MONOCULAR DEPRIVATION OF FOURIER PHASE INFORMATION BOOSTS THE DEPRIVED EYE'S DOMINANCE DURING INTEROCULAR COMPETITION BUT NOT INTEROCULAR PHASE COMBINATION

JIANYING BAI, [a] XUE DONG, [a,c] SHENG HE [b,d] AND MIN BAO [a,b]*

[a] *CAS Key Laboratory of Behavioral Science, Institute of Psychology, Beijing 100101, China*

[b] *State Key Laboratory of Brain and Cognitive Sciences, Beijing 100101, China*

[c] *University of Chinese Academy of Sciences, China*

[d] *Department of Psychology, University of Minnesota, United States*

Abstract—Ocular dominance has been extensively studied, often with the goal to understand neuroplasticity, which is a key characteristic within the critical period. Recent work on monocular deprivation, however, demonstrates residual neuroplasticity in the adult visual cortex. After deprivation of patterned inputs by monocular patching, the patched eye becomes more dominant. Since patching blocks both the Fourier amplitude and phase information of the input image, it remains unclear whether deprivation of the Fourier phase information alone is able to reshape eye dominance. Here, for the first time, we show that removing of the phase regularity without changing the amplitude spectra of the input image induced a shift of eye dominance toward the deprived eye, but only if the eye dominance was measured with a binocular rivalry task rather than an interocular phase combination task. These different results indicate that the two measurements are supported by different mechanisms. Phase integration requires the fusion of monocular images. The fused percept highly relies on the weights of the phase-sensitive monocular neurons that respond to the two monocular images. However, binocular rivalry reflects the result of direct interocular competition that strongly weights the contour information transmitted along each monocular pathway. Monocular phase deprivation may not change the weights in the integration (fusion) mechanism much, but alters the balance in the rivalry (competition) mechanism. Our work suggests that ocular dominance plasticity may occur at different stages of visual processing, and that homeostatic compensation also occurs for the lack of phase regularity in natural scenes. © 2017 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: ocular dominance, monocular deprivation, fourier phase, binocular rivalry, interocular phase combination.

INTRODUCTION

A classical model for neuroplasticity is ocular dominance plasticity. To date, mounting evidence has demonstrated residual ocular dominance plasticity in the adult visual system (Xu et al., 2010a; Lunghi et al., 2011, 2013; Ooi et al., 2013; Zhou et al., 2013, 2015; Lo Verde et al., 2017), which is conventionally thought to be hard-wired (Wiesel and Hubel, 1963; Hubel and Wiesel, 1970).

There is a long history of using monocular deprivation to study ocular dominance plasticity. During deprivation, no pattern information is transmitted through the eye patch. In vision research, it is widely accepted that the early visual neurons could be considered as "Fourier filters", analyzing the amplitude and phase of the input images (Schade, 1956; Campbell and Robson, 1968; Graham and Nachmias, 1971; Westheimer, 2001). In accordance with this notion, monocular deprivation blocks both the Fourier amplitude and phase information from entering the patched eye. In the signal processing literature, phase has long been realized to be more important than amplitude in image reconstruction and scene recognition (Oppenheim and Lim, 1981; Piotrowski and Campbell, 1982; Ni and Huo, 2007). Naturally, a question arises: what is the consequence of depriving the Fourier phase information alone, will the eye dominance be altered?

One way to answer this question is to test whether the eye dominance shifts or not after one eye is deprived of the phase-aligned frequencies describing contours and higher level spatial representations, on the premise that the Fourier amplitude spectra of the visual inputs remain identical across the two eyes. Note that while the global average power of the phase-scrambled stimuli is the same as the original, locally there are important differences, and this defines the features (Morrone and Burr, 1988). Therefore, a decoder could pick the difference easily (Perna et al., 2005, 2008; Castaldi et al., 2013).

Notably, a recent study (Zhou et al., 2014) has attempted to test whether the deprivation of phase regularity may alter the eye dominance. In their work, the

---

*Correspondence to: M. Bao, Rm. 4-814, 16 Lincui Road, Chaoyang District, Beijing 100101, China.

E-mail address: baom@psych.ac.cn (M. Bao).

two eyes see the same movie except that in one eye the Fourier phase spectrum of the input is scrambled. By using an interocular phase combination task (Ding and Sperling, 2006; Huang et al., 2010; Kwon et al., 2014), they found no change of eye dominance after watching the movie for 2.5 h. However, in Lunghi et al.'s (2011) monocular patching study, the eye dominance is measured with binocular rivalry, another method frequently used to evaluate eye dominance (Ooi and He, 2001; Handa et al., 2004, 2005; Lunghi et al., 2011, 2013; Xu et al., 2011; Platonov and Goossens, 2014; Dieter and Blake, 2015). The use of different measurements makes it difficult to compare the two studies directly. Since it is possible that the two measures are supported by different mechanisms, eye dominance measured with phase integration and binocular rivalry (competition) may reach different conclusions. Therefore, without stricter experimental control, one cannot affirmatively conclude whether the monocular deprivation of phase information can reshape the eye dominance like monocular patching. In the present study, we therefore adopted both the binocular rivalry and interocular phase combination tasks to measure the eye dominance prior to and following the simulated monocular patching and monocular deprivation of phase regularity. Such a more complete design allowed us to examine a possibility that the monocular deprivation of phase regularity alone may lead to changes in eye dominance, but only when measured with direct inter-ocular competition rather than inter-ocular phase combination. Besides, Zhou and colleagues' (2014) negative results derive from the observations of only three subjects, it remains appealing to re-examine this question in a larger amount of subjects for stronger statistical power.

To achieve the monocular deprivation of phase regularity, we developed an ''altered reality'' system, with which subjects could interact with the natural world that had been changed through real-time image process. For 3 h, one eye's inputs were replaced with spatially correlated (or ''pink'') noises (see Method). Instead of off-line image processing (Zhou et al., 2014), our method realizes the phase scrambling in real-time, and guarantees identical amplitude spectra in both eyes by strictly preserving the complex conjugations of the Fourier transforms throughout adaptation.

