 6^\circ$ was presented ten times in a random order. In a trial, a test grating was presented for 200 ms and

subjects were asked to make a 2-AFC judgment of whether the grating was left or right tilted (Fig. 3b). The measurement was performed in both the upper and the lower visual fields in a balanced order. In the former case, a test grating was presented at the trained location. In the latter case, it was presented at an untrained location symmetrically across the horizontal meridian of the visual field. For each measurement, all of the data from nine blocks were pooled together to generate a psychometric function: the percentage of trials in which subjects indicated that a test grating was perceived to tilt to the left plotted as a function of its real orientation. We used a cumulative normal function to fit the psychometric values and interpolated to find the perceived vertical (Fang et al. 2007).

At Post 1, we then measured subjects' orientation discrimination thresholds at the orientations of 15° and 75° right tilted from the vertical in the upper visual field. Twelve QUEST staircases (same as above) were completed for each orientation. The two orientation conditions were counterbalanced across subjects. Discrimination thresholds from the 10 staircases for each orientation were averaged as a measure of subjects' discrimination performance. Subjects' performance improvement after training at an orientation was calculated as $(\text{pre-training threshold} - \text{post-training threshold}) / \text{pre-training threshold} \times 100\%$. At Posts 2 and 3, only the threshold at the orientation of 15° was measured.

Experiment 2 has a similar design as that of Experiment 1 except that (1) subjects were trained at the orientation of 75° and (2) there was only one post-training test on day 7. Prior to the experiments, subjects practiced two staircases (80 trials) at the orientations of 15° and 75° to get familiar with the stimuli and the experiment procedure.

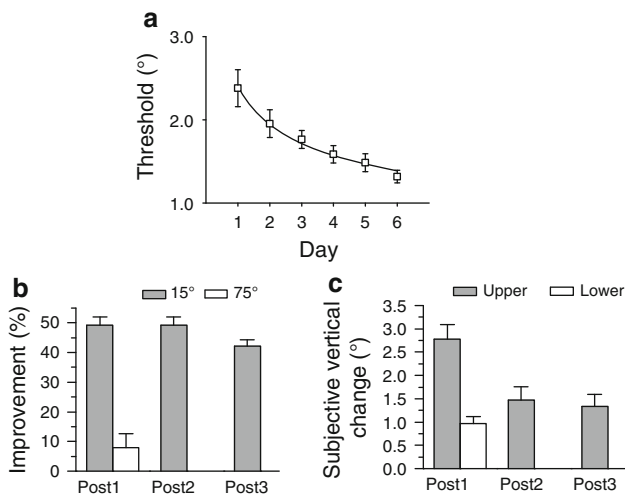


Fig. 4 **a** Learning curve. Orientation discrimination thresholds at 15° are plotted as a function of training day. **b** Percent improvement in orientation discrimination performance at 15° at Posts 1–3 and at 75° at Post 1. **c** Subjective vertical change in the *upper* visual field at Posts 1–3 and in the *lower* visual field at Post 1. Data were averaged across eight subjects. Error bars denote 1 SEM calculated across subjects

Results

In Experiment 1, subjects practiced an orientation discrimination task in the upper visual field at the orientation of 15° right tilted from the vertical (i.e., 0°) on days 1–6, for 8,160 trials in total. Throughout the training course, their discrimination thresholds gradually decreased (Fig. 4a). Before and after training, we measured subjects' orientation discrimination thresholds at 15° and 75°. At Post 1 on day 7, relative to the performance before training, the percent improvements in discrimination performance at 15° and 75° were 49 and 8%, respectively. The improvement at 15° was significantly larger than that at 75° ($t(7) = 6.33$, $P < 0.001$), which demonstrated that the orientation discrimination learning was highly specific to the trained orientation (Fig. 4b).

To examine the persistence of the learning effect, we measured the discrimination threshold at 15° about 1 week (Post 2 on day 14) and 2 months (Post 3 on day 68) after training. Relative to the performance before training, the performance improvements were 49 and 43% at Posts 2 and 3, respectively, which were not significantly different from the improvement at Post 1 (both $t(7) < 2.08$, $P > 0.05$; Fig. 4b). This result means that the learning effect was long-lasting and it was completely kept even after 2 months.

Having shown the specificity and persistence of the orientation discrimination learning, we used the method of constant stimuli to measure subjects' perceived vertical before and after training. Five test gratings with orienta-

tions of 0°, ±3°, and ±6° were presented randomly, and subjects were asked to make a 2-AFC judgment of whether the grating was left or right tilted. Psychometric functions were constructed and fitted with a cumulative normal function. Perceived vertical was found through interpolation.

