Vision Research 50 (2010) 368–374

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Decoupling location specificity from perceptual learning of orientation discrimination

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ARTICLE INFO

Article history:
Received 19 May 2009
Received in revised form 19 August 2009

Keywords:
Perceptual learning
Orientation discrimination
Location specificity

ABSTRACT

Perceptual learning of orientation discrimination is reported to be precisely specific to the trained retinal location. This specificity is often taken as evidence for localizing the site of orientation learning to retinotopic cortical areas V1/V2. However, the extant physiological evidence for training improved orientation turning in V1/V2 neurons is controversial and weak. Here we demonstrate substantial transfer of orientation learning across retinal locations, either from the fovea to the periphery or amongst peripheral locations. Most importantly, we found that a brief pretest at a peripheral location before foveal training enabled complete transfer of learning, so that additional practice at that peripheral location resulted in no further improvement. These results indicate that location specificity in orientation learning depends on the particular training procedures, and is not necessarily a genuine property of orientation learning. We suggest that non-retinotopic high brain areas may be responsible for orientation learning, consistent with the extant neurophysiological data.

1. Introduction

Among various visual perceptual learning tasks, the neuronal mechanisms of orientation learning have been most intensively studied (Ghose, Yang, & Maunsell, 2002; Raiguel, Vogels, Mysore, & Orban, 2006; Schoups, Vogels, Qian, & Orban, 2001; Yang & Maunsell, 2004). These neurophysiological studies are in large measure inspired by psychophysical evidence that orientation discrimination learning is precisely specific to the trained retinal location (Schoups, Vogels, & Orban, 1995; Shiu & Pashler, 1992). The Schoups et al. (1995) study has been particularly influential, since they showed that orientation learning did not transfer to an untrained retinal location merely 2.5° away from the trained location at 5° retinal eccentricity in the visual periphery. Equally precise location specificity was also reported in learning of a spatial localization (bisection) task which was also specific to the stimulus orientation (Crist, Kapadia, Westheimer, & Gilbert, 1997). Because cortical areas V1/V2 are highly retinotopic, and their small receptive fields are most capable of performing fine orientation discrimination, it is natural that neurophysiological studies first focused on neurons in the early visual cortex, seeking evidence for training induced sharpening of receptive field orientation tuning.

However, to date, the neurophysiological evidence linking orientation learning to V1/V2 neuron orientation tuning sharpening is controversial and weak at best. Schoups et al. (2001), inspired by their own psychophysical findings, found a correlation between improved monkey orientation discrimination and steeper V1 neuron orientation tuning functions; however, Ghose et al. (2002) found no orientation tuning changes in either V1 or V2 neurons. More significant orientation tuning changes have been reported in V4 neurons by the same two research groups (Raiguel et al., 2006; Yang & Maunsell, 2004). Even so, these changes in V4 neurons were still too small to account for behavioral orientation learning (Raiguel et al., 2006).

While neurophysiologists debate the exact brain site of orientation learning, here we demonstrate that the highly cited psychophysical evidence for precise location specificity in orientation learning deserves a second look. Specifically, we show that perceptual learning of orientation discrimination actually transfers substantially across retinal locations, either from the fovea to the periphery, or among peripheral locations. Moreover, we found that location specificity in orientation learning could be eliminated with appropriate training procedures, which suggests that location specificity is not necessarily a genuine property of orientation learning. Our results shed new light on the current neurophysiological debate regarding the brain sites of orientation learning and help illuminate the mechanisms of perceptual learning in general.

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doi:10.1016/j.visres.2009.08.024

2. Methods

2.1. Observers and apparatus

Thirty six observers (undergraduate students in their early 20s at Beijing Normal University) with normal or corrected-to-normal vision participated in this study. All were new to psychophysical experiments and were unaware of the purposes of the study.