Besides a possible null effect that Zhou et al. have reported (Zhou et al., 2014), two distinct positive results might be observed. First, if monocular deprivation of phase regularity shifts the eye dominance to the deprived eye, sharing mechanisms may underlie the phase deprivation and patching. Instead, if deprivation increases the eye dominance of the non-deprived eye, we would speculate that a later mechanism selectively promotes the signal transmission pathway for the non-deprived eye because of its superior signal-to-noise ratio. Through three experiments, our results showed significant shift in eye dominance to the deprived eye when the eye dominance was measured with a binocular rivalry task. We also replicated Zhou et al.'s (2014) null effect when measuring the eye dominance with an interocular phase combination task.

EXPERIMENTAL PROCEDURES

Experimental procedures for all the experiments of the present study were approved by the Institutional Review Board of the Institute of Psychology, Chinese Academy of Sciences. Informed consents were obtained from all the subjects. All the experiments described have been carried out in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki) for experiments involving humans.

Comparing monocular phase regularity deprivation with patching (Experiment 1)

Participants. Twelve subjects (11 females; age: 19–25 years old) participated in Experiment 1. All were naive to the experimental hypotheses, and had normal or corrected-to-normal vision.

Apparatus. Binocular rivalry measurements were conducted on a Dell OptiPlex 7010 computer using MATLAB (Mathworks Inc., Natick, MA, United States) and Psychtoolbox 3.0.11 Extensions (Brainard, 1997). Stimuli were presented on a 27.2-inch LCD monitor (Asus VG278HE, 1920 × 1080 pixel resolution at the refresh rate of 120 Hz), and viewed through a pair of shutter goggles (NVIDIA 3D Vision2 P1431). The monitor was calibrated with a spectrophotometer (Photo Research, PR-655) with the sensor attached behind the shutter goggles. To calibrate the display, we measured the luminance gamma curves and inverted them with a look-up table. The mean luminance of the monitor was 48.68 cd/m^2, but reduced to 18.76 cd/m^2 when viewed through the shutter goggles. Participants viewed the stimuli through the shutter goggles in a dark and quiet room from a distance of 100 cm. A chin-rest was used to help minimize head movement.
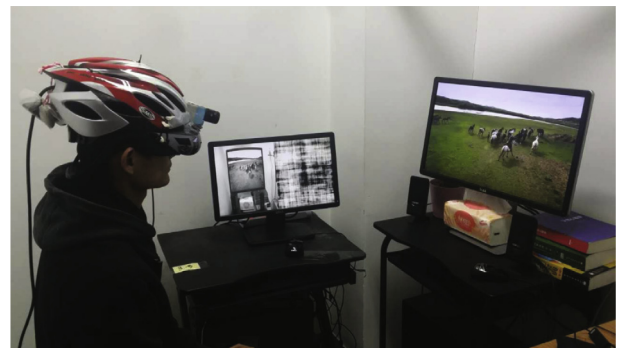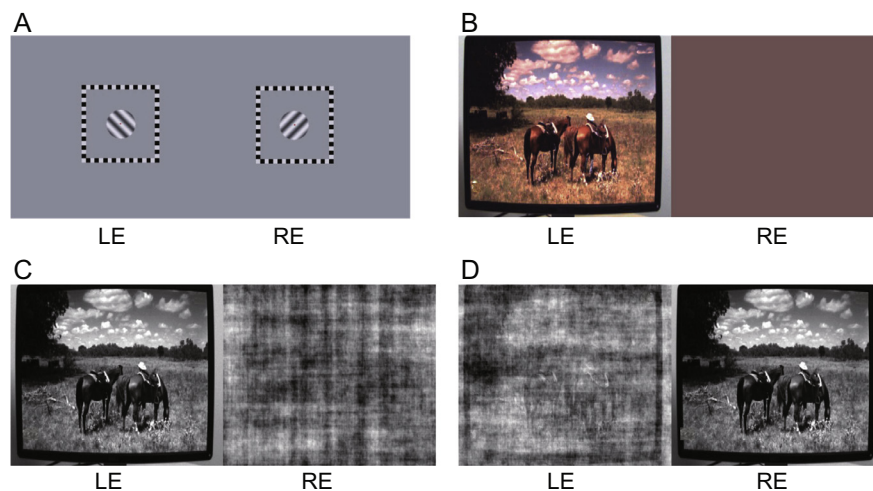

Fig. 1. The alter reality system and an example of the experimental scene. The system comprised of a camera connected to a computer that fed into the HMD. This computer processed the images taken by the camera in real-time, and then presented the images to the HMD. The original image was presented to one eye, while the altered image to the other eye. Participants wore the HMD during adaptation when they could view the world freely or watch movies as shown in the figure. The small LCD monitor was also connected to the computer, which worked in a clone mode with the HMD. This enabled the experimenters to see what the subject viewed. In this example, the subject was watching the original camera video through the left eye, and the pink noise video through the right eye.

We developed two altered reality systems for the present study (see Fig. 1). Each system comprised of a camera (The Imaging Source) connected to a computer that feeds into a head-mounted display (HMD). One system was equipped with a DFK-23UM021 USB3.0 camera (640 × 480 RGB32@60 Hz) connected to a Dell XPS 8700 computer with an NVIDIA Geforce GTX770 graphic processing unit. The other one used a DFx-22AUC03 USB2.0 camera (640 × 480 RGB32@87 Hz) connected to a Dell XPS 8700 computer with an NVIDIA Geforce GTX770 graphic processing unit. The HMDs were Sony HMZ-T2 (OLED display, 49.4° in horizontal, 27.8° in vertical, 1280 by 720 pixels) and Sony HMZ-T3 (OLED display, 49.4° in horizontal, 27.8° in vertical, 1280 by 720 pixels). The HMDs were also calibrated with a Photo Research PR-655 spectrophotometer.

Stimuli. For the binocular rivalry measurements, the rival stimuli were two dichoptically presented orthogonal sine-wave grating disks (±45° from vertical, 80% Michaelson contrast, see Fig. 2A), whose edges had been smoothed with a Gaussian filter. The patches subtended 1°, and were displayed foveally, surrounded by a high contrast checkerboard "frame" (size: 2.5° × 2.5°; 0.15° thick) that promoted stable binocular alignment. The spatial frequency of the gratings was 3 cpd. A red central fixation point (0.04° in diameter) was presented to both eyes.

