

# Dichoptic Perceptual Training and Sensory Eye Dominance Plasticity in Normal Vision

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**PURPOSE.** We introduce a set of dichoptic training tasks that differ in terms of (1) the presence of external noise and (2) the visual feature implicated (motion, orientation), examining the generality of training effects between the different training and test cues and their capacity for driving changes in sensory eye dominance and stereoscopic depth perception.

**METHODS.** We randomly assigned 116 normal-sighted observers to five groups (four training groups and one no training group). All groups completed both pre- and posttests, during which they were tested on dichoptic motion and orientation tasks under noisy and noise-free conditions, as well as a binocular phase combination task and two depth tasks to index sensory eye dominance and binocular function. Training groups received visual training on one of the four dichoptic tasks over 3 consecutive days.

**RESULTS.** Training under noise-free conditions supported generalization of learning to noise-free tasks involving an untrained feature. By contrast, there was a symmetric learning transfer between the signal-noise and no-noise tasks within the same visual feature. Further, training on all tasks reduced sensory eye dominance but did not improve depth perception.

**CONCLUSIONS.** Training-driven changes in sensory eye balance do not depend on the stimulus feature or whether the training entails the presence of external noise. We conjecture that dichoptic visual training acts to balance interocular suppression before or at the site of binocular combination.

**Keywords:** sensory eye dominance, dichoptic visual training, perceptual learning, stereopsis, plasticity

Binocular vision is a fundamental feature of the primate brain. Under ideal conditions, binocularity allows combining information from the two eyes equally to form a single and stable percept. However, the visual cortex may not always give a balanced weighting to the two eyes' input, resulting in functional asymmetry of the two eyes, commonly termed *sensory eye dominance*. Sensory eye dominance is a prominent characteristic exhibited by certain clinical groups, particularly in strabismic amblyopes,<sup>1,2</sup> where the amblyopic brain largely prefers one eye's input over the other, manifesting in impaired binocular function.<sup>3</sup> Interocular suppression is thought to play a primary role in binocular visual deficits of amblyopes on the grounds that binocular cortical mechanism is intact in amblyopia if the interocular stimulation is artificially adjusted to balance the two monocular signals before binocular summation.<sup>4,5</sup> Of immediate relevance to the present work, variations in sensory eye dominance can be found outside of the clinical setting: in the normal population, around 60% of the healthy population show mild dominance while 30% to 40% show stronger dominance.<sup>6-8</sup>

There is emerging evidence that mechanisms underlying sensory eye dominance in adults, both in the visually impaired and in visually normal individuals, is more plastic

than previously believed,<sup>9-11</sup> opening a window of opportunity for modulating sensory eye dominance in both populations. Training protocols that adopt dichoptic presentation of motion-in-noise stimuli have been shown to successfully promote eye rebalancing and reestablish binocular visual capacities in amblyopes<sup>12,13</sup>; however, the mechanisms underlying these improvements have yet to be elucidated. The two-stage model for binocular interactions in the visual system may provide some hints.<sup>14</sup> This model suggests that the integration of the left and right eye signals occurs in two distinct stages. The first stage happens before binocular summation, where each eye receives inhibitory input from the contralateral eye, while the second stage of contrast gain control occurs after binocular summation (i.e., the summation of monocular excitatory channels of the two eyes). Theoretically, changes brought by dichoptic visual training using motion-in-noise stimuli<sup>12,13</sup> could be driven by any or some combination of the following: (1) changes in interocular suppression before binocular summation, (2) changes at or after binocular summation within the primary visual cortex, or (3) changes in postbinocular-summation mechanisms in the extrastriate cortex such as the regions that known to serve motion perception or even signal-noise-segregation.<sup>15</sup>

Previous work involving perceptual learning in healthy adults has revealed that training effects are largely task dependent: training on signal-in-noise (extracting signals embedded in noise) versus fine discrimination (discriminating between two closely positioned features) tasks led to different degrees of learning transfer<sup>16</sup> that are accompanied by differences in functional reweighting along the dorsal and ventral pathways.<sup>15</sup> Specifically, besides improving the immediately trained task, training on a fine task has been consistently shown to enhance performance on the signal-in-noise task for the same visual feature.<sup>16–19</sup> By contrast, training on a signal-in-noise task only had minimal benefits on the fine task involving the same feature, but it drove a broader transfer of learning that could be generalized to the signal-in-noise tasks for other visual features.<sup>16</sup> It is important to emphasize that all the previous work showing a clear pattern of learning generalization was conducted under binocular presentation settings (i.e., with the same stimulus presented to both eyes). It is therefore unclear as to the breadth of improvements that training in signal-in-noise and fine discrimination tasks could achieve if the stimuli are instead shown dichoptically.

Here, we aimed to characterize the breadth of improvements that dichoptic visual training under different tasks and feature-demands could attain. Specifically, we compared the generality of perceptual learning under dichoptic signal-noise training and novel dichoptic fine training paradigms involving different cues (motion, orientation). Critically, we were interested in probing the changes in sensory eye dominance and binocular function (i.e., stereoscopic depth perception) that can be attained under the different training conditions. These capacities were indexed using additional binocular phase combination and signal-in-noise and fine depth tasks, the latter two of which have been shown to engage different depth processing loci in the human brain.<sup>15,20</sup>

The various training paradigms introduced here differ in terms of the presence or absence of external noise, as well as in terms of the particular visual feature involved, but share in common the fact that binocular integration is required for solving each task. We predicted that if dichoptic training paradigms act to balance interocular suppression before or at the site of binocular summation, all four dichoptic training tasks could lead to a similar degree of reduction in sensory eye dominance. We should also observe broad learning transfer across tasks and stimulus features. However, if dichoptic training drives changes in postbinocular-summation mechanisms, such as signal-noise segregation mechanisms in the dorsal cortex,<sup>15</sup> we should observe the best learning outcomes with dichoptic signal-in-noise training only.

## METHODS

### Participants

A total of 116 (age 19–33 years, mean 22.3 years; 36 males) visually normal observers, unaware of the purpose of the experiment, were tested. All participants had normal or corrected-to-normal visual acuity, normal binocular fusion (Worth-4-Dot test), and stereopsis (Titmus test,  $\leq 40$  arcsec). All participants provided written informed consent in line with the procedures approved by the Human Research Ethics Committee (HREC), The University of Hong Kong. These participants were randomly assigned to five groups:

48 trained on motion tasks (24 signal-in-noise; 24 fine discrimination), 48 trained on orientation tasks (24 signal-in-noise; 24 fine discrimination), and 20 received no visual training (control group).