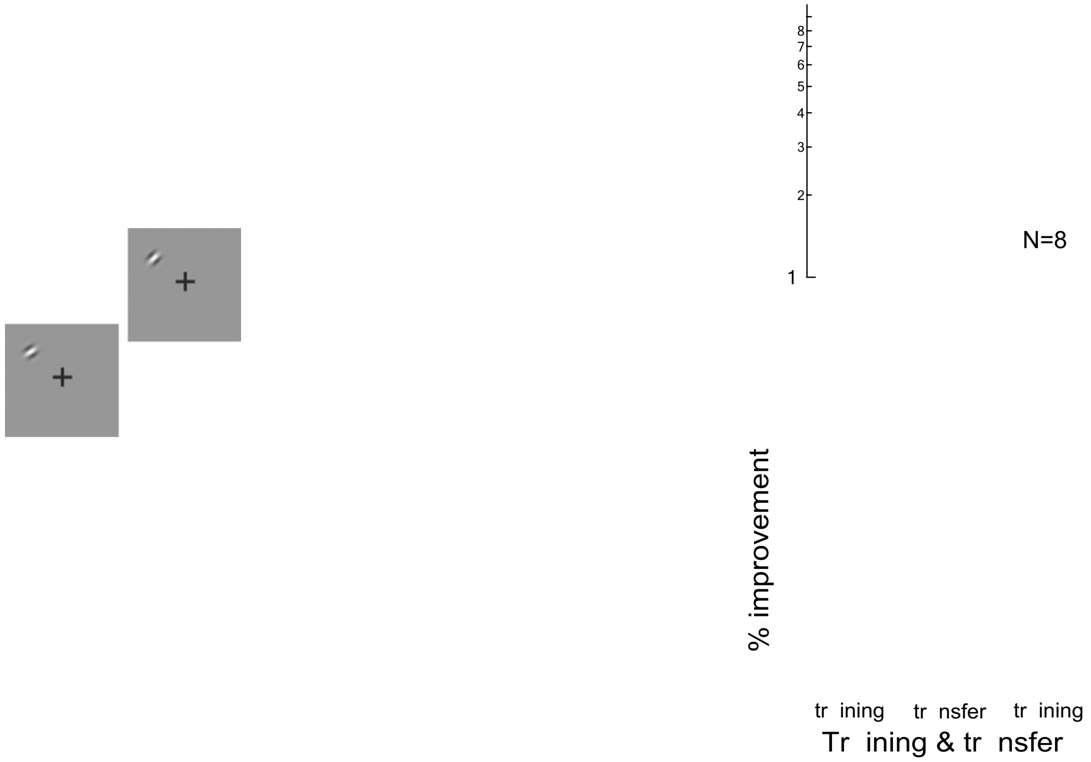
The stimuli were generated by a PC-based WinVis program (Neurometrics Institute, Oakland, CA) and presented on a 21-in. NEC MultiSync FE2111 color monitor (1024 pixel × 768 pixel, 1.3 min (H) × 1.3 min (V) per pixel, 120 Hz frame rate, 33.4 cd/m^2 mean luminance). Luminance of the monitor was linearized by an 8-bit look-up table. Viewing was monocular, and a chin-and-head rest helped stabilize the head of the observer. The viewing distance was 1 m. Experiments were run in a dimly lit room.

