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Report

# Effectively Reducing Sensory Eye Dominance with a Push-Pull Perceptual Learning Protocol

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## Summary

**Much knowledge of sensory cortical plasticity is gleaned from perceptual learning studies that improve visual performance [1–7]. Although the improvements are likely caused by modifications of excitatory and inhibitory neural networks, most studies were not primarily designed to differentiate their relative contributions. Here we designed a novel push-pull training protocol to reduce sensory eye dominance (SED), a condition that is mainly caused by unbalanced interocular inhibition [8–10]. During the training, an attention cue presented to the weak eye precedes the binocular competitive stimulation. The cue stimulates the weak eye (push) while causing interocular inhibition of the strong eye (pull). We found that this push-pull protocol reduces SED (shifts the balance toward the weak eye) and improves stereopsis more so than the push-only protocol, which solely stimulates the weak eye without inhibiting the strong eye. The stronger learning effect with the push-pull training than the push-only training underscores the crucial involvement of a putative inhibitory mechanism in sensory plasticity. The design principle of the push-pull protocol can potentially lend itself as an effective, noninvasive treatment of amblyopia.**

## Results and Discussion

The binocular visual system provides a model for investigating how competition from excitatory interactions and mutual inhibition between two independent inputs (eyes) shape the sensory system [11]. Figure 1A shows a simplified framework to conceptually understand the putative excitatory and inhibitory networks [12]. Inputs of hypothetical cortical units with common orientation preference from the two eyes converge while monocular units with preference for orthogonal orientation inhibit one another. The mutual inhibition between the two eyes' inputs is largely balanced in the normally developed adult. But when the mutual inhibition is unbalanced, resulting in sensory eye dominance (SED), binocular vision is degraded [9, 10]. Figure 1B conceptualizes an example in which the right eye's (RE) inhibition on the left eye (LE) is stronger. When stimulated with dichoptic orthogonal gratings of the same contrast to induce binocular competition, signals in the LE's channel are suppressed, whereas signals in the RE's channel travel upstream, leading to its image being perceived.

To quantify SED, we present the two eyes with dichoptic vertical and horizontal gratings [9]. Figure 2A shows an example in which the contrast of the LE's vertical grating is fixed. The contrast of the RE's horizontal grating is adjusted using a QUEST procedure [13] until the observer reports equal chance (percentage) of perceiving either grating. We refer to this contrast as the RE balance contrast. We then switch the gratings between the two eyes (Figure 2B) to measure the LE balance contrast. SED is the difference between the LE and RE balance contrast values. The eye with the higher balance contrast is the weak eye [9].

We sought to reduce SED by using a push-pull protocol (Figure 2C). During the training, a rectangular frame (attention cue) is presented to the weak eye, followed by a pair of dichoptic orthogonal gratings. The cue activates transient attention to cause the weak eye's grating to be perceived, and the strong eye's grating is suppressed [8] by a putative interocular inhibitory mechanism. Similarly, in the second half of stimulus presentation, the grating in the weak eye is perceived. The observer discriminates the grating orientation from the two presentations (seen by the weak eye).

Separately, we used a push-only protocol (Figure 2D), which is similar to the push-pull protocol, except the strong eye is not stimulated. Similarly, both protocols repeatedly stimulate the weak eye to perceive its signals (push), which presumably enhance the efficacy of the weak eye's channel. In contrast, and additionally, the push-pull protocol repeatedly suppresses the signals in the strong eye, which presumably strengthens the weak eye's inhibition on the strong eye (pull; Figure 1A). We predict that the additional "pull" action renders the push-pull protocol more effective than the push-only protocol in reducing SED.