### General Procedures

All groups completed both “pre” and “post” tests, during which they were tested on the motion and orientation signal-noise and fine tasks. Additionally, during these tests, we indexed their sensory eye dominance using the binocular phase combination task<sup>21</sup> and broader binocular function using the two depth tasks.<sup>16</sup> The training groups received visual training on one of four dichoptic tasks: signal-in-noise motion task, fine motion task, signal-in-noise orientation task, or fine orientation task over 3 consecutive days (1 hour per day, 3600 trials in total). We selected a training protocol of this length based on previous binocular training work showing large effects attained with this training duration,<sup>16</sup> in addition to pilot dichoptic training data showing performance saturation with this same training period. Training groups were then retested on all tasks (“post” tests) on the day immediately following the last training session. The control group did not receive training but completed the pre- and posttraining tests with an equivalent time window in between the two tests as for the other groups. The order of the tasks in pre- and posttests was counterbalanced. During the training (but not test) sessions, participants were provided with auditory feedback.

### Apparatus

Stimuli were generated using custom software written in MATLAB (MathWorks, Natick, MA, USA) with extensions from Psychtoolbox<sup>22,23</sup> and presented dichoptically on a 27-in. ASUS 3D-vision ready LCD display (AsusTek Computer Inc., Taipei, Taiwan; resolution: 1920 × 1080 pixels; refresh rate: 120 Hz) paired with shutter goggles (NVIDIA 3D Vision 2; Nvidia Corporation, Santa Clara, CA, USA). At the start of each session, we verified for (the lack of) crosstalk between eyes by presenting geometric test patterns independently to each eye and ensuring clean separation of signals. Participants were asked to rest their head on a chinrest to maintain a viewing distance of 50 cm.

### Stimuli and Tasks

Stimuli were presented on a uniform gray background with a binocularly presented grid-like frame composed of solid black and white squares (each 1.5 degrees in size) serving to provide an unambiguous background reference (i.e., to promote binocular fusion).

**Motion Stimuli and Tasks.** We generated two types of motion stimuli, both with an equal number of black and white dots presented at 100% contrast. Each dot subtended 0.2 degrees, moved with a velocity of 2 deg/s, and had a limited lifetime of 1 second. We derived the signal-in-noise motion stimulus from Li et al.,<sup>7</sup> such that the moving dots were presented within a central aperture subtending 9 degrees in diameter. We manipulated the signal-to-noise ratio such that the detectability of motion direction depended on the percentage of signal dots that moved coherently in a single direction. At 100% signal, all the dots carried either left or rightward coherent motion direction, whereas a 0% signal stimulus consisted only of noise

dots that randomly moved within the aperture. On each trial, signal dots carrying a coherent motion direction were presented to one eye, while noise dots carrying a random motion direction were presented to the alternate eye.<sup>7</sup> Observers were required to judge the net motion direction of the dots (either leftward or rightward) by pressing arrow keys on the keyboard. The fine motion stimulus was derived from the binocular variant introduced by Chang et al.<sup>16</sup> It had the same overall size as the signal-in-noise stimulus but was made up of a central aperture (4.5 degrees diameter) and a surrounding annulus (9 degrees diameter). The dots located in the central aperture and the surround moved coherently and had a density of 3 dots/deg<sup>2</sup>. The dots in the surround (i.e., reference motion direction) moved on an average 30 degrees clockwise or counterclockwise from vertical with a random jitter offset ranging from  $-3$  to  $3$  degrees introduced on each trial. For this task, the dots in the surrounding annulus that carried a reference motion direction and those carrying the target motion direction in the center were presented to different eyes on each trial. Observers were asked to judge whether the motion direction of the dots in the central target was offset clockwise or counterclockwise relative to the reference motion direction in the surround by pressing arrow keys on a keyboard. To ensure that judgments were made in the same quadrant, a maximum motion direction difference of 30 degrees was adopted.

For both tasks (and for both test and training runs), we manipulated task difficulty by adjusting the signal-to-noise ratio (signal-in-noise task) or the degree of motion direction offset between the central target and the reference surround (fine task) on each trial using the QUEST staircase procedure sampling thresholds at an 82% correctness level.<sup>24</sup> A block of trials consisted of two interleaved staircases of 60 trials each that randomly presented the signal dots (signal-in-noise task) or the central target (fine task) to either the left (Figs. 1a, 1b, configuration 1) or the right eye (Figs. 1a, 1b, configuration 2). By randomly interleaving the two staircases, observers could not determine the eye of origin for signal (or center) and noise (or surround) on each trial once the stimuli were fused. Participants completed one practice block to get familiarized with the stimuli and one test block in the pretest and two test blocks in the posttest. Stimuli were presented for 500 ms, and the interstimulus interval was fixed at 300 ms.

#### Glass Pattern Orientation Stimuli and Tasks.

We generated two types of glass pattern orientation stimuli, again derived from the binocular variants introduced by Chang et al.<sup>16</sup> Both the signal-in-noise and fine stimulus contained an equal number of black and white static dots displayed at 100% contrast. The dots were arranged in dipole configurations, such that each dipole comprised a single color, and were generated by shifting one of the dots by a distance of 0.2 degrees in the direction  $\theta$ . For the *signal-in-noise orientation* stimulus, the dipoles were positioned within a central aperture 9 degrees in diameter. The signal dipoles carried either a horizontal or vertical orientation, while the noise dipoles had a random orientation sampled from between 0 and 180 degrees. The proportion of signal-to-noise dipoles was adjusted on each trial. At 100% signal, all dipoles were either horizontally or vertically orientated. Task difficulty increased when the percentage of signal dipoles decreased relative to the noise dipoles. At 0% signal, all dipoles conveyed a random orientation. We presented the signal dipoles to one eye and noise dipoles to the other eye on each trial (Fig. 1c, configurations 1 and

