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Short-term monocular deprivation reduces inter-ocular suppression of the deprived eye

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Abstract

The adult visual system was traditionally thought to be relatively hard-wired, but recent studies have challenged this view by demonstrating plasticity following brief periods of monocular deprivation (Lunghi, Burr, & Morrone, 2011; Lunghi, Burr, & Morrone, 2013). When one eye was deprived of spatial information for 2-3 hours, sensory dominance was shifted in favour of the previously deprived eye. However, the mechanism underlying this phenomenon is unclear. The present study sought to address this issue and determine the consequences of short-term monocular deprivation on inter-ocular suppression of each eye. Sensory eye dominance was examined before and after depriving an eye of all visual input using a light-tight opaque patch for 2.5 hours, in a group of adult participants with normal binocular vision (N=6). We used a percept tracking task during experience of binocular rivalry (BR) to assess the relative dominance of the two eyes, and an objective probe detection task under continuous flash suppression (CFS) to quantify each eye's susceptibility to inter-ocular suppression. In addition, the monocular contrast increment threshold of each eye was also measured using the probe detection task to ascertain if the altered eye dominance is accompanied by changes in monocular perception. Our BR results replicated Lunghi and colleagues' findings of a shift of relative dominance towards the eye that has been deprived of form information with translucent patching. More crucially, using CFS we demonstrated reduced inter-ocular suppression of the deprived eye with no complementary changes in the other eye, and no monocular changes in increment threshold. These findings imply that short-term monocular deprivation alters binocular interactions. The differential effect on inter-ocular suppression between eyes may have important implications for the use of patching as a therapy to recover visual function in amblyopia.

1 Introduction

Neural plasticity has been extensively studied in mammalian visual systems and is a prominent feature of developing brains. If exposed to abnormal visual input during development, structural and functional changes are induced in visual cortex, presumably driven by mechanisms for maintaining an adaptive and stable environment in the brain (Keck et al., 2017; Turrigiano & Nelson, 2000). A well documented example is the shift in ocular dominance induced by monocular deprivation (Hubel & Wiesel, 1964). Prolonged disruption of visual input to one eye in young animals (e.g. kittens, monkeys, mice), leads to a shrinkage of ocular dominance columns associated with that eye and weakened responses from the deprived eye in response to visual stimulation (Baker, Grigg, & von Noorden, 1974; Blakemore, Garey, & Vital-Durand, 1978; Crawford, Blake, Cool, & von Noorden, 1975; Frenkel & Bear, 2004; Hubel, Wiesel, & LeVay, 1977; Le Vay, Wiesel, & Hubel, 1980; Wiesel & Hubel, 1963). These changes are specific to imbalanced input, since deprivation of both eyes together does not produce the same effects (Crawford et al., 1975; Wiesel & Hubel, 1965). The shift in ocular dominance, nonetheless, can be reversed by subsequently depriving the previously open eye, although the effectiveness of this reversal is restricted to a critical time window (Blakemore et al., 1978; Swindale, Vital-Durand, & Blakemore, 1981). Interestingly, recent research in human adults has demonstrated effects of short-term monocular deprivation in the opposite direction. Specifically, perceptual eye dominance is shifted in favour of the previously deprived eye (Lunghi et al., 2011; Lunghi et al., 2013), though the precise mechanism underpinning this effect remains unclear.

In a series of studies, Lunghi and colleagues covered one eye of participants using a translucent lens for 2.5 hours, depriving it of spatial information but matching average luminance to that of the other eye. Sensory eye dominance was subsequently measured (after patch removal) using a binocular rivalry (BR) task and revealed that the patched eye dominated perception for longer periods. This effect decays over time and the temporal dynamics of rivalry returns to the pre-deprivation level approximately 15–60 minutes after uncovering the eye (if tested with achromatic stimuli). Coupled with behavioural changes, physiological evidence has shown increased and decreased cortical responsiveness associated with the deprived eye and the non-deprived eye, respectively (Binda et al., 2018; Chadnova, Reynaud, Clavagnier, & Hess, 2017; Lunghi, Berchicci, Morrone, & Di Russo, 2015; Zhou, Baker, Simard, Saint-Amour, & Hess, 2015). An opaque eye patch, which eliminates all visual input, induces similar effects on binocular balance (Chadnova et al., 2017; Zhou, Clavagnier, & Hess, 2013) suggesting that changes in light adaptation do not underpin this shift in eye dominance.

In addition to measuring rivalry, other work has used tasks requiring a combination of binocular inputs such as binocular phase combination and binocular contrast matching tasks (Zhou, Clavagnier, & Hess, 2013; Zhou, Reynaud, Kim, Mullen, & Hess, 2017; Zhou, Thompson, & Hess, 2013). One of these studies (Zhou, Clavagnier, & Hess, 2013) compared the consequences of short-term deprivation, induced by both opaque and translucent patching, on ocular balance measured with a binocular combination task. They obtained similar results in both cases—the relative contribution from the treated eye was increased. However, when the phase information presented to one eye is scrambled (a form of monocular phase deprivation) different effects are found depending on the task used to measure sensory eye dominance (Bai, Dong, He, & Bao, 2017; Zhou, Reynaud, & Hess, 2014). If a rivalry task is used, the pattern of results is consistent with previous work (Bai et al., 2017). However, for a binocular combination task there is no change in eye dominance (Bai et al., 2017; Zhou et al., 2014). This raises the possibility that there are multiple mechanisms involved in the plasticity of sensory eye dominance and that binocular contrast combination between fusible stimuli, and binocular rivalry between incompatible stimuli, are differentially affected by monocular deprivation. In light of this it is difficult to generalise these effects across different forms of monocular deprivation and methods of quantifying sensory eye dominance. Therefore, we first aimed to replicate Lunghi's findings on BR dynamics, but using an opaque patch rather than a translucent one.

An alternative way of characterising the sensory balance between eyes is to examine the susceptibility of each eye to continuous flash suppression (CFS). This is a phenomenon where a dynamic, contour-rich, image presented to one eye gains immediate dominance such that the perception of another less salient stimulus (e.g. a static grating) simultaneously presented to the other eye is suppressed, for a relatively prolonged period (often several minutes) (Tsuchiya & Koch, 2005). Although there is a positive association between the depth of suppression produced by CFS and that under BR, the eye dominance measured with the two tasks is not necessarily the same for an individual (M. Wang, McGraw, & Ledgeway, 2019a, 2019b). Whether short-term monocular deprivation affects eye dominance estimated via BR and CFS in the same way remains unknown.

Whilst it is possible to quantify the depth of inter-ocular suppression under BR, it is usually much weaker than that produced by CFS (Tsuchiya, Koch, Gilroy, & Blake, 2006; M. Wang, McGraw, & Ledgeway, 2019a, 2019b). Alongside the well documented individual and inter-ocular variations (Dieter, Sy, & Blake, 2017; M. Wang, McGraw, & Ledgeway, 2019b), this poses a problem in that post-deprivation eye dominance can sometimes be unmeasurable under BR. For example if one eye of an individual is already suppressed comparatively weakly during BR, enhancing its relative dominance by monocular deprivation may make it even less susceptible to suppression by the other eye, but quantifying such a small effect can be challenging. This issue can be overcome when the magnitude of suppression is sufficiently large—as is found under conditions of CFS. For these reasons, the effect of monocular patching was also examined in a CFS task in this study, to determine the relative modulation of inter-ocular suppression of each eye.

If the previously deprived eye becomes more sensitive, and/or the other eye becomes less sensitive following monocular patching, the relative perceptual contribution of each eye to binocular tasks will be changed accordingly. However, evidence for this proposal is mixed. In Lunghi et al.'s (2011) original study, no change in each eye's contrast discrimination threshold was found following monocular deprivation. This was also the case in later studies (e.g. Baldwin & Hess, 2018). Baldwin and Hess (2018) showed that the magnitude of the deprivation effect revealed with different binocular tasks is not significantly correlated. A correlation would be expected if the changes in binocular balance were underpinned by a single effect such as a change in monocular threshold following patching. Other work has shown a lowered monocular detection threshold in the previously deprived eye along with an elevated threshold for the non-deprived eye (Zhou, Clavagnier, & Hess, 2013; Zhou et al., 2017; Zhou, Thompson, & Hess, 2013). The inconsistencies in results might be related to different types of thresholds being measured (e.g. discrimination vs. detection). Nevertheless, the number of subjects tested in previous studies was limited (e.g. 2 subjects in Zhou, Clavagnier, and Hess's (2013) study), and the magnitude of effects was small. Therefore, we sought to clarify whether or not monocular visual processing is systematically affected by short-term monocular deprivation, by measuring contrast increment thresholds separately for each eye using a probe task analogous to that used to study CFS (see Tsuchiya et al., 2006).

In sum, the aims of this study were threefold. First, we sought to replicate previous findings that brief periods of monocular deprivation alter the relative contribution of the two eyes to perception during binocular rivalry, in favour of the eye that has been patched (Lunghi et al., 2011; Lunghi et al., 2013). Second, the effect of short-term deprivation on eye dominance was also measured using an objective, forced-choice task—CFS. An advantage of the CFS task is that, unlike rivalry, the contribution of each eye can be measured independently. Finally, we addressed whether changes in monocular contrast increment threshold in one or both eyes accompany changes in eye dominance.

2 Methods

2.1 Observers

Six observers participated in the study (age range: 22–49 years, one female), including the three authors (S1, S2 and S3), and all had normal or corrected-to-normal vision. The TNO test (Laméris Ootech, Nieuwegein, The Netherlands) was used to assess stereo vision. The participant wore a pair of red-green anaglyph spectacles to detect the orientation of a disparity-defined (cyclopean) object depicted within random-dot stereograms. The smallest disparity at which the judgement could be reliably performed was recorded as a measure of stereoacuity. The results indicated that stereoacuity was in the normal range for all observers tested. The study was conducted with the approval of University of Nottingham, School of Psychology Ethics Committee and all participants gave informed consent. All were experienced observers in psychophysical experiments.