We tested the prediction by applying both protocols (in an interleaved procedure) on the same observer (n = 7) at two different retinal locations with similar magnitudes of SED over a 10 day training phase. To monitor progress of each training session, we measured balance contrast, with the orientation of the test grating being either the same as or orthogonal to the orientation of the training grating. For simplicity, we shall refer to such stimuli orientation as same, or orthogonal, from here onward. The balance contrast was measured using the QUEST procedure before and after each day's training session. Figure 3A and 3B show the average results with the push-pull and push-only protocols, respectively. The x axis plots the training session, and the y axis plots the interocular balance contrast, which is the difference between the measured balance contrast and fixed contrast (1.5 log unit).

With the push-pull protocol (Figure 3A), the same interocular balance contrast (open symbols) declines as training progresses (before: slope = $-0.026$, $R^2 = 0.881$, $p < 0.001$; after: slope = $-0.021$, $R^2 = 0.895$, $p < 0.001$), indicating perceptual learning. However, the orthogonal interocular balance contrast (filled symbols) changes little (before: slope = $-8.82 \times 10^{-5}$, $R^2 = 0.001$, $p = 0.919$; after: slope = 0.004, $R^2 = 0.297$, $p = 0.103$), suggesting that the learning effect is limited to the trained stimulus orientation and eye. We also measured the balance contrast using the method of constant stimuli before and after the entire training period. From the psychometric functions obtained (see Figure S1A available online), we

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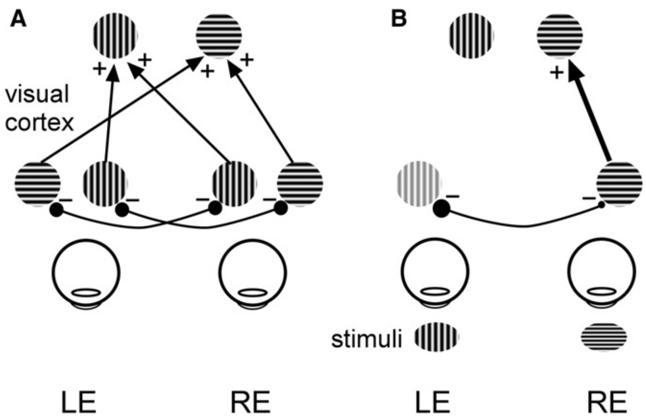


Figure 1. A Conceptual Cortical Model of Binocular Interaction

(A) At the first level, monocular units with different orientation preference from each eye inhibit one another. At the second level, monocular units from each eye with the same orientation preference converge. Interocular inhibition is activated when the two eyes are stimulated with orthogonal gratings.

(B) Sensory eye dominance with strong inhibition of the left eye (LE). When the two eyes are presented with orthogonal gratings of equal contrast, the right eye's (RE) grating (strong eye) is perceived while the LE's grating (weak eye) is suppressed because of the stronger inhibition on the LE's monocular units.

calculated the interocular balance contrast (gray symbols, Figure 3A), which confirms a significant learning effect for the same interocular balance contrast ($t(6) = 4.318$, $p = 0.005$), but not for the orthogonal interocular balance contrast ($t(6) = 0.218$, $p = 0.835$).

The push-only protocol (Figure 3B), however, shows no learning (same interocular balance contrast: before: slope = 0.003, $R^2 = 0.279$, $p = 0.095$; after: slope = 0.001, $R^2 = 0.028$, $p = 0.646$; orthogonal interocular balance contrast: before: slope = −0.001, $R^2 = 0.079$, $p = 0.403$; after: slope = 0.001, $R^2 = 0.038$, $p = 0.587$). The interocular balance contrast obtained by the method of the constant stimuli also fails to demonstrate a significant learning effect (t test, $p > 0.05$).

We calculated SED, i.e., the difference between the same and orthogonal interocular balance contrast values, in Figure 3A and 3B. Figure 3C plots the SED obtained before each day's training session. The push-pull protocol significantly reduces SED (black squares, slope = −0.026, $R^2 = 0.850$, $p < 0.001$), but the push-only protocol does not (gray diamonds, slope = 0.004, $R^2 = 0.293$, $p = 0.086$). We obtained similar results (data not shown) from the SED measured after each day's training session (push-pull: slope = −0.025, $R^2 = 0.896$, $p < 0.001$; push-only: slope = −0.001, $R^2 = 0.012$, $p = 0.761$). Essentially, our experiment with the push-pull protocol reveals that repeatedly suppressing the image in the strong eye from perception, i.e., "negatively" stimulating the strong eye, is necessary to significantly reduce SED.