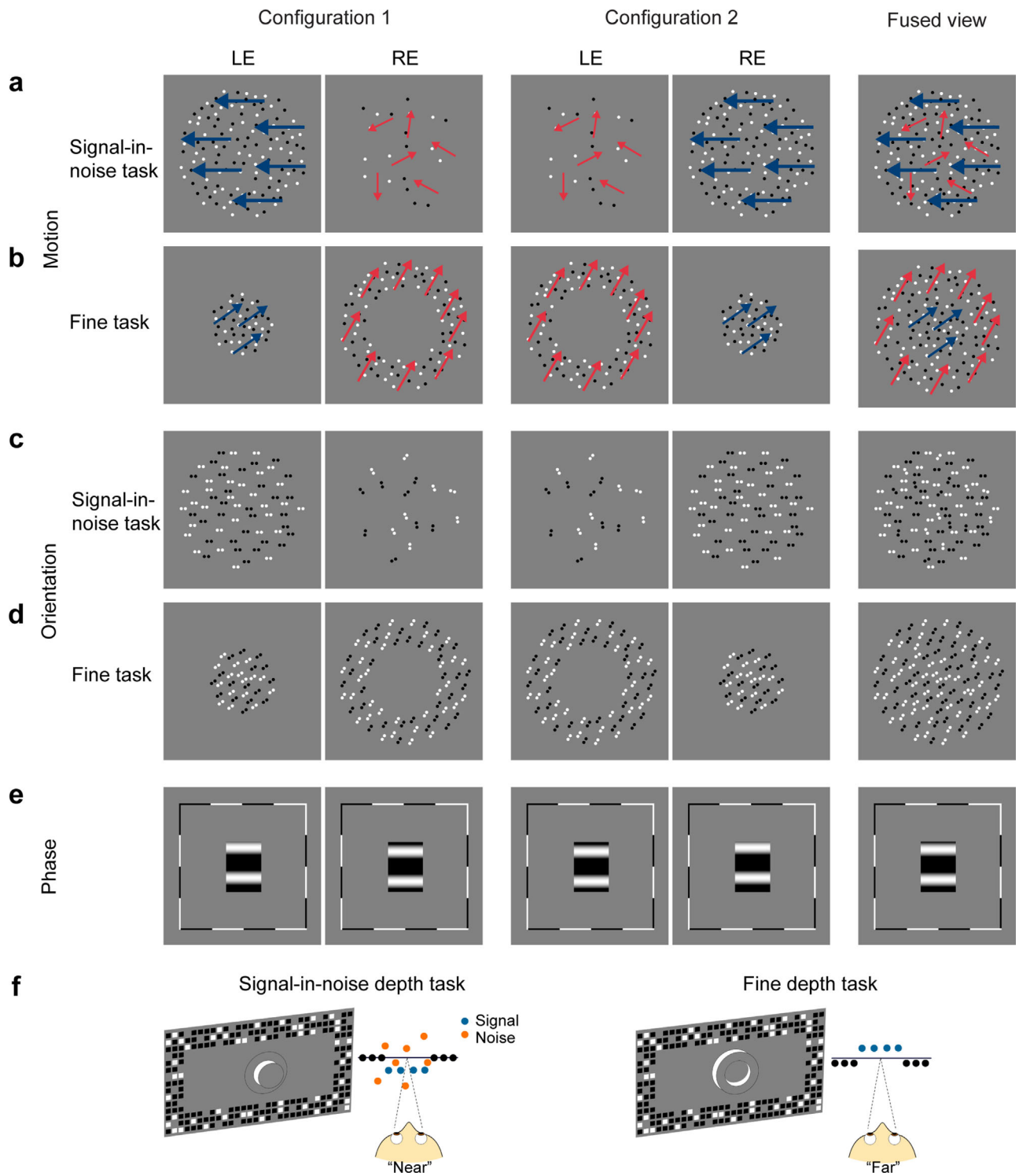
2). Observers had to judge the net orientation of the dipoles (either horizontal or vertical) by pressing arrow keys on the keyboard. The *fine orientation* stimulus adopted a center (4.5 degrees diameter) and surround (9 degrees diameter) configuration but maintained an identical overall size as the signal-in-noise stimulus. The dipoles in the center and the surround were coherently oriented. On each trial, the orientation carried by the surrounding dipoles (i.e., reference orientation) was on average 30 degrees clockwise or counterclockwise from vertical with an additional random offset of  $-3$  to  $3$  degrees. Task difficulty was manipulated by varying the orientation difference between the central target and the reference surround. The dipoles in the surrounding annulus and the center were presented dichoptically on each trial such that one eye viewed the central target while the alternate eye viewed the reference surround (Fig. 1d, configurations 1 and 2). For this task, observers were asked to indicate whether the orientation carried by the dipoles in the center was offset clockwise or counterclockwise with respect to the reference orientation in the surround by pressing arrow keys on a keyboard. All other task parameters were identical to those described above for the dichoptic motion tasks.

**Binocular Phase Combination Task.** Two horizontal sine-wave gratings ( $3.6 \times 5.3$  degrees) with a spatial frequency of 0.3 cycles per degree were generated at 100% contrast. The two sine-wave gratings were created with opposite vertical phase shifts of  $-22.5^\circ$  and  $22.5^\circ$ , selected based on previous work,<sup>9,10,21</sup> and, when presented dichoptically, are easily fused to form a cyclopean percept.

Each trial began with a fixation cross surrounded by a binocularly presented frame to aid fusion. Each eye was presented with a white fixation cross and two diagonally positioned dots, and observers were asked to perform a calibration with arrow keys that allowed the shifting of the images until a single fixation cross and four symmetrically placed dots were perceived. Once calibration was complete, observers were instructed to press a key to bring up the main stimulus. The two sine-wave gratings with opposite phase shift were then delivered to the two eyes dichoptically, along with a horizontal reference line 0.04 degrees in thickness presented to both eyes. The observers' task was to indicate their perceived phase of the grating by adjusting the position of the reference line in a fixed step size of 0.04 degrees (equivalent to a change of  $4^\circ$  in grating phase angle) to their perceived center of the fused grating. The initial position of the reference line was randomly selected within a vertical range of  $-2$  and  $2$  degrees from the center on each trial. The observers were given a maximum of 120 seconds to finalize their adjustment.

The perceived phase of the grating after binocular combination is determined by the internal weighting of the two monocular inputs; therefore, sensory eye dominance can be reflected by how much the perceived phase deviates from zero.<sup>21</sup> To avoid positional bias, two configurations were used such that the  $-22.5^\circ$  phase shift grating was randomly presented to either the left (Fig. 1e, configuration 1) or the right (Fig. 1e, configuration 2) eye on each trial. Each configuration was measured 40 times, yielding a total of 80 trials that were randomly interleaved in one block. Participants completed one block in both the pre- and posttests.

**Depth Stimuli and Tasks.** Stimuli were random-dot stereograms (RDSs) that depicted a central circular target plane 4.5 degrees in diameter and a surround 9 degrees in diameter. Dots of the RDS were randomly black or white



**FIGURE 1.** Schematics of the dichoptic signal-in-noise (a) and fine (b) motion tasks and the dichoptic signal-noise (c) and fine (d) orientation tasks. For all four dichoptic tasks, signal dots/dipoles (signal-in-noise task) or the central target (fine task) were randomly presented to either the left (configuration 1) or the right eye (configuration 2) on each trial. (e) Binocular phase combination task. Two horizontal sine-wave gratings with an opposite phase shift of  $-22.5^\circ$  and  $22.5^\circ$  were dichoptically presented to the two eyes. (f) Signal-in-noise and fine depth tasks. For the signal-in-noise task, the signal dots in the central plane were either near or far relative to the surrounding plane that was fixed at zero disparity; for the fine task, the disparity of the surrounding plane was fixed at  $\pm 12$  arcmin while the disparity of the central plane varied finely relative to it.

