ERP P1-N1 changes associated with Vernier perceptual learning and its location specificity and transfer

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Our recent studies demonstrate that perceptual learning can transfer completely to untrained retinal locations upon proper training procedures, which suggests perceptual learning being a high-level learning process occurring beyond the retinotopic visual areas. We propose that whether learning is location specific depends on the functional connections between high-level learning and the sensory inputs corresponding to the untrained retinal locations. These inputs may be suppressed by intensive training and focused (spatial) attention on the trained location to obstruct learning transfer. Here we present event-related potential (ERP) evidence that Vernier perceptual learning and its transfer are associated with P1 reduction and N1 enhancement. However, location specificity is only associated with N1 suppression corresponding to the untrained retinal location. These results are consistent with our proposal that the blockage of top-down influences or functional connections and the inhibition of visual inputs corresponding to untrained locations may contribute to location specificity in perceptual learning.

Introduction

Visual perceptual learning is known to be mostly specific to the trained retinal locations, which is often taken as evidence for neural plasticity in the retinotopic early visual cortex (Karni & Sagi, 1991; Schoups, Vogels, & Orban, 1995; Crist, Kapadia, Westheimer, & Gilbert, 1997; Bejjanki, Beck, Lu, & Pouget, 2011). However, recently we demonstrated that perceptual learning often transfers completely to untrained retinal locations upon proper training procedures (Xiao et al., 2008; J. Y. Zhang et al., 2010; T. Zhang, Xiao, Klein, Levi, & Yu, 2010; Wang, Zhang, Klein, Levi, & Yu, 2012). For example, we found that foveal orientation discrimination learning can transfer completely to a peripheral location with a pretest of approximately 200–250 trials at the peripheral transfer location, and additional training at the peripheral location cannot produce further learning (T. Zhang et al., 2010). The same foveal orientation learning is location specific without such a short pretest (Schoups et al., 1995; T. Zhang et al., 2010). We also found with a double training paradigm (Xiao et al., 2008) that highly location-specific Vernier learning transfers completely to a diagonal visual quadrant when an irrelevant contrast discrimination task is also trained at the diagonal visual quadrant (Wang et al., 2012). These results suggest that perceptual learning is a high-level learning process beyond the retinotopic visual areas. To explain why high-level perceptual learning shows location specificity, we hypothesized that location specificity results from functional disconnections between the high-level learning unit and the visual inputs corresponding to the untrained retinal locations (J. Y. Zhang et al., 2010). Multiple sessions of intensive training with focused spatial attention may have

Citation: Zhang, G.-L., Cong, L.-J., Song, Y., & Yu, C. (2013). ERP P1-N1 changes associated with Vernier perceptual learning and its location specificity and transfer. *Journal of Vision*, *13*(4):19, 1–13, http://www.journalofvision.org/content/13/4/19, doi:10.1167/13.4.19.

doi: 10.1167/13.4.19 Received April 16, 2012; published March 26, 2013 ISSN 1534-7362

suppressed the untrained retinal locations (J. Y. Zhang et al., 2010), as hinted by the known neurophysiological impacts of spatial attention inhibiting unattended regions (Moran & Desimone, 1985; Treue, 2001; Slotnick, Schwarzbach, & Yantis, 2003), even if these regions are unstimulated (Smith, Singh, & Greenlee, 2000; Shmuel, Augath, Oeltermann, & Logothetis, 2006), as is typical in perceptual learning studies.

In addition, location-specific learning may transfer to a mirrored location in the opposite hemisphere when the training and transfer locations are close to (~1°–3° from) the vertical meridian (Berardi & Fiorentini, 1987; Tanaka, Miyauchi, Misaki, & Tashiro, 2007). Similarly, in our previous studies we found that even the highly location-specific Vernier learning may show transfer in some observers when learning and transfer are each measured at a mirrored retinal location 5° from the vertical meridian. Figure 1 summarizes the individual transfer indices of Vernier learning from our published (Xiao et al., 2008; Wang et al., 2012) and unpublished data under various transfer location conditions. The transfer index (TI) is defined as the ratio of percent improvements at the transfer location versus the training location. TI = 1 when the learning transfer is complete, but TI = 0 when there is zero transfer. It is evident that although the grand mean of TI is near zero, the individual TIs vary greatly. To the interest of our current study, the TIs distribute nearly evenly from 0 to 1 when Vernier learning and transfer are tested at mirrored locations across the vertical meridian in the lower visual field.

In this study we tested Vernier learning and its transfer in two mirrored locations across the vertical meridian in the lower visual field. Similar to the Figure 1 data, we found diverse transfer effects of Vernier learning among individual observers (i.e., some observers showed more transfer and some showed less transfer), which allowed different ERP responses associated with location specificity and transfer of Vernier learning to be compared. We found posterior P1 reduction and N1 enhancement with learning transfer, which may indicate top-down influence of high-level learning. However, location specificity was associated with no such P1-N1 changes, but with suppressed N1 corresponding to the untrained retinal location. These results provide neurophysiological evidence for our proposal regarding the mechanisms underlying perceptual learning and its specificity and transfer.

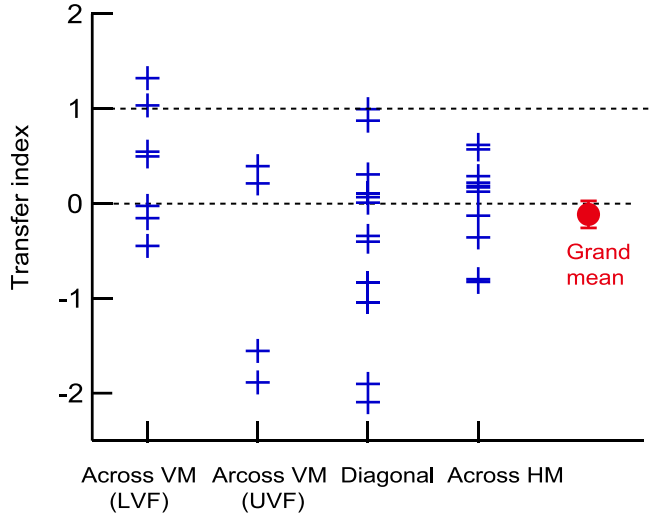

Figure 1. Summary of individual transfer indices at various Vernier learning and transfer location conditions and the grand mean. More than one condition was tested in some of the observers. VM - Vertical meridian; HM - Horizontal meridian; LVF - Lower visual field; UVF - Upper visual field.

Methods

Observers and apparatus

Twenty-eight right-handed observers (undergraduate students at Beijing Normal University; 13 males and 15 females; mean age = 21.7 years) with normal or corrected-to-normal vision participated in this study. All were new to psychophysical and ERP experiments and were unaware of the purpose of the study. Informed written consent was obtained from each observer before data collection. This study adhered to the Declaration of Helsinki.