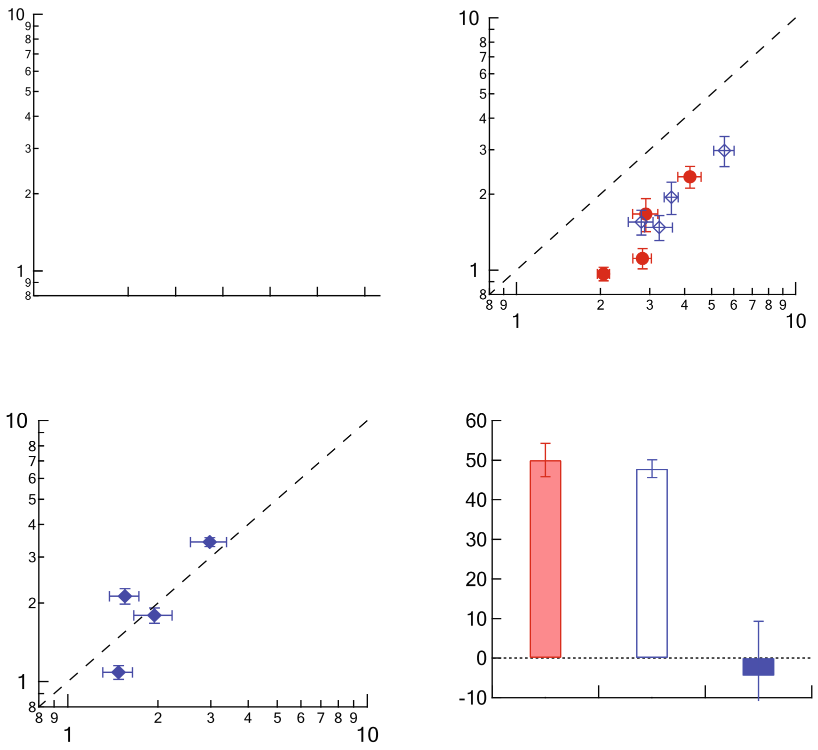
2.2. Stimuli and procedure

Two types of stimuli were used. One was a Gabor patch (Gaussian enveloped sinusoidal grating, with spatial frequency = 1.5 cpd, standard deviation = 0.29°, contrast = 0.47 and phase randomized for every presentation, Fig. 1A) presented on a mean luminance background. The other was identical to the stimulus used by Schoups et al. (1995), which was a circular field (diameter = 2.5°) consisting of 1-dimensional white noise (white and black bars of varying widths, which were randomized from 0.077° to 0.312° and were reset in each trial, Fig. 2A). Both stimuli were viewed through a circular aperture (diameter = 17°) of a black cardboard that covered the entire monitor screen. This control prevented observers from using monitor edges as external references to determine the stimulus orientation.

Orientation thresholds were measured for both discrimination and identification tasks. Orientation discrimination thresholds (for Gabors in Figs. 1 and 4) were measured with a temporal 2AFC staircase procedure. For each trial, the reference (36° or 126°) and test (reference ± an orientation offset) were separately presented in the two brief stimulus intervals (92 ms each) in a random order separated by a 500-ms inter-stimulus interval. An observer's task was to judge which stimulus interval contained the more clockwise-oriented stimulus. Orientation identification thresholds (for Schoups et al.'s stimuli in Figs. 2 and 3) were measured with a single-interval staircase procedure, in which only the test was presented for 300 ms, oriented 45° or 135° ± an orientation offset. Here an observer's task was to judge whether the test was more anti-clockwise or clockwise relative to the implicit oblique orientation reference (45° or 135°) that was never shown. Auditory feedback was given on incorrect responses. Each trial was preceded by a 25′ × 25′ fixation cross (300 ms) that stayed through the trial if the stimulus was presented in the periphery, or disappeared 250 ms before the onset of the first stimulus interval if the stimulus was presented in the fovea.

Each staircase consisted of four preliminary reversals and six experimental reversals. The initial orientation difference between





the test and the reference was sufficiently large, so that the observers could always make a correct discrimination. The steps of the staircase were separated by 0.05 log units above and below the reference. A classical 3-down-1-up staircase rule was used, which resulted in a 79.4% convergence level. The geometric mean of the experimental reversals was taken as the threshold for each staircase run. An observer typically completed 14–16 staircases in a 2-h training session.