Figure 3A and 3B reveal that the magnitudes of the interocular balance contrast are larger after each daily training session with both push-pull (same: $F(1,6) = 92.435$, $p < 0.001$; orthogonal: $F(1,6) = 3.617$, $p = 0.106$, two-way analysis of variance [ANOVA] with repeated measures) and push-only (same: $F(1,6) = 46.802$, $p < 0.001$; orthogonal: $F(1,6) = 4.464$, $p = 0.079$) protocols than before each daily training session. The after versus before differences do not vary significantly with the number of training sessions (interaction effect between the order of measurement [after versus before] and training

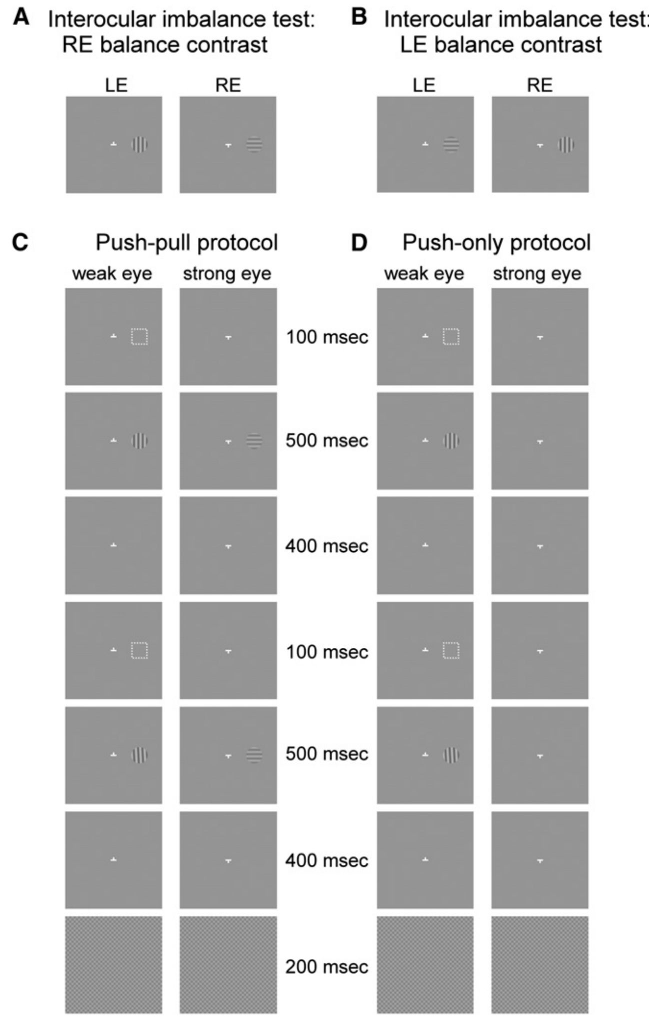


Figure 2. Experimental Protocols for Sensory Eye Dominance and Perceptual Learning

(A and B) Orthogonal gratings used to measure the balance contrast in the RE and LE, whose difference defines the sensory eye dominance.

(C) Push-pull protocol. The white rectangular frame acts as a cue to attract transient attention, causing the (vertical) grating in the weak eye to be perceived while the (horizontal) grating in the strong eye is suppressed.