2.2 Apparatus and Stimuli

The tasks were completed in a dimly lit room. The grey scale stimuli were generated using custom software written in C, on an Apple Macintosh, and were displayed on a pair of identical LCD monitors (22 inch Samsung Sync-Master 2233RZ; 1024 × 768-pixel resolution; 60 Hz refresh rate; 318 cd/m^2 maximum luminance). The utility of using these displays in vision experiments (in terms of spatial, timing and luminance characteristics) has been validated (P. Wang & Nikolic, 2011). The temporal synchronisation of the two monitors was achieved by driving them with the dual outputs of the same video card. They were carefully calibrated to produce output luminance as a linear function of the digital representation of the image. The noisy-bit method, applied to each colour channel separately, was used to increase the effective number of intensity levels available on each screen (Allard & Faubert, 2008).

A Wheatstone mirror stereoscope was employed to enable the dichoptic presentation of the stimuli, which produced an optical viewing distance of 231.5 cm. The angle of the pair of full-silvered mirrors was nominally ±45° with regard to the median plane of the head, but the angle was adjusted, if necessary, for individual observers to attain stable binocular fusion. On each display stimuli were presented within a central square region, enclosed by a high contrast checkered fusion frame (2.21° × 2.21°), with a pair of vertically and horizontally oriented Nonius lines, to assist binocular fusion, against a uniform “grey” background (159 cd/m^2). A binocular fixation cross was also presented at the centre of the displays between trials and a chin rest was used to stabilise head position.

The stimuli used to elicit CFS or BR were spatially two-dimensional random noise patterns consisting of square elements (0.128° × 0.128°) presented to one eye, and a horizontally-oriented sinusoidal grating (spatial frequency 1.8 cpd) to the other eye (see Figure 1). For the noise pattern, the luminance of each element was assigned by random sampling with replacement from a uniform probability distribution spanning a range determined by a Michelson contrast of 20%. The grating had the same level of Michelson contrast. The phase of the grating was randomly assigned to either +sine or −sine phase on each trial, with respect to the horizontal midline, and each half of the square display window contained an integer number of cycles, preventing luminance artefacts. For CFS the noise pattern was replaced with a new stochastic sample at a rate of 10 Hz, forming a dynamic sequence, which served to suppress the grating viewed by the other eye. For BR the pair of stimuli were identical to those used in the CFS task, except that the noise pattern was static rather than dynamic.

2.3 Procedure

The CFS task has been previously described in M. Wang, McGraw, and Ledgeway (2019b). A two-alternative forced choice (2-AFC) probe detection task was used to quantify inter-ocular suppression under CFS (Tsuchiya et al., 2006) and an example trial is demonstrated in Figure 1. The probe method is designed to measure the contrast increment required to break the suppression produced by the dynamic noise in the other eye. On each trial participants were asked to fixate the central cross and wait until the noise pattern was exclusively perceived before pressing a key to immediately trigger the presentation of a probe stimulus. This ensured that the contrast increment threshold was measured under complete suppression. The probe stimulus was a contrast increment, lasting for 500 ms, applied to either the top or bottom half of the grating, chosen at random on each trial. The temporal onset and offset of the probe were smoothed using a Gaussian envelope with a SD of 100 ms. The dynamic noise stopped refreshing following the offset of the probe. The task was to judge the spatial location of the probe (top vs. bottom). Following a response, the noise and grating were replaced with a uniform "grey" interior within the fusion frame and then the fixation cross was displayed for 1000 ms until the next trial began.

Probe contrast started at 40% and was then adjusted using a three-down, one-up adaptive staircase procedure, converging on the 79.3% correct performance level. A proportional step size of 30% was used before the fourth reversal of the staircase and was 15% thereafter. The staircase terminated after 12 reversals and the geometric mean of the contrast level at the last four reversals was adopted as the probe contrast increment threshold for that particular set of trials.

To utilise the depth of suppression evoked by CFS as an indication of the relative strength of each eye, increment thresholds were measured with both configurations of eye of presentation. That is, in half the conditions tested the grating was presented to the left eye and the dynamic noise sequence to the right eye, and for the remaining conditions the converse was true. Monocular increment thresholds for each eye were also obtained using an identical procedure (i.e. the probe detection task), with the exception that there was no noise viewed by the other eye. Participants completed a minimum of five staircases (range 5 to 8) for each condition tested, and the final threshold for each condition was calculated as the arithmetic mean of these values. To provide a measure of inter-trial variability, the standard error of the mean (SEM) was also calculated.

For BR, temporal dynamics were measured to quantify sensory eye dominance. At the beginning of each trial participants initiated the presentation of the noise and grating, by pressing a key, once stable binocular fusion was achieved. They then reported their percepts continuously by key presses over a 60-second period. There were three possible responses: exclusive noise, exclusive grating, and a mixed percept containing portions of both stimuli. In the case that a key was still being pressed at the end of the 60-second period, the trial continued until the percept changed (i.e. indicated by key release), or once a maximum duration of 120 seconds was reached. This was done in order to record the total duration of the last percept. Like CFS, both configurations of eye of presentation were tested and each condition was repeated at least five times.

The measurements of CFS and BR were made both before patching and immediately after a 150-minute period of occluding one eye with an opaque patch that deprived the eye of all visual information. For both pre- and post-deprivation testing, all the conditions (including the BR and CFS tasks, monocular increment thresholds and both configurations of eye of presentation) were completed in a pseudorandom order. As the effect produced by monocular patching wanes over time (see Lunghi et al., 2013), the post-patching measurements were completed within a window of 35 minutes after the patch was removed, over three sessions separated by at least 24 hours (the pre-patching measurements were made separately and the length of testing sessions did not need to be so tightly constrained). During monocular deprivation, the participant’s non-dominant eye was patched (normal activities allowed), which was the eye less susceptible to CFS as determined on the basis of pilot studies and practice trials before formal data collection began.

Although a response for a mixed percept was recorded in our study, we did not analyse the dynamics associated with it. However, it was taken into account when calculating the metrics for the other two percepts because it typically occupies some proportion of time being perceived in a particular trial (i.e. the sum of proportions for the exclusive noise and exclusive grating percepts never reached 1).

2.4 Mixed-effects model analysis

The effects at the group level were statistically evaluated using mixed-effects model analysis. Linear models were fitted to the data using the function *fitlme* in MATLAB (MathWorks, version R2017a). These models consisted of both fixed effects and subject-dependent random effects, where all the random effects were assumed to be uncorrelated with one another.

For the mean phase duration or the predominance measured with the BR task, the model comprised fixed effects of *Percept* (noise vs. grating), *Eye* (patched vs. non-patched), *Time* (pre- vs. post-patching) and the interaction of all combinations. Intercepts and slopes for all these predictors were included for the random effects. In addition, separate models were then constructed with the data for each eye, including a fixed effect of *Time* and random effects of the intercept and the slope for *Time*.

For the increment thresholds measured with the probe task, the model incorporated fixed effects of *Eye* (patched vs. non-patched), *Time* (pre- vs. post-patching), and their interaction, and random effects of these factors plus the intercept. This analysis was performed for both the monocular increment thresholds, and the depth of inter-ocular suppression evoked by CFS (after discounting the monocular increment threshold of the corresponding eye), using the following equation:

$$Suppression = 20 \times log_{10}(\frac{Threshold_{CFS}}{Threshold_{Monocular}}) \text{ .} \qquad (1)$$

In an analogous manner to the BR data, separate mixed models were subsequently constructed for the patched eye and the non-patched eye, to evaluate the effects of monocular deprivation on each eye. The models included a fixed effect of *Time* and random effects of the intercept and the slope for *Time*.

Furthermore, informal analysis with mixed-effects models was conducted to investigate if our data replicate the decay of the patching effect over time observed by Lunghi et al. (2013). This analysis was performed for the post-patching measurements, including the BR phase duration and predominance for each type of exclusive percept (i.e. noise and grating), and the monocular and CFS increment thresholds. The time since the removal of the eye patch (within each of the 3 testing sessions) was coded according to the time stamp of the raw data files (one file corresponds to a one-minute trial of the BR percept tracking task or a run of the CFS task containing one staircase). Each mixed-effects model comprised fixed effects of

Time course and *Eye*, and their interaction, and a random intercept and random slopes for all predictors.

3 Results

Distributions of phase durations (i.e. probability density functions, PDF; bin size: 0.2) are shown in Figure 2 and Figure 3[1], for every participant. Each has been normalised to the individual's mean duration measured before patching, for exclusive noise and grating percepts, respectively. The corresponding cumulative density functions (CDF) were then fitted using a nonlinear least squares method with a gamma distribution defined by the following equation:

$$g(x) = \frac{\lambda^{\rho}}{\Gamma(\rho)} \int_0^x t^{\rho-1} e^{-\lambda t}\, dt, \tag{2}$$

where Γ is the gamma function, ρ indicates the shape of the distribution (shape parameter) and λ describes the width (scale parameter). The CDF rather than PDF was chosen for fitting, to eliminate subjectivity due to introducing an arbitrary bin size. However the fitted curves are plotted as PDF in Figure 2 and Figure 3, using the estimated parameters based on the CDF fits, to allow direct comparison to the results presented in previous work by Lunghi et al. (2013). On the whole, there is a rightward shift in the distribution for the stimulus shown to the deprived eye and a leftward shift in the other eye, consistent with the findings of Lunghi et al. (2013). These changes also apply to the normalised phase durations pooled across the participant group (Figure 4).

Lunghi et al. (2013) found that the ratio of the shape parameter (ρ) to the scale parameter (λ), which describes the mean of the gamma distribution, was approximately unity in the absence of prior deprivation. However, it was increased for the deprived eye and decreased for the non-deprived eye after monocular deprivation. The time course of this effect resembles that for the changes in the mean phase duration for each eye (Lunghi et al., 2013). In our study a similar effect on the ratio of ρ to λ was observed, as depicted in Figure 5. For both exclusive noise (Figure 5a) and exclusive grating percepts (Figure 5b), the ratio for each eye was close to unity before patching, with little inter-ocular or inter-individual variation (mean data across all the subjects shown by the large crosses). The ratio was altered after monocular patching, in opposite directions for the two eyes—it was increased for the patched eye (i.e. an upward shift) and decreased for the non-

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[1] For interpretation of the references to colour in the figure legends and the related text in this article, the reader is referred to the web version.

patched eye (i.e. a leftward shift). Based on the meaning of ρ/λ, these results imply an increased mean exclusive phase duration for the patched eye and a decreased mean duration for the non-patched eye. Nevertheless, not all observers showed a pronounced effect, and there were larger inter-individual variations compared to the pre-patching level (see S2, noise percept, and S5, grating percept).