2.3. Eye movements

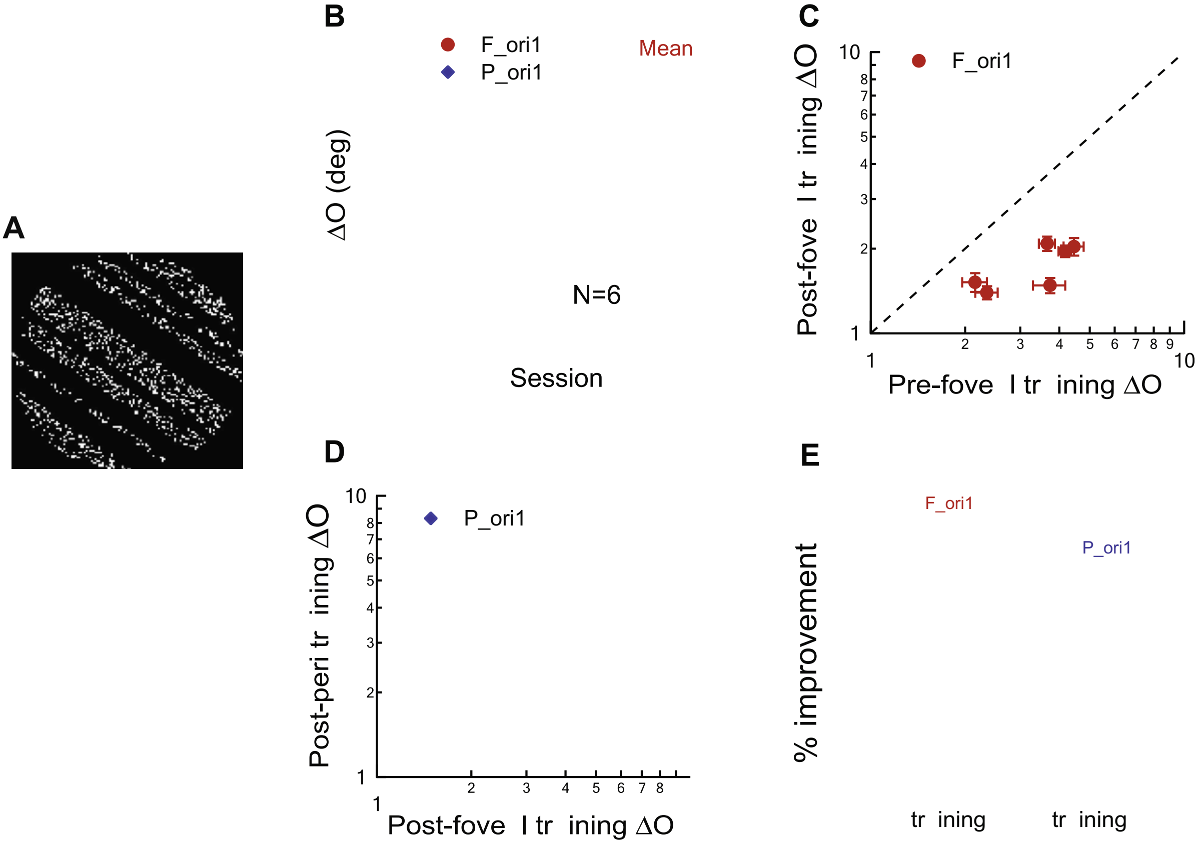
We used an Eyelink II eye tracker to assess the impact of eye movements when peripheral orientation discrimination was performed. Five new observers performed a 2AFC orientation discrimination task for 3–5 sessions. During the first interval, the eye positions on the average were within 0.5° and 1° from the fixation in 90.3% and 98.9% of the trials, respectively, similar to those in a fixation-only control condition ($p = 0.29$ and 0.37, respectively). The eye positions during the second interval were within 0.5° and 1° from the fixation in 78.3% and 96.1% of the trials, respectively, suggesting some involuntary eye drifts (mainly within −0.5°). Importantly, practice did not reduce the second-interval eye drifts to improve visual discrimination. The last-/first-day ratios of these off-fixation percentages in the second interval were 0.954 (<0.5°) and 0.995 (<1°), suggesting no reduction of eye drifts after training. Therefore, learning data reported in this paper were not significantly affected by eye movements.