and positioned with a density of 12 dots/deg<sup>2</sup>, with each dot subtending 0.2 degrees. For the signal-in-noise depth stimulus, the surrounding plane was kept at zero disparity,

and we assigned a disparity of 6 arcmin (either crossed or uncrossed) to the central target plane. We varied the percentage of signal dots defining the target plane relative to noise

dots on each trial. At 100% signal, the dots that defined the target plane all fell on  $-6$  or  $6$  arcmin. At 0% signal, the target plane consisted purely of noise, with dots randomly positioned within  $\pm 12$  arcmin. Task difficulty (% signal) was adjusted according to the QUEST staircase procedure, measuring the percentage of signal required to achieve 82% correct level.<sup>24</sup> For the fine depth stimulus, the disparity of the surround was fixed at  $\pm 12$  arcmin while the disparity of the target plane was varied finely from 1 to 240 arcsec relative to the surround. Task difficulty was manipulated by adjusting the disparity difference between the target plane and the surround using the QUEST staircase procedure. For both tasks, observers were asked to indicate whether the central target plane was in front (“near”) or behind (“far”) of the surround (Fig. 1f). Each block comprised two stair-

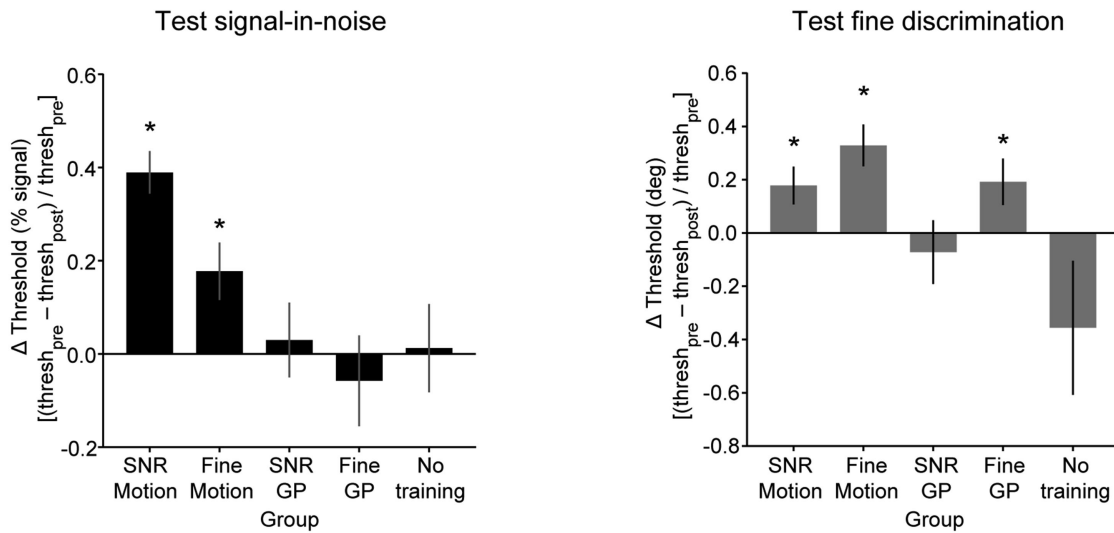
cases of 52 trials. Participants completed one practice block and one test block in the pretest and two test blocks in the posttest. Stimulus duration was fixed at 500 ms, and trials were separated by an interval of 500 ms.

**RESULTS**

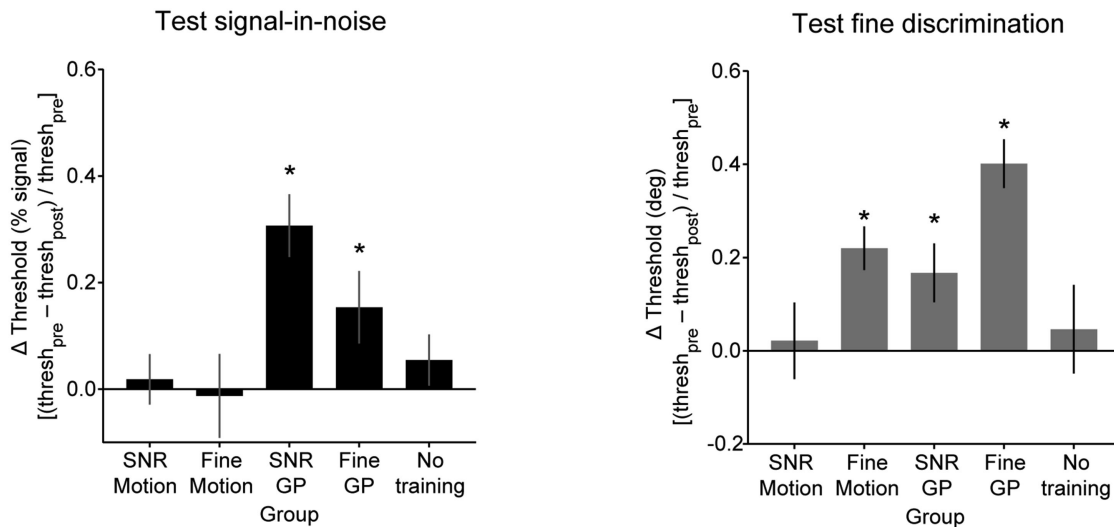
**Transfer of Learning With Dichoptic Visual Training**

We first examined the degree and specificity of improvements attained across the various training tasks. Thresholds for each *test task* were analyzed with independent 5 (group—including the control group)  $\times$  2 (time—before and after training) repeated-measures ANOVAs that were subsequently Bonferroni corrected for multiple comparisons.

**Motion**

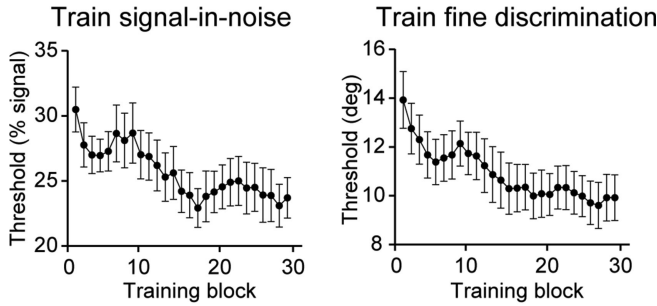


**Orientation**



**FIGURE 2.** Normalized differences in pretest versus posttest thresholds for groups trained on the signal-in-noise (SNR) motion task ( $n = 24$ ), fine motion task ( $n = 24$ ), signal-in-noise (SNR) orientation (glass pattern [GP]) task ( $n = 24$ ), and fine orientation (GP) task ( $n = 24$ ) and for the group that received no training ( $n = 20$ ), presented independently for each dichoptic task. Error bars represent  $\pm 1$  SEM. \* $P < 0.01$ .