The stimuli were generated with a Matlab toolbox Psychtoolbox-3 (Pelli, 1997) and presented on a 21-in. Iiyama MA203DT color monitor (1920 × 1440 pixel resolution, 0.21 × 0.21 mm pixel size, 75 Hz frame rate, and 39 cd/m^2 mean luminance [Iiyama Corporation, Nagano, Japan]). The luminance of the monitor was linearized by an 8-bit look-up table. A chin-and-head rest helped stabilize the head of the observer. Experiments were run in a dimly lit room. Viewing was binocular at a distance of 1.5 m.

Stimuli

The Vernier stimulus (Figure 2a) consisted of a pair of identical Gabors on a mean luminance background and was presented at the center of the lower right or lower left visual quadrant at 5° retinal eccentricity. The two Gabors had the same spatial frequency (3 cpd), standard deviation (0.4°), contrast (0.45), orientation (vertical), phase (90°), and a center-to-center distance of 1.67° (5λ). The position of each Gabor shifted half the Vernier offset in opposite directions perpendicular to the Gabor orientation.

Psychophysical procedure

Vernier alignment thresholds were measured with a single-interval 2AFC staircase procedure. In each trial, the stimulus was presented for 200 ms. The observer's task was to judge whether the upper Gabor was to the left or right of the lower Gabor. A small foveal fixation cross (25′ × 25′) preceded each trial by 500 ms and stayed throughout the trial. Auditory feedback was given on incorrect responses in behavioral sessions, but not in ERP sessions. The staircase followed a 3-down-1-up rule, which resulted in a 79.4% convergence rate (Levitt, 1971). The step size of the staircase was 0.05 log units. The geometric mean of the reversals, excluding the first five, was taken as the threshold. Each staircase consisted of 125 trials in training sessions but in a pretraining baseline session, these trials also interleaved with another 125 trials with a fixed subthreshold Vernier offset (see Results). There was a brief rest every 42 trials to reduce fatigue.

EEG recording

The electroencephalogram (EEG) was recorded by a NeuroScan system (Neurosoft, Inc., Sterling, VA, USA) with 64 silver chloride electrodes mounted on an elastic cap according to the international 10-20 system. The electrode activity of the brain was amplified and digitized continuously (bandpass filtered at 0.05–100 Hz) at a sample rate of 1000 Hz. The horizontal electrooculogram (EOG) was recorded from two electrodes positioned at the outer canthus of each eye, and the vertical EOG was recorded from two electrodes located below and above the left eye. All electrodes, except those for monitoring eye movements, were physically referenced to the left mastoid and were then off-line re-referenced to the average of the left and right mastoids. Electrode impedances were kept below 5 kΩ.

Experimental procedure

The experiment consisted of eight sessions in seven different days (Figure 2b): A practice session (S0) and an ERP baseline session (S1) on the first day, four behavioral training sessions (S2–S5), an ERP posttraining session (S6), and a behavioral posttraining session (S7). In the practice session (S0), each observer practiced 40 trials in a staircase at the to-be-trained location to get familiar with the task. The baseline session (S1) consisted of four 250-trial blocks, in which the EEG signals were recorded. Half the trials in each block were controlled by a staircase procedure to converge the Vernier offset to the threshold level (mean Vernier offset = 4.53 ± 0.26 arcmin). The other half remained at a fixed subthreshold level based on practice performance (mean Vernier offset = 2.88 ± 0.08 arcmin). To determine these subthreshold offset values, the Vernier offset was first set 3 arcmin, close to the mean posttraining threshold of a separate group of eight observers who in a prep experiment performed the same near-threshold Vernier training without ERP recording. This measure would not only approximately determine the mean Vernier offset subthreshold, but also allow near-threshold ERP comparisons before and after training (Figure 7). Then this 3-arcmin subthreshold offset was compared to a very rough estimate of the threshold offset in S0 (the mean of the last 25 trials) for each observer. Depending on the difference between these two offsets, the final subthreshold offset was adjusted individually by 0, ±0.5, or ±1 arcmin for most observers (with a few exceptions in which the adjustment did not use the exact 0.5-arcmin steps, see Figure 3c). These two types of trials were randomly interleaved trial by trial. Each training session (S2–S5) included eight 125-trial staircases. The ERP posttraining session (S6) included four 250-trial blocks. The Vernier offset in half the trials of each block was fixed at the pretraining threshold level, and in the other half was at the pretraining subthreshold baseline level. These trials were also randomly interleaved trial by trial. The behavioral posttraining session (S7) consisted of four 125-trial staircases, two at the trained location and two at the untrained location in a counterbalanced order. Vernier training was always performed in the lower-left visual quadrant (S2–S5), and the pre- and posttraining behavioral and ERP performance were measured in both the trained lower-left and untrained lower-right visual quadrants, each quadrant with half of the trials (S1, S6, and S7).

Data analysis

Behavior data analysis

The amount of perceptual learning was quantified by the accuracy improvement from S1 to S6 and by the percent threshold improvement from S1 to S7. The amount of learning transfer was quantified by the transfer index (TI) that was calculated as the accuracy improvement at the untrained location divided by the accuracy improvement at the trained location, so that TI $\geq$ 1 indicated complete transfer and TI $\leq$ 0 indicated no transfer. Here we used accuracy changes to calculate TIs because the accuracies were measured during ERP recording, so that the relationship between TIs and ERP changes could be directly examined.

