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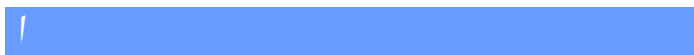
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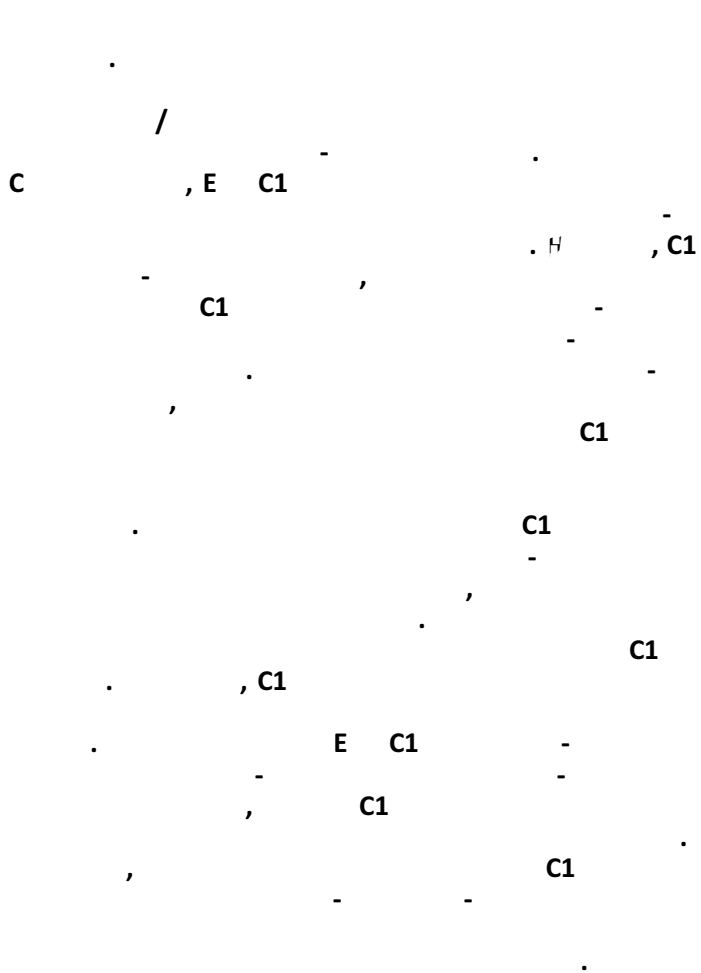
Whether training can induce plasticity in the early visual cortex remains a central issue in perceptual learning research. Traditionally, psychophysical observations of location and orientation specificities have been cited as evidence for learning occurring in V1 where neurons are most retinotopic and orientation selective (e.g., Karni & Sagi, 1991; Schoups, Vogels, & Orban, 1995). However, reweighting models suggest that perceptual learning may result from improved readout of outputs from early visual neurons representing a trained location or orientation, rather than tuning changes of these neurons per se (e.g., Dosher & Lu, 1998). Moreover, our psychophysical evidence demonstrates that perceptual learning can transfer significantly, and often completely, to a new location or orientation with double training, in which the observers are additionally exposed to the new location or orientation via an irrelevant task (Xiao et al., 2008; J. Y. Zhang et al., 2010; Wang, Zhang, Klein, Levi, & Yu, 2012; Wang, Cong, & Yu, 2013; Wang, Zhang, Klein, Levi, & Yu, 2014; J. Y. Zhang, Cong, Klein, Levi, & Yu, 2014). These transfer results indicate that perceptual learning may primarily occur in high-level brain areas beyond the retinotopic and orientation-selective early visual cortex.