Motion



Orientation

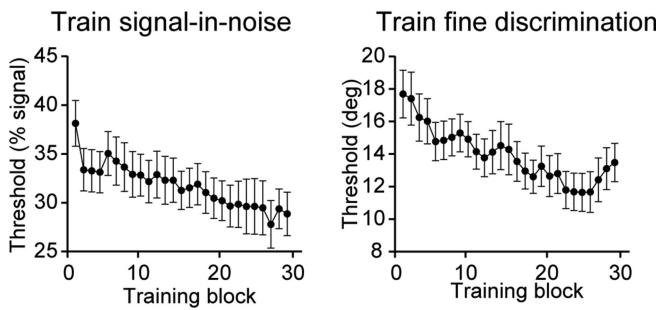
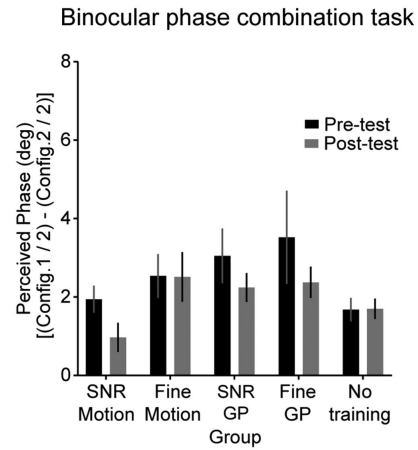


FIGURE 3. Group-averaged training data presented independently for each training group. Each point represents a three-block moving average. Error bars represent  $\pm 1$  SEM.  $*P < 0.01$ .

First, we examined learning improvements for the signal-in-noise tests. Considering first the signal-noise *motion* task (Fig. 2, top left, visualized in terms of threshold changes, computed as  $[(\text{thresh}_{\text{pre}} - \text{thresh}_{\text{post}})/\text{thresh}_{\text{pre}}]$ ), the ANOVA indicated a significant group  $\times$  time interaction ( $F_{(4, 111)} = 6.40, P < 0.001, \eta^2_p = 0.19$ ). In particular, we observed that signal-noise thresholds improved not only for the group who received dedicated training on the same signal-in-noise motion task ( $t_{(23)} = 7.48, P < 0.001$ ) but also for those who received fine motion training ( $t_{(23)} = 3.41, P = 0.002$ ). Thresholds for this task did not improve for those trained on the orientation cue (signal-in-noise orientation training,  $t_{(23)} = 0.87, P = 0.40$ ; fine orientation training,  $t_{(23)} = 0.40, P = 0.69$ ) or for the control group ( $t_{(19)} = 1.55, P = 0.14$ ). The ANOVA for the signal-noise *orientation* test (Fig. 2, bottom left) indicated a comparable group  $\times$  time interaction ( $F_{(4, 111)} = 3.65, P = 0.008, \eta^2_p = 0.12$ ). Improvements were limited to participants trained on the two tasks involving the orientation cue (signal-in-noise orientation training,  $t_{(23)} = 5.33, P < 0.001$ ; fine orientation training,  $t_{(23)} = 2.87, P = 0.009$ ). Thresholds for those trained on the motion cue (signal-in-noise motion training,  $t_{(23)} = .57, P = 0.58$ ; fine motion training,  $t_{(23)} = 1.62, P = 0.12$ ) and for the control group ( $t_{(19)} = 1.87, P = 0.08$ ) did not improve.

Subsequently, we considered the degree of learning on the fine discrimination tests. The ANOVA for both the fine motion and fine orientation discrimination tests similarly indicated a significant group  $\times$  time interaction (fine motion test,  $F_{(4, 111)} = 3.74, P = 0.007, \eta^2_p = 0.12$ ; fine orientation test,  $F_{(4, 111)} = 4.55, P = 0.002, \eta^2_p = 0.14$ ; Fig. 2a, right panel). Thresholds for the fine *motion* test improved for those who received dedicated training on the fine motion

a



b

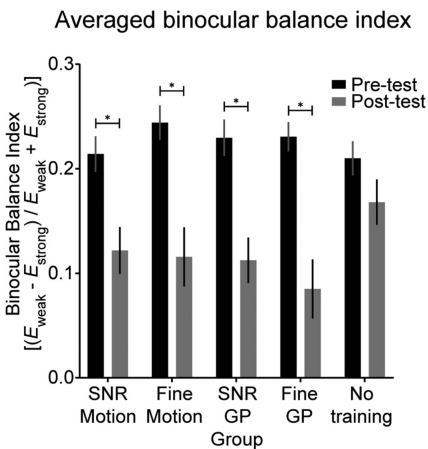


FIGURE 4. Sensory eye dominance in the pre- and posttest for all the groups as indexed by the (a) perceived phase captured from the binocular phase combination task and (b) the averaged binocular balance index derived from the four dichoptic tasks. For both indices, an index of zero represents no dominance. Error bars represent  $\pm 1$  SEM.  $*P < 0.01$ .

task ( $t_{(23)} = 4.44, P < 0.001$ ) but also for those who received signal-in-noise motion training ( $t_{(23)} = 3.01, P = 0.006$ ) and fine orientation training ( $t_{(23)} = 3.41, P = 0.002$ ). The same pattern of improvements was observed for the fine *orientation* test. Thresholds for this test improved not only for the group who received dedicated training on the fine orientation task ( $t_{(23)} = 6.79, P < 0.001$ ) but also for those who trained on the signal-in-noise orientation task ( $t_{(23)} = 2.81, P = 0.01$ ) and the fine motion task ( $t_{(23)} = 4.95, P < 0.001$ ). Thresholds for the control group did not improve on either of the fine test tasks (motion test,  $t_{(19)} = -.25, P = 0.81$ ; orientation test,  $t_{(19)} = .96, P = 0.35$ ).

It is important to note that the pretest thresholds for all four dichoptic tasks were not significantly different among groups (signal-in-noise motion test,  $F_{(4, 111)} = .57, P = 0.69$ ; fine motion test,  $F_{(4, 111)} = 1.09, P = 0.37$ ; signal-in-noise orientation test,  $F_{(4, 111)} = .40, P = 0.81$ ; fine orientation test,  $F_{(4, 111)} = .44, P = 0.78$ ; Supplementary Fig. S1). Therefore, learning effects observed here cannot be due to mere differences in pretest performances. Moreover, all groups attained asymptotic performance well before the end of the training protocol ( $\sim$ block 20, Fig. 3); thus, the differences observed

here cannot be attributed to insufficient training in one task versus another.

In sum, learning transfer between signal-in-noise and fine discrimination training for the *same* visual feature was symmetrical—training on either task enhanced performance on both test tasks. However, between-cue facilitation was only observed for fine discrimination training. Learning under signal-noise conditions did not transfer to improvements in tasks involving other cues.