3. Results

3.1. Decoupling location specificity in Schoups et al. (1995) from orientation learning

The Schoups et al. (1995) study provided the most striking and influential psychophysical evidence for precise location specificity in orientation learning. In this study, observers first practiced orientation identification at the fovea, which reduced orientation thresholds by approximately 72% on the average (from 5.4° to 1.5°, their Fig. 3), before they continued orientation training in peripheral locations at 5° eccentricity. After foveal training, practice at a peripheral location at 5° eccentricity improved peripheral orientation performance significantly, but this peripheral learning did not transfer to an untrained retinal location that was 2.5° away from the trained location but at the same retinal eccentricity. Schoups et al. did not test how much the substantial foveal learning would transfer to the peripheral locations, and there was no baseline measurement of peripheral orientation thresholds before foveal training. Nevertheless, fovea-to-periphery transfer is strongly hinted at by their data. For example, orientation thresholds at 5° eccentricity after foveal training were either similar to, or lower than, the initial foveal thresholds (mean thresholds were 4.8° vs. 5.4° over three observers, their Figs. 2–4). Considering that peripheral orientation thresholds are typically higher than foveal thresholds (e.g., Figs. 1B and 2B), some foveal learning may well have transferred to the periphery in the Schoups et al. study.

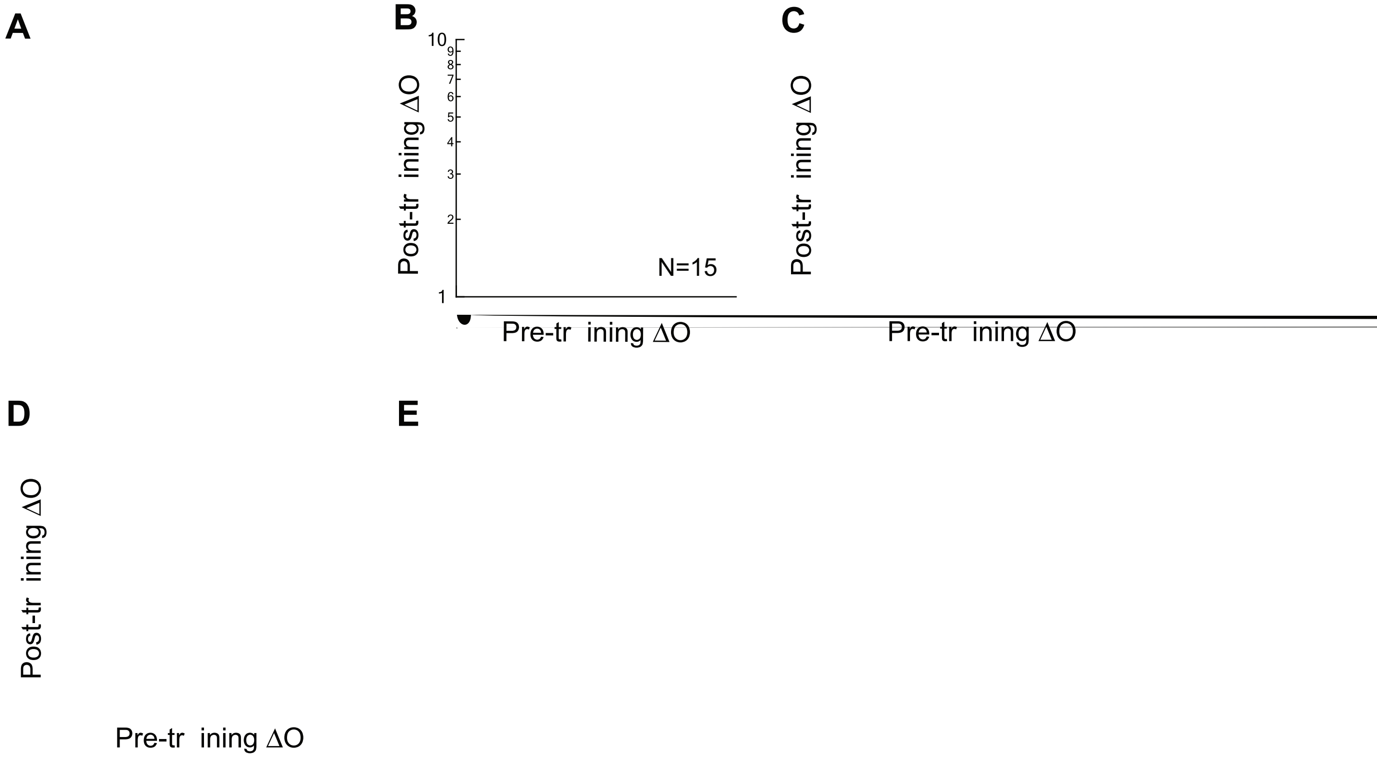
We therefore measured the transfer of foveal orientation learning to the periphery, with the expectation that this would at least