On the other hand, significant changes of ERP C1 are regarded as strong evidence for neural plasticity in

the early visual cortex as a result of perceptual learning (Pourtois, Rauss, Vuilleumier, & Schwartz, 2008; Bao, Yang, Rios, He, & Engel, 2010). C1 is the first in a series of ERP components that are activated by visual stimuli. It is commonly considered to mainly reflect neural activities in V1 because of its fast peak latency that may be earlier than feedback from later processing (Martinez et al., 1999; Noesselt et al., 2002). Topographic and source localization also reveal that C1 is mainly generated in V1 (Clark, Fan, & Hillyard, 1994; Gomez Gonzalez, Clark, Fan, Luck, & Hillyard, 1994; Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002). Moreover, a distinct characteristic of C1 is its polarity reversals when stimuli are presented in upper versus lower visual fields, which is consistent with the cruciform organization of V1 around the calcarine fissure (Jeffreys & Axford, 1972b; Butler et al., 1987). More recent evidence suggests that C1 may also originate in V2 and V3 that also have the polarity reversal property (Ales et al., 2010). Therefore, C1 changes would suggest learning-induced neural plasticity in one or more areas of V1–V3.

However, recent evidence shows that C1 can also be top-down modulated (Kelly, Gomez-Ramirez, & Foxe, 2008; Rauss, Pourtois, Vuilleumier, & Schwartz, 2009). Neuronal recording studies also suggest top-down modulation of V1 responses by perceptual learning (Li, Piech, & Gilbert, 2004, 2008; Yan et al., 2014). Thus, we hypothesized that C1 changes could at least partially result from top-down modulation of high-level perceptual learning. To single out this top-down effect, we measured C1 changes at an untrained location after training of a peripheral orientation discrimination task. Our previous study has shown that perceptual learning of orientation discrimination at a peripheral location can transfer significantly to other untrained locations (T. Zhang, Xiao, Klein, Levi, & Yu, 2010; also see a recent replication by Hung & Seitz, 2014). Therefore, any potential C1 changes associated with learning transfer would suggest top-down modulation, rather than early visual cortical plasticity at this untrained transfer location. Moreover, such C1 changes would indicate that high-level perceptual learning is able to remap top-down modulation to untrained neurons at a new location to achieve similar functionality.

Thirty-three right-handed observers (16 males and 17 females, mean age = 24.2 years, *SD* = 2.8 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. Dell P1130 color monitor (1024- × 768-pixel resolution, 0.39- × 0.39-mm pixel size, 120-Hz frame rate, and 0.8 cd/m^2 minimal luminance and 111.4 cd/m^2 maximal luminance). A black cardboard with a circular aperture (diameter = 17°) covered the entire monitor screen. Viewing was binocular at a distance of 1 m. A chin-and-head rest helped stabilize the head of the observer during training and behavioral posttest sessions (see Experimental design section below). Experiments were run in a dimly lit room.

The stimulus for orientation discrimination was a circular noise grating originally designed by Schoups et al. (1995): A circular field (diameter = 3.8°) consisting of one-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; Figure 1a, left panel). In a control experiment a "donut" noise grating was also used, in which the center of the noise grating was filled with a circular blank field (diameter = 1.5°; Figure 1a, right panel). The stimuli were presented in various peripheral locations at 5° retinal eccentricity.

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The experiment consisted of nine sessions on 9 different days (Figure 1c): A preliminary visual field location probe session (S0), An ERP baseline session (S1), five behavioral training sessions (S2–S6), an ERP posttraining session (S7), and a behavioral posttraining session (S8).

P be e i n (S0)

The topography distribution of C1 varies greatly among observers (Proverbio, Del Zotto, & Zani, 2007). It is also sensitive to the stimulus retinal locations (Jeffreys & Axford, 1972a; Clark et al., 1994). To select the best locations for C1 recordings, we employed a visual field location probe session. In the 1.5-hr session, an observer discriminated the shape of the gratings (circular or donut; 80% of the trials were circular gratings at 36°) and counted the number of donut gratings in each block of 100 trials for 30 blocks. The stimulus was presented at one of the eight locations at a retinal eccentricity of 5° (Figure 1b) in a random

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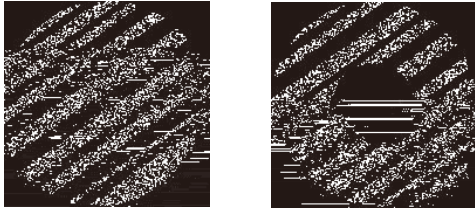
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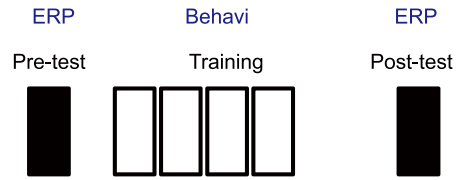
sequence. A pair of locations (Loc A and Loc B in Figure 1c) in two diagonal visual quadrants that evoked the largest C1 component were then selected for each observer as training and transfer locations in all later sessions (S1–S8). These locations were counter-balanced between upper visual field (UVF) and lower visual field (LVF) among observers. Four observers were excluded after the probe session (S0) because typical C1 components could not be found with any pair of diagonal probe locations. Prior to this session each observer practiced 10 trials consisting of eight circles and two donuts.