(D) Push-only protocol. The stimulus presentation sequence is the same as in the push-pull protocol, except no grating is presented to the strong eye.

session, $p > 0.05$). The after versus before difference in magnitude is significantly larger with the same stimuli than with orthogonal stimuli in the push-pull ($F(1,6) = 56.935$, $p < 0.001$, two-way ANOVA with repeated measures) and push-only ($F(1,6) = 27.576$, $p = 0.002$) training. This is highly suggestive of stimulus orientation and eye specificity. However, this after versus before difference is unlikely to be caused by fatigue during the afternoon session, because the orientation discrimination threshold data are similar between the morning and afternoon sessions (Figure S1C). Rather, the after versus before difference in interocular balance contrast resembles the performance deterioration observed during training of texture discrimination [14–16].

Separately, we trained three other observers over 10 days of push-pull protocol, followed by 10 days of push-only protocol (sequential procedure). Figure 3A and 3B plot the average interocular balance contrast data obtained with the

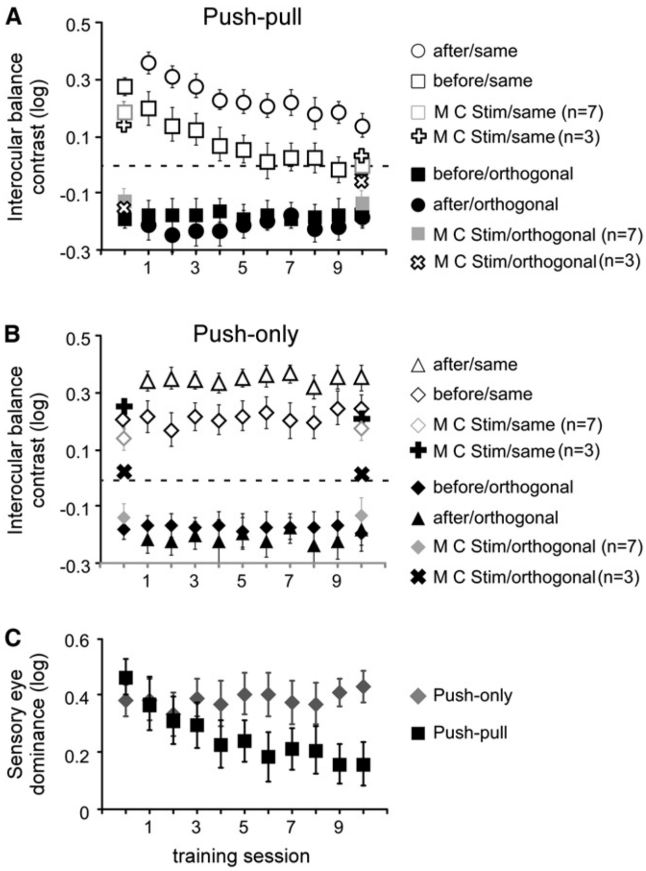


Figure 3. Outcomes of the Perceptual Learning Protocols on Sensory Eye Dominance of Seven Observers Trained with the Interleaved Procedure

(A) The average interocular balance contrast with the push-pull protocol. The interocular balance contrast was obtained with grating whose orientation was the same as, or orthogonal to, the grating used in the training, respectively, and was measured before and after each day's training. The balance contrast reduces with days in training when tested with the same orientation grating.

(B) The interocular average balance contrast with the push-only protocol. The interocular balance contrast does not change with training.

(C) Sensory eye dominance (SED; measured before each day's training session) reduces with the push-pull but not the push-only protocol.

Both (A) and (B) also include the average data of observers (n = 3) trained in a sequential procedure (plus and cross symbols; error bars are not shown to reduce clutter). See also Figures S1A and S1B. Error bars indicate 1 standard error of the mean (SEM).

method of constant stimuli (plus and cross symbols; see also Figure S1B). They show a similar trend to the seven observers' data (push-pull: same: $t(2) = 4.052$, $p = 0.056$; orthogonal: $t(2) = -3.497$, $p = 0.073$; push-only: same: $t(2) = 0.895$, $p = 0.465$; orthogonal: $t(2) = 0.325$, $p = 0.776$).