### Changes in Sensory Eye Dominance

Next, we examined if dichoptic visual training led to alterations in sensory eye dominance by computing two indices: one derived from the binocular phase combination task and a second derived from the dichoptic signal-noise and fine tests. Indexing sensory eye dominance first using the binocular phase combination task, eye dominance was represented by the perceived phase, defined as the perceived phase difference between configuration 1 and configuration 2 [(config. 1 – config. 2) / 2].<sup>9,10</sup> Having a binocularly perceived phase of zero, then, represented no dominance. To index sensory eye dominance using the four dichoptic tasks, we quantified a binocular balance index, computed as  $(E_{\text{weak}} - E_{\text{strong}}) / (E_{\text{weak}} + E_{\text{strong}})$ , where  $E_{\text{strong}}$  represents the configuration that had a lower threshold (threshold obtained when the signal or the target was presented to the dominant eye), and  $E_{\text{weak}}$  represented the configuration that had a higher threshold (threshold obtained when the signal or the target was presented to the nondominant eye). Thus, an index of zero represented perfect balance, and the more the index deviated from zero, the stronger the dominance. For each subject, we averaged the binocular balance index acquired from the four dichoptic tasks to generate a second index of sensory eye dominance. The dominant eye was defined for each task in the pretest. Based on the above formula, this therefore yields a positive binocular balance index in the pretest. A decrease in the index after visual training would indicate a reduction in dominance, with a negative value (if any) representing a change of the dominant eye.

Each set of sensory eye dominance indices was entered into separate, Bonferroni-corrected ANOVAs comparing the pre- and posttest index across the five groups. The ANOVA for the perceived phase measurement (Fig. 4a) indicated no significant main effects or interaction. By contrast, the ANOVA for the binocular balance index derived from the four dichoptic tasks (Fig. 4b) indicated a significant group  $\times$  time interaction ( $F_{(4, 111)} = 3.47$ ,  $P = 0.01$ ,  $\eta^2_p = 0.11$ ). Notably, all groups who received dichoptic visual training demonstrated a shift in sensory eye dominance (i.e., binocular balance index was closer to zero after training) (signal-in-noise motion training,  $t_{(23)} = 5.50$ ,  $P < 0.001$ ; fine motion training,  $t_{(23)} = 5.26$ ,  $P < 0.001$ ; signal-in-noise orientation training,  $t_{(23)} = 6.34$ ,  $P < 0.001$ ; fine orientation training,  $t_{(23)} = 5.76$ ,  $P < 0.001$ ). No change in the binocular balance index was observed for the control group ( $t_{(19)} = 2.71$ ,  $P = 0.014$ ). We additionally verified that the binocular balance index obtained in the pretest was not significantly different among groups ( $F_{(4, 115)} = .70$ ,  $P = 0.59$ ).

As the previous analysis was computed using an averaged binocular balance index derived from all four tasks, we further examined the task and training specificity of eye balance changes by analyzing indices for each of the four tasks independently (Supplementary Fig. S2). We excluded

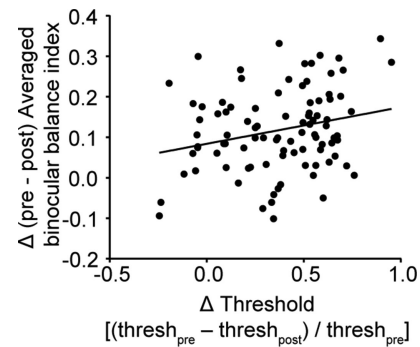


FIGURE 5. Relationship between the change in averaged binocular balance index (pre – post) and threshold improvements in the trained task. Individuals with larger training-related improvements (i.e., threshold changes) tended to have larger improvements in binocular balance.

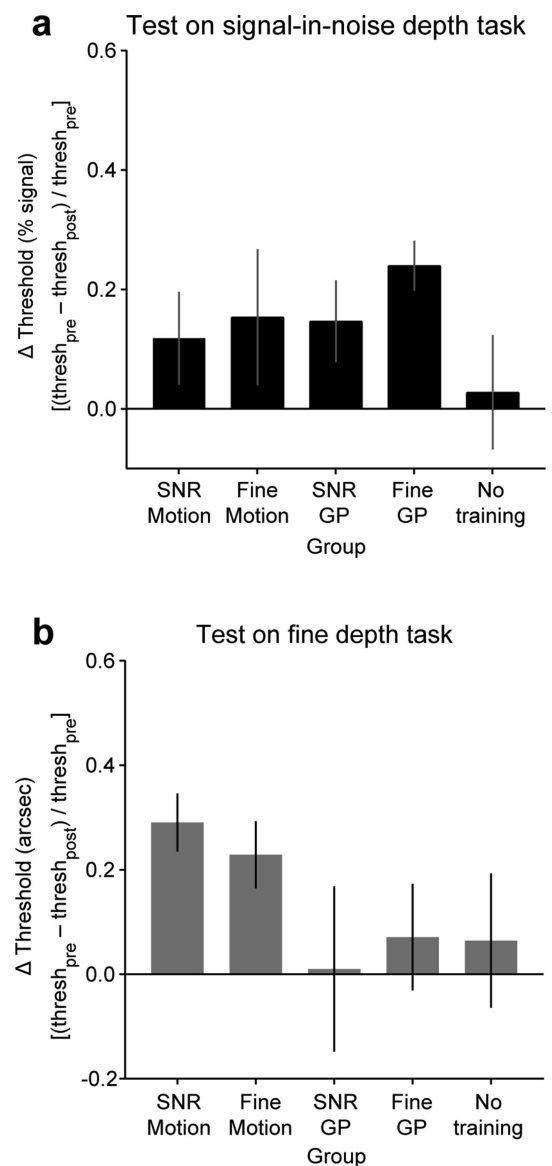


FIGURE 6. Normalized differences in pretest versus posttest thresholds for all the groups on the (a) signal-in-noise depth task and the (b) fine depth task. Error bars represent  $\pm 1$  SEM.

the control group at this stage of analysis based on the fact that they did not show threshold improvements on all the tasks and demonstrated no significant changes with the averaged binocular balance index. We found that for each of the four tasks, only the main effect of time was significant (signal-in-noise motion task,  $F_{(1, 92)} = 35.46, P < 0.001, \eta^2_p = 0.28$ ; fine motion task,  $F_{(1, 92)} = 73.28, P < 0.001, \eta^2_p = 0.44$ ; signal-in-noise orientation task,  $F_{(1, 92)} = 7.17, P = 0.009, \eta^2_p = 0.07$ ; fine orientation task,  $F_{(1, 92)} = 34.20, P < 0.001, \eta^2_p = 0.27$ ), indicating that changes in balance as indexed by each test task were not significantly different among training groups.