During the 3 h of adaptation, subjects viewed the world through the HMDs of our altered reality systems. Custom software controlled the image processing.

Acquisition and display were performed in MATLAB using the plugin for MATLAB supported by The Imaging Source and Psychtoolbox. The camera images were clipped to 640 × 360 resolution, and then expanded to 1280 × 720 resolution to fit the screen of goggles.

The original camera video was presented to the left eye, while the camera video to the right eye was processed with two options. One was to replace each image with its mean color. This simulated monocular patching in Lunghi et al.'s studies (Lunghi et al., 2011, 2013). The other option was to replace the camera images with pink noises. The power spectra of the pink noises matched exactly those of the camera images (the difference between them was less than 10^{-5}%). However, the phase spectra of the camera images were replaced by the phase spectrum of a white noise (randomly selected from 30 pre-defined white noises every 2–5 s). To speed up the real-time image processing, camera video was monochrome in the pink noise condition. Fig. 2B, C illustrates these two adaptation conditions.

Procedure. Each session of binocular rivalry measurements consisted of 20 trials. Each trial lasted for 1 min, including a 55-s presentation of the rival gratings and a 5-s blank interval. The orientation of the grating for each eye was kept constant within a trial, but randomly changed across the trials. Participants were required to report whether they perceived one of the two gratings or piecemeal by holding down one of the three keys (Left, Right, or Down arrows) on the keyboard.

Before the formal experiment, participants practiced the binocular rivalry task for 3–4 days to ensure that they were familiar with the task and the estimated eye dominance became relatively stable. They practiced four sessions per day, with 20-min break between the sessions (but only 5-min break between the first two sessions). Literature indicates that perceptual dominance durations widely fluctuated in the first several trials of a day (Suzuki and Grabowecky, 2007). Therefore, the first session included only five warm-up trials, the data of which were not analyzed. The three subsequent sessions each included 20 trials.

The practice sessions were also used to screen the subjects for balanced sensory eye dominance. An eye ratio index for the left vs. right eye (abbrev. as LvsR) was calculated by the formula $(T_L + T_M/2)/(T_R + T_M/2)$. Here, T_L, T_R, and T_M represented the summed phase durations for perceiving the stimulus in the left eye, the stimulus in the right eye, and mixed percepts in a trial, respectively. Subjects were allowed to proceed to the formal

Fig. 2. Stimuli for binocular rivalry test and 3 h of adaptation. (A) Binocular rivalry stimuli. Two orthogonal gratings (±45°) were presented centrally but to different eyes. LE (left eye), RE (right eye). The orientations of the gratings were constant within a trial but alternated across trials. (B) Depiction of the visual inputs for the mean color adaptation condition in Experiment 1. The display in the right eye was uniform in the mean color of the camera image. (C) Depiction of the visual inputs for the pink noise adaptation condition in Experiment 1. The Fourier phase spectrum of the right-eye image was replaced by the phase spectrum of a white noise image. (D) Depiction of the visual inputs for the semi-pink noise adaptation condition in Experiment 2. Here, 50% elements of the phase spectrum matrix were replaced with the corresponding elements from the phase spectrum of a white noise image. Selection of the to-be-replaced elements was random, but with the restriction to ensure the complex conjugation. Visual inputs for the pink noise condition in Experiment 2 were identical to those in Experiment 1 except that the pink noise (and semi-pink noise) video was presented to the left eye.

experiment as long as the average LvsR across the last three practice sessions were between 0.9 and 1.1. In Experiment 1, the dominant eye was the right (deprived) eye in 5 out of the 12 subjects. The grand average LvsR across all subjects was 0.997 ± 0.062.

Before adaptation, subjects completed 20 trials of binocular rivalry test, which served as a baseline measurement ("Pre" test). As in the practice, they also completed a 5-min warm-up test, the data of which were not included for analysis. After the pre-test, subjects adapted to one of the aforementioned altered realities for 3 h. The post-tests were conducted immediately after adaptation ("Post0" test, 20 trials), or 24 h later ("Post24" test). No warm-up trials were completed before the two post-tests. This was reasonable for the "Post0" test, since we were interested in the immediate effects following adaptation. However, it was a small procedural mistake for the "Post24" test. Thus, the data in the first few trials of the "Post24" test could be contaminated (Suzuki and Grabowecky, 2007), which was also mentioned in the Result section.

Each subject finished the above procedures four times on different days. Each adaptation condition was repeated twice, with the sequence counter-balanced.

Monocular deprivation of all or half the phase regularity (Experiment 2)

Participants. Twelve subjects (6 females; age: 20–25 years old) participated in Experiment 2. Three of them also participated in Experiment 1. All subjects except one were naive to the experimental hypotheses, and all had normal or corrected-to-normal vision.

Apparatus. The apparatuses were the same as in Experiment 1 except that we only used the 2nd altered reality system for Experiment 2.

Stimuli. Binocular rivalry stimuli were the same as those in Experiment 1 (see Fig. 2A). During adaptation, participants' left eyes were presented with the pink noise or semi-pink noise video in different days. The pink noise condition resembled that in Experiment 1, while in the semi-pink noise condition, only 50% elements of the phase spectrum matrix were replaced with the corresponding elements from the phase spectrum of a white noise image. Selection of the to-be-replaced elements was random, but with the restriction to ensure the complex conjugation.

Procedure. The task and procedures were the same as those in Experiment 1 except that only an immediate test ("Post0") was performed following each adaptation session since no reliable residual effects were observed after 24 h in Experiment 1. Each adaptation condition was repeated 4 times (with pre- and post-tests) on different days, with the sequence counter-balanced.

As in Experiment 1, participants were also screened for balanced sensory eye dominance during the practice stage. Subjects were allowed to participate in the formal experiment if their average LvsRs in the last three

sessions were between 0.8 and 1.2. In Experiment 2, the dominant eye was the left (deprived) eye in 5 out of 12 subjects. The grand average LvsR across all subjects was 0.977 ± 0.078.

Measuring the eye dominance with the interocular phase combination task (Experiment 3)

Participants. Eight subjects (2 females; age: 19–25 years old) participated in Experiment 3. All were naive to the experimental hypotheses, and had normal or corrected-to-normal vision.