In addition to the balance contrast measurements, we conducted three sets of pre- and posttraining tests on the observers with the interleaved training procedure. Our first set of tests evaluated the hypothesis that the underlying plasticity occurs mainly in the early visual cortex by focusing on the location and orientation specificity of learning [17–22]. A finding that no learning occurs at the push-only training location could also indicate that learning at the push-pull location cannot be transferred to another training location. This suggests that learning at the push-pull location occurs at cortical areas where the local feature information has not been integrated across a larger visual field [23–25]. To support this, we examined whether the learning is transferable to an untrained retinal location 1.53° from the trained location with the same eccentricity. We found that SED reduction (0.011 ± 0.033 log unit) is much smaller than at the trained location (0.304 ± 0.043 log unit; $t(6) = 6.418$, $p = 0.001$). We further investigated the orientation specificity of learning by narrowing the test orientation from 90° to 45° by measuring SED at the trained location using 45° and 135° dichoptic gratings. We only found a small reduction in SED (0.021 ± 0.048 log unit).

Our second set of tests investigated whether the learning is accompanied by (1) reduced efficiency of the strong eye and/or (2) increased efficiency of the weak eye (Figure 1A). Such modifications in monocular efficiency can be reflected in corresponding changes in monocular contrast and orientation discrimination thresholds after training. We thus measured monocular contrast thresholds at the push-pull and push-only locations using grating with either the same orientation as the orientation of the weak eye's training grating or orientation orthogonal to it. Figure 4A shows threshold reduction in all but the strong eye (in the same/push-pull and orthogonal/push-only conditions); however, the reduction is much smaller than the reduction in SED at the push-pull location (Figure 3A). This suggests that modifications of efficiency within each ocular pathway are unlikely to be the main factor responsible for learning. Similarly, we measured monocular orientation discrimination thresholds and found a statistically insignificant improvement after training, except in the strong eye (orthogonal/push-pull condition; Figure 4B). These findings indicate that alterations of monocular efficiency (factors 1 and 2) are unlikely to significantly contribute to learning (reduced SED). Instead, they suggest that the learning with the push-pull protocol is attributable to the activation of interocular inhibition, whereby the weak eye suppresses the strong eye during training ("pull"). That is, repeatedly stimulating the putative inhibitory mechanism leads to perceptual learning.

Our third sets of tests investigated whether reducing SED is beneficial for binocular depth processing. We measured binocular disparity threshold and reaction time to detect the depth of a disc in a random-dot stereogram at the trained and untrained locations [26, 27]. We found that depth threshold reduces significantly at the push-pull ($t(6) = 5.354$, $p = 0.002$) but not the push-only ($t(6) = 1.294$; $p = 0.243$) location (Figure 4C), with a significantly larger reduction in the former ($t(6) = 2.824$, $p = 0.030$). Reaction times to detect depth are reduced significantly at the push-pull location ($t(6) = 3.104$, $p = 0.021$) but insignificantly at the push-only location ($t(6) = 2.086$, $p = 0.082$). However, the pre- and postreaction time difference does not reveal a statistically significant effect of training protocol ($t(6) = 1.600$, $p = 0.161$). At the untrained locations (>1.53° from the trained location), there are no reliable changes in depth threshold ($t(4) = -1.712$, $p = 0.162$) and reaction time ($t(4) = -0.055$, $p = 0.958$). Effectively, stereopsis is improved as a consequence of the push-pull protocol that aims to rebalance interocular inhibition. Such a learning effect on stereopsis is particularly significant because the training stimuli carried no binocular disparity and the observers were never trained on the stereo task.