The mean phase durations and proportion of time that each percept was perceived (i.e. predominance), before (red) and after patching (black), are plotted in Figure 6a-d for the patched (ordinate) and non-patched eye (abscissa). A diagonal line with unity slope marks the balance of the two eyes, and data points deviating from this line indicate dominance of one eye (see figure legend). As can be seen, the mean phase duration (Figure 6a, b) and predominance of each exclusive percept (Figure 6c, d), were increased when the corresponding stimulus was presented to the patched eye (i.e. an upward shift), or decreased when presented to the non-patched eye (i.e. a leftward shift). The absolute changes in each eye's measures appear inconsistent across individuals. Therefore, we took the ratio of the eye dominance after patching over that prior to patching using the following equation (a similar deprivation effect index has been previously used by Lunghi, Emir, Morrone, & Bridge, 2015):

$$Patching\ effect = 20 \times log_{10}\left(\frac{Patched\ eye_{post}/Nonpatched\ eye_{post}}{Patched\ eye_{pre}/Nonpatched\ eye_{pre}}\right), \qquad (3)$$

where a *Patching effect* index of zero denotes no difference between the pre- and post-patching measures and non-zero values indicate a change in the degree of eye dominance as a consequence of patching. Note that for BR dynamics a positive index signifies enhanced dominance of the eye that was previously patched, whereas for threshold measures the converse is true.

The resultant index for all BR measures is plotted in Figure 6e. The plot essentially reflects the results shown in Figure 6a-d, but it extracts a common component that captures the patching effect across individuals and conditions (i.e. changes in relative eye dominance). The computed indices for these BR measures illustrate an obvious shift of the relative sensory eye dominance towards the previously patched eye in our group of participants.

The results of mixed-effects model analysis for the BR mean phase duration showed significant main effects of *Percept* ($t_{(40)} = 3.84$, $p < .001$) and *Time* ($t_{(40)} = -2.07$, $p = .045$), and an interaction effect between *Eye* and *Time* ($t_{(40)} = 7.71$, $p < .001$). Overall, the exclusive percept phase duration was longer for the noise than that for the grating stimulus and was slightly shortened after patching. Moreover, the analyses of the models including only the effects of *Time* for the two eyes separately suggested that the decrease in mean phase duration for the non-patched eye ($t_{(22)} = -2.41$, $p = .025$) was more consistent across individuals than the changes for the patched eye ($t_{(22)} = .647$, $p = .524$).

The results for the model constructed for predominance revealed a significant main effect of *Percept* ($t_{(40)} = 6.52$, $p < .001$), and *Eye* × *Time* ($t_{(40)} = 9.39$, $p < .001$) and *Percept* × *Eye* × *Time* ($t_{(40)} = 2.05$, $p = .047$) interactions. Like phase duration, the noise stimulus was also perceived for more time in total than the grating. When looking at the effect of *Time* on each eye, the results showed an increased predominance for the patched eye after monocular deprivation ($t_{(22)} = 2.42$, $p = .024$), and decreased predominance for the non-patched eye ($t_{(22)} = -2.77$, $p = .011$). The three-way interaction associated with predominance is more complicated to interpret, and further breakdown of the term suggested that it may result from the larger difference between the noise and grating predominance viewed by the non-patched eye relative to that presented to the patched eye; this was only true for the pre-patching measurements, and was absent when tested after patching.

In a similar vein, we show each individual's mean increment threshold measured before and after patching, in the monocular condition and under CFS in Figure 7a and b, for the patched and non-patched eyes. The results in Figure 7a suggest that monocular increment thresholds, measured in each eye in the absence of a suppressing noise pattern in the other eye, were minimally affected, and that there was no consistent change across individuals. The data points for all observers are close to the unity line. In contrast, the effect of patching is revealed when measured under CFS (Figure 7b). The increment threshold for the previously patched eye decreased for all participants except S1, who exhibited very little suppression for either pre- or post-patching measurements. On the other hand, the suppression measured with the non-patched eye was not consistently influenced across observers. Pearson's correlation tests were performed to assess if any changes in monocular increment thresholds predicted those measured under CFS. A ratio of the post-patching threshold to the pre-patching threshold was taken for each eye to indicate changes produced by patching. The results showed that the ratios computed from the monocular contrast increment thresholds were not significantly correlated with the ratios computed from the thresholds under CFS (patched eye: $r = .421$, $p = .406$; non-patched eye: $r = -.409$, $p = .421$). An index of *Patching effect* (Equation 3) was also computed for monocular and CFS increment thresholds (Figure 7c). The sensory eye dominance indicated by the inter-ocular suppression evoked by CFS, on average, was moved towards the patched eye following monocular deprivation, but this effect was absent when the increment threshold was measured monocularly. Unlike the mixed effects found with BR dynamics (i.e. an enhancement of the patched eye, a diminution of the non-patched eye, or a combination of both contributed to the alteration of relative eye dominance), the patching effect revealed with the CFS task is largely driven by the reduction in susceptibility of the patched eye to inter-ocular suppression (see Figure 7b).

Whilst the *Patching effect* for the monocular contrast increment threshold is very similar for all observers, there are some differences between individuals for conditions involving inter-ocular suppression. Notably, individuals exhibiting larger patching effects in the CFS condition also tend in general to be more susceptible to CFS (see Figure 7). This is probably because the patching effect measured with CFS manifests in reduced inter-ocular suppression of the patched eye and those observers who were already very resistant to suppression before patching are therefore less able to exhibit a reduction in this effect (e.g. S1).

For the mixed-effects model analyses of the increment thresholds, measured with the probe task, the results showed that none of the factors included in the linear model significantly predicted monocular increment thresholds (*Time*: $t_{(20)} = -0.11$, $p = .913$; *Eye*: $t_{(20)} = -0.20$, $p = .840$; *Eye* × *Time* interaction: $t_{(20)} = -0.46$, $p = .651$). For the *Suppression* index calculated using Equation 1, by contrast, there was a significant main effect of *Time* ($t_{(20)} = -2.36$, $p = .029$) and its interaction with *Eye* ($t_{(20)} = -2.77$, $p = .012$). When averaged across eyes, a decrease in inter-ocular suppression was revealed after monocular patching. The interaction term is of more interest, suggesting a distinct influence of monocular patching on the two eyes. Furthermore, as expected from Figure 7b, the results of separate models for the two eyes showed a decline in suppression after patching only for the patched eye ($t_{(10)} = -3.08$, $p = .012$), whereas there was no change for the non-patched eye ($t_{(10)} = -.40$, $p = .70$). This result reinforces the differential effect patching has on the two eyes.

Interestingly, the analysis of the time course of the patching effects suggested that the difference between eyes decayed over the period of testing but only for the increment thresholds measured with CFS. This was indicated by a significant *Time course* × *Eye* interaction ($t_{(68)} = 2.81$, $p = .006$), while no such effect was found for monocular increment thresholds, BR phase duration, or BR predominance for either noise or grating. Specifically, the CFS threshold for the patched eye increased as time passed, meaning a return to the level before patching. There was no systematic time effect for the threshold measured for the non-patched eye.

4 Discussion

In the current study, monocular deprivation for 2.5 hours altered the relative balance between the two eyes, measured with BR and CFS. Previous research has shown that varying the severity of deprivation (e.g. form vs. light exclusion) results in similar effects on the subsequent contribution of each eye to binocular combination (Zhou, Clavagnier, & Hess, 2013). Our study extends this work to show that opaque patching (c.f. translucent patching used by Lunghi et al., 2011; Lunghi et al., 2013) can also bias ocular dominance measured using tasks involving inter-ocular suppression where the two eyes' images are not fusible. The results highlight the robustness of this plasticity and suggest that the mode of sensory deprivation does not matter for its effect on BR dynamics.

More importantly, by using a CFS task, we were able to show that short-term monocular deprivation changed inhibitory interactions between the two eyes, leaving the monocular contrast increment thresholds unaffected. Specifically, the deprived eye became less susceptible to suppression, (or equivalently the non-deprived eye may become too weak to induce suppression) whereas complementary changes were not found in the other eye. It is worth noting that Sheynin, Proulx, and Hess (2019) reported decreased exclusive dominance for the non-deprived eye's percept during BR with no change in that for the previously deprived eye. This finding may be interpreted in the context of our results of reduced suppression of the deprived eye. A prominent model of binocular rivalry proposes a mechanism involving mutual inhibition and self-adaptation (e.g. Wilson, 2007), implying that the exclusive dominance of one eye's percept depends on the strength of inter-ocular inhibition (elicited by the mechanism encoding the stimulus presented to this eye) of the mechanism encoding the contralateral eye's stimulus. Indeed, Sheynin et al.'s (2019) findings of increased probability of binocular combination and superimposed mixed percepts (simultaneous visibility of the two eyes' images at identical spatial locations in the visual field) also point to a reduced level of inter-ocular suppression following short-term monocular deprivation. Furthermore, the attenuated inter-ocular suppression is consistent with the observation of a reduction in resting concentration of an inhibitory neurotransmitter, gamma-Aminobutyric acid (GABA), in primary visual cortex (V1) following monocular deprivation (Lunghi, Emir, et al., 2015). Our results on the time course of post-deprivation measures, indicate that the suppression of the deprived eye recovered over time, whereas the suppression of the non-deprived eye showed no change. Thus short-term monocular deprivation leads to a unilateral, non-reciprocal change of inter-ocular suppression.