Before training, subjects' perceived vertical was very close to 0°. However, training made their perceived vertical shift toward the trained orientation. In other words, the perceived orientation of a test grating around 0° was pushed away from the trained orientation. This phenomenon resembles a well-known visual illusion—tilt aftereffect. At Post 1, the subjective vertical changes in the upper and lower visual fields were 2.78° and 0.96°, respectively (Fig. 4c). Both were significantly larger than zero (both $t(7) > 6.19$, $P < 0.001$). The change in the upper visual field was significantly larger than that in the lower visual field ($t(7) = 6.76$, $P < 0.001$), showing that the perceived vertical change was specific to the trained location. At Posts 2 and 3, we examined the persistence of the perceived vertical change. Unlike the orientation discrimination performance, the perceived vertical changes dropped to about half of that at Post 1 (both $t(7) > 4.76$, $P < 0.01$), but both were still significantly larger than zero (both $t(7) > 5.00$, $P < 0.01$; Fig. 4c). These results suggest that the discrimination performance improvement and the subjective vertical change after training had distinctive time courses.

Experiment 2 was performed to examine whether the perceived vertical change depends on the angular difference between the trained orientation and the vertical. Subjects underwent the same training as that in Experiment 1 except that they were trained at the orientation of 75° right tilted from the vertical. Throughout the training course, their discrimination thresholds gradually decreased (Fig. 5a). Before and after training, we measured subjects' orientation discrimination thresholds at 15° and 75°. At Post 1 on day 7, relative to the performance before training, the percent improvements in discrimination performance at 15° and 75° were 6 and 49%, respectively. The improvement at 75° was significantly larger than that at 15° ($t(7) = 4.95$, $P < 0.01$), which demonstrated that the orientation discrimination learning was highly specific to the trained orientation (Fig. 5b). The subjective vertical changes in the upper and lower visual fields were 0.21° and -0.06°, respectively, both of which were not significantly different from zero (both $t(7) < 0.87$, $P > 0.41$; Fig. 5c). This result suggests that the orientation discrimination training at 75° had little effect on perceived vertical.

Discussion

The present study examined the change of perceived vertical by the orientation discrimination learning, its time

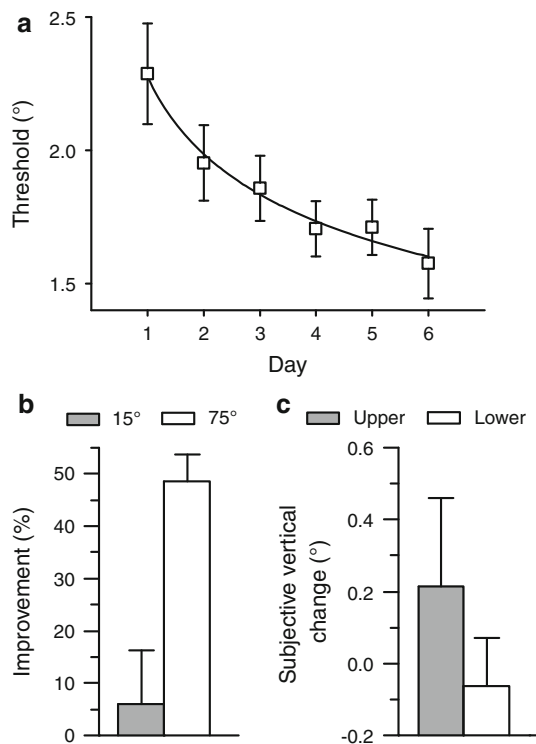


Fig. 5 **a** Learning curve. Orientation discrimination thresholds at 75° are plotted as a function of training day. **b** Percent improvement in orientation discrimination performance at 15° and 75° at Post 1. **c** Subjective vertical change in the *upper* and *lower* visual fields at Post 1. Data were averaged across eight subjects. *Error bars* denote 1 SEM calculated across subjects

course and its relation to the performance improvement. Experiment 1 showed that training not only improved subjects' orientation discrimination performance as demonstrated by many previous studies, but also shifted subjects' perceived vertical toward the trained orientation. Interestingly, the change of perceived vertical and performance improvement had different dynamics. Subjects' performance levels were maintained at a constant level, even 2 months after training. However, their perceived vertical changes reduced dramatically 1 week after training. In addition, Experiment 1 showed that there was only a weak transfer of the perceived vertical change from the trained location (i.e., the upper visual field) to the untrained location (i.e., the lower visual field). Experiment 2 demonstrated that, when trained at 75°, subjects' perceived vertical was not affected, although their orientation discrimination performance was improved.