In summary, our push-pull protocol produces a stronger learning effect on SED and stereopsis than the standard push-only protocol. The effectiveness of the push-pull protocol can be traced to the simultaneous stimulation of the weak and strong eyes during training, with the image in the

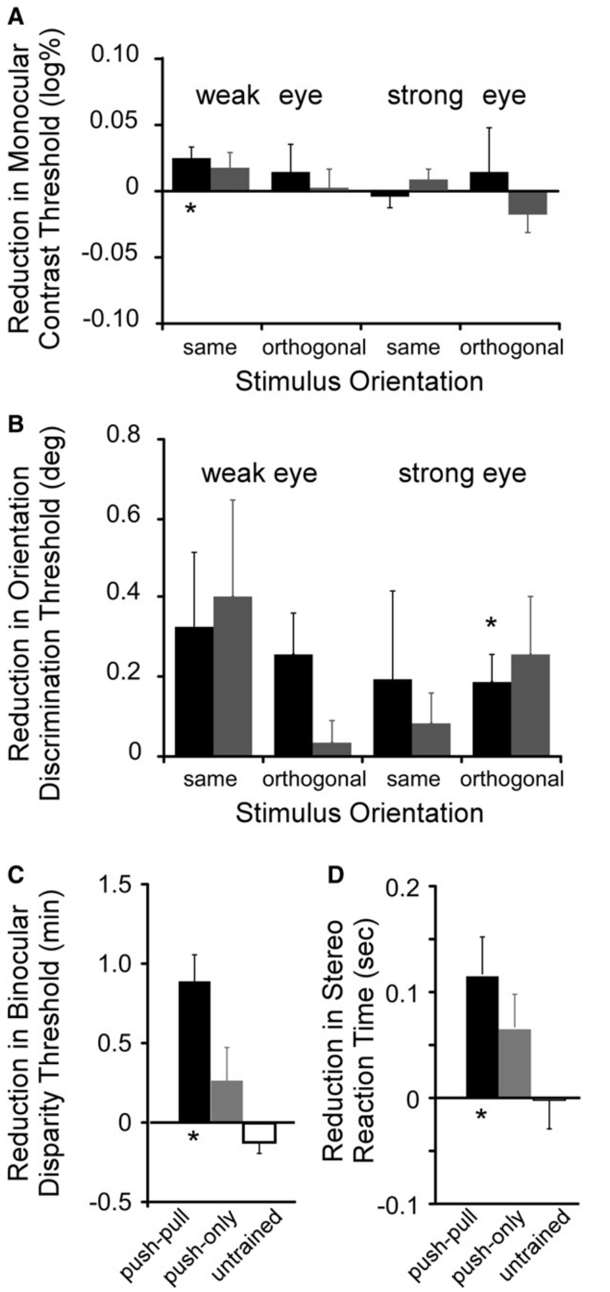


Figure 4. Outcomes of the Perceptual Learning Protocols on Unrelated Monocular and Binocular Functions

(A) Reduction in monocular contrast threshold at the push-pull (black bars) and push-only (gray bars) training locations in the weak and strong eye.
(B) Reduction in monocular orientation discrimination threshold.
(C and D) The reduction in stereo threshold and reaction time, respectively, at the push-pull (black bar), push-only (gray bar), and an untrained (open bar) location. *$p < 0.05$. Error bars indicate 1 SEM.

strong eye being actively suppressed by the putative interocular inhibitory mechanism. This is opposite to the push-only protocol, wherein the strong eye is not stimulated, precluding the need for interocular inhibition because there is no image to suppress. (The push-pull protocol is reminiscent of the approach used in spatial context-induced perceptual learning of contrast discrimination [28].) Our findings thus suggest a substantial role of interocular inhibition in the plasticity of the adult binocular visual system. This view is highly pertinent and provides the strongest behavioral support for the recent discoveries of the differential roles of the excitatory and inhibitory circuitries in juvenile and adult cortical plasticity. Specifically, the maturation of local inhibitory network in non-primate visual cortex correlates closely with the critical period for the formation of ocular dominance columns, and the inhibitory network is involved in the reestablishment of adult cortical plasticity [29–32].

