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Attentional eye selection modulates sensory eye dominance

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Abstract:	Brief periods of monocular deprivation significantly modify binocular visual processing. For example, patching one eye for a few hours alters the inter-ocular balance, with the previously patched eye becoming dominant once the patch is removed (Lunghi, Burr, & Morrone, 2011; Lunghi, Burr, & Morrone, 2013). However, the contribution of higher-level visual processing to this phenomenon is still unclear. Here, we compared changes in sensory eye dominance produced by three types of monocular manipulations in adult participants with normal binocular vision. One eye was covered for 150 minutes using either an opaque patch, a diffusing lens, or a prism that inverted the image. All three manipulations altered dominance duration and predominance during binocular rivalry (BR) in favour of the treated eye and the time courses of the changes were similar. These results indicate that modifications of luminance or contrast are not strictly necessary to drive shifts in eye dominance, as both were unaltered in the prism condition. Next, we found that shifts in eye dominance were dependent on attentional demands during the monocular treatment period, providing support for the role of attentional eye selection in modulating eye dominance. Finally, we found relatively rapid build-up of the ocular dominance shift after the onset of monocular treatment. Taken together, our results suggest that modifications to monocular input alter inter-ocular balance via selective attentional mechanisms that bias output towards the deprived eye. Eye-based attention may play an important role in conditions where normal input to one eye is disrupted, such as childhood amblyopia.

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Abstract

Brief periods of monocular deprivation significantly modify binocular visual processing. For example, patching one eye for a few hours alters the inter-ocular balance, with the previously patched eye becoming dominant once the patch is removed (Lunghi, Burr, & Morrone, 2011; Lunghi, Burr, & Morrone, 2013). However, the contribution of higher-level visual processing to this phenomenon is still unclear. Here, we compared changes in sensory eye dominance produced by three types of monocular manipulations in adult participants with normal binocular vision. One eye was covered for 150 minutes using either an opaque patch, a diffusing lens, or a prism that inverted the image. All three manipulations altered dominance duration and predominance during binocular rivalry (BR) in favour of the treated eye and the time courses of the changes were similar. These results indicate that modifications of luminance or contrast are not strictly necessary to drive shifts in eye dominance, as both were unaltered in the prism condition. Next, we found that shifts in eye dominance were dependent on attentional demands during the monocular treatment period, providing support for the role of attentional eye selection in modulating eye dominance. Finally, we found relatively rapid build-up of the ocular dominance shift after the onset of monocular treatment. Taken together, our results suggest that modifications to monocular input alter inter-ocular balance via selective attentional mechanisms that bias output towards the deprived eye. Eye-based attention may play an important role in conditions where normal input to one eye is disrupted, such as childhood amblyopia.

Introduction

Patching one eye for several hours, while maintaining normal visual input to the other eye, induces changes in the balance between the two eyes' contributions to binocular vision (e.g. Lunghi et al., 2011; Lunghi et al., 2013; Zhou, Clavagnier, & Hess, 2013). That is, after removing the patch the previously occluded eye becomes more dominant, revealed by both psychophysical and physiological measures (Begum & Tso, 2015, 2016; Binda et al., 2018; Chadnova, Reynaud, Clavagnier, & Hess, 2017; Lunghi, Berchicci, Morrone, & Di Russo, 2015; Tso, Miller, & Begum, 2017; Zhou, Baker, Simard, Saint-Amour, & Hess, 2015). The neural locus of these changes is thought to be in primary visual cortex (V1) (Binda et al., 2018; Chadnova et al., 2017; Lunghi, Berchicci, et al., 2015; Lunghi, Emir, Morrone, & Bridge, 2015), where neurons whose responses are predominately driven by inputs from either eye are arranged in alternating ocular dominance columns (Adams, Sincich, & Horton, 2007; Hubel & Wiesel, 1969; Tootell, Hamilton, Silverman, & Switkes, 1988). Crucially, observations of reciprocal changes in the responsiveness of both eyes (Lunghi, Berchicci, et al., 2015; Zhou, Clavagnier, & Hess, 2013; Zhou, Reynaud, Kim, Mullen, & Hess, 2017; Zhou, Thompson, & Hess, 2013), and an altered depth of inter-ocular suppression after controlling for monocular contrast sensitivity (Wang, Ledgeway, & McGraw, 2019; Wang, McGraw, & Ledgeway, 2020) suggest a binocular effect. These findings point to ocular dominance plasticity in human adults whose visual system is believed to be relatively hard wired. Understanding the processes that drive the shifts of ocular dominance following unusual binocular visual experience may not only deliver useful insights into binocular vision in general, but also help treatment of visual anomalies involving large asymmetries in spatial vision between the two eyes, such as amblyopia (Barrett, Bradley, & McGraw, 2004).

In the work by Lunghi and others (2011, 2013), a translucent occluder was used to deprive one eye of spatial information for 2.5 hours, giving rise to (approximately) matched luminance in the two eyes. Recently we have similarly shown that an opaque patch, which eliminates all visual input to an eye, is also effective in increasing the patched eye's subsequent relative dominance in a binocular rivalry (BR) task (Wang et al., 2019; Wang et al., 2020). Some work has compared the effects of translucent and opaque patching in the same study, and comparable shifts in eye dominance were observed (Begum & Tso, 2016; Chadnova et al., 2017; Zhou, Clavagnier, & Hess, 2013). The result that full occlusion is no more effective than contrast deprivation may imply that inter-ocular imbalance in spatial information may be a key factor in modulating sensory eye dominance. In support, it has been found that reducing the contrast of a monocular image for some time, increased relative dominance of the treated eye (Kim, Kim, & Blake, 2017; Zhou, Reynaud, & Hess, 2014), whilst changes in relative inter-ocular luminance differences failed to produce any effect on subsequent eye dominance (Yao et al., 2017). By comparing various forms of short-term monocular manipulation we may gain important insights into the mechanisms regulating ocular balance.

A few previous studies have investigated the effects produced by several variants of monocular deprivation, but they have focused on manipulation of low-level sensory input, such as elimination of a certain range of spatial frequencies or disruption of phase regularity (Bai, Dong, He, & Bao, 2017; Zhou et al., 2014). However, it has been shown that cognitive mechanisms, such as selective attention, are also involved in some forms of eye dominance plasticity (Dieter, Melnick, & Tadin, 2016; Ooi, Su, Natale, & He, 2013; Xu, He, & Ooi, 2010). Consequently, it remains unknown whether higher-level processes also contribute to changes in sensory eye dominance following manipulations of monocular input. Therefore, in the current study we sought to compare the effects of luminance (opaque patch), contrast (diffusing lens), and spatial mismatches (inverting prism) on sensory eye dominance. In the latter case the mismatch in low-level spatial and temporal input is minimised, presumably revealing the influence of selective attention.

Experiment 1: How do different types of monocular treatment modulate subsequent sensory eye dominance?

Methods

Observers

Nine participants who had normal or corrected-to-normal vision took part in the study (age range: 23–51 years, one female), and were staff or students at the University of Nottingham. All but three (the authors) were naïve to the purpose of the study. Two of the participants were only available to complete the opaque patch and diffuser conditions, and another participant only completed the inverting prism condition. The remaining participants (N = 6) completed all three treatment conditions. Normal stereo vision for all observers was indicated by the results of the TNO stereo test (Laméris Ootech, Nieuwegein, The Netherlands). All observers completed extensive practice trials before formal data collection began to familiarise themselves with the binocular rivalry task. The study was conducted with the approval of the University of Nottingham, School of Psychology Ethics Committee and all participants gave informed consent.

Apparatus and Stimuli

Observers performed the experimental task in a dimly lit room. Stimuli were computer generated grey-scale images, produced using an Apple Macintosh computer running custom software written in the C programming language, 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 with respect to their spatial characteristics, timing and luminance properties has previously been documented (Wang & Nikolic, 2011). Precise temporal synchronisation between the two monitors was achieved by driving them using the dual outputs of the same video card. The monitors were carefully checked and calibrated to produce a linear luminance output function for the digital representation of the image. The noisy-bit method was applied to each colour channel independently, to effectively produce an infinite number of intensity levels available for presenting stimuli on the display, enabling precise control of luminance contrast (Allard & Faubert, 2008).

A monocular image was presented to each display, and the participant viewed the pair of stimuli dichoptically through a Wheatstone mirror stereoscope, with an optical viewing distance of 231.5 cm. The two full-silvered mirrors were placed symmetrically with respect to the median plane of the head, and the angle was adjusted (if necessary) for individual observers to maintain stable binocular fusion. The background of each display was a uniform grey field, with a luminance of 159 cd/m^2. The stimuli subtended 2.21° × 2.21°, enclosed by a high contrast checkered fusion frame (alternating black and white square elements), with a pair of vertically- and horizontally-oriented Nonius lines, to assist binocular fusion. A binocular central fixation cross was presented at the beginning of each trial, and head position was stabilised with the use of a chin rest.

To trigger the perceptual experience of binocular rivalry, a horizontally-oriented sinusoidal luminance grating (Michelson contrast 20%; spatial frequency 1.8 cpd) was presented to the participant's left eye, and an identical but vertically-oriented grating was presented to the right eye simultaneously. The grating contained 4 cycles and was randomly assigned to either +sine or –sine phase on each trial, with respect to the horizontal or vertical midline.

Procedure

Temporal dynamics of BR were recorded to quantify sensory eye dominance. The measurement was completed both in the absence of (i.e. baseline), and immediately following monocular treatment for a duration of 150 minutes (Figure 1a). The effects of three types of treatment were examined. First, one eye was covered with an opaque patch where all visual input to that eye was eliminated. Second, a diffusing lens was used where all contour information was removed such that subjects could not count fingers at a distance of 10 cm. The luminance level at the eye was largely preserved, with a small attenuation of ~15% as measured by a spot photometer. For the third treatment condition, a Porro prism was placed over one eye using a trial frame, to invert the image viewed by that eye. In this way the two eyes' images were matched in luminance, contrast, chromatic and temporal information over a central region of the visual field, whilst binocular fusion was prevented. The field of view through the inverting prism was limited, subtending 33.40° vertically and 28° horizontally, but was sufficiently larger than the angle subtended by the visual displays used for presenting the stimuli. The effect of monocular treatment of each eye was measured separately, so that we could determine if the treatment altered eye balance independently of any inherent baseline eye dominance.

In the BR task, at the beginning of each trial the participant viewed the fixation cross and pressed a key when stable binocular fusion was achieved, to initiate stimulus presentation. Subjective percepts were tracked continuously by key presses over 30 minutes, with a brief break every three minutes. There were three types of response allowed: an exclusive horizontal grating, an exclusive vertical grating, and a mixed percept that contained both gratings. The BR measurement was completed at least twice for each eye condition (in separate sessions). For analyses the data were collapsed across both eye conditions, such that there were a minimum of four repetitions for each treatment condition. A minimum of two repetitions were also completed for the baseline measurement.

Data analyses

Distributions of phase durations

Relative eye dominance was quantified by comparing the mean phase duration of exclusive percepts viewed by the two eyes. The raw durations, binned every three minutes, were pooled across all testing sessions of the corresponding treatment condition (i.e. all repetitions including both eye conditions), and grouped based on whether the stimulus was presented to the previously treated eye or the non-treated eye, which discounts any existing biases of eye and/or orientation. As there were marked individual differences in measures, phase duration values for the treated and the non-treated eyes were normalised to each observer's mean phase duration measured during the corresponding three-minute time bin in the baseline condition. The resulting distributions reveal differences between eyes attributable to monocular treatment, and how these effects may have diminished over time, independently of potential prolonged measurement effects on BR dynamics. The mean baseline duration, used as the basis of this normalisation procedure, was calculated from the durations pooled across both eyes/orientations and all repeated testing sessions. The normalised phase durations were then pooled across all individuals, and the distributions of these durations are plotted as a probability density function (PDF; bin size: 0.2). Using the method of nonlinear least-squares, the corresponding cumulative density function (CDF) was then fitted with a gamma distribution defined by the following equation:

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

where Γ is the gamma function, ρ indicates the shape of the distribution (shape parameter) and λ describes the spread (scale parameter). To eliminate subjectivity caused by introducing an arbitrary bin size, the CDF rather than PDF was used for fitting. However the fitted curves are plotted in the PDF form, with the estimated parameters from the CDF fits, to allow direct comparison to the results presented in previous work (Lunghi et al., 2013).