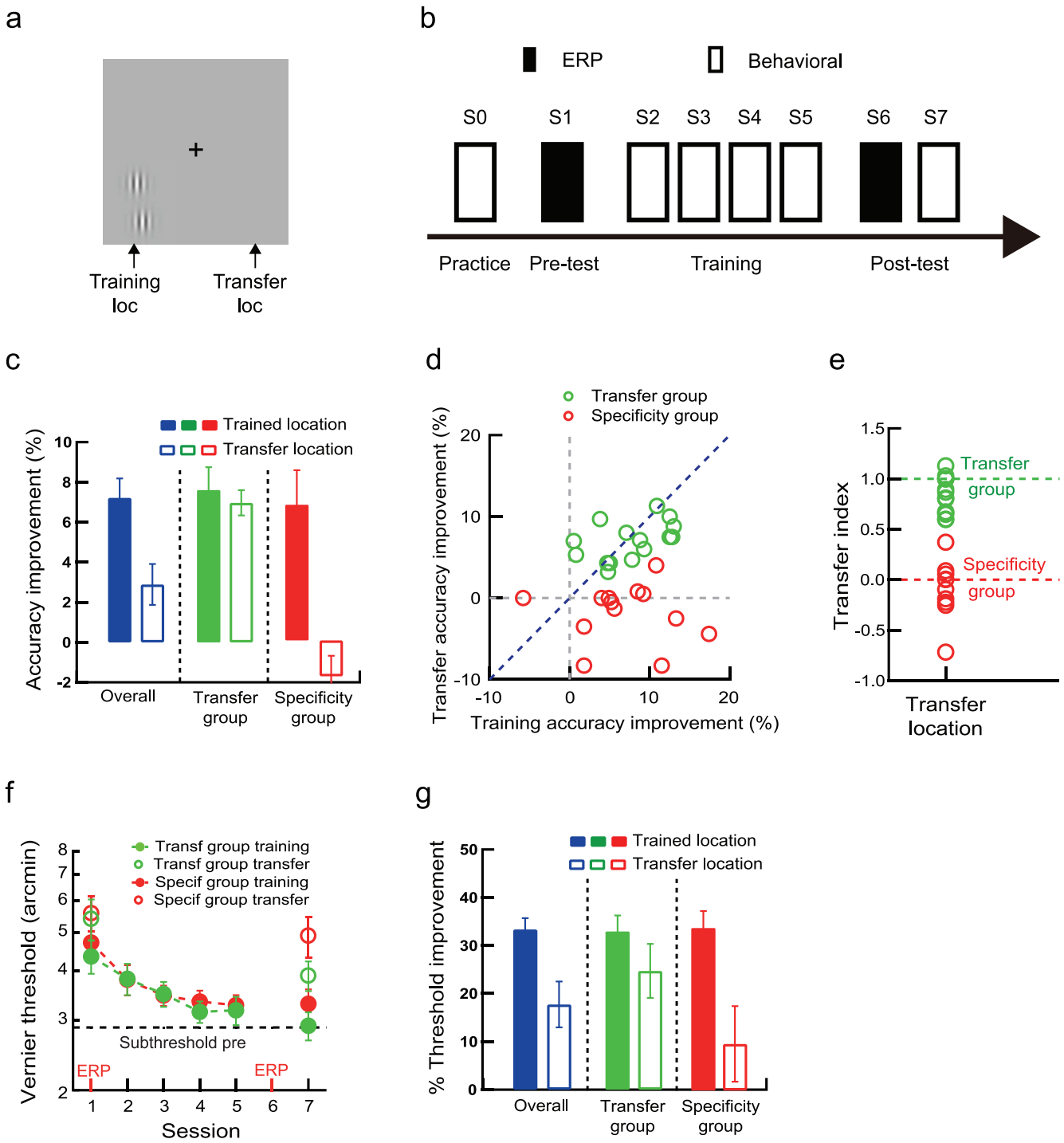

Figure 2. Psychophysical data for Vernier learning and transfer. (a) The Vernier stimuli and the training and transfer locations. (b) An illustration of the training procedure. S0 was a practice session. S1 was a behavioral and ERP baseline session that measured Vernier thresholds as well as accuracies at subthreshold Vernier offsets while ERPs were simultaneously recorded. S2–S5 were behavioral training sessions in which the Vernier task was practiced near threshold. S6 measured posttraining accuracies with Vernier offsets fixed at pretraining threshold and subthreshold levels while ERPs were simultaneously recorded. S7 measured posttraining thresholds. (c) Vernier accuracy improvements at the trained and untrained locations for all observers and for the "transfer" and "specificity" groups, respectively. Error bars indicate one standard error of the mean. (d) Individual accuracy improvements due to transfer plotted against due to training. (e) Transfer indices for individual observers in the "transfer" and "specificity" groups. (f) The learning curves and the pre- and posttraining thresholds at the untrained location for both "transfer" and "specificity" groups. (g) Threshold improvements at the trained and untrained locations for all observers as well as for the "transfer" and "specificity" groups.

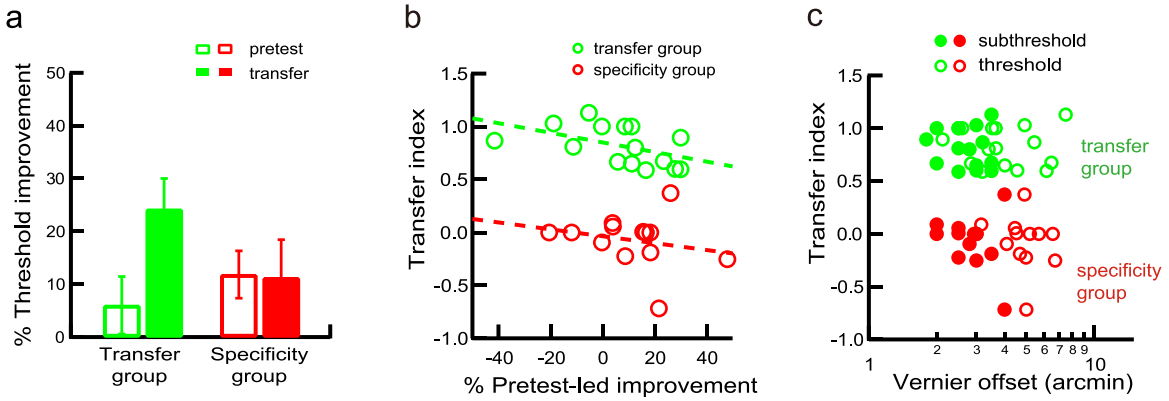

Figure 3. The impact of pretests on learning transfer. (a) The estimated threshold improvements due to pretest and the overall threshold improvements at the untrained location due to transfer in "transfer" and "specificity" groups. (b) Individual transfer index versus the pretest-led improvement (the estimated threshold improvement due to pretest). (c) Individual transfer index versus initial Vernier offsets at threshold and subthreshold levels for "transfer" and "specificity" groups.

EEG data analysis

Raw EEG data were first off-line filtered with a digital band-pass of 0.1–40 Hz. Each epoch of EEG ranged from 200 ms before stimulus onset to 800 ms after stimulus onset. Baseline was corrected by subtracting the mean of the signals within the time window of −200 ms to 0 ms (stimulus onset). Trials with eye blinks, eye movements, muscle potentials exceeding ±50 μV at any electrode, or with incorrect behavioral responses, were excluded from ERP averaging. The numbers of trials were matched between ERP baseline sessions and ERP posttraining sessions by randomly selecting epochs from sessions containing more trials in each observer. There were about 150 stimulus-related EEG epochs averaged for each condition.