ERP ba eline e i n (S1)

This session consisted of 25 blocks of trials, 60 trials per block. In 80% of the trials, the stimulus orientation was 36°. In other trials the orientation was deviated by 15° (21° or 51°), approximately five times the baseline threshold (Figure 2). Observer judged the stimulus orientation and pressed a key only when the orientation was not 36°. Prior to ERP recording, each observer practiced 40 trials at the to-be-trained location.

O ien a i n aining e i n (S2 S6)

Each training session consisted of 20 staircases and lasted for about 1.5 hours. The training was always performed at one of the two selected locations (see details later).

ERP aining e i n (S7)

This session consisted of 30 blocks of trials. The observers performed the same orientation discrimina-tion task as in S1 with the first 22 blocks of trials (60 trials/block). In the remaining eight blocks of trials they discriminated whether the stimulus was a circular grating or a donut grating by counting the number of donut gratings in each block (100 trials/block). Within each block the stimulus was displayed at one of two selected locations (Loc A and Loc B) in a random order.

Beha i al aining e i n (S8)

The session consisted of 10 staircases, five at the trained location and five at the transfer location in a counterbalanced order.
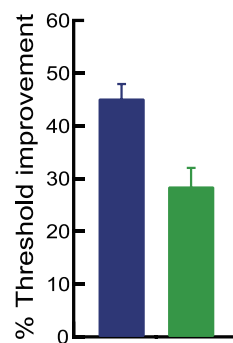
In the behavioral training and testing sessions (S2–S6 and S8), orientation [discrimination] thresholds were measured with a single [...] [a]lternative forced choice staircase proce[dure...d). In each trial a foveal fixation cross ([...]red 500 ms before the onset of the grat[ing...] [t]hroughout the trial. The grating stimu[lus...] [presente]d for 100 ms. The observer's task wa[s...] press whether the orientation wa[s...]wise or clockwise relative to an im[...] [ori]entation (36°) that was never shown[...] [and] always followed by a fixation cro[ss...] [...]0 ms. A trial ended automatically i[f...] [...]ress 1200 ms after the grating offse[t...] [inter]val (ITI) was fixed at 150 ms. The [...] [ap]peared during the ITI, so it appe[ared...] [...] a block of trials ended. Auditory [...] [o]n incorrect responses. (Tri[als...] [traini]ng were similar, except that the [...] [a]nd 300 ms, and no feedback wa[s...] description of S1 for de[...] [t]he responses).

Each staircase consis[ted...] [re]versals and six experimental r[...] [orient]ation difference between the [...] [differ]ence was 8.9°, sufficiently l[...] [orientat]ion. The step of the stairca[se...] [clockw]ise or anticlockwise to the c[...] [clas]sical three-down-one-up st[...] resulted in a 79.4% c[...] [geome]tric mean of the experim[...] [...] the threshold for each s[...] [automati]cally completed 20 stairca[ses...] [...and] the geometric mean [...] the

threshold for the session unless specified. There was a minimal 1.5-min rest after each staircase.

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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 (band-pass 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 offline rereferenced to the average of the left and right mastoids. Electrode impedance was kept below 5 kΩ.