Time course of treatment effect

The effect of monocular treatment on eye dominance was then quantified as the ratio of mean phase duration, or predominance (i.e. proportion of total time), for the exclusive percept viewed by the treated eye to that for the non-treated eye. A ratio was computed for the measurements within each of the ten, three-minute time bins, so that a time course of the treatment effect could be obtained. A ratio above unity indicates an enhanced dominance of the treated eye relative to the other eye. Note that a ratio of one does not mean a perfect balance between the two eyes, but rather no change in eye dominance after treatment. To show the variability across the group, while utilising the variability in raw phase durations within each individual observer, bootstrapping (10,000 repetitions) was performed to obtain 95% confidence intervals for the computed mean ratio within each time bin. This procedure was only conducted for the ratio obtained using mean phase durations, whilst for predominance ratio the standard error of the mean (SEM) was computed instead.

A power function was fitted to the computed ratio as a function of time after removing the treatment for each condition, in the form of the following equation with 3 free parameters (a, b, c):

$$y = (\frac{a}{t+b})^c + 1, \quad (2)$$

where y is the ratio, t is the time elapsed in minutes, a is the amplitude, b indicates the horizontal position of the function, and c defines the decay rate. The parameters a and b together determine the initial size of the effect at t = 0. The constant term defines the lower asymptote, which is set to one, assuming that the effect on sensory eye dominance would eventually return to zero ($y \approx 1$). The method of weighted nonlinear least-squares was used for fitting, where the inverse of the variance of each data point was used as a weight. For the optimisation of parameters, the constraints of $a > 0$ and $c > 0$ were applied.

Mixed percept predominance

Apart from exclusive dominance of the two eyes, the predominance of mixed perception (i.e. non-exclusive percepts) may also provide some information about binocular visual processing following monocular treatment. Hence, the proportion of time that mixed percepts occurred during each of the ten time bins was also obtained. This was extracted for the baseline condition, and all the three treatment conditions, to investigate how mixed perception during BR varied over time, and whether monocular treatment influenced the pattern. Again, to control for individual differences, the data were first normalised to the observer's baseline mixed percept proportion over the whole measurement period, before being averaged across all observers to obtain the group means.

It is possible that any treatment effect which would presumably decay over time, may be confounded with potential changes caused by prolonged BR measurement (see Klink, Brascamp, Blake, & Van Wezel, 2010). Therefore, we also conducted bin-wise normalisation on these data. That is, mixed percept proportion for each treatment condition within each time bin, was divided by that measured in the corresponding bin (instead of the overall proportion) in the baseline condition, to reveal the time course of post-treatment changes (if any) in mixed percept predominance.

Finally, as there was a brief break every three minutes when BR was measured, we examined if any changes in mixed perception occurred during each measurement run. To this end, the data within each run were broken down into three, one-minute, sub-bins, and the difference in mixed percept proportion was calculated between the last and the first sub-bins. Consequently, negative values indicate a reduction in mixed perception over time within a given run, whereas positive values indicate increased mixed perception.

Group level statistical tests

For statistical tests based on the General Linear Model, only the participants who completed all the conditions for a given test were included. Effect size is reported as Cohen's d for t-tests and (partial) η^2 for ANOVA. For linear mixed-effects model analyses, all the nine participants were included. The following hypotheses were examined.

i. Was there a shift in dominance towards the treated eye following each type of monocular treatment?

One-sample, one-tailed, t-tests were performed to compare the log-transformed eye dominance ratio with zero. This was conducted for each of the ten time bins, for each treatment condition separately. For the ratio computed using mean phase durations, equivalent permutation tests (number of permutations: 10,000) using the individuals' raw phase durations were also performed.

ii. Did the type of treatment matter?

First, a one-way (three levels) repeated-measures ANOVA was performed to examine the effect of treatment on the log-transformed eye dominance ratio, for each of the ten time bins. For the duration ratio, equivalent permutation F-tests (number of permutations: 10,000) were also conducted using the individuals' raw phase durations.

In addition, permutation tests were performed on the basis of the curve fits obtained using Equation 2. This was conducted for pairwise comparisons of the entire time course between conditions. Specifically, the raw phase durations for each observer were randomly permuted across the two conditions to be compared. A permuted ratio was then computed for every time bin for each observer based on the mean permuted durations for the two eyes. The mean ratio across observers was subsequently obtained for each time bin, and a curve given by Equation 2 was fitted to the resultant time course. The fitting method was identical to that used for the original data as described above. This procedure was repeated 10,000 times. Consequently, a p value for the given pairwise comparison was obtained (computed from the permuted and the original data) for each parameter (a, b, or c) of the curve fits.

Finally, to utilise all data without excluding any participants, linear mixed-effects model analyses were performed. The fixed effect of treatment type on the slope, and the random effect of subject on the intercept, were included in the model.

iii. Did mixed percept predominance change following each type of monocular treatment?

A paired-sample, two-tailed, t-test was performed to compare the mixed percept predominance following each type of monocular treatment with that for the baseline, pre-treatment measurements, for each of the ten time bins.

iv. Did mixed percept predominance differ between treatment conditions?

A one-way repeated-measures ANOVA was performed to compare the mixed percept predominance between the three treatment conditions, for each of the ten time bins. In addition, linear mixed-effects model analyses were also performed to utilise all data without excluding any participants. The fixed effect of treatment type on the slope, and the random effect of subject on the intercept, were included in the model.

Results

Binocular rivalry dynamics were measured to assess sensory eye dominance before and after a 150-minute monocular treatment. Figure 2 shows the distributions of normalised exclusive phase durations for the stimulus presented to the previously treated eye and the non-treated eye in the three treatment conditions (opaque patch, diffuser and inverting prism), pooled across all participants. Only the durations measured during the first, the second and the last three-minute bins are plotted for simplicity. The distribution of the normalised baseline durations for the corresponding bin is also shown in each plot. Figure 2 shows that for the first six minutes after the treatment stopped, the distributions were distinct for the two eyes—there were more longer durations for the previously treated eye than the non-treated eye, and more shorter durations for the non-treated eye. This signals a shift of eye dominance in favour of the previously treated eye after monocular treatment. These changes in the relative difference between the two eyes were consistent for all the three treatment conditions, though there were some variations in terms of the shape and scale of the distributions. When tested 27–30 minutes after the treatment stopped, the difference between the two eyes diminished and the distributions approached those measured in the baseline condition, indicating recovery of the effects induced by the monocular treatment.

To quantify changes in relative eye dominance, the ratio between the metrics (mean phase duration or predominance) for the treated and the non-treated eyes was obtained for each of the ten time bins (Figure 3). For all forms of monocular treatment, the log-transformed ratio was significantly greater than zero immediately after stopping the treatment (0–3 min), for both mean phase durations (opaque: $t_{(7)} = 7.30$, $p < .001$, $d = 2.58$; diffuser: $t_{(7)} = 6.46$, $p < .001$, $d = 2.28$; inverting: $t_{(6)} = 7.06$, $p < .00$, $d = 2.67$), and predominance (opaque: $t_{(7)} = 9.13$, $p < .001$, $d = 3.23$; diffuser: $t_{(7)} = 6.91$, $p < .001$, $d = 2.44$;

inverting: $t_{(6)} = 7.12$, $p < .001$, $d = 2.69$). These results confirmed that monocular treatment of an eye increased its dominance relative to the other, non-treated eye. As can be seen, this effect declined rapidly within the first 9 minutes before gradually reaching a plateau, and this time course was well characterised by a power function (see Table 1 for fit results). Nevertheless, the difference remained significant at least 30 minutes after finishing the treatment for all conditions in terms of mean phase durations (opaque: $t_{(7)} = 2.63$, $p = .017$, $d = 0.93$; diffuser: $t_{(7)} = 3.30$, $p = .007$, $d = 1.17$; inverting: $t_{(6)} = 12.23$, $p < .001$, $d = 4.62$), and predominance (opaque: $t_{(7)} = 3.73$, $p = .004$, $d = 1.32$; diffuser: $t_{(7)} = 4.32$, $p = .002$, $d = 1.53$; inverting: $t_{(6)} = 7.95$, $p < .001$, $d = 3.00$). Moreover, the results of permutation tests confirmed these findings (all $p < .001$). Overall, the time course of these effects, and the shift in eye dominance in favour of the treated eye, were consistent with Lunghi et al. (2013).

Table 1: Fit results (Equation 2) of the time course of the eye dominance ratio shown in Figures 3c (mean phase duration) and 3d (predominance). The estimates of the three parameters, *a*, *b* and *c* (with 95% confidence intervals shown in brackets), and the goodness of fit indicated by R^2 are shown.

	a	*b*	*c*	R^2
		Mean phase duration		
Opaque	0.64 (-1.09, 2.38)	1.16 (-1.64, 3.96)	0.43 (0.08, 0.79)	.872
Diffuser	2.00 (-0.34, 4.33)	1.88 (-0.74, 4.50)	0.53 (0.25, 0.81)	.936
Inverting	2.14 (-0.20, 4.48)	1.62 (-0.64, 3.88)	0.60 (0.34, 0.86)	.931
		Predominance		
Opaque	4.24 (-0.039, 8.51)	1.73 (-1.36, 4.82)	0.56 (0.20, 0.92)	.905
Diffuser	4.76 (2.64, 6.88)	0.61 (-0.19, 1.41)	0.45 (0.30, 0.61)	.944
Inverting	4.91 (2.49, 7.33)	1.09 (-0.19, 2.37)	0.63 (0.42, 0.84)	.943

The results of one-way ANOVA suggested that the ratio within the first time bin (0–3 min) did not differ significantly between treatment conditions (mean phase duration: $F_{(2,10)} = 0.664$, $p = .536$, $\eta^2 = .028$; predominance: $F_{(2,10)} = 1.81$, $p = .214$, $\eta^2 = .070$), nor did it become significant for the subsequent time bins (all $p > .05$, except for the predominance ratio during 12–15 min: $F_{(2,10)} = 4.34$, $p = .044$, $\eta^2 = .18$). The lack of a significant effect of treatment type was also found when individuals' raw phase durations were randomly permuted among conditions ($p = .565$ for 0–3 min, and $p > .05$ for all subsequent time bins). The results of permutation tests performed on the estimated parameters of curve fits, further suggested that none of the parameters differed significantly between conditions over the entire 30-minute measurement period (Table 2). When data from all nine participants were included, the linear mixed-effects model analysis revealed consistent results, whereby the fixed effect of treatment type was not significant (0–3 min: mean phase durations, $F_{(2,20)} = 1.77$, $p = .195$; predominance: $F_{(2,20)} = 2.41$, $p = .115$; $p > .05$ for all subsequent time bins for both metrics, except for the predominance ratio during 12–15 min: $F_{(2,20)} = 5.01$, $p = .017$). All the above results support the conclusion that the form of monocular treatment did not make a significant difference.

Table 2: The results of permutation tests (number of permutations: 10,000), in *p* values, for three pairwise comparisons between different types of monocular treatment in terms of the estimated parameters, *a*, *b*, and *c* from the curve fits (Table 1) of the time course shown in Figure 3c. The reported *p* values are uncorrected, or have been corrected for multiple comparisons using the Holm-Bonferroni method as proposed by Holm (1979).

	Opaque-Diffuser			Opaque-Inverting			Diffuser-Inverting		
	a	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*
Uncorrected *p*	.852	.682	.87	.453	.584	.398	.229	.256	.136
Corrected *p*	.907	1	.87	.907	1	.797	.686	.768	.408

It is worth noting that mixed percepts were fairly common in our measurements, in addition to exclusive dominance of one or the other grating. Figure 4 demonstrates the time course of mixed percept predominance over the 30-minute measurement period. A clear pattern can be seen for both the baseline measurement and the data measured after each type of monocular treatment—the predominance of mixed percepts declined over the course of the BR measurement (Figure 4a). The similarity between the pre- and post-treatment data also implies that no consistent changes in the overall level of mixed percept predominance, or its time course, were induced by monocular treatment.

The results of paired-sample t-tests showed no significant alterations in mixed percept predominance following monocular treatment compared to baseline measurements (0–3 min: opaque: $t_{(7)} = 0.18$, $p = .86$, $d = 0.065$; diffuser: $t_{(7)} = -0.078$, $p = .94$, $d = -0.027$; inverting: $t_{(6)} = -0.27$, $p = .797$, $d = -0.102$; $p > .05$ for all subsequent time bins except for the data during 27–30 min in the opaque patch condition: $t_{(7)} = -2.66$, $p = .032$, $d = -0.941$). Furthermore, the results of one-way ANOVA indicated that the post-treatment mixed percept predominance did not differ between the three treatment types (0–3 min: $F_{(2,10)} = 0.84$, $p = .459$, $\eta^2 = .046$; $p > .05$ for all subsequent time bins). Consistent results were obtained from the linear mixed-effects model analysis, where all subjects' data were included (0–3 min: $F_{(2,20)} = 0.61$, $p = .553$; $p > .05$ for all subsequent time bins).