Six posterior electrodes in each hemisphere (P1, P3, P5, PO3, PO5, and PO7 in the left hemisphere and P2, P4, P6, PO4, PO6, and PO8 in the right hemisphere), which covered the posterior cortex with the most visible P1-N1 changes (Figure 4), were selected for statistical analysis. For each observer, we averaged signals from six electrodes at each hemisphere to increase the signal-to-noise ratio. Paired two-tailed t-tests were applied to test ERP differences between pre- and posttraining conditions in each of the 5-ms bins. Most comparisons were performed within a time window between 120 and 200 ms, with an exception for waveforms evoked by stimuli presented at the untrained location with the "specificity" group (see Results), under which a time window between 165 and 200 ms was selected (the pre- and posttraining ERPs between 120 and 165 ms had no visible differences). Multiple comparisons with respect to the number of bins were corrected using the Benjamini-Hochberg (1995) false discovery rate (FDR) correction with $\alpha = 0.05$.

Results

Psychophysical data

The accuracy of discriminating the Vernier offset in the trained lower-left visual quadrant was improved significantly by 7.2% ± 1.0% (averaged over both Vernier offset conditions, $p < 0.001$, one-tailed paired t test; Figure 2c) from S1 to S6. The accuracy in the untrained lower-right quadrant was also improved by 2.9% ± 1.0% ($p = 0.004$) over the same period, indicating overall partial transfer of Vernier learning (TI = 0.41 ± 0.10). However, the amount of learning transfer varied greatly among observers, as can be appreciated by the individual accuracy improvement at the transfer location plotted against the accuracy improvement at the trained location (Figure 2d), as well as by individual TI variations (Figure 2e). We divided the observers into a "transfer" group ($n = 15$; TI > 0.5) and a "specificity" group ($n = 13$; TI < 0.5), which allowed later transfer versus specificity comparisons of ERP changes. The mean Vernier accuracy at the untrained locations was improved by 7.0% ± 0.7% ($p < 0.001$) in the "transfer" group (TI = 0.84 ± 0.05) and −1.1% ± 1.1% ($p = 0.16$) in the "specificity" group (TI = −0.03 ± 0.08; Figure 2c). These results were confirmed by significant threshold decreases (24.2% ± 5.8%, $p < 0.001$) in the "transfer" group and insignificant threshold changes (11.3% ± 7.3%, $p = 0.07$) in the "specificity" group at the untrained location from S1 to S7 (Figure 2f and g). Here the "transfer" and "specificity" groups had similar pretraining accuracies with subthreshold Vernier stimuli (71.4% ± 1.3% vs. 69.6% ± 1.3%, $p = 0.34$, two-tailed Student's t-test; the theoretical accuracies at threshold were identical at 79.4%) and pretraining thresholds (4.3

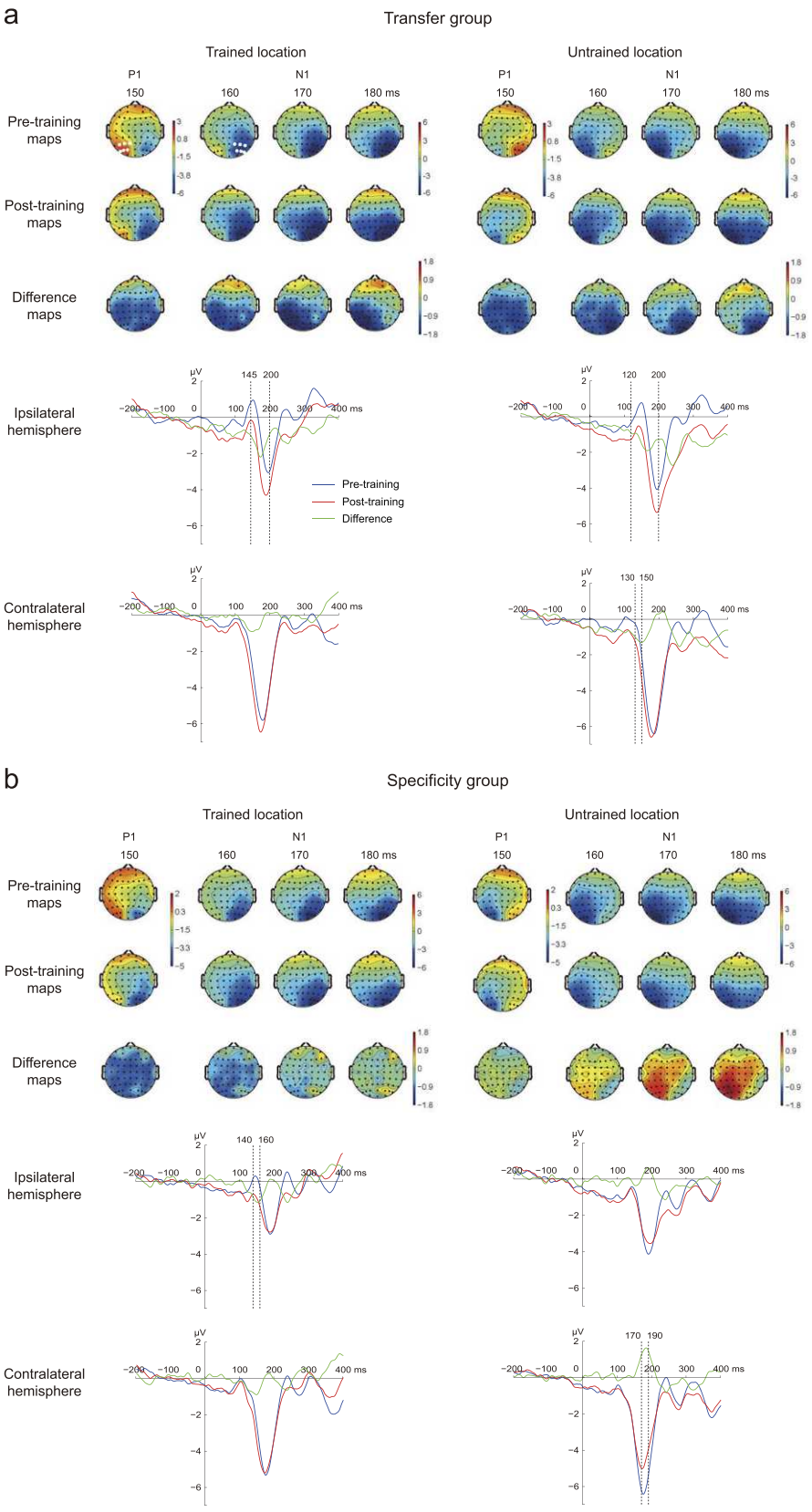

Figure 4. ERP N1-P1 changes associated with Vernier learning and its specificity and transfer under the ‘‘subthreshold pre’’ condition. (a) and (b) show the ‘‘transfer’’ and ‘‘specificity’’ group data, respectively. The top three rows of (a) or (b) show the pretraining, posttraining, and difference topographical maps when the Vernier task was performed at the trained location (left) and untrained location (right). The bottom two rows show pretraining and posttraining grand average ERPs and their difference waveforms over

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± 0.4 arcmin vs. 4.8 ± 0.3 arcmin, $p = 0.28$, Figure 2f), as well as accuracy improvements (7.6% ± 1.1% vs. 6.8% ± 1.7%, $p = 0.67$, Figure 2c) and threshold improvements (32.9% ± 3.3% vs. 33.8% ± 3.5%, $p = 0.85$, Figure 2g) after training, all at the trained location. Therefore the observers in two groups were homogeneous in these dimensions.