Finally, our finding that the push-pull, and not the push-only, protocol effectively reduces SED has implications for developing a new paradigm for treating amblyopia (an extreme form of SED). The conventional amblyopic treatment comprises depriving vision of the good eye [33, 34]. Recent amblyopia research has found that extensive perceptual training of the amblyopic eye improves its visual functions [35–40]. However, the common motivation of existing treatment modalities is based on the design principle of the push-only protocol, wherein the strong eye is not actively inhibited. Our findings suggest that an amblyopic therapy that adopts the design principle of the push-pull protocol will likely increase treatment efficacy.

## Experimental Procedures

A Macintosh computer running Matlab and Psychophysics Toolbox [41, 42] generated the stimuli on a flat cathode ray tube monitor. All observers (one author and nine naive observers with informed consent) had clinically normal binocular vision. The experiments performed conformed with the regulatory standards of the Institutional Review Board of the University of Louisville and of Salus University. We first measured SED with vertical and horizontal grating discs at eight concentric retinal locations 2° from the fovea (Figure 2A and 2B). Two locations with the largest SED were chosen for the training (see Supplemental Experimental Procedures for details).

Seven naive observers were trained in an interleaved procedure wherein both push-pull (Figure 2C) and push-only (Figure 2D) protocols were implemented on the same day. During the training, and for each observer, the push-pull protocol was assigned to one retinal location, and the push-only protocol was assigned to the second retinal location. To accomplish this, each observer came to the laboratory for a 1 hr morning session and a 1 hr afternoon session (12 blocks per session) for a total of 10 days. The sequence of selecting the training protocol (push-pull versus push-only) for each session was counterbalanced with an ABBA within-subject design. To monitor the learning progress, we measured the observer's balance contrast before each morning's training session and after each afternoon's training session. To further assess the learning effect, we ran three sets of tests in the pre- and posttraining phase: (1) SED with 45° and 135° grating discs, (2) monocular contrast thresholds and orientation discrimination thresholds with vertical and horizontal grating discs (see Supplemental Experimental Procedures and Figure S2), and (3) stereo threshold and reaction time (see Supplemental Experimental Procedures and Figure S3). For the stereo tests, an untrained location with the least SED was also measured. All seven observers participated in the three sets of tests, except for the untrained location condition in the third set of tests ($n = 5$). Additionally, SED with horizontal and vertical gratings was measured before and after the training at locations (±45°) adjacent to the two training locations and was tested on all seven observers.

Separately, three observers were trained with the push-pull protocol for 10 days, followed by the push-only protocol for a subsequent 10 days (sequential procedure). They received 1 hr of training during each daily session and were assessed for the learning effect on SED. Data from both groups of observers were pooled separately for statistical analysis.

### The Push-Pull Training Protocol

A trial began with fixation at the nonius target and the presentation of an attention cue (1.25° × 1.25° frame with dashed outline, width = 0.1°, 1.56 log unit, 70 cd/m$^2$) for 100 ms. After a 100 ms cue lead time, the first dichoptic gratings (500 ms, 1.25°, 3 cpd, 35 cd/m$^2$) were presented. The same 100 ms cue was presented again 400 ms later, followed by a 100 ms cue lead time and the second dichoptic gratings with a slightly different orientation in the weak eye (500 ms). A 200 ms checkerboard sinusoidal grating mask (7.5° × 7.5°, 3 cpd, 35 cd/m$^2$, 1.5 log unit) terminated the trial 400 ms later. The contrast values of the dichoptic gratings were those that led to equal predominance with the interocular imbalance test. The observer reported whether the first or second grating had the slight counterclockwise orientation, and an audio feedback was given. (Before the proper training, we determined for each observer that the cue successfully suppressed the grating viewed by the strong eye.) The orientation discrimination threshold was obtained using the QUEST procedure. Twelve blocks (50 trials per block) were performed in each training session.

### The Push-Only Training Protocol

The procedure was identical to the push-pull protocol, with an important exception. Instead of presenting a pair of dichoptic gratings to the training location, only a monocular grating was presented to the weak eye's training location while the corresponding location in the strong eye viewed a homogeneous gray (blank) field.

## Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and three figures and can be found with this article online at doi:10.1016/j.cub.2010.09.043.

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