These findings confirm our prediction. If the orientation tuning curves of neurons in human visual cortex have undergone a similar narrowing to that found with monkey subjects (Raiguel et al. 2006; Schoups et al. 2001; Yang and Maunsell 2004), orientation discrimination learning should have induced tilt aftereffect. However, we cannot

simply deduce from the observation of tilt aftereffect that associated neuronal changes must occur within the visual cortex. An alternative explanation is that perceptual learning could lead to a cognitive or category bias, which is associated with neuronal changes in high cortical cortex (e.g., frontal area). Two pieces of evidence argue against this explanation. First, Experiment 1 demonstrated that the tilt aftereffect was highly specific to the trained location, which showed a very weak transfer between the trained and untrained locations separated by 5° of visual angles. This result suggests that the aftereffect was subserved by retinotopic visual areas. Second, Experiment 2 demonstrated that training at 75° did not generate tilt aftereffect. If the tilt aftereffect could be attributed to a cognitive/category bias, training at any right tilted orientation (e.g. 75°) should bias the percept of the vertical to be left tilted. Instead, this null effect of training at 75° can be better explained by the orientation selectivity property of neurons in visual areas. McAdams and Maunsell (1999) measured half-height tuning bandwidths of orientation-selective neurons in V1 and V4. The mean values in both areas were about 74° (see Figs. 1, 2), which means that the overlap between neuronal populations responding to the orientations of 0° and 75° was very small. Thus, the distribution of neuronal activity representing the vertical should be affected little by the training at 75° and no tilt aftereffect should be observed.

Our results suggest that the orientation discrimination training changed neuronal response properties in human retinotopic visual areas, as manifested by the tilt aftereffect. It is natural to ask whether the changes are functionally related to the performance improvement after training. The different dynamics of the tilt aftereffect and performance improvement in the time course of the learning suggests that this is a complicated issue. As discussed above, shortly after training, the narrowing of orientation tuning curves could contribute to both the tilt aftereffect and performance improvement. However, 1 week after training, the magnitude of the tilt aftereffect was reduced by about 50%, while the performance remained constant. Here are two possible explanations to the dissociation. One is that the orientation tuning curves of all those neurons modified by training had partially recovered to the status before training. The recovery would inevitably lose some discrimination capacity. But the loss could be compensated by a high-level decision unit, as suggested by many theoretical and empirical studies on perceptual learning (Doshier and Lu 1998; Law and Gold 2008; Poggio et al. 1992). The other explanation is that a long-term narrowing occurred only with the most informative neurons for discriminating the trained orientation, while other neurons fully recovered 1 week after training. Both explanations suggest that the development of perceptual learning is comprised of more than one phase. Our finding and speculation is resonant with a recent fMRI

study by Yotsumoto et al. (2008). They examined the dynamics of performance on a texture discrimination task (TDT) and brain activation in human V1 over a long-time course of perceptual learning. Shortly after training, both V1 activation and task performance increased. However, 2 weeks after training, while performance levels were maintained at a constant level, V1 activation decreased to the level observed before training. Based on this finding, they proposed a two-stage model for the development of perceptual learning. Our results provide further support for this model.

An important characteristic of perceptual learning is its persistence. The benefit of perceptual learning with visual feature detection could last up to 2 years (Karni and Sagi 1991). In high-level vision, training effect with a shape/object recognition task could last several months (Bi et al. 2010; Furmanski and Engel 2000; Sigman and Gilbert 2000). Most of previous single-unit and brain imaging studies on perceptual learning focus on cortical changes immediately after training. Our study highlights the importance of studying the development of neural mechanisms of perceptual learning at different temporal stages.

Tilt aftereffect is typically generated by visual orientation adaptation, which selectively depresses the responses of neurons sensitive to the adapted orientation (Carandini et al. 1998; Fang et al. 2005; Movshon and Lennie 1979). Although tilt aftereffect from perceptual learning here is ostensibly similar to that from the adaptation, it is supposed to result from the narrowing of orientation tuning curves because no neurophysiological study has found neuronal response suppression by the orientation discrimination learning (Raiguel et al. 2006; Schoups et al. 2001; Yang and Maunsell 2004). A recent fMRI study (Jehee et al. 2010) also failed to find any blood-oxygenation-level-dependent (BOLD) signal change in early visual areas after orientation discrimination learning, but the multi-voxel pattern analysis (MVPA) suggested that orientation selectivity was increased by the learning. The overall evidence to date suggests that these two tilt aftereffects have different underlying mechanisms.

In summary, in the present study, we found that the orientation discrimination training at 15° not only improved discrimination performance, but also led to a location-specific tilt aftereffect. The two perceptual effects had different temporal dynamics through the time course of perceptual learning—the former one maintained at a constant level, but the latter one dropped dramatically 1 week after training. These findings suggest that the orientation discrimination training could modify neuronal responses in human retinotopic visual areas and the development of perceptual learning is not a single neural process. Future studies will be required to address whether similar phenomena could be found with other types of visual perceptual learning.

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