Figure 4b depicts the time course of the changes in mixed percept predominance following monocular treatment relative to that measured during the corresponding time bin in the baseline condition (see *Data analyses*). When variations arising from prolonged BR measurement were discounted, a flat curve was revealed for all treatment conditions. In other words, the only source of variations in mixed perception was related to measuring BR over time. Moreover, Figure 4c shows the change in mixed percept proportion within each of the ten time bins. As can be seen, negative values were predominant, suggesting that the proportion of mixed percepts declined over time, even within a measurement run. This rules out the possibility that the observed pattern of results was due to artefacts introduced by the brief break between runs. Rather, the data show that mixed perception decreases as BR measurement continues, in contrast to previous findings by Klink et al. (2010) (see *General discussion*). As the methodologies were very similar, we considered the possibility that the discrepancies in this result might have arisen from the small differences in the stimuli used. However, the same pattern of reducing mixed percept predominance was found when we retested the baseline time course in three subjects using stimuli with identical spatial frequency, luminance contrast and grating orientation to those used by Klink et al. (2010).

In summary, the results of Experiment 1 show that covering one eye for 2.5 hours with an opaque patch, a diffusing lens, or an inverting prism produced similar effects on binocular rivalry dynamics. That is, the previously treated eye was strengthened relative to the other eye. Despite the fact that the type of visual information available was different in the three treatment conditions, the magnitude and time course of this phenomenon were comparable. This implies that a lack of luminance or contrast information in one eye is not a necessary requirement for the shift in sensory eye dominance produced by short-term monocular deprivation.

Experiment 2: Role of top-down attention in driving the changes in sensory eye dominance

The results of Experiment 1 indicate that altering low-level sensory input is not a prerequisite for producing shifts in eye dominance. This raises the possibility of higher-level processing contributing to the effect, at least in the prism condition. Interestingly, our participants claimed that they were able to perceive the upright image in the non-treated eye predominately, while ignoring the inverted image viewed through the prism. Therefore, a plausible driver of the changes in eye dominance following monocular inversion seems to be selective attention to one eye, or inattention to the other. However, the activities the participants undertook during the treatment period were not constrained or monitored in Experiment 1, such that attention was not strictly controlled. Therefore, we sought to manipulate the degree to which selective attention was required during the monocular treatment. If top-down attention does play a role in the prism condition, one might expect to find larger effects when participants engage in a task that requires them to actively attend to the normal visual input in the non-treated eye. In addition, it remains unknown whether attentional processes also contribute to the effects found following modification of low-level input. Therefore, we also tested the opaque patch condition in Experiment 2. A difference in the size of effects for different levels of attentional demand during monocular luminance deprivation, would indicate a contribution of attention in this condition too.

Methods

Observers

Six observers with normal binocular vision (TNO stereo acuity within the normal range) took part in this experiment, three of whom also participated in Experiment 1.

Procedure

A schematic illustration of the procedure is shown in Figure 1b. One hour of monocular treatment was applied, to an eye randomly selected for each participant and fixed throughout the experiment. Two treatment conditions were completed for each participant: using an opaque patch or an inverting prism as in Experiment 1. During the period of monocular treatment, the participant either did a jigsaw puzzle (Gibsons *London from Above*), which was attentionally demanding (active condition), or simply stared at a plain curtain (passive condition), before they were tested in a BR percept tracking task for 30 minutes to assess sensory eye dominance. Note that in the passive condition the participants viewed the curtain from a close distance, such that the textural detail and undulation of the curtain were readily visible, as was the directional component of the lighting. Baseline measurements of BR without any monocular treatment were also completed for each observer. The apparatus, stimuli, and procedure for the BR task were identical to those used in Experiment 1 with the following exception. For half of the conditions, the horizontal grating was presented to the left eye and the vertical grating was presented to the right eye; for the remaining conditions the converse was true. The data were combined across both configurations, yielding two sets of measurement for each treatment × attention condition and for the baseline condition (each configuration was completed once for each condition).

Data analyses

Eye dominance was quantified in terms of the exclusive phase duration distributions and the ratio of mean phase duration or predominance between the two eyes. The normalisation and fitting procedures for phase duration distributions were identical to those used in Experiment 1. For the measure of ratio, note that a value of one indicates balanced BR dynamics between the two eyes (cf. no difference depending on whether the eye has received monocular treatment in Experiment 1), because only one of the observer's eyes was patched.

Group level statistical tests

The following hypotheses were assessed for Experiment 2.

i. Was there a shift in dominance towards the treated eye following each type of monocular treatment relative to the baseline measurements?

Paired-sample, one-tailed, t-tests were performed to compare the log-transformed eye dominance ratio for each treatment condition with baseline, conducted for each of the ten time bins. In addition, equivalent permutation tests (number of permutations: 10,000) using the individuals' raw phase durations were performed for the ratio computed using mean phase durations.

ii. Did the type of treatment and the attentional demand matter?

A 2 (treatment type) × 2 (attentional demand) repeated-measures ANOVA was performed to assess the effects on the log-transformed eye dominance ratio, for each of the ten time bins. For the duration ratio, equivalent permutation F-tests (number of permutations: 10,000) were also conducted using the individuals' raw phase durations. Specifically, the interaction term was tested using unrestricted permutations of the raw phase durations among the four conditions. The main effects were tested by restricting permutations between the two levels of the factor of interest within each level of the other factor.

Results

The group distributions of exclusive phase durations (normalised) for the treated and the non-treated eyes, pooled from the measurements within the first (0–3 min) and the last time bins (27–30 min), are shown in the form of PDF for the five conditions in Figure 5.

The similarity between the distributions for the two eyes in the baseline condition signified little or no bias in eye dominance before monocular treatment. In the passive conditions of both forms of monocular treatment, almost no change was found in the difference between the two eyes' distributions, compared to baseline. This result means that monocular treatment, with minimal engagement of attention, failed to produce any changes in subsequent sensory eye dominance. In contrast, a separation between the two eyes' distributions was observed in the two active conditions, when measured immediately after treatment. In both cases, this eye difference diminished when measured 27–30 minutes following the treatment offset.

This pattern of results was also revealed with respect to the treated to non-treated eye ratio in terms of both mean exclusive phase duration and predominance (Figure 6). For both treatment conditions, whilst a shift towards to the treated eye can be seen immediately after removing the treatment in the active conditions (i.e. an increase in the ratio relative to that in the baseline condition), this effect was absent in the passive conditions (i.e. an unaltered ratio). Moreover, the effect of the inverting prism in the active condition was larger than that for the opaque patch. The time course of these effects was similar to Experiment 1: any increase in the treated eye's dominance declined rapidly within the first few minutes and then gradually reached the baseline level.

Statistically, the results of paired-sample t-test revealed a significant increase in the log-transformed eye dominance ratio during the first time bin (0–3 min) following treatment termination for both active conditions (mean phase durations: opaque, $t_{(5)}$ = 4.28, d = 1.75; inverting, $t_{(5)}$ = 4.34, p = .004, d = 1.77; predominance: opaque, $t_{(5)}$ = 3.29, p = .011, d = 1.34; inverting, $t_{(5)}$ = 4.00, p = .005, d = 1.63), but not for the passive conditions (mean phase durations: opaque, $t_{(5)}$ = 0.437, p = . 218, d = 0.35; inverting, $t_{(5)}$ = 0.92, p = .200, d = 0.38; predominance: opaque, $t_{(5)}$ = 0.08, p = .468, d = 0.03; inverting, $t_{(5)}$ = 0.40, p = .354, d = 0.16). While any effects (for the active conditions) on the ratio declined over time, these remained significant at least 21 minutes after the treatment was completed (18–21 min, mean phase durations: opaque, $t_{(5)}$ = 3.04, p = .014, d = 1.24; inverting, $t_{(5)}$ = 6.09, p < .001, d = 2.49; predominance: opaque, $t_{(5)}$ = 2.35, p = .033, d = 0.96; inverting, $t_{(5)}$ = 10.39, p < .001, d = 4.24). Similar results were obtained from the permutation tests, which took into account individuals' raw phase durations (0–3 min: opaque passive, p = .215; opaque active, p < .001; inverting passive, p = .154; inverting active, p < .001).

The results of two-way ANOVA revealed a significant main effect of attentional demand (0–3 min: mean phase durations, $F_{(1,5)}$ = 25.26, p = .004, η_p^2 = .835; predominance, $F_{(0.36,1.82)}$ = 21.46, p = .006, η_p^2 = .811) until 24 minutes after treatment removal (21–24 min: mean phase durations, $F_{(1,5)}$ = 14.34, p = .013, η_p^2 = .742; predominance, $F_{(1,5)}$ = .29, p = .043, η_p^2 = .593). Although for the active condition the inverting prism produced larger changes than the opaque patch, as shown in Figure 6, the main effect of treatment type was not significant for the ratio in terms of mean phase durations (0–3 min: $F_{(1,5)}$ = 1.02, p = .360, η_p^2 = .169; p > .05 for all subsequent time bins except for 12–15 min: $F_{(1,5)}$ = 10.90, p = .022, η_p^2 = .686), nor was the interaction term significant (0–3 min: $F_{(1,5)}$ = 3.68, p = .113, η_p^2 = .424; p > .05 for all subsequent time bins except for 18–21 min: $F_{(1,5)}$ = 13.42, p = .015, η_p^2 = .729). For the ratio computed using predominance, however, there was a significant main effect of treatment type ($F_{(0.36,1.82)}$ = 26.65, p = .004, η_p^2 = .842) and an interaction ($F_{(0.36,1.82)}$ = 14.59, p = .012, η_p^2 = .745) during the first 3 minutes, but not subsequently (all p > .05 except for the main effect of treatment type during 12–15 min, $F_{(1,5)}$ = 13.67, p = .014, η_p^2 = .732, and during 21–24 min, $F_{(1,5)}$ = 12.41, p = .017, η_p^2 = .713). Moreover, similar findings were obtained with the permutation F-test performed on individuals' raw phase durations, in terms of the main effect of attentional demand (p = .002 for 0–3 min and p < .05 until 24 min) and treatment type (p = .883 for 0–3 min and all p > .05 subsequently), and the interaction term (p = .093 for 0–3 min and all p > .05 except for 18–21 min, p = .009).

Overall, the differences found in the passive and the active conditions support the proposal of a substantial contribution of top-down attention in driving the shifts in sensory eye dominance following short-term monocular treatment.

Experiment 3: What is happening to sensory eye dominance during monocular inversion?

One could argue that the boost in eye dominance following short-term monocular deprivation is a rebound effect once the deprived eye is re-exposed to normal visual input. A prediction based on this account is that any effect would be induced only when the deprivation ends. The eye dominance shifts observed in both the current and previous studies were measured at the point when monocular treatment was terminated. This tells us little about visual processing taking place during the treatment period, and how these changes might build up over the course of monocular treatment. Begum and Tso (2015, 2016) have demonstrated in adult macaques that physiological changes of V1 neurons occur during the course of monocular deprivation; the responsiveness of the non-deprived eye is gradually decreased. These changes started to recover once the deprivation period was terminated. The early onset of neuronal changes during the deprivation period suggests that shifts in ocular dominance may not simply be a rebound effect. However, complementary behavioural evidence is yet to be obtained.

With the opaque patch or the diffuser, it is impossible to measure sensory eye dominance behaviourally without removing the occluder from the patched eye. This limitation can be overcome however with the inverting prism, as the treated eye is still stimulated with spatial information and allows the measurement of perception during binocular rivalry. In this experiment, therefore, sensory eye dominance was measured with the same BR task as used in Experiment 1, at several time points during monocular treatment with the inverting prism.

Methods

Observers

Six participants, including four who took part in Experiment 1 and another two observers, participated in this experiment. The newly recruited participants also had normal binocular vision.

Procedure

The apparatus, stimuli for the BR task, and procedure were identical to those used in Experiment 1, with the exception of the time point at which BR was measured. Participants performed the BR task immediately after the introduction of the inverting prism, and subsequently every 30 minutes, until the end of the 150-minute treatment period, yielding six measurements for each observer. The prism was then removed and BR was measured again, immediately, and at 30 minutes following the prism removal. A schematic illustration is shown in Figure 1c. Each measurement lasted 3 minutes. The procedure was repeated at least twice for each eye.

Data analyses

The data were treated in the same manner as in Experiment 1, with the exception that the exclusive phase durations were normalised to the mean baseline durations pooled over only the first three-minute time bin. This is because BR was not measured continuously for 30 minutes in this experiment, but rather in discrete three-minute runs.

Group level statistical tests

The following hypotheses were assessed for Experiment 3.

i. Was there a shift in dominance towards the treated eye at each time point of measurement?

One-sample, one-tailed, t-tests were conducted to compare the log-transformed eye dominance ratio with zero, for each of the 8 measurements. For the ratio computed using mean phase durations, equivalent permutation tests (number of permutations: 10,000) using the individuals' raw phase durations were performed additionally.

ii. Did the eye dominance change at each time point compared to the first measurement?