It was unlikely that the transfer of Vernier learning in the "transfer" group was a result of the S1 pretest at the untrained location. We calculated the average Vernier threshold improvement from S1 to the mean of the first four staircases (half of the total staircases) in S2 at the trained location in the "transfer" group to estimate the impact of pretest at the untrained location, which was very small (6.0% ± 5.4%, $p = 0.15$), about a quarter of the 24.2% overall threshold improvement at the untrained location (Figure 3a). For the "specificity" group, the corresponding S1 pretest effect was 11.8% ± 4.5% ($p = 0.01$), similar to the 11.3% threshold improvement at the untrained location. In addition, the slopes of the simple regression lines of the transfer index versus the pretest impact functions were insignificantly different from zero in both the "transfer" groups (slope = −0.0045, $p = 0.064$) and the "specificity" group (slope = −0.0032, $p = 0.46$) (Figure 3b), indicating that how much Vernier learning transfers was not significantly affected by pretests in this experiment. The transfer of Vernier learning was also not affected by initial group differences of Vernier offsets, as the initial Vernier offsets did not differ between the "transfer " group and "specificity" group at the threshold ($p = 0.28$) and subthreshold levels ($p = 0.47$) (Figure 3c).

ERP data

ERP was recorded under two Vernier offset conditions pre- and posttraining in S1 and S6: The "subthreshold pre" condition and the "threshold pre" condition. Under the "subthreshold pre" condition, the Vernier offsets fixed at the pretraining subthreshold levels changed to near-threshold after training at the trained location (mean offset = 2.88 ± 0.08 arcmin, which was lower than the mean pretraining threshold 4.53 ± 0.26 arcmin and near the mean post-training threshold 3.10 ± 0.19 arcmin in S7). Under the "threshold pre" condition, the pretraining Vernier offsets were not fixed but varied around the thresholds under the control of the staircases. Although this measure would increase the noise of ERP responses (the first 30 trials of each staircase were thrown out to reduce the Vernier offset variation to SD = 0.34 arcmin), the more problematic practice effect was avoided if behavioral pretraining thresholds were measured before ERP pretraining baselines. The post-training Vernier offsets were fixed at the pretraining threshold levels. Therefore, under the "threshold pre" condition the Vernier offsets changed from threshold levels to suprathreshold levels after training at the trained location.

The mean topographic maps and ERP waveforms are presented in Figure 4 for the "subthreshold pre" condition and Figure 5 for the "threshold pre" condition. The first visual ERP component C1 could not be reliably identified and analyzed, likely due to the small stimulus size and low stimulus contrast, as well as the possibility that some observers may not show significant C1 responses to the stimulus presented at this specific location (Kelly, Gomez-Ramirez, & Foxe, 2008). Two issues are worth noting before detailed analysis of the impacts of learning and its specificity/transfer on ERP responses. First, the pretraining ERP waveforms were not significantly different between the two groups ($p > 0.05$ after FDR correction) in the ipsilateral and contralateral posterior cortices under the "subthreshold pre" and "threshold pre" conditions, respectively, within a time window of 120–200 ms (covering P1 and N1, see below). Therefore, learning transfer/specificity was unrelated to neither the pre-training thresholds (Figure 2f) nor the pretraining ERPs. Second, when the Vernier task under the "threshold pre" condition was performed at the untrained location (Figure 5), the peaks of difference waveforms (posttraining – pretraining) of the "transfer" group were significantly different from those of the "specificity" groups within the 120–200 ms time window. ($F(1, 26) = 12.8$, $p = 0.001$, mean amplitudes of 10-ms time windows around the peak over six selected electrodes in each hemisphere were entered into a repeated measures ANOVA. We did not run t tests here because the latencies of peaks were different between the "transfer" and "specificity" groups, see green lines in Figures 4 and 5.) These differences indicated that the observers could be reliably divided into "transfer" and "specificity" groups on the basis of not only behavioral improvements, but also ERP changes.

Some interesting patterns of ERP changes, which were similar under "subthreshold pre" and "threshold pre" Vernier offset conditions, emerged that were

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six posterior electrodes in each hemisphere (highlighted in the top left two maps of (a) when the Vernier task was performed at the trained location (left) and untrained location (right). A pair of vertical lines show the time window within which the post- and pre-training ERPs showed significant differences.