Contrast increment thresholds have often been measured as a function of the pedestal contrast to construct Threshold vs Contrast (TvC) curves that have been used to make inferences about the underlying neural contrast response function of the visual pathways (Legge & Foley, 1980). Although no study has yet characterised the full TvC function following monocular deprivation, factors that influence the shape of the TvC curve have been postulated as the result of concomitant changes (e.g. rescaling) in the response gain and/or contrast gain of the neural response (Bex, Mareschal & Dakin, 2007; Bonds, 1989; Carandini, Heeger, & Movshon, 1997; Geisler & Albrecht, 1992; Heeger, 1992). Indeed, modulation of the gain of the neural contrast response function has been proposed to explain changes in contrast increment thresholds measured during binocular rivalry suppression (Ling, Hubert-Wallander & Blake, 2010). An explanation of the consequences of short-term monocular deprivation favoured by many researchers is that the modulation of ocular dominance arises from reciprocal changes in each eye's contrast gain (Chadnova et al., 2017; Lunghi et al., 2013; Zhou, Clavagnier, & Hess, 2013). Whilst our results did show reduced susceptibility of the previously deprived eye to inter-ocular suppression, which is consistent with that idea, the fact that the non-deprived eye is largely unaffected argues against it. This is because inter-ocular suppression, in either direction, is expected to be influenced when the balance in contrast gain between the two eyes changes. Our results indicate that the suppression of each eye is modulated independently by monocular deprivation.

Crucially, our findings have demonstrated that altered ocular balance is not accompanied by changes in monocular increment threshold. Therefore, we propose that monocular deprivation elicits direct effects on binocular interactions, rather than acting on the monocular contrast gain of each eye which later interactions may be dependent on. Indeed, results from Chadnova et al. (2017) also revealed that changes in eye dominance could only be seen when stimulated dichoptically, whereas monocular stimulation was not able to reveal the bias. Although some studies have reported modified monocular thresholds following deprivation (Zhou, Clavagnier, & Hess, 2013; Zhou et al., 2017; Zhou, Thompson, & Hess, 2013), they measured contrast detection, rather than contrast increment, thresholds. Furthermore in Zhou, Clavagnier, and Hess's (2013) and Zhou, Thompson, and Hess's (2013) studies, only 2 or 3 subjects were tested and the observed changes in monocular thresholds were relatively small[2]. Zhou et al. (2017) tested the same number of subjects (i.e. 6) as the current study, but their analyses only examined differences between the two eyes after the patch was removed (i.e. a main effect of eye). Whether or not monocular thresholds for each eye were altered by patching was not statistically evaluated. Further research is needed to address the reliability of this finding but at present it is sufficient to conclude that monocular increment thresholds are unchanged by short-term monocular deprivation and cannot predict the pattern of changes in CFS thresholds (see Figure 7a and b).

Our findings in the context of binocular rivalry appear to be consistent with models where inter-ocular suppression is driven by opponency units detecting

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[2] Zhou, Thompson, and Hess (2013) examined the effect of monocular deprivation on monocular detection thresholds in three amblyopic subjects. Two of the subjects showed significant changes, whereas reciprocal changes in the two eyes were not always present. The third subject did not show any significant changes in monocular thresholds.

conflicts between the two eyes' inputs (Katyal, Engel, He, & He, 2016; Katyal, Vergeer, He, He, & Engel, 2018; Said & Heeger, 2013). The neurophysiological basis is thought to be neurons that can compute either the sum or difference in input between the eyes (Smith III, Chino, Ni, Ridder, & Crawford, 1997). Psychophysical evidence suggests that these summation and differencing mechanisms are independently adaptable (May & Zhaoping, 2016; May, Zhaoping, & Hibbard, 2012). This form of opponency provides a plausible account for our results in that the strength of inter-ocular inhibition may be changed by directly modifying the activity of opponency channels without affecting monocular processing. Notably, a signature of this class of model is the prediction of weaker inter-ocular inhibition after selective adaptation of the opponency channel. In binocular rivalry studies, this notion receives empirical support from the observation of increased probability of mixed perception over prolonged exposure to non-fusible dichoptic stimulation (Klink, Brascamp, Blake, & Van Wezel, 2010; Said & Heeger, 2013). Here, the dampened activity in the opponency channel from adaptation produces lower inter-ocular inhibition and over time becomes less able to sustain exclusive dominance of one eye's percept over the other. One way of evaluating whether opponency channels are modified by short-term monocular deprivation would be to look at changes in rivalry perception (dominance versus mixed percepts) before and after patching. However, the current experimental design, where the order of measurements was randomised and intermingled between conditions is not well suited to examine this. We are however conducting other work that we hope to report in the near future that should be able to address this issue more directly. At present we cannot rule out an opponency-based scheme, but it is not the only possible explanation.

Alternatively, our findings can be interpreted within the framework offered by gain control models of binocular vision (Ding, Klein, & Levi, 2013a, 2013b; Ding & Sperling, 2006; Meese, Georgeson, & Baker, 2006). These models are based on the idea that the visual system relies on contrast gain control to optimise sensitivity (Gardner et al., 2005; Ohzawa, Sclar, & Freeman, 1985). Specifically, the input from each eye (C_L and C_R for the left and right eye, respectively) undergoes divisive inhibition before the monocular outputs from the two eyes' channels are summed for binocular perception. Figure 8 illustrates the components of such types of model in which our results may be explained. If deprivation only acts on the inter-ocular suppression of the patched eye (say the left eye) by the non-patched eye (S_{RL}), as indicated by our results, the monocular gain of the patched eye (ε_L) will not be altered. Note that the models suggest a dependence of the inter-ocular suppression of one eye (S_{RL} or S_{LR}) on the other eye's gain (ε_R or ε_L), known as inter-ocular gain control. This predicts that the reduced suppression of the patched eye may result from a decreased gain of the non-patched eye (possibly due to a lowered gain efficiency, μ_R), which is, however, not the pattern seen in our results. Our results, therefore, indicate an extra parameter of the intrinsic susceptibility of the eye to inter-ocular inhibition (I_L and I_R), that weights the gain-dependent inter-ocular suppression component (S_{RL} and S_{LR}), and which can be adjusted by short-term monocular deprivation. This notion can be incorporated into the first stage (i.e. before binocular summation) of Meese et al.'s (2006) two-stage model, by including independent weights to monocular and inter-ocular gain control such that the latter is subject to the influence of monocular deprivation (see also Spiegel, Baldwin, and Hess, 2017).

Our study extends the finding of opaque patching on binocular contrast combination between fusible stimuli to binocular rivalry between non-fusible stimuli. A recent study has revealed a lack of relationship between the deprivation effects on different binocular processes despite using similar measurement (Baldwin & Hess, 2018). In Baldwin and Hess's (2018) study, the effect of monocular deprivation was assessed in two variations of dichoptic masking, when the orientations of the two eyes' stimuli were the same (i.e. parallel condition) and when they were very different (i.e. cross-orientation condition). Their results showed a reduction in masking effects (i.e. elevated thresholds) in the deprived eye on both tasks, but that the individual differences in magnitude of this deprivation effect revealed in the two tasks were not correlated. Based on the binocular fusibility of stimuli, Baldwin and Hess (2018) proposed a mechanistic link between parallel dichoptic masking and binocular contrast combination, and between cross-orientation dichoptic masking and binocular rivalry, respectively. It is therefore reasonable to place a caveat on the conclusion—although we have shown consequences on eye dominance in binocular rivalry similar to those found previously in binocular contrast combination (e.g. Zhou, Clavagnier, & Hess, 2013), these do not necessarily posit a common mechanism of plasticity.

A binocular phase combination task is frequently used to assess the effect of deprivation on ocular dominance (Bai et al., 2017; Y. Wang, Yao, He, Zhou, & Hess, 2017; Yao et al., 2017; Zhou, Clavagnier, & Hess, 2013; Zhou et al., 2014; Zhou et al., 2017; Zhou, Thompson, & Hess, 2013). However, there may be multiple binocular processes involved in this task, making it hard to disentangle the underlying mechanisms. Evidence suggests that binocular fusion and inter-ocular suppression are both likely to occur for a blurred, horizontally-oriented edge that has a small vertical disparity between the two eyes, but these two consequences are mutually exclusive (Georgeson & Wallis, 2014). When it comes to using the phase combination task as a measure of binocular perception, we cannot tell whether a biased perception occurs because the two monocular images (with a vertical offset) are fused to form a binocular percept (whereby the contributions from the two eyes are imbalanced), or because of suppression of one of the images. The probability of suppression is even higher when there is an imbalance in the contrast between the two eyes' inputs (Georgeson & Wallis, 2014). Although fusion and suppression both reflect aspects of each eye's contribution to perception after binocular interactions, they may be differentially affected by deprivation.

In the present study, an opaque patch was used, suggesting that the plastic changes observed are mostly input driven. There may be other circumstances, where other sources of inter-ocular imbalance are involved. For example, Kim, Kim, and Blake (2017) have illustrated that both a lack of conscious awareness in one eye, rendered by CFS, and a reduction in contrast energy relative to the other eye, are able to induce a bias favouring the affected eye. In addition, the shift in eye dominance can also be demonstrated in a rivalry task when the inputs to the two eyes have matched Fourier amplitude spectra but scrambled spatial phases (Bai et al., 2017). A plausible explanation is that the scrambled image is less useful than the normal image viewed by the other eye, and the participant selectively attends to the untreated eye's input. In this view it is the imbalanced allocation of attention that drives the subsequent, compensatory, enhancement of the treated eye. It is reasonable to assume that the consequences of an imbalance in attention between eyes may be revealed only with dichoptic stimuli that are not fusible. This is because there is no competition between eyes in terms of attention when tested with fusible stimuli, and therefore compensatory processes may not be triggered. Nonetheless, the hypothesis that higher-level factors may also play a role in ocular dominance plasticity is still preliminary and systematic examinations are needed, which we are currently exploring in our laboratory.