tell us how much general learning foveal training would generate. Eight observers practiced foveal orientation discrimination of a Gabor stimulus at either 36° or 126° (F_ori1) in 2AFC trials for seven sessions, and all showed improved orientation discrimination (Mean percent improvement (MPI) = 1-post-/pre-training threshold = 39.6 ± 4.4%, $p < 0.001$, one tail paired t-test; mean session-by-session thresholds shown in the left half of Fig. 1B, and individual pre- and post-training thresholds contrasted in Fig. 1C). The error bar corresponds to one standard error of the mean. Before and after foveal training, their orientation thresholds for the same oriented Gabor (P_ori1) and an orthogonal Gabor (P_ori2), both centered in either the lower- or upper-left visual quadrant at 5° retinal eccentricity, were also measured (each averaged over six staircases). The results showed that peripheral orientation thresholds were also significantly reduced for both P_ori1 and P_ori2 (MPI = 29.2 ± 5.6%, $p < 0.001$, and MPI = 29.6 ± 6.5%, $p = 0.002$, respectively; Fig. 1B and C). Peripheral performance on the average improved about 75% as much as did foveal performance, but the differences among peripheral and foveal improvements were not statistically significant ($p = 0.192$, repeated measures ANOVA). Although we expected some improvement of peripheral orientation discrimination because of general learning, the very substantial transfer far exceeded our expectation.

With statistically similarly improved performance at the trained fovea and untrained peripheral locations, we wondered whether the foveal training had taught the periphery all there was to learn. That is, had foveal orientation training already optimized peripheral orientation discrimination, so that additional training at the peripheral location would not further improve the performance? To examine this possibility, the same eight observers performed peripheral orientation training for the fovea-trained orientation (P-ori1) for five to six sessions at the same peripheral location where the transfer was tested. Following peripheral training, orientation discrimination only improved significantly in two observers but not in other six observers (overall MPI = 9.8 ± 7.5%, $p = 0.12$; mean session-by-session thresholds shown in the right half of Fig. 1B, and individual pre- and post-training thresholds contrasted in Fig. 1D), suggesting that foveal orientation training indeed had optimized peripheral performance in most observers. These data are seemingly inconsistent with Schoups et al. (1995) who reported nearly 50% improvement of peripheral orientation discrimination as a result of additional peripheral training following foveal training (their Fig. 3). Our further experiments will explain why there is this discrepancy.