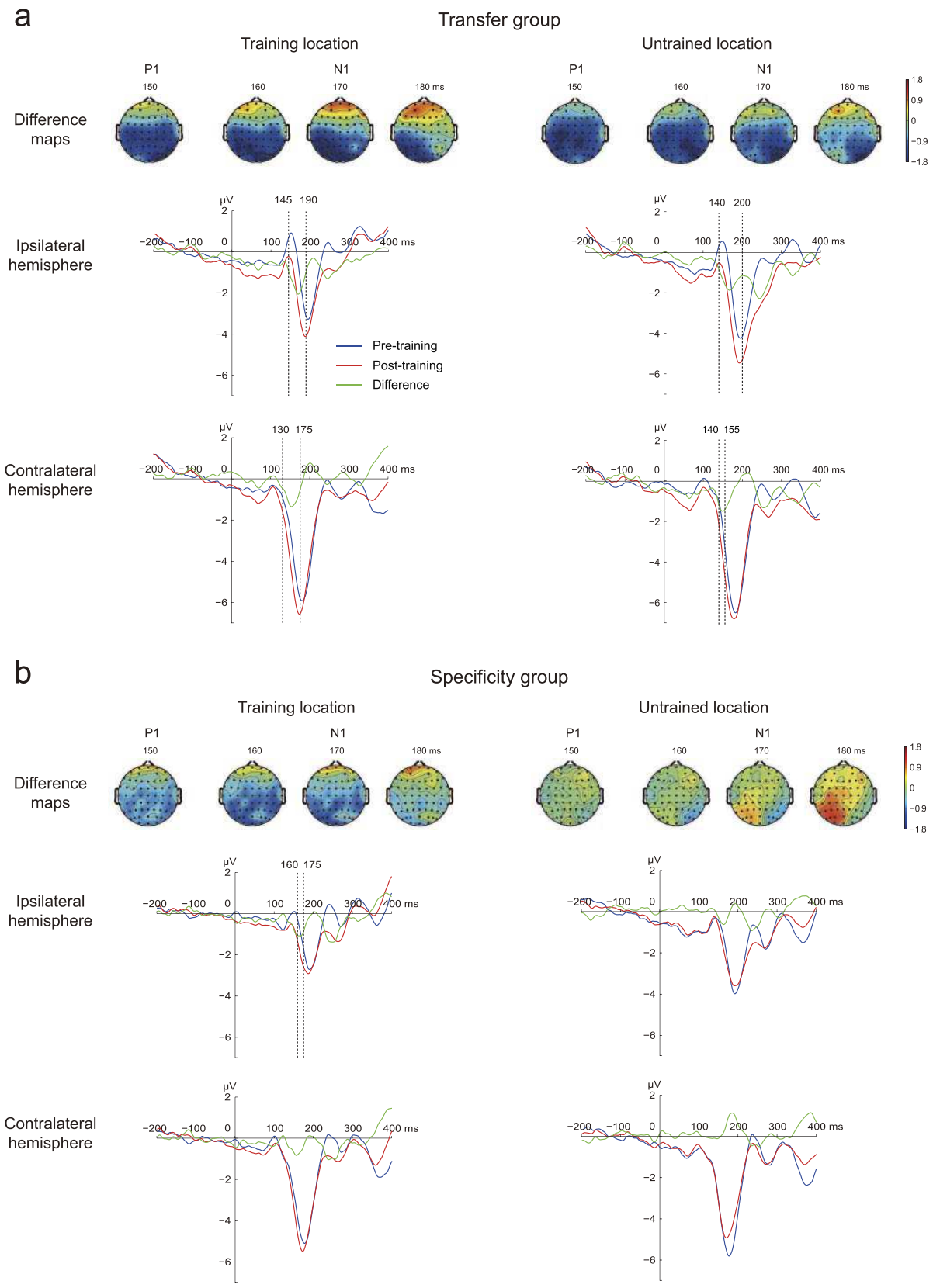

Figure 5. ERP N1-P1 changes associated with Vernier learning and its specificity and transfer under the "threshold pre" condition. (a) and (b) show the "transfer" and "specificity" group data, respectively. The top row of (a) or (b) shows the posttraining – pretraining difference topographical maps when the Vernier task was performed at the trained location (left) and untrained location (right). The bottom two rows of (a) or (b) show pretraining and posttraining grand average ERPs and their difference waveforms over the

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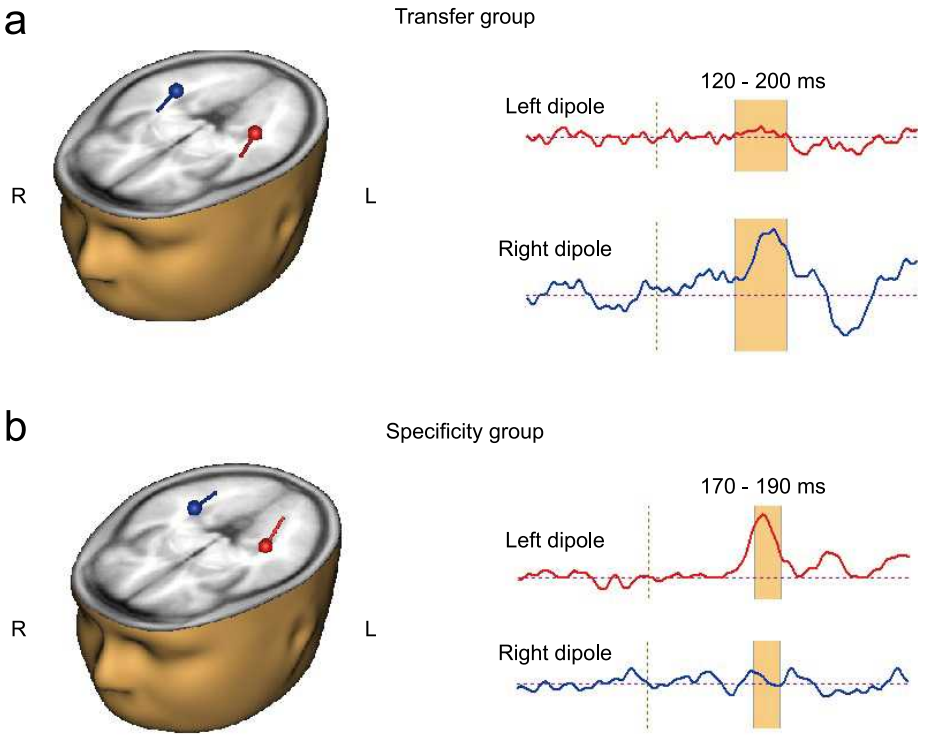

Figure 6. Source location of ERP changes after Vernier learning. (a) and (b) show the "transfer" and "specificity" group results, respectively. Left: Dipole modeling of the intracranial source of the difference waveforms between pretraining and posttraining over the P1-N1 interval when the "subthreshold pre" Vernier task was performed at the untrained retinal location. Right: Source waveforms showing the time courses of modeled activity of the dipoles.

distinctly associated with the "transfer" and "specificity" groups, respectively. Under the "subthreshold pre" condition (Figure 4), the Vernier task performed by the "transfer" group at the trained lower-left visual quadrant evoked reduced P1 and enhanced N1 in the ipsilateral posterior cortex (145–200 ms), although there were no significant ERP changes in the contralateral posterior cortex. The same task performed at the untrained lower-right visual quadrant also revealed reduced P1 and enhanced N1 (120–200 ms) in the ipsilateral hemisphere, as well as reduced contralateral P1 (130–150 ms). The patterns of these P1-N1 changes due to training and transfer are thus similar, and at least the ERP changes with the Vernier task at the untrained location should reflect top-down influences. However, ERP changes associated with Vernier task performed by the "specificity" group at the trained location were weaker and more limited, and those at the untrained location were very different or even opposite. When the Vernier task was performed at the trained location, only P1 in the ipsilateral posterior cortex (140–160 ms) was reduced. There was no significant N1 change, in contrast to widespread N1 enhancement in the "transfer" group. When the Vernier task was performed at the untrained location, no P1 reduction and N1 enhancement were observed, in contrast to significant P1 reduction and N1 enhancement in the "transfer" group. In addition, N1 in the contralateral posterior cortex (170–190 ms) was suppressed.