Paired-sample, two-tailed, t-tests were performed to compare the log-transformed eye dominance ratio at each time point from the second measurement with the first one (i.e. immediately after putting on the prism). Equivalent permutation tests (number of permutations: 10,000) were also performed using individuals' raw phase durations for the duration ratio.

Results

The group distributions of normalised exclusive phase durations are shown in Figure 7. Each subplot depicts the durations for the treated eye and the non-treated eye pooled over a three-minute measurement run. For the measurements taken during the monocular inversion period, only the data for the first, the second, and the last run are shown for the sake of simplicity. The distributions for normalised baseline durations for these observers are also plotted. When measured immediately after the onset of monocular inversion (leftmost plot in Figure 7), the distributions for the two eyes showed little difference and both resembled the baseline distribution. An increased probability of longer durations for the treated eye and shorter durations for the non-treated eye was revealed after 30 minutes of wearing the prism. This pattern of results remained evident until the end of the monocular inversion period (i.e. 150 minutes after the onset) and was also the case immediately after removing the inverting prism. As in the other two experiments, the distributions for the two eyes were similar when measured 30 minutes after removing the prism.

The ratio of mean exclusive phase duration or predominance between the two eyes, as a function of time after the onset or offset of monocular inversion, is shown in Figure 8. Immediately after putting on the prism, this ratio was close to one which signals no changes. Interestingly, as early as 30 minutes following the onset of monocular inversion, a shift in eye dominance towards the inverted eye can be clearly seen. This increase in the inverted eye's dominance thereafter remained evident throughout the course of monocular inversion. The ratio was shifted towards the eye that had received monocular inversion (greater than unity) when measured immediately following prism removal, and it returned to its equilibrium after 30 minutes.

The results of one-sample t-tests suggested that the log-transformed eye dominance ratio was not greater than zero for the first measurement at the time when the prism was put on (mean phase durations: $t_{(5)}$ = -0.81, *p* = . 774, *d* = -0.33; predominance: $t_{(5)}$ = -1.06, *p* = .832, *d* = -0.43), but became significantly larger than zero after 30-minutes of monocular treatment (mean phase durations: $t_{(5)}$ = 4.70, *p* = . 003, *d* = 1.92; predominance: $t_{(5)}$ = 4.10, *p* = .005, *d* = 1.67). This effect remained significant throughout the whole period before the prism was removed (150 min, mean phase durations: $t_{(5)}$ = 6.23, *p* < . 001, *d* = 2.54; predominance: $t_{(5)}$ = 3.74, *p* = .007, *d* = 1.53). Immediately after the prism was removed, the log-transformed ratio was still significantly larger than zero (mean phase durations: $t_{(5)}$ = 4.34, *p* = . 004, *d* = 1.77; predominance: $t_{(5)}$ = 4.80, *p* = .002, *d* = 1.96). The difference was not significant after 30 minutes for the ratio of mean phase durations ($t_{(5)}$ = 2.17, *p* = . 041, *d* = 0.89), whereas it was still significant when the ratio was computed using predominance ($t_{(5)}$ = 2.95, *p* = .016, *d* = 1.21). For duration ratio, the permutation test yielded similar results for the measurements following prism onset (0 min: *p* = .958; all *p* < .001 for subsequent measurements), and the effects remained significant following prism offset which lasted at least 30 minutes (0 min: *p* < .001; 30 min: *p* < .001).

When compared to the eye dominance measured at the onset of monocular inversion, the ratio increased significantly as soon as 30 minutes elapsed, indicated by the results of paired-sample t-tests (mean phase durations: $t_{(5)}$ = 4.14, *p* = .009, *d* = 1.69; predominance: $t_{(5)}$ = 8.43, *p* < .001, *d* = 3.44). This difference remained significant throughout the whole period of monocular inversion with the prism (150 min, mean phase durations: $t_{(5)}$ = 7.54, *p* < .001, *d* = 3.08; predominance: $t_{(5)}$ = 2.98, *p* = .031, *d* = 1.22). The log-transformed ratio immediately after prism offset was significantly larger than that measured at prism onset (mean phase durations: $t_{(5)}$ = 4.38, *p* = .007, *d* = 1.79; predominance: $t_{(5)}$ = 11.03, *p* < .001, *d* = 4.50), but the difference was not significant after 30 minutes (mean phase durations: $t_{(5)}$ = 1.91, *p* = .114, *d* = 0.78; predominance: $t_{(5)}$ = 2.10, *p* = .090, *d* = 0.86). The results of permutation tests suggested that all subsequent measurements, including both those during and after monocular inversion, were significantly larger than the first measurement at prism onset (all *p* < .001).

These results demonstrate that the effect of monocular inversion on sensory eye dominance became measurable as early as 30 minutes following the introduction of the prism. Indeed, past research has also shown such a short duration was able to produce shifts in eye dominance measured with binocular rivalry (Kim et al., 2017; Lunghi et al.,

2013) and binocular phase combination (Min, Baldwin, Reynaud, & Hess, 2018), though the effect lifetime was reduced to a few minutes. The finding that re-exposure to normal binocular input is not a necessary requirement for producing the changes in sensory eye dominance, is consistent with physiological evidence from Begum and Tso (2015, 2016). These observations make an account based on a rebound effect of the treated eye less likely, as the onset of the changes in eye dominance does not depend on the termination of monocular treatment. Nonetheless, a caveat is that the orientation of the grating stimulus appeared identical when viewed with and without the prism. During testing the prism only mattered with respect to the appearance of the scene in the background environment (e.g. the monitor, desk etc.) which was dimly lit.

General discussion

The influence of short-term monocular deprivation on inter-ocular balance in adults has recently been demonstrated in a number of studies by showing increased relative contributions from the deprived eye on a range of binocular tasks (e.g. Lunghi et al., 2013; Zhou, Clavagnier, & Hess, 2013). However, the mechanism driving this phenomenon remains elusive. This issue was addressed here by comparing changes in BR dynamics following different types of monocular manipulation. It has been assumed that the occurrence of this phenomenon requires deprivation of low-level sensory input to one eye. On the contrary, here we found similar shifts in eye dominance whilst maintaining spatial and temporal input to both eyes. We propose that the primary contributor of the effects observed in the prism condition arises from higher-level cognitive processes – monocular image inversion may have guided attentional eye selection in favour of the non-treated eye.

It is intriguing that both the magnitude and time course of the changes in eye dominance in all three conditions in Experiment 1 were not significantly different. This suggests that these forms of monocular treatment may have acted on a single mechanism that regulates inter-ocular balance. A key factor in this phenomenon appears to be the direction-specificity of the changes – the eye which is strengthened depends on whether it is the previously treated or the non-treated eye. Notably, ocular dominance plasticity in human adults has also been demonstrated elsewhere; inter-ocular imbalance can be reduced through training directed to using the two eyes together (Bao, Dong, Liu, Engel, & Jiang, 2018). In this case, the direction of changes in eye dominance depends on which eye is more dominant prior to training. This should not be confused with the form of changes addressed in the present study, where the key determinant is the inter-ocular imbalance induced by monocular treatment.

In Experiment 1, the inter-ocular imbalance was realised through degrading the stimulation through one eye in the opaque patch and the diffuser conditions. In the prism condition, the information from the upright image is more biologically relevant, potentially engaging attentional eye selection mechanisms. The results of Experiment 2 further supported this idea. When attentional demand was minimised by preventing the participant from engaging in activities requiring visual information (passive condition), the effect of monocular treatment on sensory eye dominance was eliminated. The active and passive conditions were designed to place different attention demands on the observer during the monocular treatment, but they also differed in the richness of visual stimulation available and cognitive load. Although the latter might be a potential confound, responsible in part for the shifts in eye dominance found (Kim et al., 2017), the fact that the prism produced larger shifts than the opaque patch in the active condition (especially in terms of predominance), where these factors were identical, suggests some role for top-down attentional selection. The inverting prism is likely to engender greater levels of inter-ocular conflict than the opaque patch, and hence place greater demands on attentional selection to suppress any irrelevant information. Similarly, although it is possible that the restricted field of view through the prism (reduced amount of visual information), rather than attentional eye selection, led to a shift in eye dominance, that there was no shift in eye dominance in the inverted passive condition does not support this assertion. Assuming that short-term monocular deprivation exclusively alters binocular interactions (Wang et al., 2020), our results reinforce the notion that changes in monocular attention, can produce shifts in eye balance (Wong, Baldwin, Hess, & Mullen, 2021).

It has been well documented in both humans and other primates that spatial attention enhances neuronal responses in subcortical and early visual areas (e.g. Brefczynski & DeYoe, 1999; Carrasco, 2006; Heinze et al., 1994; Katyal & Ress, 2014; Luck et al., 1994; McAlonan, Cavanaugh, & Wurtz, 2008; Motter, 1993; O'Connor, Fukui, Pinsk, & Kastner, 2002; Reynolds, Chelazzi, & Desimone, 1999). This attentional modulation is thought to be accomplished by top-down feedback projections that increase contrast gain of the attended objects or regions (Reynolds & Chelazzi, 2004). It is tempting to speculate that there may be also an analogous role for attention in regulating ocular dominance, whereby selective attention to one eye's input strengthens responses of neurons which have a preference to the stimulation of that eye. In support of this idea, an electroencephalogram (EEG) study has revealed neural correlates of attentional eye selection; the P1 component of event related potentials (ERPs) was larger when attention was directed to a stimulus presented to one eye but not the other, and this effect was absent if the selection occurred in only one eye (i.e. the two competing stimuli were monocularly presented to the same eye) (Mishra & Hillyard, 2009). Additional support comes from studies of binocular rivalry showing that selectively attending to one of the rivalrous stimuli boosts the dominance of the attended stimulus relative to the unattended one (Chong & Blake, 2006; Chong, Tadin, & Blake, 2005; Hancock & Andrews, 2007; Zhang, Jiang, & He, 2012). For instance, Zhang et al. (2012) have shown using inter-ocular suppression that stimulus suppression time was reduced when attention was directed to an external cue (at a non-overlapping location in the visual space) presented to the same eye, compared to when the cue was presented to the other eye viewing the suppressing stimulus. The finding that this effect increased with attentional load and did not depend on the low-level attributes of the cue indicates a specific role for attention.

Crucially, as it was the external cue, rather than either of the competing stimuli that was selectively attended to, these results revealed attentional facilitation of the eye and not of the stimulus or spatial location.

The imbalance in visual processing between eyes induced by attentional eye selection could be mediated through inter-ocular suppression. Notably, Dieter and Tadin (2011) proposed that the degree of attentional control over binocular rivalry dynamics increases with the difference in behavioural relevance between the two eyes' images. Indeed, an emerging body of evidence suggests that stimulus predominance during binocular rivalry can be modulated by higher-level cognitive and social factors (e.g. Alpers & Pauli, 2006; Anderson, Siegel, & Barrett, 2011; Bannerman, Milders, De Gelder, & Sahraie, 2008; Chong et al., 2005; Engel, 1956; Goryo, 1969; LoSciuto & Hartley, 1963; Mudrik, Deouell, & Lamy, 2011; Yu & Blake, 1992), presumably through increased attention to one eye's stimulus because of its superior relevance. In particular, a stimulus created through inversion of faces or other real-life images, resembling that produced by an inverting prism, has been shown to be less predominant than an upright image viewed by the other eye during binocular rivalry (Bannerman et al., 2008; Engel, 1956; Yu & Blake, 1992). This reinforces the notion that the inverted prism image was suppressed for longer (and probably to a greater extent) than the upright image viewed by the non-treated eye during rivalry, leading to a general imbalance in binocular visual processing.

Consistent with an account that suppression-driven inter-ocular imbalance contributed to the effects found in our prism condition, Kim et al. (2017) have demonstrated increased dominance of an eye after it has undergone inter-ocular suppression evoked by conditions of continuous flash suppression (CFS). This is a phenomenon where a stimulus presented to one eye is suppressed from awareness when the other eye is simultaneously presented with a fast-changing, high-contrast stimulus. The finding that inter-ocular suppression of an adaptor interfered with the formation of afterimages suggests impaired visual processing under CFS (Tsuchiya & Koch, 2005). Similar to our prism condition, the suppressed eye in Kim et al.'s (2017) study was not physically deprived of sensory input, but the directional changes in eye dominance still arose, possibly due to compromised processing caused by suppression. Nonetheless, the to-be-suppressed stimulus used by Kim et al. (2017) may have evoked weaker low-level neuronal responses compared to the suppressing stimulus viewed by the other eye, independently of inter-ocular suppression. By contrast, we provide more convincing evidence in this regard by using an inverting prism where any potential low-level inter-ocular imbalance was minimised.