Apparatus. The stimuli for the interocular phase combination task were presented on a 21 in. Sony CRT monitor with a resolution of 1600 × 1200 pixels and a refresh rate of 85 Hz. The mean luminance of the screen was 81.03 cd/m^2. Subjects viewed the monitor through a stereoscope from a distance of 75 cm in a dark room. Other apparatuses were similar to those in Experiment 1.

Stimuli. The stimuli for the interocular phase combination task were sinusoidal gratings (6.67° × 6.67°, 0.3 cpd) whose edges had been smoothed with a Gaussian filter. A square frame (each side subtended 9.3°) was always displayed binocularly to help fusion.

Procedure. A modified interocular phase combination task was adopted to measure the eye dominance (see Fig. 4). Two horizontal sine-wave gratings were presented dichoptically on the center of the mid-gray background. The phase of the two gratings shifted in the opposite direction by 22.5° each, yielding two different configurations C1 and C2. Specifically, in the configuration C1, the phase of the grating in the left eye was 22.5° and that in the right eye was -22.5°. While in C2, the phase of grating in the left eye was −22.5° and that in the right eye was 22.5°. In binocular combination, when different images are displayed on the two retinae, only a single combined "cyclopean" image is perceived (Ding and Sperling, 2006). Participants were asked to adjust the vertical position of a one-pixel reference line to indicate the center of such a "cyclopean" perceptual grating using the Up Arrow and Down Arrow keys. The initial position of the reference line was randomly assigned within a range of −20 to 22 pixels from the center of screen. The step size of the adjustment was 1 pixel, corresponding to 1.85° phase angle of the grating. Before starting each trial, participants had to ensure that they could see an intact nonius cue used to verify binocular fusion. The nonius cue was composed of eight dichoptically presented white rectangles. The test started 500 ms after the fusion was confirmed. To avoid binocular rivalry, in each trial, the gratings (displayed for 100 ms) and a 400-ms blank interval were presented alternatively until the participants finished the adjustment by pressing the space key. The next trial started 1 s after the participant's response. If no key presses were detected within 20 s after the test started, successive beeps would
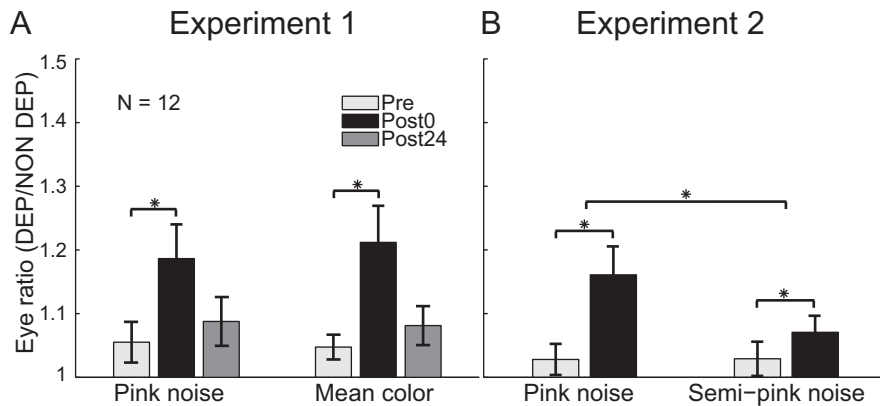
Fig. 3. Results of Experiments 1 and 2. (A) Grand average eye ratio index for the pre- and post-tests for the pink noise and mean color adaptation conditions in Experiment 1. Asterisk represent that there was a significant deprivation effect, i.e. difference between the post-test and the pre-test, as evaluated with a paired *t*-test. (B) Grand average eye ratio index for the pre- and post-tests in the pink noise and semi-pink noise adaptation conditions in Experiment 2. The asterisk above each pair of bars represents a significant deprivation effect. The top asterisk denotes that the deprivation effect differed significantly between the two adaptation conditions. All the paired *t*-tests were corrected for multiple comparisons. Error bars in all the figures represent standard errors of means.
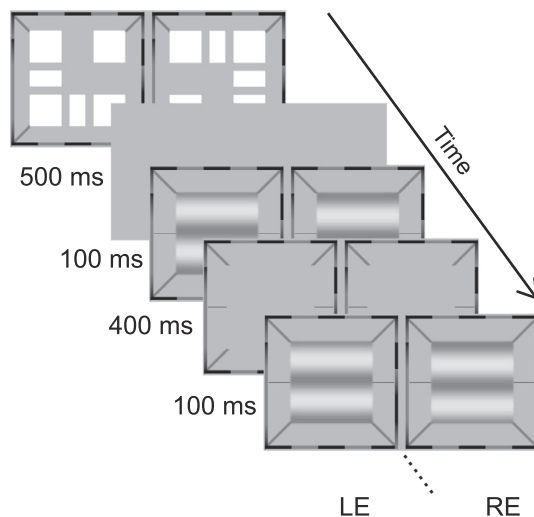
Fig. 4. A typical trial of the interocular phase combination task. Participants had to ensure the nonius cue was intact first. The test started 500 ms after the fusion was confirmed. Two horizontal sine-wave gratings were presented dichoptically on the center of the mid-gray background. The spatial phase of the two gratings shifted in the opposite direction by 22.5°. Participants were asked to adjust the vertical position of a one-pixel reference line to indicate the center of such a "cyclopean" perceptual grating using the Up Arrow and Down Arrow key. The initial position of the reference line was randomly assigned within a range of -20 to 22 pixels from the center of screen. The step size of adjustment was 1 pixel, corresponding to 1.85° phase angle of the grating. In each trial, the gratings (displayed for 100 ms) and a 400-ms blank interval were presented alternatively until the participants finished the adjustment by pressing the space key.

prompt the participants to complete the adjustment quickly.