In order to better understand the functional relationship between changes in sensory eye dominance (as indexed by the group-averaged dichoptic tasks) and training, we then correlated changes in sensory eye dominance (pretest averaged binocular balance index – posttest averaged binocular balance index) and threshold improvements in the trained task  $[(\text{thresh}_{\text{pre}} - \text{thresh}_{\text{post}})/\text{thresh}_{\text{pre}}]$  using Pearson correlation. The analysis indicated a significant positive correlation between the two measures ( $r(92) = 0.24, P = 0.02$ ; Fig. 5).

### Learning Effects on Stereoscopic Depth Perception

Last, we tested whether dichoptic visual training led to any changes in stereoscopic depth perception. Thresholds for each of the depth tasks were analyzed using a repeated-measures ANOVA. For both tasks, the analysis indicated an overall main effect of time only (signal-in-noise task,  $F_{(1, 111)} = 28.61, P < 0.001, \eta^2_p = 0.21$ ; fine task,  $F_{(1, 111)} = 17.90, P < 0.001, \eta^2_p = 0.14$ ). While the control group's thresholds showed little change from pre- to posttraining, the interaction was not significant (for both test tasks) (signal-in-noise task,  $F_{(4, 111)} = 0.41, P = 0.80$ ; fine task,  $F_{(4, 111)} = .63, P = 0.64$ ; Fig. 6).

## DISCUSSION

We compared the breadth of perceptual learning obtained under dichoptic signal-noise training and dichoptic fine training paradigms involving different visual cues and examined their effects on sensory eye dominance and binocular function (depth perception). Using dichoptic presentation protocols, we found a different pattern of learning transfer as compared to those attained previously using binocular presentation.<sup>16,18,19</sup> Notably, dichoptic training on the signal-in-noise task only boosted performance on the fine task for the same visual feature, while dichoptic training on the fine task benefited the signal-in-noise task for the same visual property but also supported generalization of learning to the fine task involving an untrained feature. Moreover, dichoptic visual training promoted eye rebalancing regardless of the task type (extracting signal in noise or discriminating fine feature) and stimulus feature (motion or orientation) but did not drive changes on stereoscopic depth perception.

### Learning Within and Across Visual Features

First, we consider the symmetric transfer of learning observed within a given visual cue. Previous work on perceptual learning using binocularly presented stimuli has consistently demonstrated that training on a low-noise task (i.e., here, our fine task) transferred to improvements

on a high-noise task, but the transfer for the converse was limited.<sup>16,18,19</sup> Here, under dichoptic presentation, we observed a more robust within-cue transfer such that there was a significant improvement on the fine task after training on the signal-in-noise task. According to the augmented Hebbian reweighting model,<sup>19</sup> training in clear displays optimizes weights for the relevant features, which, in turn, supports target detection in noise. By contrast, training in noisy displays trims the weight given to irrelevant features (noise exclusion) but cannot optimize weights for relevant features. Therefore, learning transfer to a low-noise task is usually minimal. This model appears sufficient to explain away results obtained previously under binocular presentation. However, it is, at first glance, unclear as to how it might explain the data observed here.

Cai et al.<sup>25</sup> compared performance on a signal-noise motion task under dichoptic (signal and noise dots presented to different eyes), binocular (signal and noise dots presented to both eyes), and monocular (signal and noise dots presented to just one eye) conditions. They found that segregating signal and noise dots into different eyes led to better performance than that attained under the binocular and monocular conditions when the stimuli had high contrast and speed. It thus appears that more efficient signal-noise segregation mechanisms may be at work when the signal and noise are presented to different eyes than when they are presented binocularly. It is well established that processing motion in noise involves visual area V5/human middle temporal complex (hMT<sup>+</sup>),<sup>26</sup> where neurons are binocular in nature. However, neurophysiologic studies have indicated that while around 45% to 60% of neurons in middle temporal area (MT) are binocularly unbiased or balanced, the remaining neurons show clear ocular preference.<sup>27–29</sup> We conjecture that ocular preference of hMT<sup>+</sup> neurons may enable better motion signal extraction under dichoptic viewing conditions. For example, if the signal is shown to the left eye, left eye–preferring hMT<sup>+</sup> neurons may be able to read out signal with little interference from the noise presented to the right eye. In this way, signal-noise training under the dichoptic presentation mode may be better suited for promoting signal extraction and noise filtering simultaneously as compared to training under binocular presentation in which both signal and noise must be segregated by both eyes. While motion signal integration is associated with hMT<sup>+</sup>, the signal-noise orientation task is believed to involve V2 and V4,<sup>30–33</sup> both of which also contain neurons with ocular preference.<sup>33–36</sup> Regardless, orientation signals may be better extracted and optimized via the same signal/noise reweighting mechanisms, as described above for motion signal extraction.

An alternative manner in which dichoptic training of a signal-noise stimulus may better promote improvements in a feature discrimination task is via binocular input modulation through cortical feedback to the lateral geniculate nucleus (LGN). V2,<sup>37</sup> V4,<sup>38</sup> and MT<sup>39</sup> have been shown to provide strong feedback to V1, which drives a cascaded feedback influence on the LGN.<sup>40</sup> This cortical projection to the LGN influences the gain and responsiveness of LGN neurons to incoming visual stimuli.<sup>41</sup> In the case of a dichoptic signal-in-noise task, the cortico-geniculate feedback projection may allow adjustments of the gain between signal and noise before binocular combination. In this manner, training on the dichoptic signal-in-noise task may permit both a downweighing of irrelevant features and an optimization of weights for the relevant features. This, together with the



ocular preference properties of the extrastriate neurons, may be reasonable conduits for the apparently increased effectiveness of signal-noise training to fine task performance under dichoptic viewing observed here.