On the basis of our current sample, we were able to compare the patching effects assessed with BR and CFS, two processes that are strongly related (M. Wang, McGraw, & Ledgeway, 2019a, 2019b). Yet, the manner in which these two types of inter-ocular suppression are affected by deprivation may not be the same. Unlike the unilateral changes under CFS, for BR we found mixed effects: an enhancement of the deprived eye, a diminution of the non-deprived eye, or a combination of both contributed to the alteration of sensory eye dominance. Similar mixed patterns of changes in phase duration of each eye's image were also observed in other studies examining the effect of short-term monocular deprivation on BR (e.g. visual inspection of Figure 3a in Binda & Lunghi, 2017). This implies that the relative, but not absolute strength, of each eye's contribution is more important for BR. In support, using principal component analysis (PCA), Sheynin et al. (2019) have demonstrated that a principal component representing relative eye dominance explained the changes in BR dynamics produced by monocular deprivation whilst another principal component representing exclusive dominance independent of eye of origin did not significantly predict the results. This conclusion links to our previous finding of a discrepancy between eye dominance manifested in CFS and BR (M. Wang, McGraw, & Ledgeway, 2019a, 2019b), pointing to potentially different mechanisms.

To summarise, our study has illustrated a boost to one eye that has been deprived of input for a few hours, relative to the other eye, in two tasks involving inhibitory binocular interactions. Importantly, we found that this shift in ocular dominance is specifically due to reduced inter-ocular suppression (inhibition) of the deprived eye. This is conceivably relevant to the notion that the degraded plasticity of adult brains is associated with an altered excitation/inhibition balance (i.e. increased inhibition) compared to developing brains (Chen et al., 2011; Keck et al., 2011; van Versendaal & Levelt, 2016). Recent studies in amblyopia have shown abnormally reduced inter-ocular suppression of the fellow eye by the amblyopic eye (Ding et al., 2013a; Huang, Baker, & Hess, 2012; Zhou et al., 2018). Our findings imply that inter-ocular suppression can be modulated for each eye separately, which may be relevant when the level of inter-ocular suppression has to be adjusted in only one eye. One implication is that in adults with amblyopia, an effective method may be to occlude the amblyopic rather than unaffected eye for short periods of time.

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Figure legends

Figure 1: A typical trial sequence of the CFS protocol (a) and the corresponding contrast profiles of the stimuli over time (b). After the initiation of the trial, a noise pattern was presented to one eye (right eye in this example) and a sinusoidal grating was simultaneously presented to the other eye. The noise image was replaced with a new sample every 100 ms (i.e. at 10 Hz). Once the participant indicated the exclusive dominance of the noise pattern by pressing a key, a probe (contrast increment) was presented randomly to either the top or bottom half of the grating (the top in this diagram), lasting 500 ms and modulated by a Gaussian window with a SD of 100 ms. The location of the probe was judged after its offset.

Figure 2: Phase duration distributions for exclusive noise percepts experienced by the patched eye (yellow) and non-patched eye (red), plotted as probability density functions, separately for pre- (upper panel) and post-patching (lower panel), and for each individual. The phase durations were normalised to each observer's mean noise percept duration prior to monocular patching. The curves are plotted as the gamma PDFs, with the parameters estimated from fitting with gamma CDFs (Equation 2). The fit results, including the estimated parameters, ρ and λ, and the goodness of fit indicated by R^2 are shown.

Figure 3: Normalised phase duration distributions for exclusive grating percepts. Conventions are the same as in Figure 2.

Figure 4: Normalised phase duration distributions for exclusive noise or grating percepts pooled across all the six subjects. Conventions are the same as in Figures 2 and 3.

Figure 5: Ratios of the shape parameter (ρ) to scale parameter (λ) for the fitted phase duration distributions of (a) noise percepts and (b) grating percepts, for pre(red) and post-patching measurements (black). The ordinates indicate the ratios for the patched eye and the abscissae show those for the non-patched eye. The dotted lines indicate equal ratios for the two eyes. Small symbols represent data for different individuals. The grand means calculated across all participants are marked by the large crosses (error bars: ±1 SEM).

Figure 6: The changes of BR dynamics produced by monocular patching. The pre- (red) and post-patching measurements (black) for the patched eye versus non-patched eye are shown in (a)-(d). Small symbols represent data for individuals. The mean data across all participants are marked by the large crosses. (a) Mean phase

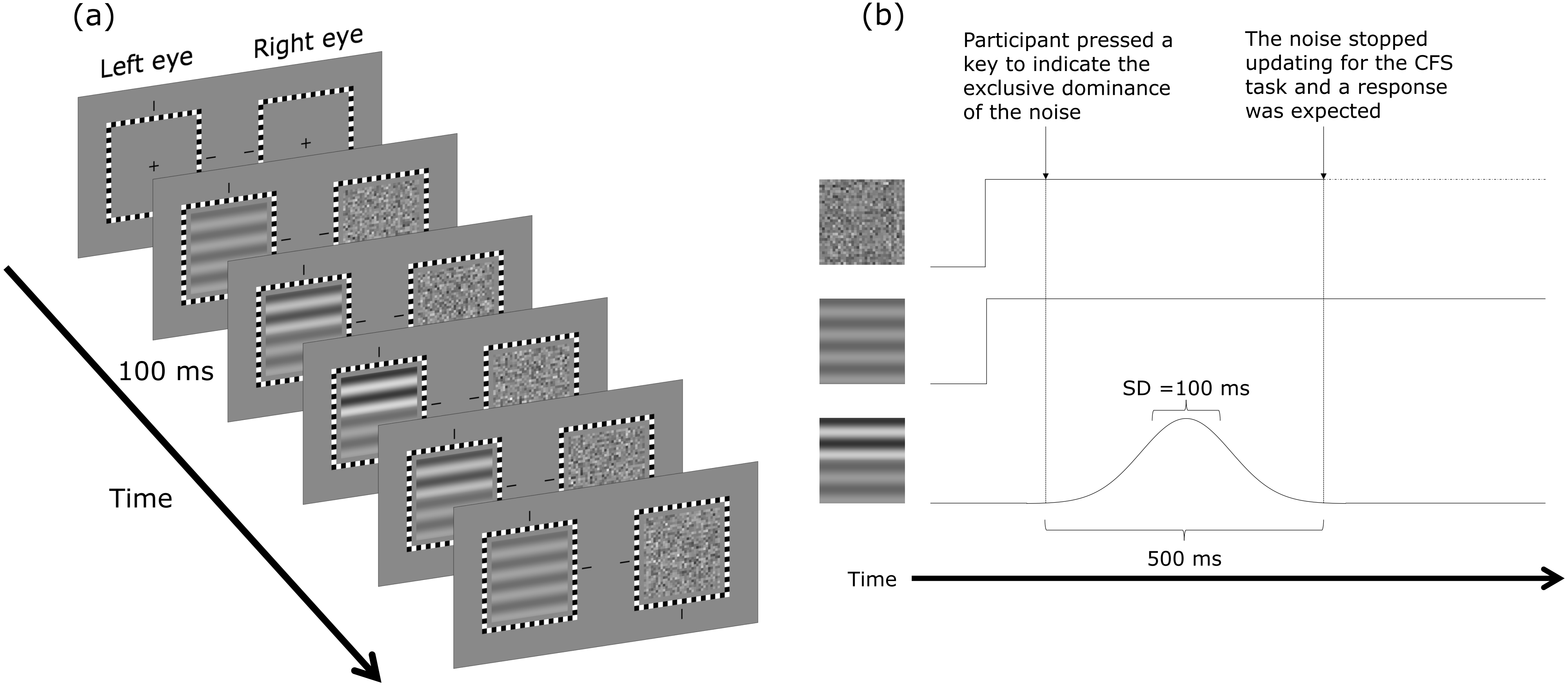
duration for exclusive noise percepts. (b) Mean phase duration for exclusive grating percepts. (c) Proportion of time (i.e. predominance) that the noise is being perceived. (d) Grating predominance. The dotted line depicts where the patched eye exhibited equal strength to the non-patched eye. Patched eye dominance is indicated by data points that fall above the diagonal dotted line, while data points below the line show non-patched eye dominance. Horizontal and vertical bars represent the ±1 SEM. The *Patching effect* index (Equation 3) quantifying the degree of eye dominance for the post-patching measurement relative to that for the pre-patching measurement is shown in (e), in terms of BR mean phase duration and predominance for each exclusive percept. Individual data are shown as grey symbols. The horizontal solid lines show the grand means calculated across all six participants for the corresponding condition. The horizontal dotted line represents no difference between measures obtained before and after monocular patching.

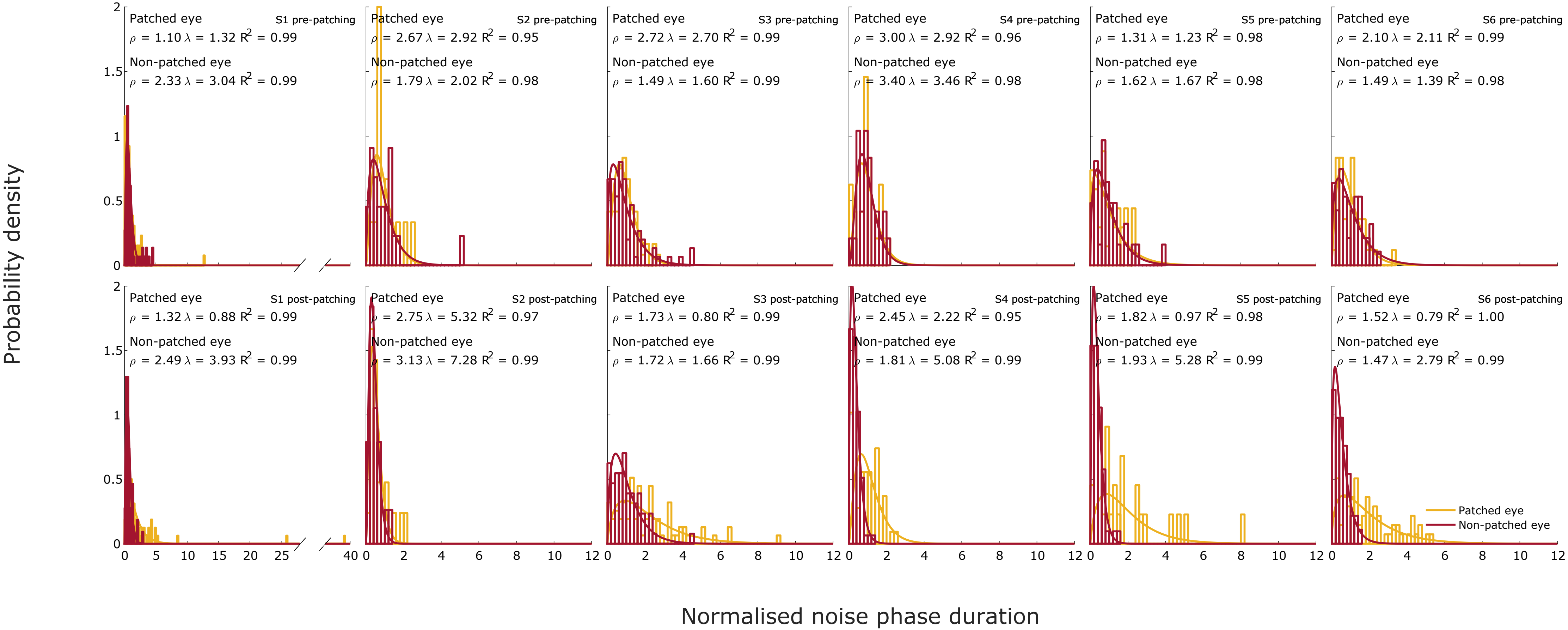
Figure 7: The effects of monocular patching on contrast increment thresholds measured with the probe detection task. The pre- and post-patching measurements of (a) monocular contrast increment thresholds for the patched eye versus non-patched eye and (b) those for the thresholds measured under CFS. (c) *Patching effect* index (Equation 3) for contrast increment thresholds measured in the monocular condition and under CFS. Conventions are the same as in Figure 6 with the following exception. In (a) and (b) data points falling below the diagonal dotted line indicate patched eye dominance. Note that in (c) the different direction of change in *Patching effect* values calculated with probe thresholds from that for BR temporal dynamics (Figure 6e) indicates the same shift in sensory eye dominance (see text for further details).