EEG da a anal i

For orientation discrimination in ERP baseline and posttraining sessions (S1 and S7), only EEG signals evoked by a 36° grating were analyzed. For the control shape discrimination task at the probe session (S0) and ERP posttest session (S7), only EEG signals evoked by the same 36° grating were analyzed. Raw EEG data were first offline filtered with a digital bandpass filter of 0.05–40 Hz. Each epoch of EEG ranged from 200 ms before stimulus onset to 400 ms after stimulus onset. The baseline was corrected by subtracting the mean of the signals within a time window of −200 to 0 ms

(stimulus onset). Trials with eye blinks, eye movements, or muscle potentials exceeding $\pm$ 50 μV at any electrode, as well as with incorrect behavioral responses, were excluded from ERP averaging. The numbers of trials were matched between ERP baseline and posttraining sessions by randomly selecting epochs from sessions containing more trials in each observer. A total of 450 $\pm$ 65 stimulus-related EEG epochs were averaged for each condition.

A paired two-tailed   test was applied to test ERP differences between baseline and posttraining conditions in each of the 10-ms bins within a time window of 0–100 ms for C1 analysis, and within a time window of 150–200 ms for N1 analysis. Multiple comparisons with respect to the number of bins were corrected using the Benjamini-Hochberg false discovery rate correction (Benjamini & Hochberg, 1995) with $\alpha = 0.05$.

Five sessions of training improved orientation discrimination significantly at the trained location, with the mean percent improvement (MPI) = 45.2 $\pm$ 2.7% (< 0.001, one-tailed paired   test in this and later analyses unless specified; Figure 2b, c). The improvement was also significant at the diagonal quadrant location where no pretest and training were performed (MPI = 28.6 $\pm$ 3.5%,   < 0.001, calculated with baseline thresholds at the trained location). To quantify the learning transfer, a transfer index (TI) was calculated as the ratio of the MPI at the transfer location over the MPI at the trained location, so that TI $\geq$ 1 indicated complete transfer and TI $\leq$ 0 indicated no transfer. The mean TI = 0.60 $\pm$ 0.07, indicating overall partial transfer of orientation learning to the untrained diagonal quadrant location, was consistent with our previous report (T. Zhang et al., 2010). However, the amount of learning transfer varied greatly among observers, which can be appreciated by individual TIs plotted in Figure 2d. As the main purpose of the current study was to measure the potential C1 changes associated with the transfer of learning, observers who showed minimal transfer with TI < 0.3 (one trained in LVF and four trained in UVF) were excluded from ERP data analysis (the adjusted mean TI = 0.72 $\pm$ 0.05).

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The baseline and posttraining ERP C1 topographies over a time window of 50–90 ms at the trained and transfer locations are presented in Figure 3 (C1 changes were significant in this time window at both trained and transfer locations; see below). These topographies show polarity reversals with stimuli presented in upper versus lower visual fields, which is a typical characteristic of C1 (Jeffreys & Axford, 1972b; Butler et al., 1987). The heights and widths of the C1 voltages were visibly increased after training at both trained and transfer locations.

To quantify the C1 changes associated with training and transfer, three electrodes where baseline C1s showed largest changes were selected for each observer at each of the trained and transfer locations (Figure 3, white dots). Their baseline and posttraining ERP functions were then averaged, respectively. The group mean ERP functions for the UVF training group ($N =$ 11) and the LVF training group ($N = 13$) again showed typical polarity reversals of C1 (Figure 4a). To test the training effects on C1, both groups' ERP data (absolute values) within a time window of 0–100 ms were pooled. Multiple comparisons with paired   tests (see Methods) showed enhanced C1 changes after training at not only the trained location from 50 to 90 ms (indicated by two vertical dash lines in Figure 4a), but also the transfer location from 40 to 90 ms. However, we did not find significant correlations between C1 changes and the amount of learning (= 0.305,   = 0.107) or transfer (= -0.093,   = 0.63).

We further compared the mean C1 changes within the 50–90 ms time window where C1 were significantly affected by learning at both locations in the above analysis. A repeated-measures ANOVA showed a significant main effect of Training, $F(1, 23) = 16.62$,   = 0.001 (Figure 4b). There were no significant main effects of Location (trained vs. transfer locations, $F[1, 23] = 0.008$,   = 0.93) and Group (UVF vs. LVF training groups, $F[1, 23] = 0.033$,   = 0.86). The interactions between Training and Location, $F(1, 23) = 0.034$,   = 0.85, and between Training and Group, $F(1, 23) = 0.53$,   = 0.48, were not significant either.