Similar patterns of ERP changes were observed under the "threshold pre" condition (Figure 5). For the "transfer" group the Vernier task at the trained location evoked smaller P1 and larger N1 responses in the ipsilateral posterior cortex (145–190 ms) and the contralateral posterior cortex (130–175 ms). The same task at the untrained location also evoked smaller P1 and larger N1 responses in the ipsilateral posterior cortex (140–200 ms), as well as larger contralateral N1 in a narrow time window (160–175 ms). For the "specificity" group the Vernier task at the trained location evoked larger ipsilateral N1 responses only in

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same six posterior electrodes as in Figure 4 in each hemisphere when the Vernier task was performed at the trained location (left) and untrained location (right). A pair of vertical lines show the time window within which the post- and pre-training ERPs showed significant differences.

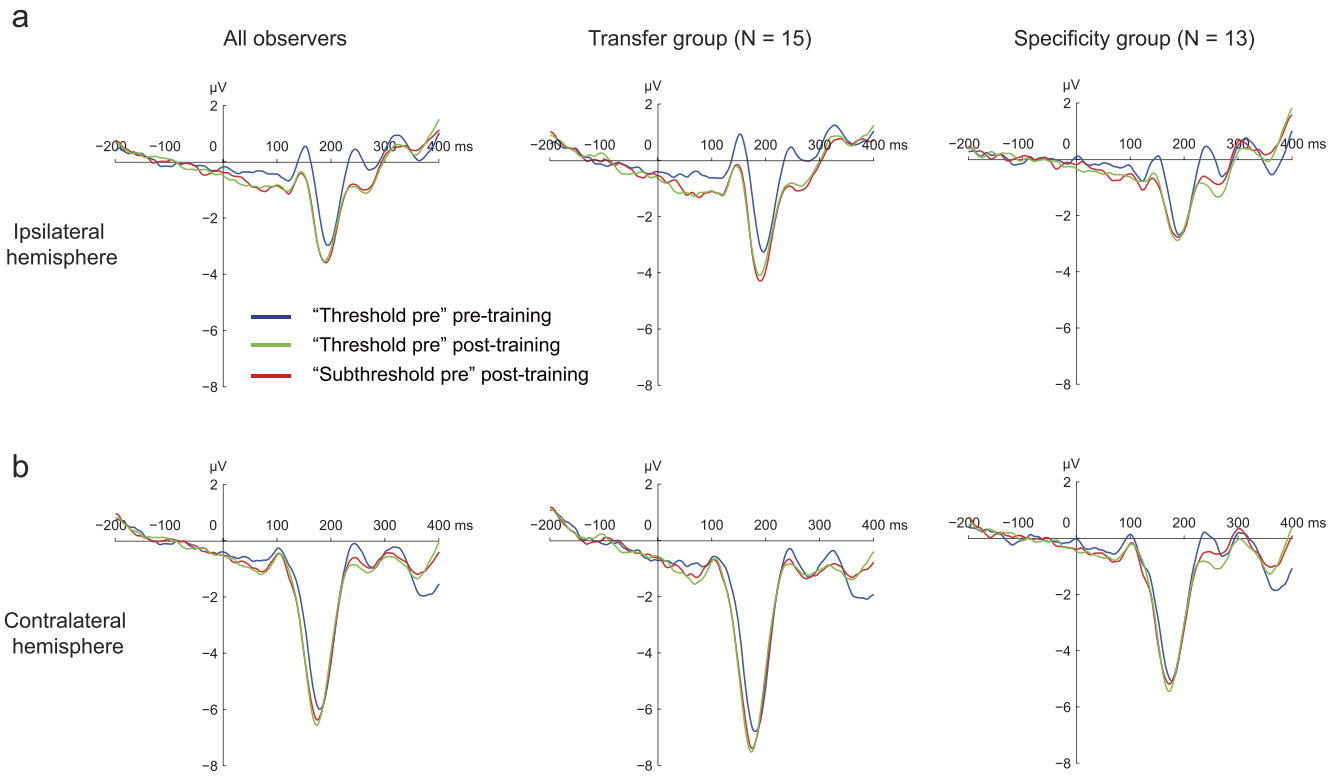

Figure 7. The impacts of learning-reduced task difficulty and attention demand on ERP P1-N1 changes. Each panel plots the ERP waveforms of pre- and posttraining ERPs under the "threshold pre" condition in which the Vernier offset changed from threshold to suprathreshold, and the post-training ERP under the "subthreshold pre" condition in which the Vernier offset became near threshold after training. (a) Ipsilateral ERP waveforms. (b) Contralateral ERP waveforms. The left, middle, and right panels show the results from all observers, "transfer" group, and "specificity" group, respectively.

a narrow time window (160–175 ms) after training. The same task at the untrained location failed to evoke any significant ERP changes, although some (insignificant) contralateral N1 suppression could be seen in the difference maps.

The ERP changes under the "subthreshold pre" and "threshold pre" conditions (Figures 4 and 5) suggest that the learning transfer is characterized by reduced P1 and enhanced N1 when evoked by the Vernier task at the untrained location, which occurred more often and stronger in the ipsilateral posterior cortex. In contrast, location specificity is characterized by much weaker or no significant P1-N1 changes, as well as contralateral N1 suppression. To localize the sources of ipsilateral P1 reduction and N1 enhancement and contralateral N1 suppression, we performed dipole modeling of intracranial sources of the averaged difference waveforms associated with the "subthreshold pre" Vernier task at the untrained retinal location with the Brain Electromagnetic Source Analysis (BESA) software (Gräfelfing, Germany; Figure 6). A four-shell spherical head model (brain, skull, cerebrospinal fluid, and scalp) was used as an approximation for dipole fitting. The P1-N1 changes were fitted over 120–200 ms ("transfer" group) and 170–190 ms ("specificity" group) with one symmetrical pairs of dipoles, respectively. The best-fitting source estimated one pair of dipoles located approximately in Brodmann area 19 of the visual cortex in both groups ("specificity" group: $x = \pm 34$, $y = -40$, $z = -1$; "transfer" group: $x = \pm 37$, $y = -40$, $z = 0$). These dipoles provided very good fits to the observed ERP difference waveforms with a low residual variance (RV) of 13.3% and 11.4% for "transfer" group and "specificity" group, respectively. Moreover, the source waveforms (Figure 6) showed that the ipsilateral dipole (blue one) mainly accounted for the P1-N1 change in the "transfer" group, whereas the contralateral dipole (red one) mainly accounted for N1 suppression in the "specificity" group.