Similar conclusions of a role of higher-level processing have been made in another recent study by Ramamurthy and Blaser (2018). They used a "kaleidoscopic" transformation to produce images that were 'fractionated and uninformative', but preserved gross luminance, contrast and spatial frequency information. In the current study we preserved the relative layout of objects in the field of view, object shapes, surface colour, luminance and texture within objects and phase regularities in the treated eye. We hoped this would engender greater levels of inter-ocular conflict and hence place greater demands on attentional selection. Furthermore, we included a passive control condition, where the need for attentional selection was greatly reduced or eliminated.

Studies of short-term learning also have a bearing on the influence of attention on eye dominance. For example, Xu and colleagues (Xu et al., 2010; Xu, He & Ooi, 2012a) used a novel push-pull training protocol to reduce sensory eye dominance. During training an exogenous attention cue presented to the weak eye, preceded binocular stimulation. The cue stimulated the weak eye (push) whilst causing inter-ocular inhibition of the strong eye (pull), shifting the balance towards the weak eye. They concluded that it is the suppression of the strong eye during training, rather than attention cueing *per se*, that is important for driving the perceptual learning effect. Interestingly, although the degree of sensory eye dominance decreased over successive days of training, the eye dominance measured after each day's training session was temporarily larger than that measured before the training on the same day (e.g. see Figure 3 of Xu, He & Ooi, 2012b). That is, the dominance of the strong eye that was suppressed during the training phase increased after the training session. This short-term learning effect is similar to the findings reported in the current manuscript. In the current study, we showed that the treated eye, which presumably received less endogenous attention due to its reduced behavioural relevance, was strengthened after monocular treatment. It is possible that our monocular treatment weakened the contribution of the eye during the treatment period, and this induced inter-ocular imbalance was subsequently compensated by a homeostatic mechanism: presumably through a reduction in inhibition of the treated eye as indicated by our previous work (Wang et al., 2020). Thus, there might be different influences of endogenous and exogenous attention on perceptual learning and monocular deprivation tasks.

In our previous work (Wang et al., 2020) we have shown that short-term monocular patching altered sensory eye dominance through reducing inter-ocular suppression, consistent with psychophysical and physiological evidence of an attenuated inhibition level following deprivation (Lunghi, Emir, et al., 2015; Sheynin, Proulx, & Hess, 2019). Consequently, a possibility has been raised that such effects may be explained through adjusting the behaviour of a binocular opponency channel (Said & Heeger, 2013). The principal idea is that binocular rivalry suppression is elicited by a set of opponency units for each eye that are sensitive to inter-ocular difference. On the assumption that mixed perception is associated with weak inter-ocular suppression (Hollins, 1980), a critical prediction of the opponency model of binocular rivalry is that mixed perception would progressively increase during the course of BR, due to adaptation in the putative opponency mechanisms over time. That is, the ability of the opponency channel to elicit inter-ocular suppression is weakened, and hence it would become less able to sustain exclusive percepts. This is indeed supported by previous reports of more mixed perception with increased exposure to binocular rivalry stimuli (Klink et al., 2010). However, our results (baseline condition) are at odds with Klink et al.'s (2010) findings: Mixed percept predominance decreased, rather than increased, over the course of BR measurement. We have shown good reliability of the observed trend for decreasing mixed percepts using a within-run analysis, and the discrepancy is unlikely to be explained by differences in methodologies or stimuli used. Nonetheless, we do not contend that this provides evidence against the idea of a binocular opponency channel. Instead, our results challenge the validity of utilising mixed perception time course to test the predictions of the opponency model. Furthermore, we found that the time course of mixed perception was not altered by any of the three treatment conditions in Experiment 1.

As a final note, a recent study has shown that baseline mixed percept predominance positively predicts the magnitude of changes in eye dominance following monocular deprivation (Steinwurzel, Animali, Cicchini, Morrone, & Binda, 2020). They interpreted this finding by linking the pre-deprivation level of inter-ocular inhibition, indicated by mixed percept predominance, to the potential for plasticity in the mature visual system. Interestingly, we did not find any significant correlation between the baseline mixed percept predominance and our measures of eye dominance after monocular treatment (log-transformed ratio during 0–3 min, averaged across treatment conditions: mean phase duration, Pearson's $r_{(7)} = .007$, $p = .984$; predominance, Pearson's $r_{(7)} = .267$, $p = .487$) — see Figure 4d, and Figures 3e and 3f for individual data for the mixed and exclusive percepts, respectively. However, like Steinwurzel et al. (2020) we also did not find any changes in mixed percept predominance after deprivation. This suggests that the exact relationship between mixed percepts and inter-ocular inhibition warrants further study.

To conclude, we have demonstrated a role for attentional eye selection in producing changes in sensory eye dominance following short-term monocular treatment. The present findings point to the importance of inter-ocular imbalance in triggering subsequent directional changes in sensory eye dominance, towards the presumably "disadvantaged" eye. That is, neuronal activities are biased towards monocular neurons that are activated by stimulation of a given eye, compared to those responding to the input from the other eye. We speculate that an inter-ocular imbalance in visual processing at or before the level of V1 determines the regulation of eye dominance, where inputs from the two eyes first converge and thus remain distinguishable (Hubel & Wiesel, 1968). This is because eye-of-origin information is essential for determining the direction of changes in ocular balance. This could be implemented in layer 4 of V1 and/or even earlier in lateral geniculate nucleus (LGN). Elimination of low-level sensory information in one eye induces direct imbalance in the input. Attentional eye selection may also lead to biased processing through feedback projections selectively to monocular neurons responding to the attended eye. In turn, this may facilitate inter-ocular suppression by amplifying intra-cortical inhibition, which further reinforces the imbalance between eyes. An implication of these findings is that top-down processes may also be important in clinical conditions where the visual system might selectively favour the input from one eye because it is less blurred (i.e. anisometropic amblyopia) or is more consistent with other maps of visual space (i.e. strabismus). This idea is supported by a recent study showing that observers with strabismic amblyopia are better able to attend to the information in their unaffected eye than the amblyopic eye (Chow, Giaschi, & Thompson, 2018). Interestingly, Lunghi et al. (2019) found that physical activity during monocular deprivation facilitates recovery of visual functions of adult amblyopic patients. It remains possible that engaging in physical exercise led to greater demands on attention and thus reduced the imbalance in ocular dominance. The relatively early onset of shifts in eye dominance implies that the visual system may start to attenuate the responsiveness of the non-treated eye shortly after the biased visual processing becomes stable, in order to maintain homeostasis, in line with the findings of intrinsic optical imaging studies in macaque (Begum & Tso, 2015, 2016).

Figure legends

Figure 1: Schematic illustrations of experimental procedures. (a) Experiment 1: Binocular rivalry was measured continuously for 30 minutes, before and immediately after 150-minute monocular treatment with an opaque patch, a diffusing lens, or an inverting prism. (b) Experiment 2: Binocular rivalry was measured continuously for 30 minutes after 1-hour monocular treatment with either an opaque patch or an inverting prism. The participant either did a jigsaw puzzle or passively looked at a plain curtain during the treatment period. A picture of the jigsaw puzzle used is shown in the right-hand panel. (c) Experiment 3: Binocular rivalry was measured for 3 minutes immediately after introducing an inverting prism, and subsequently every 30 minutes, for 150 minutes, yielding 6 measurements (unfilled grey circles). The prism was then removed and BR was measured again, immediately, and at 30 minutes after the prism removal (solid grey circles). See text for details.

Figure 2: Distributions (plotted as probability density functions) for normalised exclusive phase durations in Experiment 1, pooled across all participants. Each row corresponds to a treatment condition (i.e. opaque patch, diffuser, or inverting prism) and each column corresponds to a time bin (0–3, 3–6 and 37–30 min) within which the phase durations were pooled. Separate distributions for the stimulus presented to the previously treated eye (blue), and that for the non-treated eye (orange) are shown. Also plotted in each graph is the distribution for the pre-treatment (i.e. baseline) measurements (black). The curves are fitted PDF with the parameters estimated from the gamma fits of CDF (Equation 1). The fit results, including the estimated parameters, ρ and λ, and the goodness of fit indicated by R^2 are shown for each graph. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

Figure 3: Relative eye dominance in Experiment 1. (a)–(d) The time course of the ratio of mean exclusive phase duration (a and c), or predominance (b and d), for the treated eye to that for the non-treated eye, is plotted as a function of time (binned every three minutes) after the end of monocular treatment, for the opaque patch, diffuser, and inverting prism conditions. The results for a representative observer are shown in (a) and (b), and those averaged across all participants are shown in (c) and (d). The dashed horizontal line signifies an independence of mean phase duration or predominance on whether the stimulus was presented to the treated or non-treated eye. In (c) and (d) the fitted curves using Equation 2 are also plotted. Error bars are bootstrapped 95% confidence intervals (10,000 repetitions) for duration ratios and are ±1 SEM for predominance ratios. (e)–(f) The eye dominance ratio (log-transformed) during the first 3 minutes following treatment removal for individual observers (indicated by different symbols). Group means are shown by the short horizontal bars. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

Figure 4: The results of mixed percepts measured over 30 minutes in the baseline condition, or after 150 minutes of monocular treatment in Experiment 1. (a) The proportion of mixed percepts normalised to the individual's mean baseline proportion (averaged across 30 minutes). (b) The proportion of mixed percepts normalised to the individual's baseline proportion measured within the corresponding three-minute time bin. In (a) and (b) the horizontal dashed line represents the baseline level (i.e. unity). (c) The difference in mixed percept proportion between the last and the first one-minute sub-bins for each of the ten three-minute time bins. Negative values indicate a reduction in proportion over time within the bin. In all graphs the error bars represent ±1 SEM between individuals. (d) The mixed percept proportion during the first 3 minutes of measurements, either in the baseline condition, or following treatment removal for individual observers (indicated by different symbols). Group means are shown by the short horizontal bars. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

Figure 5: Distributions (PDF) of normalised exclusive phase durations for the treated (blue) and the non-treated eyes (orange) in Experiment 2, pooled across all participants. Each row corresponds to a condition and each column corresponds to a time bin within which the phase durations were pooled. For details of the fitted curves, see the legend of Figure 2. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

Figure 6: Relative eye dominance in Experiment 2. (a)–(d) The time course of the eye dominance ratio, in mean phase duration (a and c) or predominance (b and d), for the baseline condition, and the passive and the active conditions. The results for a representative observer are shown in (a) and (b), and those averaged across all participants are shown in (c) and (d). The dashed horizontal line indicates no difference between the observer's two eyes in a given condition. Error bars are bootstrapped 95% confidence intervals (10,000 repetitions) for duration ratios and are ±1 SEM for predominance ratios. (e)–(f) The eye dominance ratio (log-transformed) during the first 3 minutes following treatment removal for individual observers (indicated by different symbols). Group means are shown by the short horizontal bars. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

Figure 7: Distributions (PDF) of normalised exclusive phase durations in Experiment 3. Each subplot represents the durations within a three-minute measurement run as indicated at the top. The three leftmost subplots are the durations measured during the monocular inversion period (blue: treated eye; orange: non-treated eye), whereas the data plotted in the two rightmost subplots were measured after the prism was removed (yellow: treated eye; purple: non-treated eye). The normalised baseline durations are also plotted in each graph for comparison (black). For details of the fitted curves, see the

legend of Figure 2. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

Figure 8: Relative eye dominance in Experiment 3. (a)–(d) The eye dominance ratio as a function of time elapsed since the onset/offset of monocular inversion, in terms of mean phase duration (a and c) and predominance (b and d). The results for a representative observer are shown in (a) and (b) and those averaged across all participants are shown in (c) and (d). The dotted line plots the data measured during the monocular inversion period whereas the solid line is for the measurements after removing the prism. The arrow marks the time point at which the inverting prism was removed. The dashed horizontal line indicates the level where monocular treatment had no effect on the relative eye dominance. Error bars are bootstrapped 95% confidence intervals (10,000 repetitions) for duration ratios and are ±1 SEM for predominance ratios. (e)–(f) The eye dominance ratio (log-transformed) immediately after prism onset and after 30 minutes for individual observers (indicated by different symbols). Group means are shown by the short horizontal bars.