Before the formal experiment, participants practiced the task for 3–4 days, with 4 sessions per day. Each session included 4 blocks, and each block included 20

trials. In the practice sessions we simulated different ratios of output signals for the two monocular channels with five possible pairs of contrasts (0.5/0.3, 0.5/0.4, 0.5/0.5, 0.4/0.5. 0.3/0.5) for the left/right eyes. Higher contrast in one eye would cause the perceived phase of the cyclopean perceptual grating to be closer to the phase of the grating in that eye (Ding and Sperling, 2006). The practice sessions allowed us to measure the participant's cyclopean percepts under different interocular contrast ratios. Each contrast pair was tested for 4 trials (2 for C1 and 2 for C2) in a block with a counter-balanced sequence.

The practice sessions also served to screen the participants for balanced sensory eye dominance (but measured in the interocular phase combination task). Instead of LvsR, we used the perceived phase angle for the testing contrast pair of 0.5/0.5 to evaluate sensory eye dominance. The perceived phase angle would be close to zero for perfectly balanced sensory eye dominance. Therefore, participants were allowed to proceed to the formal experiment as long as their average perceived phase angles in the last four sessions were between −5 and 5. Eventually, the dominant eye was the right (deprived) eye in 5 out of 8 subjects. The grand average perceived phase angle across all subjects was −0.284 ± 2.661.

In the formal experiment, the grating contrast in both eyes was 0.5. A pre-test session was completed before adaptation, which included 16 trials (8 for C1 and 8 for C2 with the sequence counter-balanced). Four such sessions were completed immediately after the end of adaptation, and another one session was tested 30 min after the end of adaptation. The adaptation procedure was similar to that in Experiment 1 except that each adaptation condition was run twice.

DATA ANALYSIS

Experiment 1

Phase durations of the exclusively monocular percepts and mixed percepts were summed up in each trial, respectively. Unlike the previous study (Lunghi et al., 2013), the mixed (piecemeal) percepts were not very rare. In 7 out of 12 subjects, the predominance of piecemeal exceeded 10% (for all subjects, Pre: 19.2% ± 16.2%, Post0: 20.1% ± 17.5%, Post24: 19.6% ± 17.2%). Therefore, to consider the contribution of piecemeal, an eye ratio index was calculated by the formula $(T_R + T_M/2)/(T_L + T_M/2)$. Here, T_R, T_L, and T_M represented the summed phase durations for perceiving the stimulus in the right (deprived) eye, the stimulus in the left (non-deprived) eye, and mixed percepts in a trial, respectively.

For each subject in each pre- or post-test, the eye ratio indices for all the trials of a test were averaged. The mean for each pre-test served as the baseline for that session. For each condition, the mean of the baselines for the two repetitions was taken as the baseline. A 2 (adaptation condition: pink noise vs. mean color) × 3 (test: pre-test, post0-test and post24-test) repeated measurements analysis of variance (ANOVA) was used to evaluate the deprivation effect.

Experiment 2

As in Experiment 1, the eye ratio indices for all the trials of a test were averaged. The baselines were then estimated using the similar method. A 2 (adaptation condition: pink noise vs. semi-pink noise) × 2 (test: pre-test vs. post0-test) repeated measurements ANOVA was then performed.

Experiment 3

The perceived phase was calculated as the half of the difference between the adjustment results for the C1 and C2 conditions in each session. A positive perceived phase angle indicated that the left eye was more dominant, while a negative one indicated that the right eye was more dominant. The mean perceived phase in the pre-adaptation session served as the baseline. The results in the 5 post-adaptation sessions tracked the perceived phase at 0 min, 3 min, 6 min, 9 min and 30 min after the end of adaptation, respectively. A 2 (adaptation condition: pink noise vs. mean color) × 6 (test: pre-test, post0-test, post3-test, post6-test, post9-test, post30-test) repeated measurements ANOVA was performed to evaluate the deprivation effect.

RESULT

Comparing monocular phase regularity deprivation with patching (Experiment 1)

The 2 (adaptation condition: pink noise vs. mean color) × 3 (test: pre-test, post0-test and post24-test) repeated measurements ANOVA disclosed the significant main effect of test ($F(1.112, 12.236) = 12.400$, $p \leq 0.004$, $\eta^2 = 0.530$, Greenhouse-Geisser corrected). The main effect of adaptation condition was not significant ($F(1, 11) = 0.077$, $p > 0.75$, $\eta^2 = 0.007$) and there was no significant interaction between the two factors ($F(2, 22) = 0.932$, $p > 0.4$, $\eta^2 = 0.078$).

Replicating Lunghi et al.'s findings, following 3 h of monocular deprivation with the simulated patching (i.e. mean color video), the eye ratio index significantly increased ($t(11) = 3.809$, $p_{uncorrected} \leq 0.003$, $p_{corrected} \leq 0.02$, paired t-test with Bonferroni correction for multiple comparisons), suggesting that the strength for the deprived eye was promoted relative to the non-deprived eye (see Fig. 3A). Interestingly, 3 h of monocular deprivation with the pink noise video produced the similar effects ($t(11) = 3.156$, $p_{uncorrected} \leq 0.01$, $p_{corrected} \leq 0.05$, see Fig. 3A). No significant difference between them was observed ($t(11) = 1.160$, $p_{uncorrected} > 0.25$). For both conditions, the

effect abolished after 24 h (pink noise: $t(11) = 1.739$, $p_{uncorrected} > 0.1$; mean color: $t(11) = 2.545$, $p_{uncorrected} \leq 0.03$, $p_{corrected} > 0.1$).

Monocular deprivation of all or half the phase regularity (Experiment 2)

In Experiment 1, one eye was deprived of both the Fourier amplitude and phase information in the mean color condition. While in the pink noise condition, only the phase regularity that described contours and higher level spatial representations was destroyed with the amplitude spectra left unchanged. The results of Experiment 1 suggested that the deprivation of phase regularity could also lead to a substantial shift in eye dominance. Monocular patching is thought to drive homeostatic plasticity (Mrsic-Flogel et al., 2007) in adult primary visual cortex triggered by decreased resting GABA concentration (Lunghi et al., 2015b). Adaptation to monocular deprivation of phase regularity may be controlled by sharing mechanisms.