Figure 8: A schematic model within which the current findings may be interpreted. C_L and C_R (boxes) represent the input strength of the two eyes (i.e. contrast). μ_L and μ_R (green arrowed paths) are the gain efficiency of the two monocular channels. ε_L and ε_R (circles) are the monocular contrast gain for the two eyes. The gain of an eye is determined by both the input strength in this eye and the gain efficiency of the corresponding monocular channel. I_L and I_R (red dots) are the intrinsic susceptibility of each eye to inter-ocular inhibition and are independent of the monocular gain. The subscripts L and R of these parameters represent the parameters for the left and right eye, respectively. S_{RL} is the output suppression of the left eye by the right eye and S_{LR} is the inter-ocular suppression in the converse direction (black lines ending in a dot). This output suppression of an eye depends on both the intrinsic susceptibility to inter-ocular inhibition of this eye and the monocular contrast gain of both eyes. It is assumed that the outputs following such

inhibitory inter-ocular interactions will subsequently undergo binocular summation.

Figure 1


(a)
Left eye
Right eye
100 ms
Time
(b)
Participant pressed a key to indicate the exclusive dominance of the noise
The noise stopped updating for the CFS task and a response was expected
SD =100 ms
500 ms
Time


Probability density
Normalised noise phase duration
Patched eye
S1 pre-patching
ρ = 1.10 λ = 1.32 R2 = 0.99
Non-patched eye
ρ = 2.33 λ = 3.04 R2 = 0.99
Patched eye
S2 pre-patching
ρ = 2.67 λ = 2.92 R2 = 0.95
Non-patched eye
ρ = 1.79 λ = 2.02 R2 = 0.98
Patched eye
S3 pre-patching
ρ = 2.72 λ = 2.70 R2 = 0.99
Non-patched eye
ρ = 1.49 λ = 1.60 R2 = 0.99
Patched eye
S4 pre-patching
ρ = 3.00 λ = 2.92 R2 = 0.96
Non-patched eye
ρ = 3.40 λ = 3.46 R2 = 0.98
Patched eye
S5 pre-patching
ρ = 1.31 λ = 1.23 R2 = 0.98
Non-patched eye
ρ = 1.62 λ = 1.67 R2 = 0.98
Patched eye
S6 pre-patching
ρ = 2.10 λ = 2.11 R2 = 0.99
Non-patched eye
ρ = 1.49 λ = 1.39 R2 = 0.98
Patched eye
S1 post-patching
ρ = 1.32 λ = 0.88 R2 = 0.99
Non-patched eye
ρ = 2.49 λ = 3.93 R2 = 0.99
Patched eye
S2 post-patching
ρ = 2.75 λ = 5.32 R2 = 0.97
Non-patched eye
ρ = 3.13 λ = 7.28 R2 = 0.99
Patched eye
S3 post-patching
ρ = 1.73 λ = 0.80 R2 = 0.99
Non-patched eye
ρ = 1.72 λ = 1.66 R2 = 0.99
Patched eye
S4 post-patching
ρ = 2.45 λ = 2.22 R2 = 0.95
Non-patched eye
ρ = 1.81 λ = 5.08 R2 = 0.99
Patched eye
S5 post-patching
ρ = 1.82 λ = 0.97 R2 = 0.98
Non-patched eye
ρ = 1.93 λ = 5.28 R2 = 0.99
Patched eye
S6 post-patching
ρ = 1.52 λ = 0.79 R2 = 1.00
Non-patched eye
ρ = 1.47 λ = 2.79 R2 = 0.99
Patched eye
Non-patched eye
0
0.5
1
1.5
2
0
5
10
15
20
25
40
0
2
4
6
8
10
12

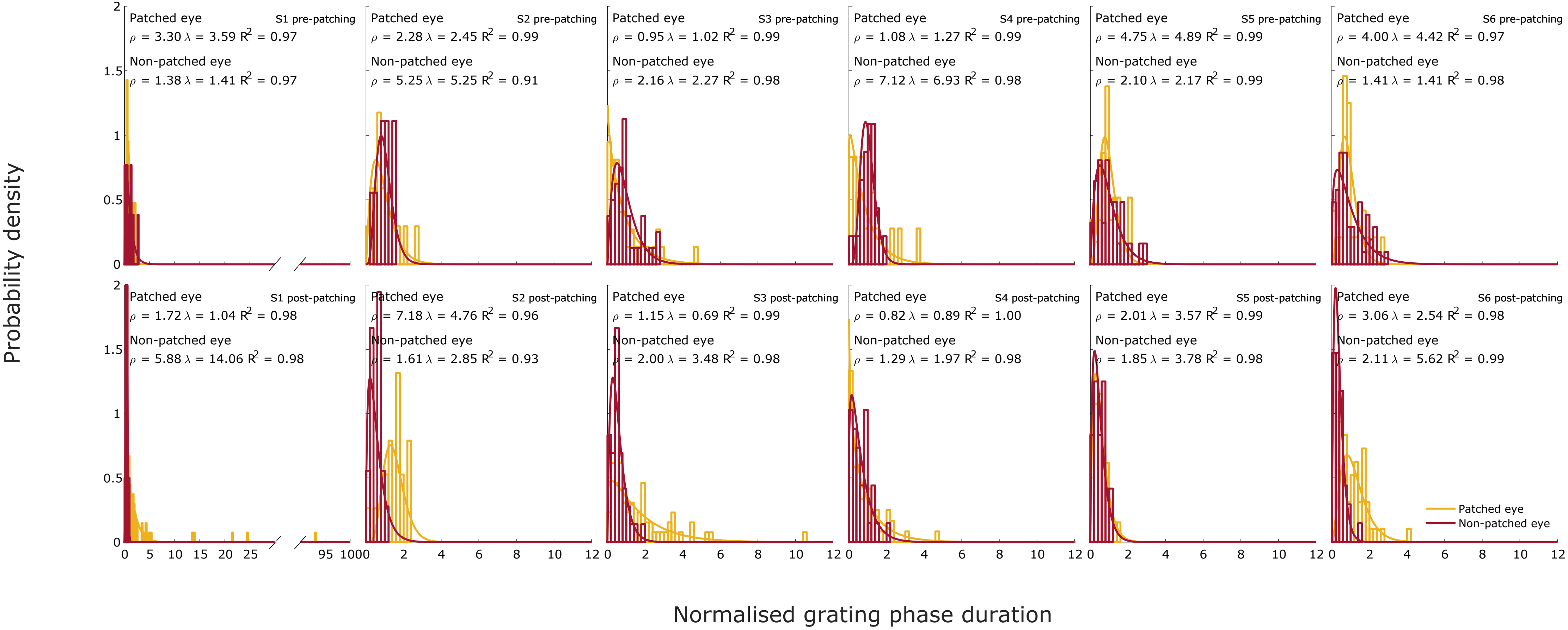
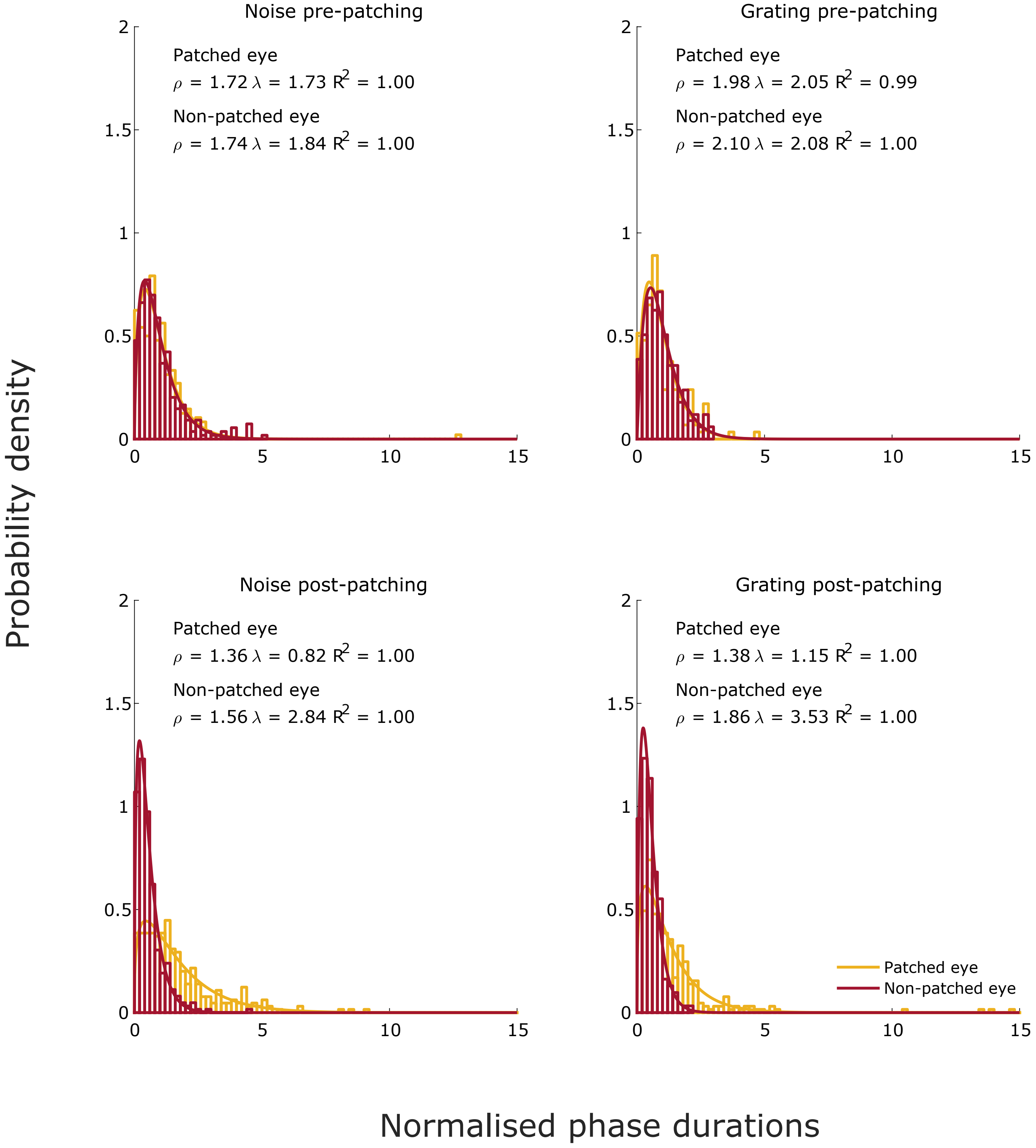