We first suspected that the discrepancies between the results of ours and Schoups et al.'s might result from stimulus and training procedure differences. Schoups et al.'s test stimuli were large (diameter = 2.5° vs. our $\sigma = 0.29°$ Gabors), and their training lasted 15–18 sessions, more than two times longer than our 6–7 sessions. So we replicated Schoups et al.'s experiment using the identical stimuli (Fig. 2A) and task (single interval orientation discrimination at either 45° or 135° oblique orientation), and our new training lasted 13 sessions. To measure the fovea-to-periphery transfer of learning, we again pretested orientation thresholds in the



periphery (5° retinal eccentricity on the horizontal meridian, left visual hemifield) before foveal training. However, the new training procedure with new stimuli produced similar data to those with the Gabor stimuli (Fig. 2B–E). First foveal orientation thresholds floored after 5–6 sessions of training, suggesting that significantly more sessions of training was redundant. Second, peripheral orientation discrimination was about equally improved (peripheral MPI = 47.9 ± 2.3%, $p < 0.001$ vs. foveal MPI = 50.0 ± 4.2%, $p < 0.001$, approximately a factor of 2 decrease in threshold), similar to the results with Gabor stimuli. Third and most importantly, like our previous data, successive peripheral training did not improve orientation discrimination further (MPI = −4.4 ± 13.8%, $p = 0.34$), suggesting again optimized peripheral orientation discrimination after foveal training.

So what made the results between the Schoups et al. and the present study so different after the differences of stimuli and training durations were excluded? The only remaining difference between two studies was that before foveal training, we briefly pretested peripheral thresholds (six staircases, or approximately 200 trials) as a baseline to gauge the fovea-to-periphery transfer of learning. Did this brief pretest enable the optimization of peripheral orientation discrimination? To test this we repeated the above experiment without the pretest in six new observers, and this time the results replicate those of Schoups et al. (Fig. 3B). That is, after foveal training (F_ori1) which reduced orientation thresholds in all observers (MPI = 46.7 ± 4.6%, $p < 0.001$; Fig. 3C), additional peripheral training at 5° retinal eccentricity on the horizontal meridian of the left visual hemifield continued to improve orientation performance at this peripheral location in five out of six observers (MPI = 33.3 ± 10.9%, $p = 0.014$, (Fig. 3D). The sixth observer had lower peripheral threshold after foveal training, which did not benefit from further peripheral training (the far left data point near the diagonal line, Fig. 3D). So this observer's data were similar to those in the previous experiment with pretesting (Fig. 2).

In summary, the above experiments (Figs. 1–3) allowed us to decouple location specificity from orientation learning by showing that location specificity in Schoups et al.'s classical study can be abolished with a brief pretest. In Section 4 we will show that this brief pretest alone enabled complete transfer of foveal learning to accomplish the optimization of peripheral performance.

3.2. Transfer of orientation learning among peripheral locations

A more common and straightforward way to study location specificity is to test the transfer of learning from a trained to an untrained peripheral location (without initial foveal training). Using this training paradigm, Shiu and Pashler (1992) in another widely cited study found no significant transfer of orientation learning from a trained quadrant of the visual field to other untrained visual quadrants. However, Shiu and Pashler's results might have been tainted by contextual cues from uncovered rectangular monitor edges (Schoups et al., 1995). Their line stimulus was presented near the corner of a 14-in. rectangular monitor screen. The edges of the monitor could have provided cues for orientation judgment. Moreover, these cues were different when the line was presented in a different monitor corner. For example, the vertical monitor edge was closer to the other line end when the line was presented in a diagonal quadrant. Taking into account this contextual cueing issue in Shiu and Pashler (1992) and the substantial fovea-to-periphery transfer of orientation learning demonstrated in Figs. 1

and 2, we decided to reinvestigate the periphery-to-periphery transfer of orientation learning.

Eighteen observers practiced 2AFC orientation discrimination for a Gabor stimulus (36° or 126°) centered in either the upper- or lower-left visual quadrant at 5° retinal eccentricity (ori1_loc1) for six sessions. For testing transfer, different subgroups of observers were tested at different locations and orientations. Fifteen observers were tested for transfer of learning to the same orientation at a new location symmetrically across the horizontal meridian of the visual field (ori1_loc2, Fig. 4B), nine were tested for transfer to an orthogonal orientation at the same trained location (ori2_loc1, Fig. 4C), and eleven were tested for transfer to an orthogonal orientation at the new location (ori2_loc2, Fig. 4D), and four were tested for transfer to the other three untrained quadrants at the same orientation (Fig. 4E) for the purpose of re-examining the results of Shiu and Pashler (1992) while having the monitor edge cues removed with a circular opening of the monitor screen (see Section 2). Orientation thresholds were pretested for the transfer location/orientation in all observers except the last four (Fig. 4E) for whom isoeccentric pretest threshold equality was assumed.