In addition, the peak latency of C1 was 2.54 $\pm$ 0.58 ms earlier at the transfer location after training (= 0.022). There was no difference at the trained location (= 0.22). So the learning and transfer effects had very small and negligible impacts on C1 peak latencies.

We found that C1 changes were unrelated to nonlearning factors such as general attention and arousal with the same stimuli. Rather C1 changes were specific to the trained task. In the posttraining ERP session (S7), the same observers also performed the same circle versus donut shape discrimination task as in S0 (Figure 5a). No significant C1 changes from S0 were evident after training at both trained and transfer locations, $F(1, 23) = 1.88$,   = 0.18 (Figure 5b, c). There were no significant main effects of Location, $F(1, 23) =$ 0.14,   = 0.71, and Group, $F(1, 23) = 0.21$,   = 0.65, and

(N = 11)

(N = 13)

quadrant location in the opposite hemisphere. Moreover, the C1 increase was specific to the trained task. The C1 changes at the untrained transfer location indicate that C1 can be top-down modulated by perceptual learning. Therefore, C1 changes after perceptual learning may not necessarily indicate neural plasticity in the early visual cortex.

We purposely selected a peripheral orientation discrimination task for training because this learning could transfer greatly to a new location in the opposite hemisphere (T. Zhang et al., 2010; Hung & Seitz, 2014). The great transfer of orientation learning is in contrast to a previous report for highly location-specific orientation learning (Shiu & Pashler, 1992). We suspect that the discrepancies may be due to the methodological differences. In Shiu and Pashler (1992) training was conducted with the method of constant stimuli that used only one stimulus level (i.e., one fixed orientation difference). Training with a single orientation difference may cause overfitting or overlearning (Sagi, 2011), which reduces learning transfer. Nevertheless, even location-specific perceptual learning can be made completely transferrable to new retinal locations with double training, in which the observers are additionally trained at the new location with an irrelevant task (Xiao et al., 2008; Wang et al., 2012; Wang et al., 2013;
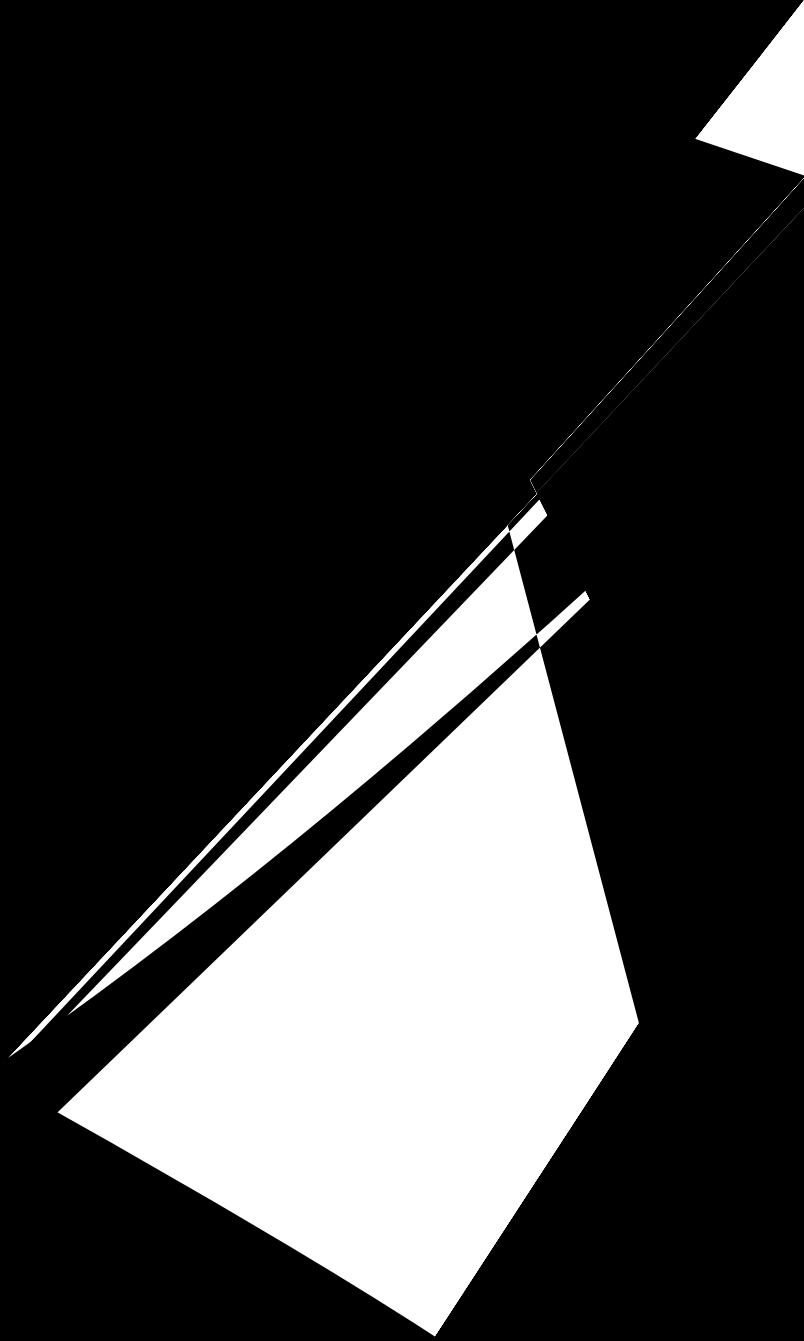
down modulation can be remapped to the responses of untrained V1 neurons to achieve similar functionality.