However, the results of Experiment 1 cannot fully exclude the later selection account. According to the later selection account, during the monocular phase deprivation the visual system could promote the neural gain of the signal transmission pathway for the non-deprived eye due to its high signal-to-noise ratio. Thus the non-deprived eye would be expected to become more dominant following the deprivation. However, the input from the deprived eye in Experiment 1 was all noise. Complete noise is an extreme condition to which the visual system might react differently as compared to a condition of low signal-to-noise ratio. It is likely that the visual system simply gives up utilizing the later selection mechanism under this extreme condition. Once there is sufficient signal (though with low signal-to-noise ratio) in the deprived eye pathway, the visual system may be confident that the inputs from the deprived eye are of low quality. Accordingly, the later selection mechanism starts to work, increasing the dominance of the non-deprived eye following adaptation. To test this alternative account, in our Experiment 2, we took a higher signal-to-noise ratio for the semi-pink noise condition, only 50% of phase regularity was destroyed from the video presented to the deprived eye (see Fig. 2D).

The 2 (adaptation condition: pink noise vs. semi-pink noise) × 2 (test: pre-test vs. post0-test) repeated measurements ANOVA disclosed a significant main effect of test ($F(1, 11) = 28.508$, $p \leq 0.0003$, $\eta^2 = 0.722$) and adaptation condition ($F(1, 11) = 8.304$, $p \leq 0.02$, $\eta^2 = 0.430$). There was also a significant interaction between the two factors ($F(1, 11) = 12.619$, $p \leq 0.005$, $\eta^2 = 0.534$).

In agreement with the homeostatic plasticity account but not the later selection account, adaptation in both conditions induced a shift of eye dominance to the deprived eye (pink noise: $t(11) = 4.900$, $p_{uncorrected} \leq 0.0005$, $p_{corrected} \leq 0.002$; semi-pink noise: $t(11) = 3.671$, $p_{uncorrected} \leq 0.004$, $p_{corrected} \leq 0.02$, paired t-tests with Bonferroni correction for multiple comparisons, see Fig. 3B). Moreover, the effects of

adaptation were significantly weaker for the semi-pink noise condition than for the pink noise condition ($t(11)$ = 3.553, $p_{uncorrected} \leq 0.005$, $p_{corrected} \leq 0.02$).

Measuring the eye dominance with the interocular phase combination task (Experiment 3)

Apparently, the findings of the first two experiments contradict with Zhou and colleagues' conclusion that monocular phase regularity deprivation does not change the eye dominance (Zhou et al., 2014). However, it remains likely that the different findings between the two studies are due to relatively weaker statistical power of Zhou et al.'s experiment. Alternatively, the contradictive results may merely result from the measurements using distinct visual tasks. Both possibilities motivated us to re-run the Experiment 1, but use the interocular phase combination task to measure the eye dominance.

The 2 (adaptation condition: pink noise vs. mean color) × 6 (test: pre-test, post0-test, post3-test, post6-test, post9-test, post30-test) repeated measurements ANOVA disclosed a significant main effect of test ($F(5, 35)$ = 21.979, $p \leq 0.0001$, $\eta^2 = 0.758$) and adaptation condition ($F(1, 7)$ = 66.465, $p \leq 0.0001$, $\eta^2 = 0.905$). The two-way interaction was also significant ($F(5, 35)$ = 33.601, $p \leq 0.0001$, $\eta^2 = 0.828$).

Fig. 5 illustrates the grand average perceived phases at different time points for the two adaptation conditions. Paired t-tests indicated no significant difference between the baseline and the perceived phase at each time point after monocular phase regularity deprivation (i.e. pink noise, $t_0(7) = 0.808$, $p_0 > 0.4$; $t_3(7) = 0.345$, $p_3 > 0.7$; $t_6(7) = 0.317$, $p_6 > 0.75$; $t_9(7) = 1.002$, $p_9 > 0.3$; $t_{30}(7)$ = 0.911, $p_{30} > 0.35$). The negative results showing no shift of the eye dominance replicated the findings of Zhou et al. (2014).

However, the perceived phase shifted in the negative direction within the first 30 min after the simulated monocular patching (i.e. mean color, $t_0(7) = 9.647$ $t_3(7)$ = 12.521, $t_6(7) = 9.195$, $t_9(7) = 11.178$, $t_{30}(7)$ = 7.132, all $p_{uncorrected} \leq 0.0002$, $p_{(0\sim9)corrected} \leq 0.0002$, $p_{(30)corrected} \leq 0.001$, paired t-tests with Bonferroni

correction for multiple comparisons). Such results suggested that the right eye (i.e. the deprived eye) became more dominant after adaptation, a replication of Zhou et al.'s previous work (Zhou et al., 2013).

DISCUSSION

In three experiments, we used both the binocular rivalry and interocular phase combination tasks to measure the eye dominance prior to and following the adaptation to either the simulated monocular patching or the monocular deprivation of phase regularity.

The first two experiments disclosed that monocular deprivation of Fourier phase regularity shifted the eye dominance to the deprived eye when the eye dominance was measured with a binocular rivalry task. Experiment 2 revealed that the partial deprivation of Fourier phase regularity still induced a shift of eye dominance in the same direction as the full deprivation, but the effect size was smaller. These results support the notion that the monocular deprivation of Fourier phase regularity is sufficient to induce a shift in eye dominance, and disprove a late selection hypothesis that the visual system adjusts the neural gain of each monocular pathway based on the signal-to-noise ratio.

Our Experiment 3 replicated Zhou et al.'s findings that removing of monocular phase regularity produced no detectable effects when measured with the interocular phase combination task (Zhou et al., 2014), but that after monocular patching, the deprived eye became stronger as measured using the same task (Zhou et al., 2013).

In short, similar changes of eye dominance after patching were observed when tested with both the binocular rivalry and interocular phase combination tasks. However, substantially different results were observed for the phase regularity deprivation when tested with exactly the same two tasks. What caused the mixed results? The reason may be two-folded. First, binocular rivalry and interocular phase combination could be supported by different neural mechanisms. Second, the monocular deprivation of phase regularity caused functional changes detectable only by the binocular rivalry task, while the patching-induced functional changes were detectable by both tasks.