Most observers showed improved orientation discrimination after training at ori1_loc1 which on the average asymptoted after four training sessions (Fig. 4A, MPI = 32.7 ± 4.3% over all 18 observers, $p < 0.001$). Moreover, orientation discrimination for the untrained ori1_loc2 was also improved significantly after training (green dots; MPI = 26.6 ± 4.5%, $p < 0.001$; Fig. 3B), suggesting substantial transfer of orientation learning at one peripheral location to an untrained peripheral location. Moreover, orientation discrimination for the untrained orthogonal orientation at the same trained location (ori2_loc1) also improved significantly (blue dots; MPI = 22.1 ± 5.4%, $p = 0.002$; Fig. 4C), suggesting significant learning transfer across orientations in the periphery. However, performance for the untrained orthogonal orientation at the untrained location (ori2_loc2) was not significantly changed (purple dots; MPI = 6.31 ± 5.1%, $p = 0.12$; Fig. 4D) in 11 participating observers.

In addition, for the four observers whose transfer of learning was tested at the other three untrained quadrants, post-training orientation thresholds at the trained and untrained quadrants were similarly improved (Fig. 4). The mean MPI = 41.0 ± 5.1% ($p = 0.002$) at the trained quadrant, and MPI = 38.0 ± 3.7% ($p = 0.001$), 36.8 ± 6.2% ($p = 0.005$), and 36.1 ± 7.6% ($p = 0.009$) at the untrained quadrants across the vertical meridian (VM), across the horizontal meridian (HM), and across the fixation (diagonal), respectively, which were not significantly different among each other ($p = 0.69$, repeated measures ANOVA). For these observers, there was no pretest of orientation thresholds at untrained quadrants, similar to Shiu and Pashler (1992), so post-training thresholds were compared to the pre-training thresholds at the trained quadrant to quantify learning transfer. These results show complete transfer of orientation learning upon the removal of contextual cues, which argues strongly against location specificity and suggests that the previous concerns about Shiu and Pashler's study (Schoups et al., 1995) were warranted.

4. Discussion

In this study we discovered that a brief pretest of orientation thresholds in the periphery (six staircases, or approximately 200 trials, originally planned as a baseline measure to gauge the transfer of learning from foveal orientation training), surprisingly overrode Schoups et al.'s classical results for location specificity in orientation learning and helped optimize peripheral orientation discrimination without additional multi-sess437(an1±)-m5ed (in= =mo322(w3at)-2sess5-394((4t) staioxim.37(and12.2154.966-1.309W287(74e tent with neurons in non-visual high brain areas not being orientation selective (e.g., Mohler, Goldberg, & Wurtz, 1973).

Perceptual learning at central brain sites would easily explain why receptive field tuning changes in visual areas up to V4 can only account for a very small part of behavioral learning data ("at least an order of magnitude smaller than the behavioral changes", Raiguel et al., 2006). We suggest that perceptual learning may reflect training induced improvements in decision making which is modeled by Dosher and Lu (1999), but this process has to occur in non-retinotopic high brain areas, which coincides with recent neurophysiological evidence that perceptual learning is correlated to neuronal changes not in sensory cortical areas, but in higher areas associated with decision making (Law & Gold, 2008). Further experimental and computational evidence is necessary to spell out the possible central mechanisms underlying perceptual learning.

Acknowledgments

This research was supported by a Natural Science Foundation of China Grant 30725018 and a Chang-Jiang Scholar professorship (CY), and by US National Institute of Health Grants RO1-04776 and RO1-01728 (DML & SAK).

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