Two interesting issues arise relevant to top-down modulation of V1 responses. The first issue, which is directly relevant to the interpretation of the current C1 results, is whether the top-down modulation could lead to long-term neural tuning changes in V1. Monkey recording evidence shows that when top-down modulation is disabled by anesthesia, V1 changes due to perceptual learning vanish (Li et al., 2008). This finding suggests that perceptual learning may not result in long-term tuning changes by modifying neural connections in V1. ERP C1 changes hence may not reflect long-term V1 tuning changes resulting from top-down modulation either. Our evidence for similar C1 changes at the trained and untrained locations is consistent with this possibility. Moreover, long-term changes in V1 neural connections cannot account for complete learning transfer to a new location/hemisphere (Xiao et al., 2008; Wang et al., 2012; Wang et al., 2013; Wang et al., 2014) or orientation (J. Y. Zhang et al., 2010; J. Y. Zhang et al., 2014) with double training.

The second related issue is whether V1 changes due to top-down modulation could, in turn, refine visual outputs to facilitate later readout. These reciprocal top-down and bottom-up interactions would be an ideal way to achieve perceptual learning. A recent monkey recording study indeed suggests this possibility (Yan et al., 2014). In theory the roles of such refined visual outputs in perceptual learning can be incorporated into reweighting models, although in these models' present formats the visual outputs are fixed, and training only changes the weights of these fixed outputs (e.g., Dosher & Lu, 1998). On the other hand, if these reciprocal interactions are the case, additional assumptions are necessary to interpret significant and often complete learning transfer after double training. It is evident from learning transfer that high-level learning is able to remap the learned rules of reweighting to a different set of sensory neurons to improve readout (J. Y. Zhang et al., 2010). However, if the readout also partially relies on refined outputs from trained sensory neurons as a result of top-down modulation, complete learning transfer may be possible only if untrained V1 neurons are also equally top-down modulated during training, or are sufficiently top-down modulated in the post-training session when the trained task is retested with the untrained condition, to produce equivalent net outputs. Whether and how these processes could take place is as yet unknown.

Previously Bao et al. (2010) used C1 changes to infer early visual cortical plasticity of perceptual learning. In their study contrast detection learning partially transferred to an untrained new location, similar to our behavioral data. However, their ERP results showed significant C1 changes only at the trained location, but not at the transfer location. The differences in C1 change patterns between Bao et al. and our study may be attributed to task differences. In Bao et al. an irrelevant RSVP task, rather than the trained contrast detection task, was performed while evoked potentials by the contrast stimulus were recorded. In addition, Bao et al.'s observers had to focus their attention on a simultaneous central task. These manipulations were to avoid the top-down influences, which is opposed to our present finding that task specific top-down modulation is mainly the cause of C1 changes with perceptual learning.

Ke   d : e ce   al lea i g, ie a i , ERP

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Commercial relationships: none.
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