Interocular phase combination is thought to depend on the absolute phase of monocular images, which highly relies on the involvement of phase-sensitive simple cells in the primary visual cortex (Huang et al., 2010). However, neural mechanisms underlying binocular rivalry are more complex, transpiring multiple levels in the visual pathway (for review, see Tong et al., 2006). For example, contour information plays a great role in strengthening image dominance in binocular competition (Baker and Graf, 2009; Xu et al., 2010b).
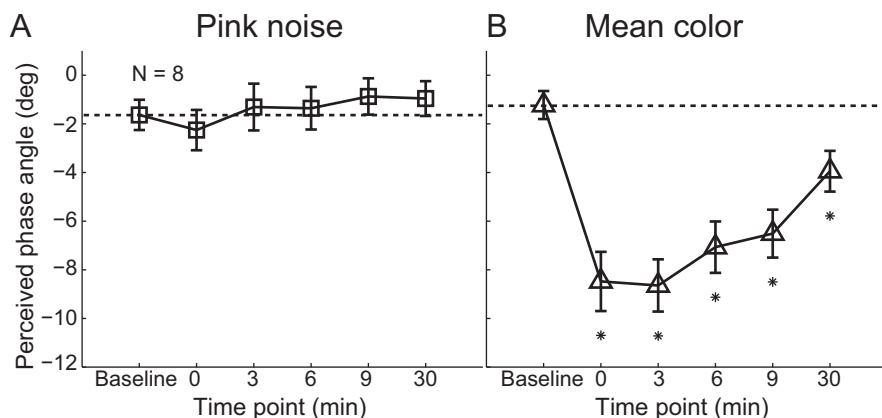
Fig. 5. The grand average of the perceived phase angles measured before and after adaptation for the (A) pink noise condition and (B) mean color condition. Dashed lines denote the baselines. Asterisks denote that the perceived phase at a given time point was significantly different from the baseline. Error bars represent standard errors of means.

Importantly, contour integration has been found to be phase invariant (Field et al., 1993). Supporting this notion, recent neurophysiological evidence has suggested that contour processing for natural images is performed in complex cells (rather than simple cells) of V1 in cats (Felsen et al., 2005), or beyond V1 in humans (Dumoulin et al., 2008; Rieger et al., 2013; Shpaner et al., 2013).

Taking the findings in all this work into consideration, the removing of phase regularity destroyed the contour information of input images in one eye. Accordingly, it is conceivable that monocular deprivation of phase regularity likely alters the balance in the rivalry mechanism that strongly weights the contour information transmitted along each monocular pathway. However, it may not change the weights in the interocular phase combination mechanism much, because the activities of phase-sensitive neurons (e.g. simple cells) for the two eyes should be about equally strong during adaptation (though the neuronal activities for the deprived eye are not locally phase-aligned over spatial scales). However, the monocular patching silences the neurons for the deprived eye, thus changes the weights for both mechanisms. As a result, the effects of monocular patching are measurable by both tasks, but those produced by monocular phase deprivation can only be detected by the binocular rivalry task.

Alternatively, the present findings can be construed in terms of different inhibitory circuitry underlying binocular rivalry and interocular phase combination. Binocular rivalry engages strong competition between the eyes and interocular suppression mechanisms that are mediated by inhibitory circuits (Tong et al., 2006). Short-term monocular patching has been shown to modulate inhibitory circuits in the primary visual cortex (Lunghi et al., 2015a,b; Lunghi and Sale, 2015). Monocular deprivation of phase regularity may alter the inhibitory circuits underlying binocular rivalry but not those underlying interocular phase combination, while monocular patching may alter both of them.

Although the effect sizes for the two types of deprivations were approximately equal in Experiment 1, we doubt a conclusion that the deprivation of phase regularity can completely account for the effects of patching. The visual inputs during adaptation were chromatic natural images in Lunghi et al.'s (2013) work. They found greater patching-induced eye dominance changes when testing the subjects with the chromatic rivalry gratings than with the luminance gratings. In our study, the test rivalry gratings were always achromatic. However, the visual inputs during adaptation were chromatic for the simulated patching but achromatic for the deprivation of phase regularity. It remains unknown whether the effects of patching in our work can become larger when the visual inputs are made achromatic for both the adaptation and tests. Therefore, although similar sizes of adaptation effects were observed for the two deprivations, it is likely that the effects of patching here were underestimated because of our particular setup. Future work may further investigate this issue. The scope of the present study is limited to showing whether the deprivation of phase regularity can lead to a shift of eye

dominance or not, and by which measurement the effects can be observed.

Our findings reveal the importance of phase in monocular deprivation, which are in good agreement with the realization of "importance of phase" in the field of signal processing in computer vision (Oppenheim and Lim, 1981). In Oppenheim and Lim's study, they reconstruct two distinct images by performing inverse Fourier transformation on the combination of one image's amplitude spectrum and the other image's phase spectrum. It is found that in nearly all the time, the reconstructed image is similar to the original one with the same phase spectrum. In fact, natural stimuli differ surprisingly little in their amplitude spectra, and phase is the predominant information on which our visual system relies to discern the world (Piotrowski and Campbell, 1982). The important role of phase in monocular deprivation thus likely reflects a consequence of biological evolution to accommodate signal processing of naturally occurring stimuli.

CONCLUSIONS

The present study found that both monocular patching and monocular phase deprivation boosted the deprived eye's dominance when measured with a binocular rivalry task. However, when measured using the interocular phase combination task, the phase deprivation showed no effects, while the effects were still observed for patching. Our work thus resolves the debate whether depriving Fourier phase information alone is sufficient to alter the eye dominance or not. The results indicate that the two measurements are likely supported by different mechanisms, and ocular dominance plasticity occurs at different stages of visual processing.

CONFLICT OF INTEREST

The authors declare no conflict of interests.

REFERENCES

Baker DH, Graf EW (2009) Natural images dominate in binocular rivalry. Proc Natl Acad Sci U S A 106:5436–5441.

Brainard DH (1997) The psychophysics toolbox. Spat Vis 10:433–436.

Campbell FW, Robson JG (1968) Application of Fourier analysis to the visibility of gratings. J Physiol 197:551–566.

Castaldi E, Frijia F, Montanaro D, Tosetti M, Morrone MC (2013) BOLD human responses to chromatic spatial features. Eur J Neurosci 38:2290–2299.

Dieter K, Blake R (2015) Sensory eye dominance varies within the visual field. J Vis 15:268.