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Figure 1

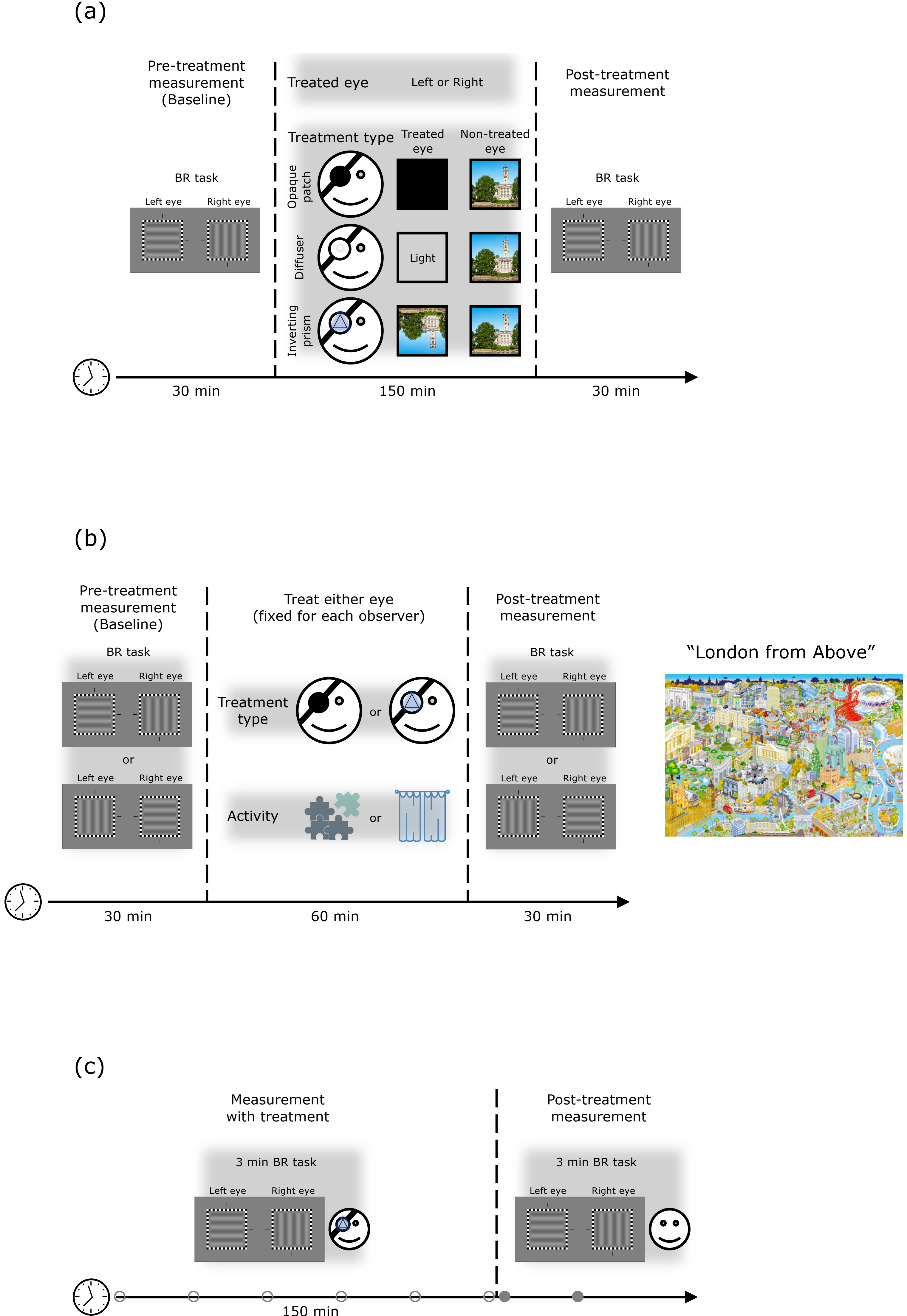

(a)
Pre-treatment measurement (Baseline)
BR task
Left eye
Right eye
30 min
Treated eye
Left or Right
Treatment type
Treated eye
Non-treated eye
Opaque patch
Diffuser
Light
Inverting prism
150 min
Post-treatment measurement
BR task
Left eye
Right eye
30 min
(b)
Pre-treatment measurement (Baseline)
BR task
Left eye
Right eye
or
Left eye
Right eye
30 min
Treat either eye (fixed for each observer)
Treatment type
or
Activity
or
60 min
Post-treatment measurement
BR task
Left eye
Right eye
or
Left eye
Right eye
30 min
"London from Above"
(c)
Measurement with treatment
3 min BR task
Left eye
Right eye
150 min
Post-treatment measurement
3 min BR task
Left eye
Right eye

Figure 2

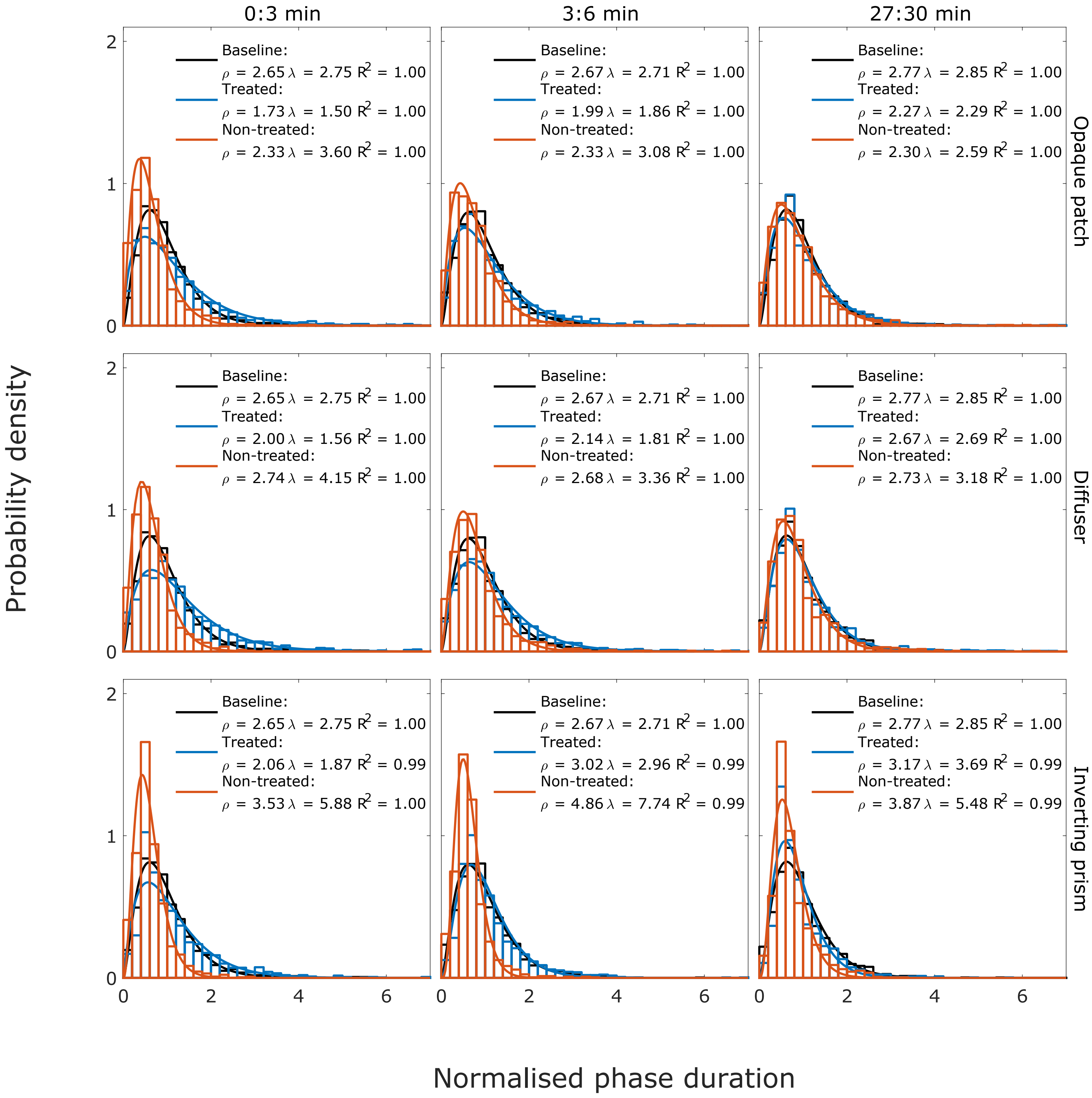

0:3 min
3:6 min
27:30 min
Opaque patch
Diffuser
Inverting prism
Probability density
Normalised phase duration
0
1
2
0
2
4
6
Baseline:
ρ = 2.65 λ = 2.75 R2 = 1.00
Treated:
ρ = 1.73 λ = 1.50 R2 = 1.00
Non-treated:
ρ = 2.33 λ = 3.60 R2 = 1.00
Baseline:
ρ = 2.67 λ = 2.71 R2 = 1.00
Treated:
ρ = 1.99 λ = 1.86 R2 = 1.00
Non-treated:
ρ = 2.33 λ = 3.08 R2 = 1.00
Baseline:
ρ = 2.77 λ = 2.85 R2 = 1.00
Treated:
ρ = 2.27 λ = 2.29 R2 = 1.00
Non-treated:
ρ = 2.30 λ = 2.59 R2 = 1.00
Baseline:
ρ = 2.65 λ = 2.75 R2 = 1.00
Treated:
ρ = 2.00 λ = 1.56 R2 = 1.00
Non-treated:
ρ = 2.74 λ = 4.15 R2 = 1.00
Baseline:
ρ = 2.67 λ = 2.71 R2 = 1.00
Treated:
ρ = 2.14 λ = 1.81 R2 = 1.00
Non-treated:
ρ = 2.68 λ = 3.36 R2 = 1.00
Baseline:
ρ = 2.77 λ = 2.85 R2 = 1.00
Treated:
ρ = 2.67 λ = 2.69 R2 = 1.00
Non-treated:
ρ = 2.73 λ = 3.18 R2 = 1.00
Baseline:
ρ = 2.65 λ = 2.75 R2 = 1.00
Treated:
ρ = 2.06 λ = 1.87 R2 = 0.99
Non-treated:
ρ = 3.53 λ = 5.88 R2 = 1.00
Baseline:
ρ = 2.67 λ = 2.71 R2 = 1.00
Treated:
ρ = 3.02 λ = 2.96 R2 = 0.99
Non-treated:
ρ = 4.86 λ = 7.74 R2 = 0.99
Baseline:
ρ = 2.77 λ = 2.85 R2 = 1.00
Treated:
ρ = 3.17 λ = 3.69 R2 = 0.99
Non-treated:
ρ = 3.87 λ = 5.48 R2 = 0.99