A topographical statistics was also performed to further confirm that the P1 reduction and N1 enhancement for the "transfer" group and N1 suppression for the "specificity" group had different cortical origins. The absolute values of these ERP changes at the untrained location were analyzed with a repeated measure ANOVA with factors of Group (specificity vs. transfer), Hemisphere (left vs. right), and Electrodes (P1, P3, P5, PO3, PO5, and PO7 in the left

hemisphere and P2, P4, P6, PO4, PO6, and PO8 in the right hemisphere). A significant Group × Hemisphere interaction, ($F(1, 26) = 5.97$, $p = 0.022$), confirmed the source difference between the P1 reduction and N1 enhancement with the "transfer" group and the N1 suppression with the "specificity" group.

In Figures 4 and 5 the ERP P1-N1 changes were estimated on the basis of pre- and posttraining ERP waveforms associated with the same physical Vernier offsets. However, at least under the "threshold pre" condition, the Vernier offsets changed from near-threshold to suprathreshold, so that the task difficulty and attention demand were reduced as a result of learning, which could have confounded the explanation of the ERP effects. To clarify this issue, we calculated the differences between pretraining waveforms under the "threshold pre" condition and posttraining waveforms under the "subthreshold pre" condition (pretraining threshold ERPs vs. posttraining threshold ERPs), and compared them to the differences between pre- and posttraining waveforms under the "threshold pre" condition (pretraining threshold ERPs vs. posttraining suprathreshold ERPs), all with the Vernier task at the trained location. The comparisons revealed no significant difference between these waveform differences in the ipsilateral and contralateral posterior cortex in both the "transfer" and "specificity" groups, as well as when all observers' data were pooled (Figure 7). Indeed, the posttraining waveforms under the "threshold pre" condition and the "subthreshold pre" condition were nearly identical within the 120–200 ms time window, regardless of one being suprathreshold and one being threshold. Therefore, the ERP P1-N1 changes shown under the "threshold pre" condition indeed resulted from Vernier learning, rather than from reduced task difficulty and attention demand.

In addition, amplitude changes of electrodes C1, Cz, and C2 in a time window of 230–250 ms were tested with the P2 component, and those of electrodes P1, P2, and CP3 in a time window of 600–700 ms were tested with the P3 component. Those electrodes were selected because they showed the largest amplitude changes. The P2 amplitudes decreased significantly (230–250 ms) at the trained and untrained locations for both "specificity" and "transfer" groups, and the decreases at the untrained location were not significantly different between the "specificity" and "transfer" groups. Thus, the changes of P2 component were unrelated to learning specificity and transfer. On the other hand, there were no significant P3 amplitude changes for both groups at the trained and untrained locations (600–700 ms), indicating that P3 was unrelated to learning and its specificity/transfer either. In addition, both vertical and horizontal EOG amplitudes did not differ significantly pre- and posttraining from 0 to 200 ms, suggesting that patterns of small eye movements cannot account for the ERP changes shown in Figures 4 and 5.

Discussion

By measuring ERP changes in observers who show either significant transfer or location specificity of Vernier learning, we demonstrate significantly reduced P1 and enhanced N1, mostly in the ipsilateral posterior cortex, with the "transfer" group when the Vernier task is performed either at the trained or untrained location. However, the "specificity" group is characterized by weaker and more limited P1-N1 changes in the ipsilateral posterior cortex with the task at the trained location, and no ipsilateral P1-N1 changes but suppressed contralateral N1 with the task at the untrained location (Figures 4 and 5). Moreover, the P1-N1 changes associated with learning are evident regardless of whether the posttraining task is near-threshold or suprathreshold (Figure 7).

Vernier learning and transfer are associated with reduced P1 and enhanced N1 mostly in the ipsilateral posterior cortex that is not directly stimulated by the Vernier stimuli. This nonretinotopic effect, as confirmed by source localization, suggests the involvement of top-down influence. This is especially true with the "transfer" group when the Vernier task is performed at the untrained location, since any significant ERP changes should be a result of top-down modulation as no training is involved at this location. Moreover, the P1-N1 changes are evident upon learning transfer, but not specificity, indicating that such top-down influence is directly related to performance improvement due to learning and transfer, although it is unclear why this top-down influence shows mostly in the ipsilateral posterior cortex.

Why is perceptual learning, if high-level, specific to the trained location? We have hypothesized that multiple sessions of intensive training with focused spatial attention to the training location could impair the functional connections between high-level learning and the sensory inputs at the untrained location to prevent learning transfer, likely by suppressing the untrained retinal locations (Xiao et al., 2008; J. Y. Zhang et al., 2010). This hypothesis is motivated by the physiological findings that spatial attention inhibits unattended locations (Moran & Desimone, 1985; Smith et al., 2000; Treue, 2001; Slotnick et al., 2003; Shmuel et al., 2006), with our extrapolation that frequent inhibition in the perceptual learning studies with multiple sessions of practice would produce long-term depression-like behavior at the untrained locations. Figures 4 and 5 provide first neurophysiological evidence for such suppression and impaired functional

connections: When Vernier learning shows location specificity, contralateral N1, which is corresponding to the untrained retinal location when the Vernier task is performed at this location, is inhibited. Moreover, the top-down influences from high-level learning, as evidenced by the P1 reduction and N1 enhancement, are blocked completely when the Vernier task is at the untrained hemisphere, as well as greatly weakened and limited when the Vernier task is at the trained hemisphere (only a small area is trained, so other areas of the same hemisphere are likely suppressed too).

Previous ERP evidence shows that the visual N1 amplitude is larger when attention is directed to a retinal location where stimuli are presented than when directed to other locations (Luck & Hillyard, 1995; Mangun, 1995). However, in our study P1-N1 changes are evident with perceptual learning regardless of whether the post-training Vernier task is near threshold or suprathreshold (Figure 7). These results excluded the possibility that P1-N1 changes result from reduced task difficulty and attention demand as a result of perceptual learning. We speculate that the P1-N1 changes may reflect top-down modulation of high level decision-making as a result of perceptual learning. On the basis of psychophysical learning transfer data, especially those showing transfer across orthogonal orientations (which also excludes perceptual learning being improved attention to a specific feature dimension, e.g., a specific orientation), we suggest that perceptual learning is decision-making learning in that the observers learn the rules of reweighing the sensory inputs through training (Zhang et al., 2010a). This decision-making learning proposal is consistent with recent neurophysiological and fMRI evidence that brain areas responsible for decision making, such as the lateral intraparietal area (LIP) and the anterior cingulate cortex (ACC), are involved in perceptual learning (Law & Gold, 2008; Kahnt, Grueschow, Speck, & Haynes, 2011).

Keywords: perceptual learning, specificity, transfer, attention, electroencephalogram

Acknowledgments

This research was supported by Natural Science Foundation of China Grants 31230030 (CY) and 31070899 (YS).

Commercial relationships: none.
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