Ding J, Sperling G (2006) A gain-control theory of binocular combination. Proc Natl Acad Sci U S A 103:1141–1146.

Dumoulin SO, Dakin SC, Hess RF (2008) Sparsely distributed contours dominate extra-striate responses to complex scenes. NeuroImage 42:890–901.

Felsen G, Touryan J, Han F, Dan Y (2005) Cortical sensitivity to visual features in natural scenes. PLoS Biol 3:e342.

Field DJ, Hayes A, Hess RF (1993) Contour integration by the human visual system: evidence for a local ''association field''. Vis Res 33:173–193.

Graham N, Nachmias J (1971) Detection of grating patterns containing two spatial frequencies: a comparison of single-channel and multiple-channels models. Vis Res 11:251–259.

Handa T, Mukuno K, Uozato H, Niida T, Shoji N, Shimizu K (2004) Effects of dominant and nondominant eyes in binocular rivalry. Optom Vis Sci 81:377–383.

Handa T, Shimizu K, Mukuno K, Kawamorita T, Uozato H (2005) Effects of ocular dominance on binocular summation after monocular reading adds. J Cataract Refract Surg 31:1588–1592.

Huang CB, Zhou J, Zhou Y, Lu ZL (2010) Contrast and phase combination in binocular vision. PLoS One 5:e15075.

Hubel DH, Wiesel TN (1970) The period of susceptibility to the physiological effects of unilateral eye closure in kittens. J Physiol 206:419–436.

Kwon M, Lu ZL, Miller A, Kazlas M, Hunter DG, Bex PJ (2014) Assessing binocular interaction in amblyopia and its clinical feasibility. PLoS One 9:e100156.

Lo Verde L, Morrone MC, Lunghi C (2017) Early cross-modal plasticity in adults. J Cogn Neurosci 29:520–529.

Lunghi C, Sale A (2015) A cycling lane for brain rewiring. Curr Biol 25: R1107–R1125.

Lunghi C, Burr DC, Morrone MC (2011) Brief periods of monocular deprivation disrupt ocular balance in human adult visual cortex. Curr Biol 21:R538–R539.

Lunghi C, Burr DC, Morrone MC (2013) Long-term effects of monocular deprivation revealed with binocular rivalry gratings modulated in luminance and in color. J Vis 13(1):1–15.

Lunghi C, Berchicci M, Morrone MC (2015a) Short-term monocular deprivation alters early components of visual evoked potentials. J Physiol 593:4361–4372.

Lunghi C, Emir UE, Morrone MC, Bridge H (2015b) Short-term monocular deprivation alters GABA in the adult human visual cortex. Curr Biol 25:1496–1501.

Morrone MC, Burr DC (1988) Feature detection in human vision: a phase-dependent energy model. Proc R Soc Ser B 235:221–245.

Mrsic-Flogel TD, Hofer SB, Ohki K, Reid RC, Bonhoeffer T, Hubener M (2007) Homeostatic regulation of eye-specific responses in visual cortex during ocular dominance plasticity. Neuron 54:961–972.

Ni X, Huo X (2007) Statistical interpretation of the importance of phase information in signal and image reconstruction. Stat Probabil Lett 77:447–454.

Ooi TL, He ZJ (2001) Sensory eye dominance. Optometry 72:168–178.

Ooi TL, Su YR, Natale DM, He ZJ (2013) A push-pull treatment for strengthening the 'lazy eye' in amblyopia. Curr Biol 23: R309–R310.

Oppenheim A, Lim J (1981) The importance of phase in signals. Proc IEEE 69:529–541.

Perna A, Tosetti M, Montanaro D, Morrone MC (2005) Neuronal mechanisms for illusory brightness perception in humans. Neuron 47:645–651.

Perna A, Tosetti M, Montanaro D, Morrone MC (2008) BOLD response to spatial phase congruency in human brain. J Vis 8 (15):1–15.

Piotrowski LN, Campbell FW (1982) A demonstration of the visual importance and flexibility of spatial-frequency amplitude and phase. Perception 11:337–346.

Platonov A, Goossens J (2014) Eye dominance alternations in binocular rivalry do not require visual awareness. J Vis 14 (2):1–17.

Rieger JW, Gegenfurtner KR, Schalk F, Koechy N, Heinze HJ, Grueschow M (2013) BOLD responses in human V1 to local structure in natural scenes: implications for theories of visual coding. J Vis 13(19):1–15.

Schade Sr OH (1956) Optical and photoelectric analog of the eye. J Opt Soc Am 46:721–739.

Shpaner M, Molholm S, Forde E, Foxe JJ (2013) Disambiguating the roles of area V1 and the lateral occipital complex (LOC) in contour integration. NeuroImage 69:146–156.

Suzuki S, Grabowecky M (2007) Long-term speeding in perceptual switches mediated by attention-dependent plasticity in cortical visual processing. Neuron 56:741–753.

Tong F, Meng M, Blake R (2006) Neural bases of binocular rivalry. Trends Cogn Sci 10:502–511.

Westheimer G (2001) The Fourier theory of vision. Perception 30:531–541.

Wiesel TN, Hubel DH (1963) Single-cell responses in striate cortex of kittens deprived of vision in one eye. J Neurophysiol 26:1003–1017.

Xu JP, He ZJ, Ooi TL (2010a) Effectively reducing sensory eye dominance with a push-pull perceptual learning protocol. Curr Biol 20:1864–1868.

Xu JP, He ZJ, Ooi TL (2010b) Surface boundary contour strengthens image dominance in binocular competition. Vis Res 50:155–170.

Xu JP, He ZJ, Ooi TL (2011) A binocular perimetry study of the causes and implications of sensory eye dominance. Vis Res 51:2386–2397.

Zhou J, Clavagnier S, Hess RF (2013) Short-term monocular deprivation strengthens the patched eye's contribution to binocular combination. J Vis 13(12):1–10.

Zhou J, Reynaud A, Hess RF (2014) Real-time modulation of perceptual eye dominance in humans. Proc R Soc Ser B 281:20141717.

Zhou J, Baker DH, Simard M, Saint-Amour D, Hess RF (2015) Short-term monocular patching boosts the patched eye's response in visual cortex. Restor Neurol Neurosci 33:381–387.