Figure 3

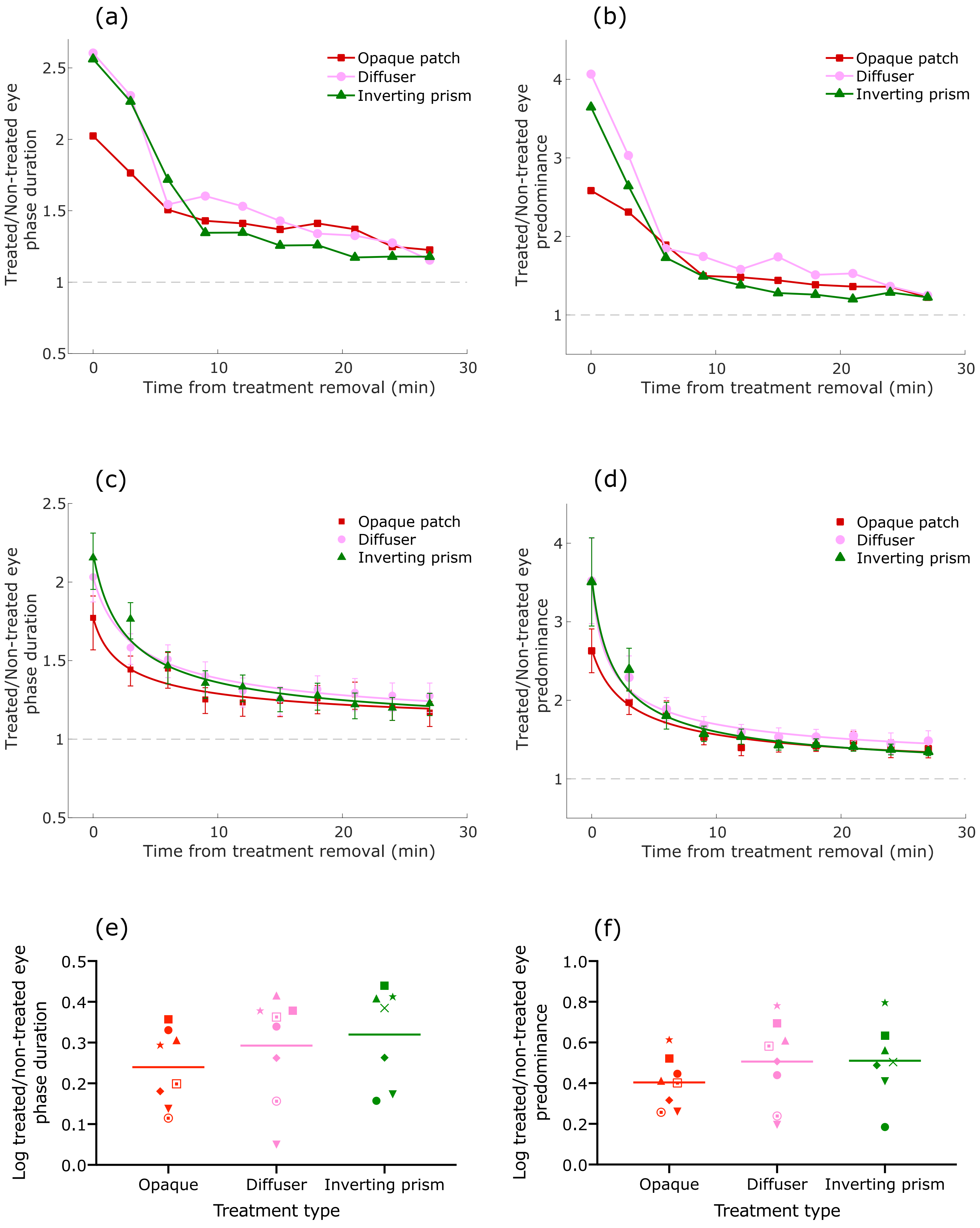

(a)
Treated/Non-treated eye phase duration
2.5
2
1.5
1
0.5
0
10
20
30
Time from treatment removal (min)
Opaque patch
Diffuser
Inverting prism
(b)
Treated/Non-treated eye predominance
4
3
2
1
0
10
20
30
Time from treatment removal (min)
Opaque patch
Diffuser
Inverting prism
(c)
Treated/Non-treated eye phase duration
2.5
2
1.5
1
0.5
0
10
20
30
Time from treatment removal (min)
Opaque patch
Diffuser
Inverting prism
(d)
Treated/Non-treated eye predominance
4
3
2
1
0
10
20
30
Time from treatment removal (min)
Opaque patch
Diffuser
Inverting prism
(e)
Log treated/non-treated eye phase duration
0.5
0.4
0.3
0.2
0.1
0.0
Opaque
Diffuser
Inverting prism
Treatment type
(f)
Log treated/non-treated eye predominance
1.0
0.8
0.6
0.4
0.2
0.0
Opaque
Diffuser
Inverting prism
Treatment type

Figure 4

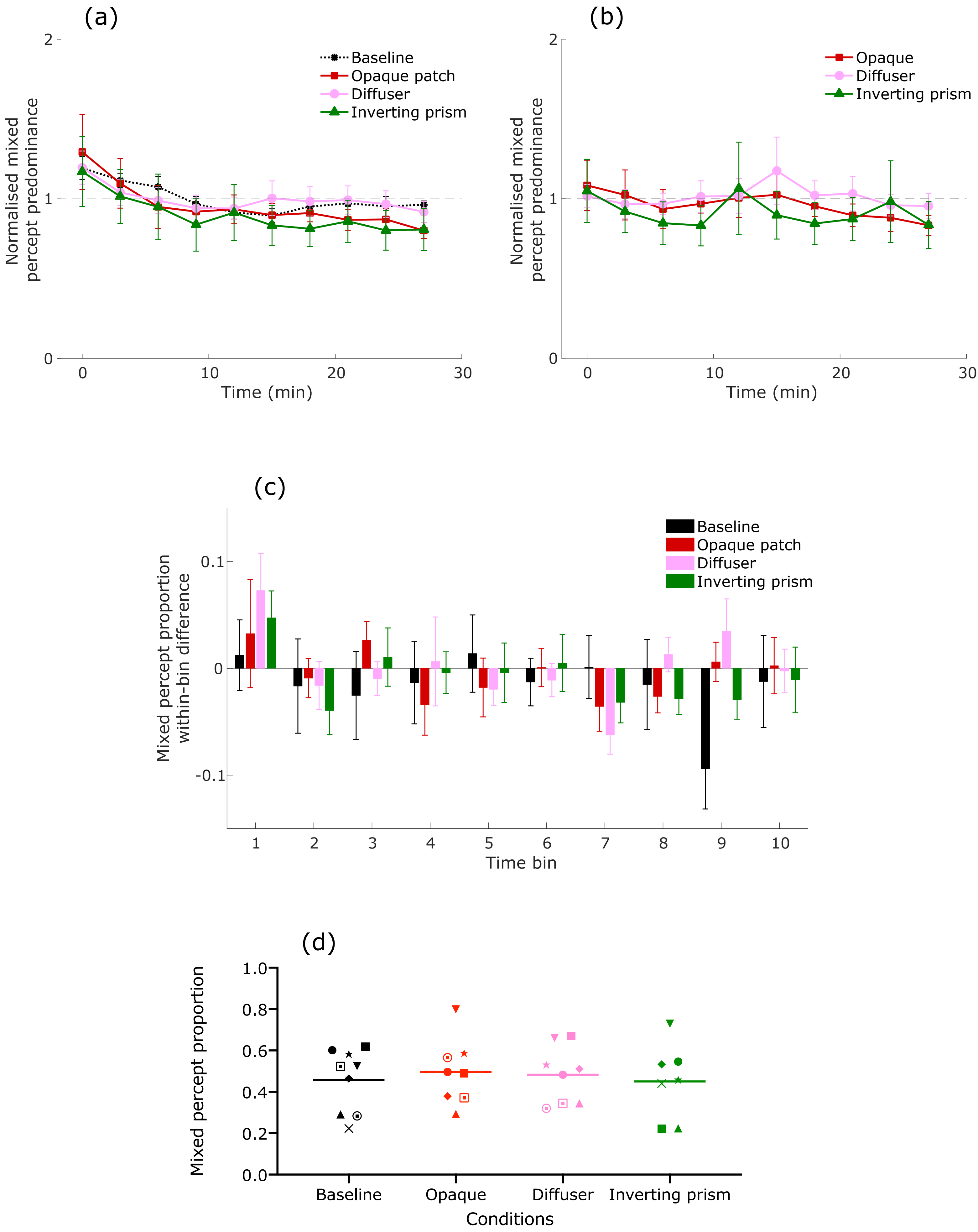

(a)
Normalised mixed percept predominance
2
1
0
0
10
20
30
Time (min)
Baseline
Opaque patch
Diffuser
Inverting prism
(b)
Normalised mixed percept predominance
2
1
0
0
10
20
30
Time (min)
Opaque
Diffuser
Inverting prism
(c)
Mixed percept proportion within-bin difference
0.1
0
-0.1
1
2
3
4
5
6
7
8
9
10
Time bin
Baseline
Opaque patch
Diffuser
Inverting prism
(d)
Mixed percept proportion
1.0
0.8
0.6
0.4
0.2
0.0
Baseline
Opaque
Diffuser
Inverting prism
Conditions

Figure 5

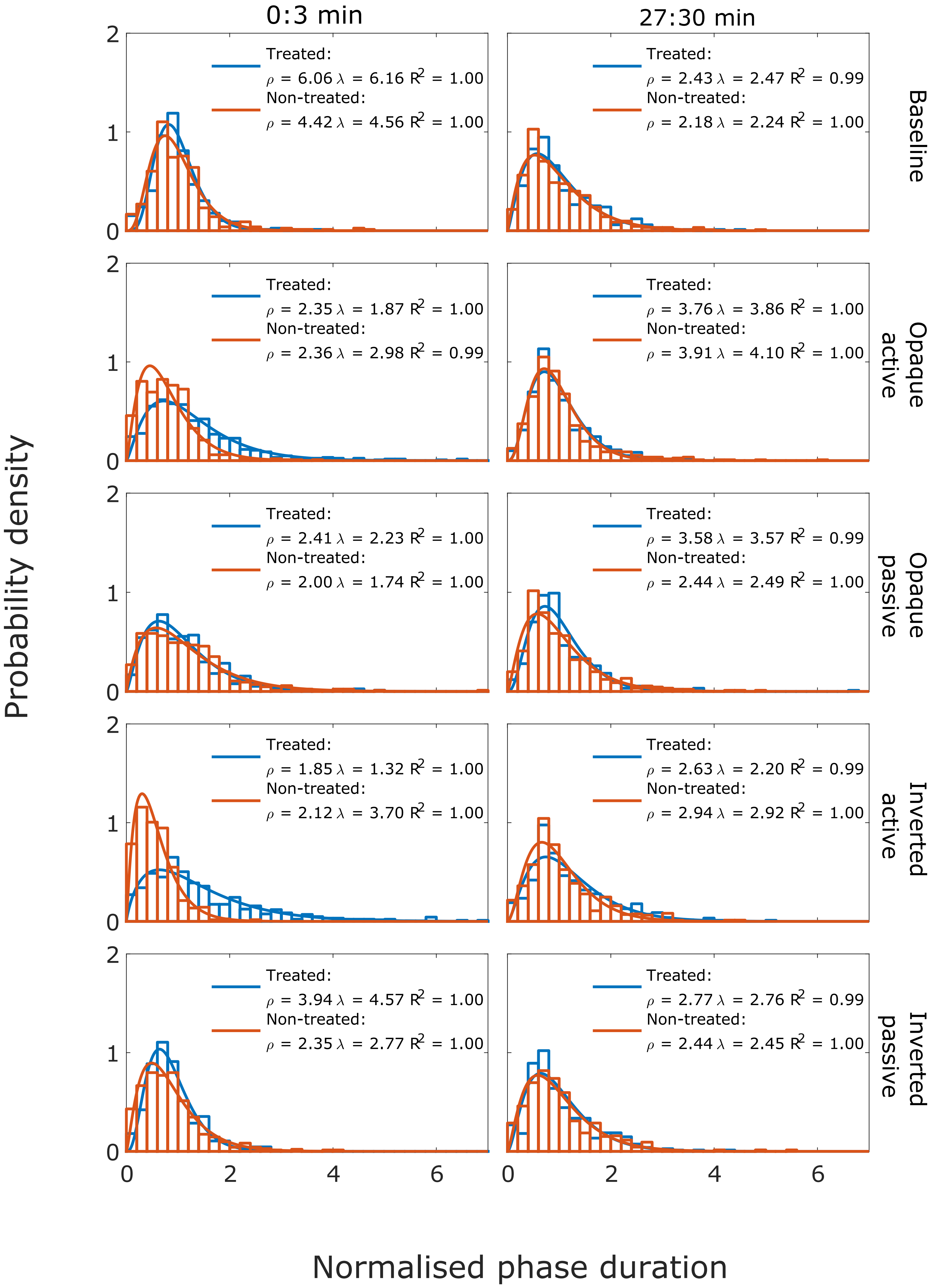

0:3 min
27:30 min
Baseline
Opaque active
Opaque passive
Inverted active
Inverted passive
Probability density
Normalised phase duration
Treated:
ρ = 6.06 λ = 6.16 R2 = 1.00
Non-treated:
ρ = 4.42 λ = 4.56 R2 = 1.00
Treated:
ρ = 2.43 λ = 2.47 R2 = 0.99
Non-treated:
ρ = 2.18 λ = 2.24 R2 = 1.00
Treated:
ρ = 2.35 λ = 1.87 R2 = 1.00
Non-treated:
ρ = 2.36 λ = 2.98 R2 = 0.99
Treated:
ρ = 3.76 λ = 3.86 R2 = 1.00
Non-treated:
ρ = 3.91 λ = 4.10 R2 = 1.00
Treated:
ρ = 2.41 λ = 2.23 R2 = 1.00
Non-treated:
ρ = 2.00 λ = 1.74 R2 = 1.00
Treated:
ρ = 3.58 λ = 3.57 R2 = 0.99
Non-treated:
ρ = 2.44 λ = 2.49 R2 = 1.00
Treated:
ρ = 1.85 λ = 1.32 R2 = 1.00
Non-treated:
ρ = 2.12 λ = 3.70 R2 = 1.00
Treated:
ρ = 2.63 λ = 2.20 R2 = 0.99
Non-treated:
ρ = 2.94 λ = 2.92 R2 = 1.00
Treated:
ρ = 3.94 λ = 4.57 R2 = 1.00
Non-treated:
ρ = 2.35 λ = 2.77 R2 = 1.00
Treated:
ρ = 2.77 λ = 2.76 R2 = 0.99
Non-treated:
ρ = 2.44 λ = 2.45 R2 = 1.00
0
1
2
0
2
4
6