Whereas we found that within a given visual cue, training on either the signal-noise or fine tasks improved performance on both tasks, the two tasks differed in the degree of learning transfer between cues. Training on the fine task supported learning that generalized to fine task performance for a different cue, but training on a signal-noise task resulted in improvements within cue only. Learning on a fine task has been thought to be specific to the stimulus feature—reflecting the strengthening of feature representations at higher levels of the visual system—and therefore does not support transfer of learning across features.<sup>16,19</sup> However, our data suggest that something beyond feature read-out strengthening needs to be considered in order to account for improvements observed under dichoptic training. When the two closely positioned features that have to be discriminated are presented to different eyes, binocular combination is a crucial first step that must occur for feature comparison to happen. We speculate that although the two fine tasks involve different visual properties, training may strengthen cue-generic interocular combination mechanisms, resulting in learning transfer between visual cues. At the very least, our data imply that extracting signal from noise under dichoptic presentation may not simply implicate a generalized segmentation process that is believed to play a key role in the binocularly presented signal-in-noise tasks.<sup>16</sup>

### Learning-Driven Changes in Sensory Eye Dominance

A key interest of the present work was to understand whether dichoptic visual training may lead to changes in sensory eye dominance. Critically, we found strong shifts in sensory eye dominance following dichoptic visual training, with the degree of shift correlating with the degree of learning. Notably, sensory eye dominance shifts were only evident when eye dominance was quantified with one of our two metrics (i.e., the dichoptic task-derived index). The alternative index was derived from the binocular phase combination task, which is widely used in both the clinical and normal populations for quantifying sensory eye dominance<sup>1,9,10,42</sup> but did not change with training. It is possible that this (binocular phase combination) task may not be sensitive to measuring changes in sensory eye dominance in normal-sighted observers. Indeed, we reported a mean (pretraining) perceived phase of just 2.5 degrees, in line with small deviations reported in previous studies testing normal observers.<sup>43–45</sup> Therefore, changes in sensory eye dominance may not be easily detected by this task due to the relatively balanced baseline performance. Unfortunately, previous studies that treated amblyopes with dichoptic training paradigms did not employ the binocular phase combination task to quantify changes in sensory eye dominance.<sup>12,13,46</sup> Thus, whether dichoptic training paradigms might be able to drive changes in the performance of the binocular phase combination task, both in visually normal individuals and in the clinical populations, still requires further investigation.

Importantly, when indexing sensory eye dominance using performance on the dichoptic presentation tasks, we found that all four training groups (but not the control group) demonstrated an improved binocular balance index

after training. Furthermore, the degree of shift in sensory eye dominance was positively correlated with the strength of improvements on the trained task. As our data indicate that training-induced changes in sensory eye dominance do not depend on the visual feature or task (external noise present or absent) trained, we therefore conjecture that the dichoptic training paradigm may at least partially act to balance interocular suppression at or before the site of binocular combination, perhaps in V1<sup>47</sup> or the LGN.<sup>48,49</sup>

### No Learning Effects on Stereoscopic Depth Perception

Next, we were also interested in probing whether dichoptic training drives broader functional changes in binocular function—in particular, in stereoscopic depth perception. Notably, dichoptic motion-in-noise training has shown hints at being effective for recovering stereo vision in amblyopes.<sup>13,46,50</sup> For instance, Hess et al.<sup>13</sup> trained amblyopic adults on a dichoptic motion-in-noise paradigm and reported improved stereosensitivity in addition to suppression reduction and binocular combination restoration; however, we did not find evidence for learning-driven changes in stereoscopic function here. It is important to remember that performance on the depth tasks requires at least two elements: (1) binocular integration and (2) readout by disparity-tuned neurons present widely in cortex. Visually normal adults and amblyopes differ in terms of their performance-limiting mechanisms. In amblyopes, suppression is assumed to be the primary factor that limits stereopsis,<sup>51</sup> resulting in disrupted binocular combination under ordinary viewing conditions.<sup>52,53</sup> Therefore, reducing suppression and promoting binocular combination may provide meaningful gains in (likely coarse) stereoscopic function. However, in normal adults with relatively balanced interocular suppression, further refining of stereoscopic function is likely limited by mechanisms further up the binocular cascade, by disparity-tuned neurons in cortex. Consequently, any training-related improvements in sensory eye dominance in normal vision may not translate to clear improvements in stereoscopic depth perception. Indeed, even for amblyopic improvements in stereoacuity that have been reported previously by Hess et al.,<sup>13</sup> it is important to note that there was no apparent relationship to reductions in suppression. Thus, stereoscopic improvements observed previously in clinical populations may still be attributed to entirely different factors, including improved visual acuity of the amblyopic eye.

### Outstanding Issues

We close with two outstanding issues that may be worth empirical attention moving forward. The first relates to the fact that the five tests employed here for indexing sensory eye dominance did not produce eye dominance classifications with a high degree of consistency. In fact, of our full pool of subjects, only 9% had the same dominant eye as indicated across all five tests. The majority of the observers (63%) showed eye dominance agreement across only three of the tests. These observations are perhaps not surprising in light of previous work that has demonstrated weak consistency when using standard sensory eye dominance

tests in determining the dominant eye in normal vision.<sup>54</sup> We suspect this may relate to the strength of dominance present in the normal population. Indeed, if we loosely classified our subjects into three groups based on their eye dominance agreement across tests (in the pretest) and compared their degree of eye dominance, we find that those who had the highest consistency across all five tests, on average, show stronger sensory eye dominance (as indexed by both the perceived phase measurement and the binocular balance index) than those who only show eye dominance agreement on four or three of the tests (Supplementary Fig. S4). Thus, we speculate that inconsistent classifications yielded by the different test indices may be due to the relatively balanced eyes in normal-sighted individuals (i.e., classifications for weakly dominant eyes come down to variance). In amblyopes or individuals with strong dominance, eye dominance may be the primary determinant of task performance. However, in individuals with relatively balanced eyes, task performance is likely influenced by other factors, yielding conflicting results across different tests. Nonetheless, it may be worth querying for a more sensitive metric for eye dominance in normal vision moving forward.

The second issue relates to the relatively short period of perceptual training employed here. Might we have observed different/amplified effects with further training? Further, can training effects be retained beyond our original test period?

To probe this, we recalled three of the original observers for further testing and training: at 22 weeks (observer 1; fine orientation training), 31 weeks (observer 2; signal-in-noise motion training), and 20 weeks (observer 3; signal-in-noise orientation training) after their original posttest. These subjects were retested on the four dichoptic tasks (posttest 2) upon recall to the laboratory and received additional training (on their original trained task) for 3 consecutive days (1 hour per day, 3600 trials in total), followed by a final posttest (posttest 3) (Supplementary Fig. S3). Inspection of these data revealed that only one subject (observer 2) benefited from additional training, with performance on the trained task (signal-in-noise motion) improving between posttest 2 and posttest 3. Critically, for all subjects, additional training did not lead to further changes in sensory eye dominance (right-most panel). Given these data, we speculate that the 3-day training protocol used here is likely to be adequate for driving stable and long-lasting changes in eye dominance in normal vision.

## CONCLUSION

We show that training protocols involving dichoptic signal-in-noise and no-noise stimuli can promote broad perceptual improvements across cues and tasks. Intriguingly, dichoptic visual training leads to robust changes in sensory eye dominance that are correlated with the strength of training task-related improvements. The task and stimulus unspecificity of eye balance improvements suggests that dichoptic visual training may potentially work to balance interocular suppression before or at the site of binocular combination. Better understanding of the mechanisms underlying learning-dependent plasticity in binocular vision and plasticity will be key for the development of optimal training-based protocols for people with visual impairments.

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