Probability density
Normalised grating phase duration
Patched eye
S1 pre-patching
ρ = 3.30 λ = 3.59 R2 = 0.97
Non-patched eye
ρ = 1.38 λ = 1.41 R2 = 0.97
Patched eye
S2 pre-patching
ρ = 2.28 λ = 2.45 R2 = 0.99
Non-patched eye
ρ = 5.25 λ = 5.25 R2 = 0.91
Patched eye
S3 pre-patching
ρ = 0.95 λ = 1.02 R2 = 0.99
Non-patched eye
ρ = 2.16 λ = 2.27 R2 = 0.98
Patched eye
S4 pre-patching
ρ = 1.08 λ = 1.27 R2 = 0.99
Non-patched eye
ρ = 7.12 λ = 6.93 R2 = 0.98
Patched eye
S5 pre-patching
ρ = 4.75 λ = 4.89 R2 = 0.99
Non-patched eye
ρ = 2.10 λ = 2.17 R2 = 0.99
Patched eye
S6 pre-patching
ρ = 4.00 λ = 4.42 R2 = 0.97
Non-patched eye
ρ = 1.41 λ = 1.41 R2 = 0.98
Patched eye
S1 post-patching
ρ = 1.72 λ = 1.04 R2 = 0.98
Non-patched eye
ρ = 5.88 λ = 14.06 R2 = 0.98
Patched eye
S2 post-patching
ρ = 7.18 λ = 4.76 R2 = 0.96
Non-patched eye
ρ = 1.61 λ = 2.85 R2 = 0.93
Patched eye
S3 post-patching
ρ = 1.15 λ = 0.69 R2 = 0.99
Non-patched eye
ρ = 2.00 λ = 3.48 R2 = 0.98
Patched eye
S4 post-patching
ρ = 0.82 λ = 0.89 R2 = 1.00
Non-patched eye
ρ = 1.29 λ = 1.97 R2 = 0.98
Patched eye
S5 post-patching
ρ = 2.01 λ = 3.57 R2 = 0.99
Non-patched eye
ρ = 1.85 λ = 3.78 R2 = 0.98
Patched eye
S6 post-patching
ρ = 3.06 λ = 2.54 R2 = 0.98
Non-patched eye
ρ = 2.11 λ = 5.62 R2 = 0.99
Patched eye
Non-patched eye
0
0.5
1
1.5
2
0
5
10
15
20
25
95
100
0
2
4
6
8
10
12

Figure 4



Noise pre-patching
Patched eye
ρ = 1.72 λ = 1.73 R² = 1.00
Non-patched eye
ρ = 1.74 λ = 1.84 R² = 1.00
Grating pre-patching
Patched eye
ρ = 1.98 λ = 2.05 R² = 0.99
Non-patched eye
ρ = 2.10 λ = 2.08 R² = 1.00
Noise post-patching
Patched eye
ρ = 1.36 λ = 0.82 R² = 1.00
Non-patched eye
ρ = 1.56 λ = 2.84 R² = 1.00
Grating post-patching
Patched eye
ρ = 1.38 λ = 1.15 R² = 1.00
Non-patched eye
ρ = 1.86 λ = 3.53 R² = 1.00
Patched eye
Non-patched eye
0
0.5
1
1.5
2
0
5
10
15
Probability density
Normalised phase durations

Figure 5

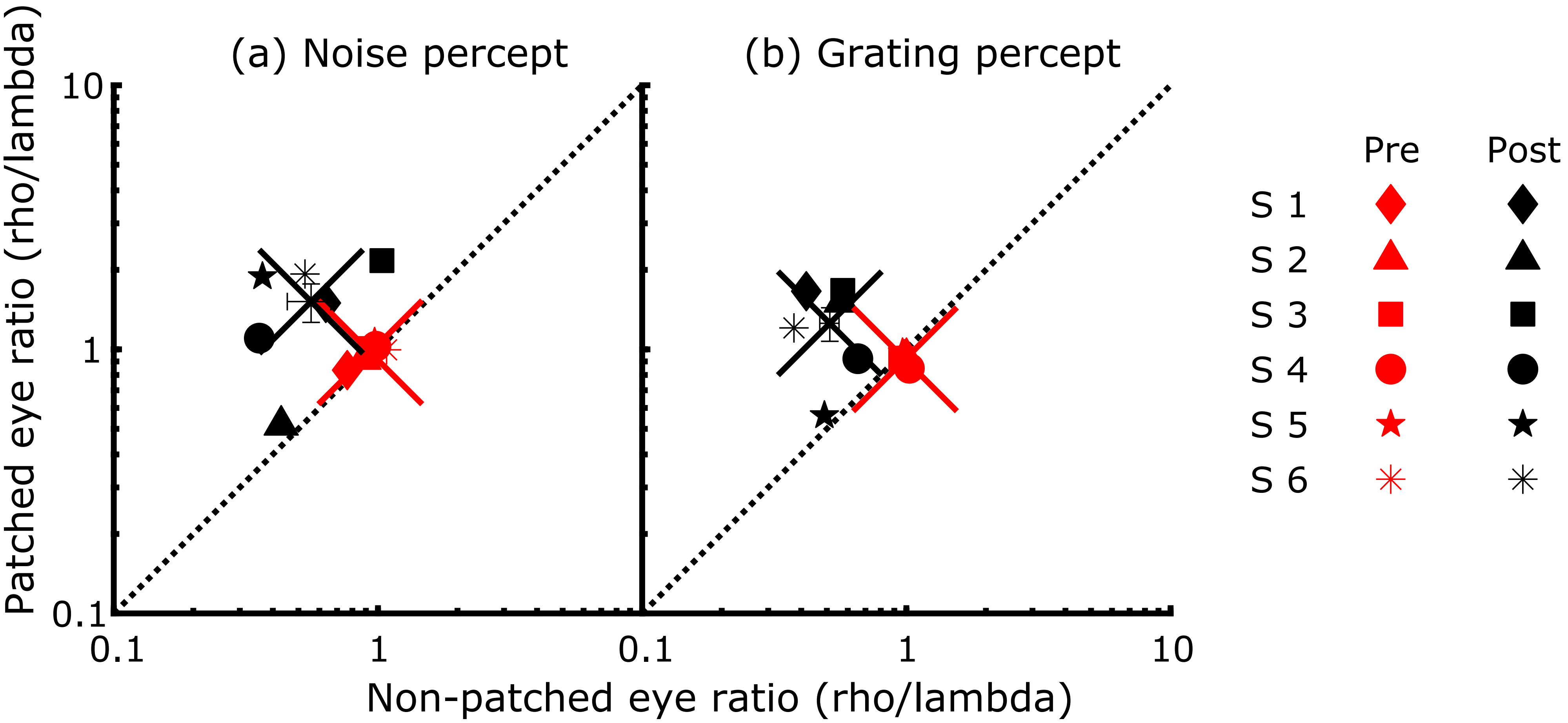

(a) Noise percept
(b) Grating percept
Patched eye ratio (rho/lambda)
Non-patched eye ratio (rho/lambda)
10
1
0.1
0.1
1
0.1
1
10
Pre
Post
S 1
S 2
S 3
S 4
S 5
S 6