Figure 6

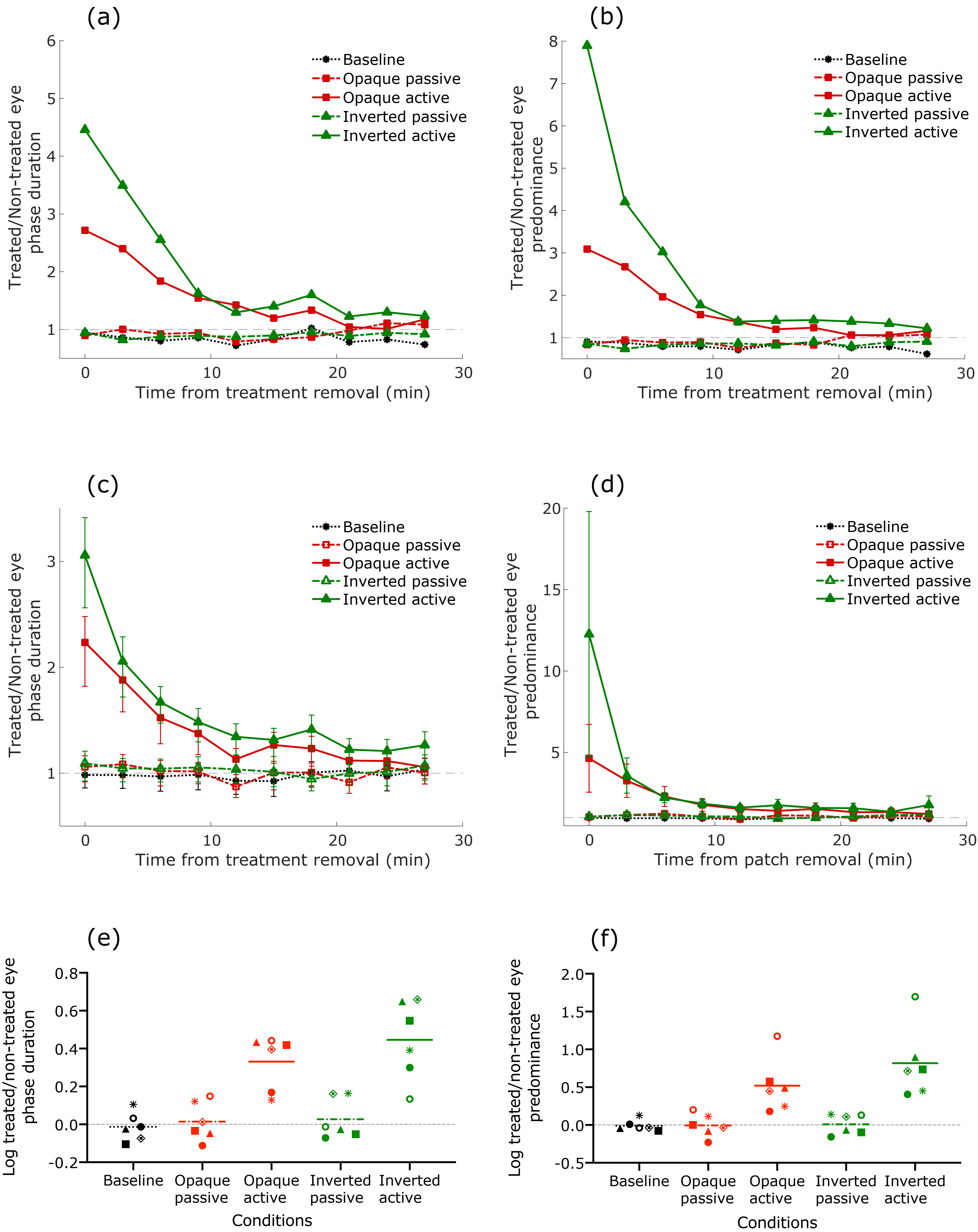

(a)
Treated/Non-treated eye phase duration
Time from treatment removal (min)
Baseline
Opaque passive
Opaque active
Inverted passive
Inverted active
(b)
Treated/Non-treated eye predominance
Time from treatment removal (min)
Baseline
Opaque passive
Opaque active
Inverted passive
Inverted active
(c)
Treated/Non-treated eye phase duration
Time from treatment removal (min)
Baseline
Opaque passive
Opaque active
Inverted passive
Inverted active
(d)
Treated/Non-treated eye predominance
Time from patch removal (min)
Baseline
Opaque passive
Opaque active
Inverted passive
Inverted active
(e)
Log treated/non-treated eye phase duration
Conditions
Baseline
Opaque passive
Opaque active
Inverted passive
Inverted active
(f)
Log treated/non-treated eye predominance
Conditions
Baseline
Opaque passive
Opaque active
Inverted passive
Inverted active

Figure 7

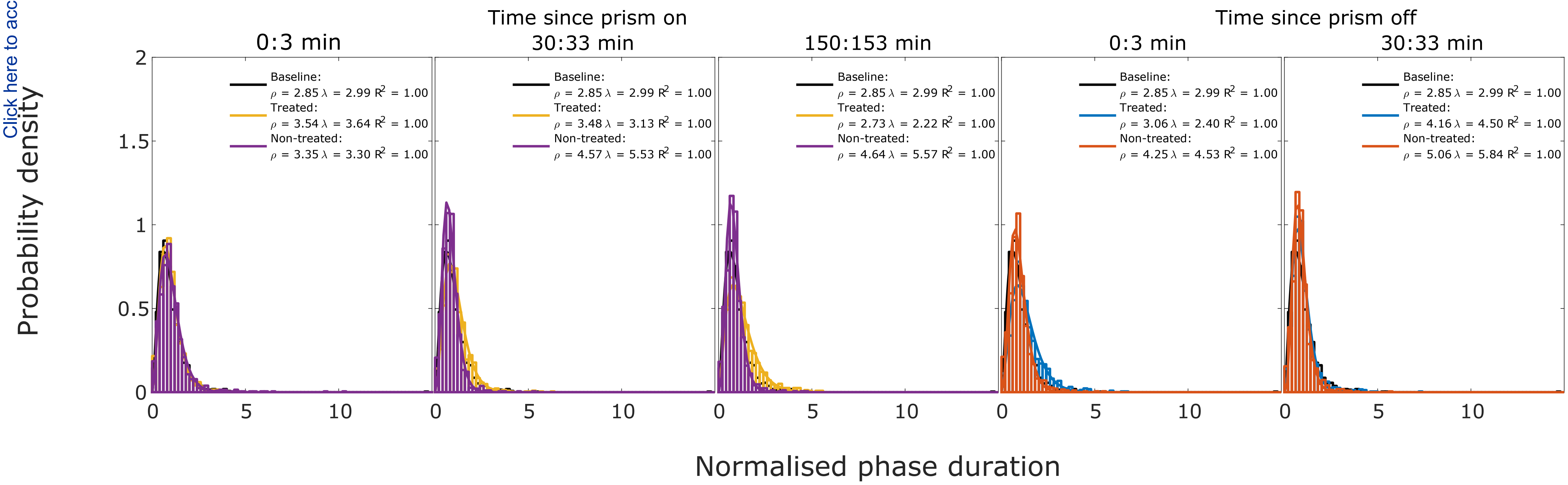
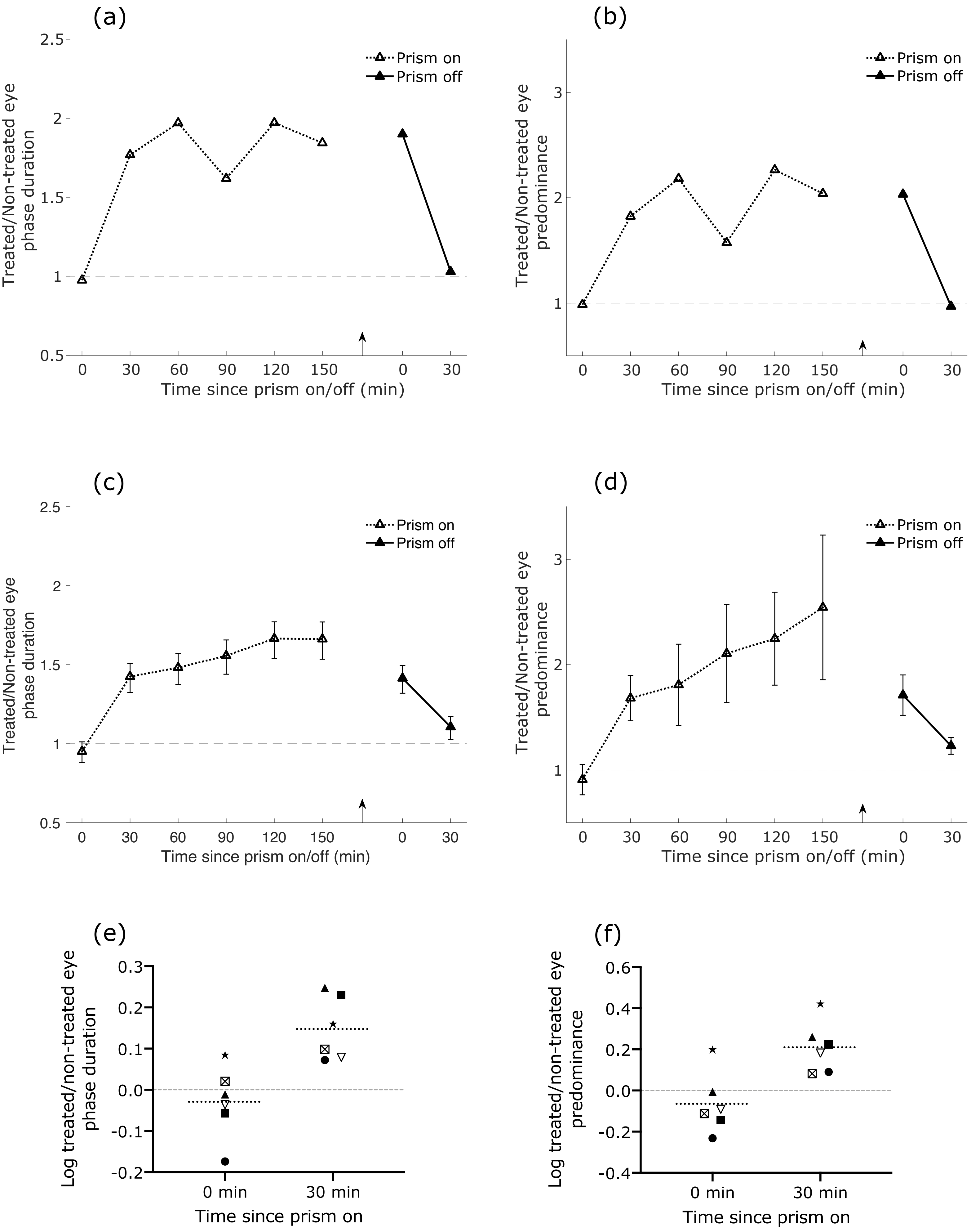

Time since prism on
Time since prism off
0:3 min
30:33 min
150:153 min
0:3 min
30:33 min
Baseline:
ρ = 2.85 λ = 2.99 R^2 = 1.00
Treated:
ρ = 3.54 λ = 3.64 R^2 = 1.00
Non-treated:
ρ = 3.35 λ = 3.30 R^2 = 1.00
Baseline:
ρ = 2.85 λ = 2.99 R^2 = 1.00
Treated:
ρ = 3.48 λ = 3.13 R^2 = 1.00
Non-treated:
ρ = 4.57 λ = 5.53 R^2 = 1.00
Baseline:
ρ = 2.85 λ = 2.99 R^2 = 1.00
Treated:
ρ = 2.73 λ = 2.22 R^2 = 1.00
Non-treated:
ρ = 4.64 λ = 5.57 R^2 = 1.00
Baseline:
ρ = 2.85 λ = 2.99 R^2 = 1.00
Treated:
ρ = 3.06 λ = 2.40 R^2 = 1.00
Non-treated:
ρ = 4.25 λ = 4.53 R^2 = 1.00
Baseline:
ρ = 2.85 λ = 2.99 R^2 = 1.00
Treated:
ρ = 4.16 λ = 4.50 R^2 = 1.00
Non-treated:
ρ = 5.06 λ = 5.84 R^2 = 1.00
Probability density
2
1.5
1
0.5
0
0
5
10
Normalised phase duration

Figure 8


(a)
Treated/Non-treated eye phase duration
2.5
2
1.5
1
0.5
Prism on
Prism off
0
30
60
90
120
150
0
30
Time since prism on/off (min)
(b)
Treated/Non-treated eye predominance
3
2
1
Prism on
Prism off
0
30
60
90
120
150
0
30
Time since prism on/off (min)
(c)
Treated/Non-treated eye phase duration
2.5
2
1.5
1
0.5
Prism on
Prism off
0
30
60
90
120
150
0
30
Time since prism on/off (min)
(d)
Treated/Non-treated eye predominance
3
2
1
Prism on
Prism off
0
30
60
90
120
150
0
30
Time since prism on/off (min)
(e)
Log treated/non-treated eye phase duration
0.3
0.2
0.1
0.0
-0.1
-0.2
0 min
30 min
Time since prism on
(f)
Log treated/non-treated eye predominance
0.6
0.4
0.2
0.0
-0.2
-0.4
0 min
30 min
Time since prism on

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