Figure 6

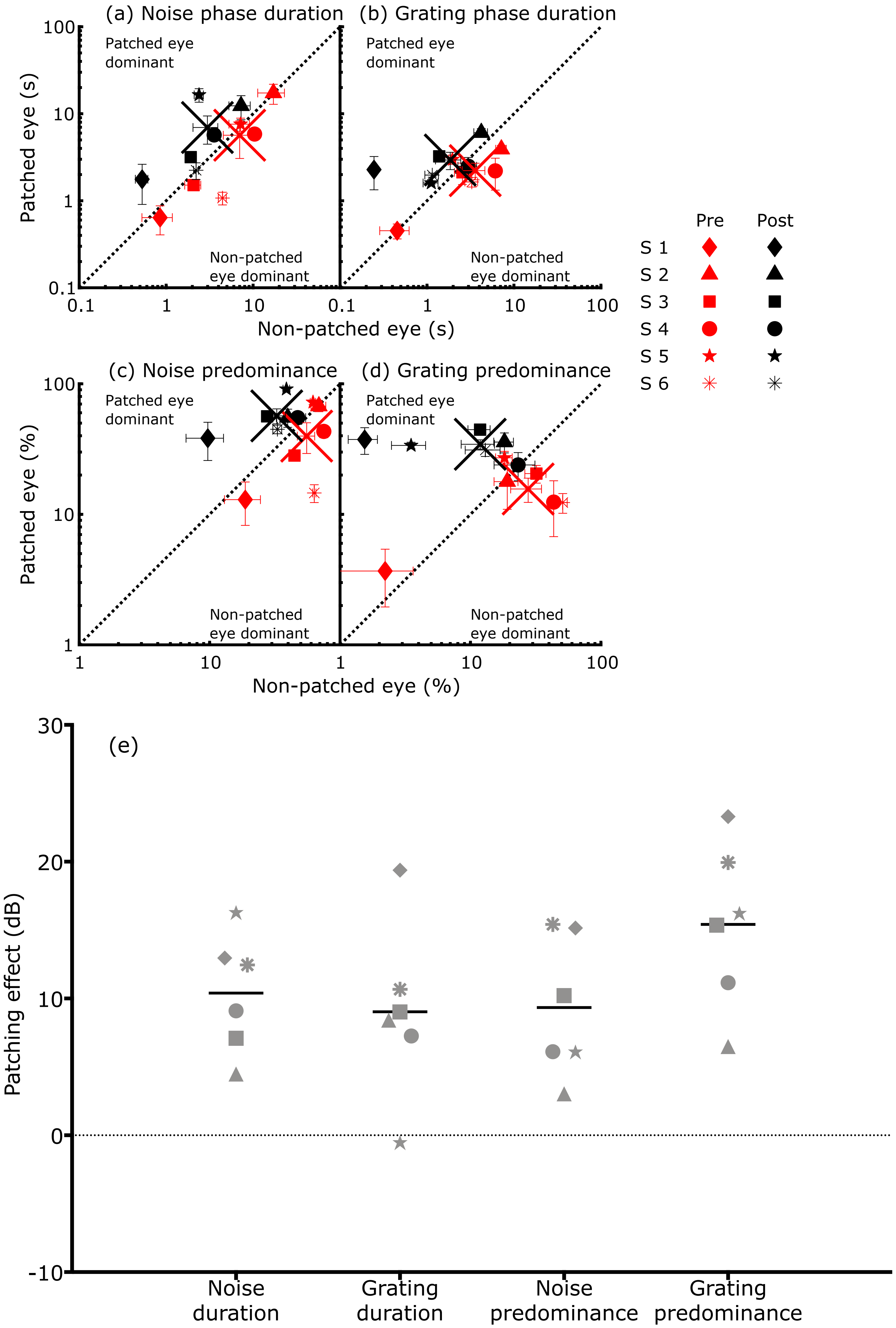

(a) Noise phase duration
(b) Grating phase duration
Patched eye dominant
Non-patched eye dominant
Patched eye (s)
Non-patched eye (s)
100
10
1
0.1
(c) Noise predominance
(d) Grating predominance
Patched eye (%)
Non-patched eye (%)
Pre
Post
S 1
S 2
S 3
S 4
S 5
S 6
(e)
Patching effect (dB)
30
20
10
0
-10
Noise duration
Grating duration
Noise predominance
Grating predominance

Figure 7

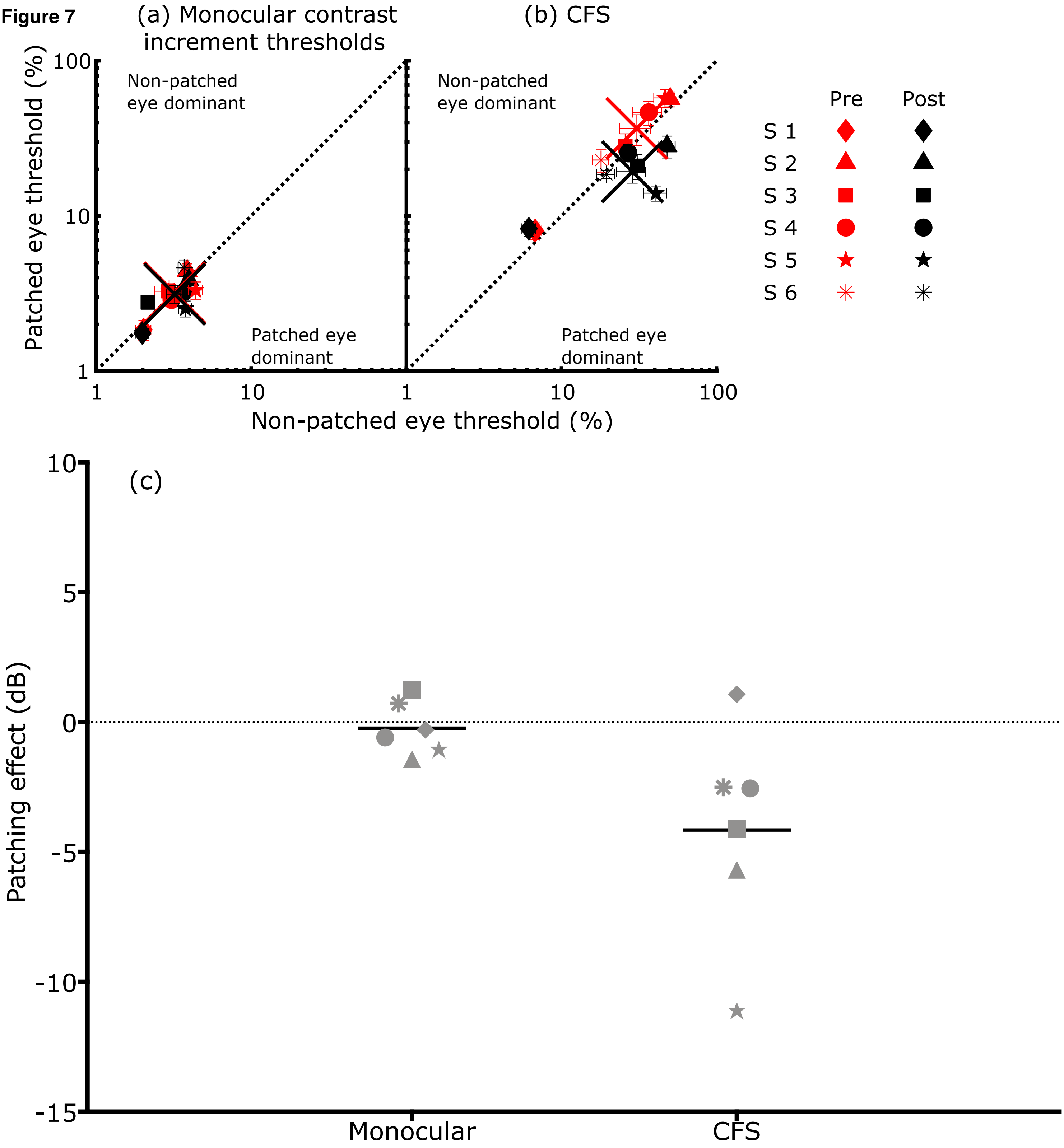
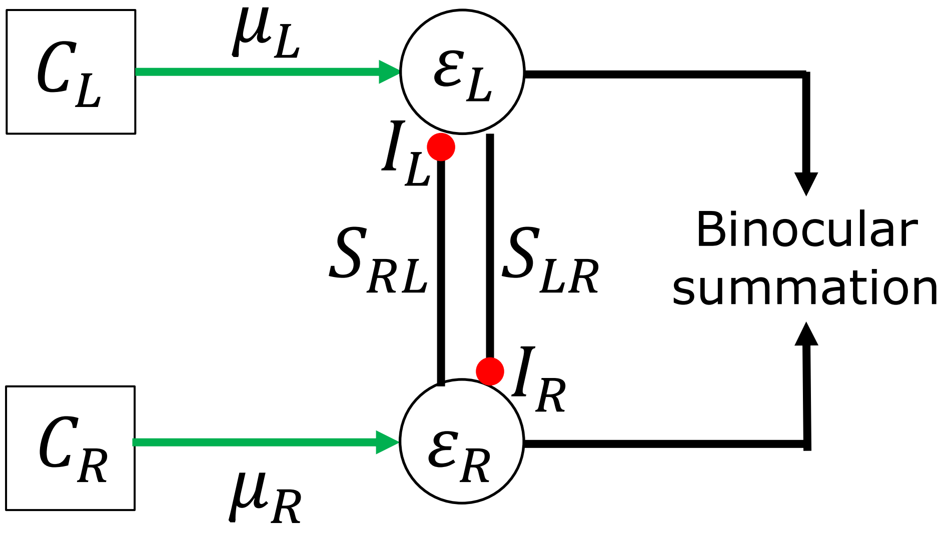

(a) Monocular contrast increment thresholds
(b) CFS
Patched eye threshold (%)
Non-patched eye threshold (%)
Non-patched eye dominant
Patched eye dominant
Non-patched eye dominant
Patched eye dominant
1
10
100
1
10
1
10
100
Pre
Post
S 1
S 2
S 3
S 4
S 5
S 6
(c)
Patching effect (dB)
10
5
0
-5
-10
-15
Monocular
CFS

Figure 8


C_L
μ_L
ε_L
I_L
S_{RL}
S_{LR}
Binocular summation
I_R
C_R
ε_R
μ_R

Mengxin Wang: Investigation, Formal analysis, Methodology, Writing — Original Draft, Writing — Review & Editing, Visualization. **Paul McGraw**: Investigation, Conceptualization, Methodology, Resources, Writing — Original Draft, Writing — Review & Editing, Supervision. **Timothy Ledgeway**: Investigation, Conceptualization, Software, Methodology, Resources, Writing — Original Draft, Writing — Review & Editing, Supervision.