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Individual variation in inter-ocular suppression and sensory eye dominance

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ABSTRACT

The competitive and inhibitory interactions between the two eyes' images are a pervasive aspect of binocular vision. Over the last decade, our understanding of the neural processes underpinning binocular rivalry (BR) and continuous flash suppression (CFS) has increased substantially, but we still have little understanding of the relationship between these two effects and their variation in the general population. Studies that pool data across individuals and eyes risk masking substantial variations in binocular vision that exist in the general population. To investigate this issue we compared the depth of inter-ocular suppression evoked by BR with that elicited by CFS, in a group (N = 25) of visually normal individuals. A noise pattern (either static for BR or dynamic for CFS) was presented to one eye and its suppressive influence on a probe grating presented simultaneously to the other eye was measured. We found substantial individual differences in the magnitude of suppression (a 10-fold variation in probe detection threshold) evoked by each task, but performance on BR was a significant predictor of performance on the CFS task. However many individuals showed marked asymmetries between the two eyes' ability to detect a suppressed target, that were not necessarily the same for the two tasks. There was a tendency for the magnitude of the asymmetry to increase as the refresh rate of the dynamic noise increased. The results suggest a common underlying mechanism is likely to be responsible, at least in part, for driving inter-ocular suppression under BR and CFS. The marked asymmetries in inter-ocular suppression at higher noise refresh rates, may be indicative of a difference in temporal processing between the eyes.

1. Introduction

When the relative differences between the two eyes' images become too large, they compete for awareness and the brain must adopt a strategy to prevent the unwanted consequences of confusion and diplopia. It has long been recognised that one possible solution is to alternate visual awareness between the two images (binocular rivalry) but another strategy is to simply suppress one image (inter-ocular suppression), so that the other one dominates perception (e.g. Alais, 2012; Blake & Logothetis, 2002; Tsuchiya & Koch, 2005). An understanding of how these processes operate is fundamentally important not only for explaining binocular vision in the normal visual system, but also for situations when it is disrupted during development (e.g. Barrett, Bradley, & McGraw, 2004).

Binocular rivalry (BR) has been studied extensively in the laboratory (Levelt, 1965) and has traditionally been measured by presenting a pair of incompatible half images to each eye, and tracking the time course (phases) of the changing subjective experiences reported by the observer (e.g. periods of exclusive perceptual dominance, mixed percepts) over the course of the trial. It is also possible to quantify the depth of inter-ocular suppression using this technique, by requiring the observer to wait until one particular stimulus dominates perception and then measuring sensitivity to a probe stimulus presented to the other eye (Fox & Check, 1968, 1972). However a potential limitation of BR is that perceptual dominance is both unstable and unpredictable, making it difficult to measure depth of suppression in a controlled manner. A more recent technique, called continuous flash suppression (CFS), has been developed to overcome these issues (Tsuchiya & Koch, 2005). CFS is a potent form of inter-ocular suppression which occurs when a dynamic, changing pattern (e.g. a series of random Mondrians) flashed continuously to one eye renders an image presented to the other eye undetectable throughout the viewing period. Despite the fact that both are the consequences of conflict between the inputs to the two eyes, the difference in the effectiveness of inter-ocular suppression evoked by BR and CFS is dramatic (Tsuchiya & Koch, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006). That is, CFS evokes suppression of the target stimulus for extended periods of time (often up to several minutes).

Over the last decade or so, our understanding of BR and CFS has advanced significantly, but we still have little understanding of the relationship between these two processes. For example, an important unresolved issue concerns whether CFS is merely an enhanced version of BR (i.e. quantitatively different), or if they rely on distinct

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mechanisms (i.e. qualitatively different). It has been suggested that CFS is not a special form of BR, based on the observation that one of Levelt (1965) propositions of BR—that increasing the strength of one rivalrous stimulus only shortens the phase duration of the other stimulus—does not apply in the case of CFS (Tsuchiya & Koch, 2005). However the generality of Levelt's original proposition has subsequently been questioned (Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006) and thus its bearing on the relationship between BR and CFS remains equivocable. Furthermore Baker and Graf (2009) have shown that depth of suppression measured using dichoptic masking is positively associated with longer phase durations during BR, suggesting that both phenomena may share a common mechanism.

Studies that have examined the effects of low-level stimulus properties on the depth of suppression evoked by either BR or CFS, are also relevant to this issue. For example, it is well established that the degree of suppression under BR, indicated by either a change in sensitivity or relative percept dominance, can be modulated by basic attributes such as the orientations and spatial frequencies of the stimuli (Fahle, 1982; Kakizaki, 1960; Song & Yao, 2009; Stuit, Cass, Paffen, & Alais, 2009; Whittle, 1965). Similarly, it is known that in CFS the spatiotemporal properties of both the dynamic flashing stimulus and the target stimulus can influence the efficacy of suppression (Han, Blake, & Alais, 2018; Han, Lunghi, & Alais, 2016; Yang & Blake, 2012; Zhan, Engelen, & de Gelder, 2018; Zhu, Drewes, & Melcher, 2016). However, some studies that have investigated how the same low-level stimulus properties affect CFS and BR suggest that they may be mediated, at least in part, by distinct mechanisms. For instance we have recently reported that CFS is not an "all-or-nothing" phenomenon and its potency as measured by the depth of suppression of a target stimulus depends critically both on the contrast and the luminance of the dynamic noise pattern inducing the suppression (Gao et al., 2016, 2018; Ledgeway, McGraw, & Thompson, 2013). This clearly suggests that CFS may engage different inhibitory mechanisms to BR, as for the latter suppression depth (but not rivalry dynamics) is supposedly independent of the contrast and luminance of the inducing stimulus (Holopigian, 1989).

The suppression evoked by CFS and BR are often assumed to reflect the same underlying process and many studies have adopted CFS as an alternative technique to BR to render a stimulus invisible (e.g. Hong & Blake, 2009; Moors, Wagemans, & De-Wit, 2014; Sterzer, Jalkanen, & Rees, 2009; Yamashiro et al., 2014; Zadbood, Lee, & Blake, 2011). However, as substantial methodological differences between studies exist, this necessarily limit the conclusions that can be currently drawn. Thus there is a need to meaningfully compare the depth of suppression evoked by BR and CFS, under directly comparable conditions using the same set of participants, in order to better understand their relationship. Investigating the relationship between BR and CFS may be crucial for understanding the role of temporal transient components in the modulation of suppression.

Individual differences in susceptibility to laboratory-induced suppression, and rivalry, are present in subjects with normal binocular vision. For example, in the literature on binocular rivalry, individual differences in the temporal dynamics of the perceptual tracking task have been frequently noted, with respect to phase duration (Bosten et al., 2015; Carter & Pettigrew, 2003; Dieter, Sy, & Blake, 2017a; Law, Miller, & Ngo, 2017; Patel, Stuit, & Blake, 2015; van Loon et al., 2013), alternation rate (Carter & Pettigrew, 2003; Dieter et al., 2017a; Fesi & Mendola, 2015; Hancock, Gareze, Findlay, & Andrews, 2012; Kleinschmidt, Sterzer, & Rees, 2012; Law et al., 2017; Miller et al., 2010), and local biases in the visual field (Dieter, Sy, & Blake, 2017b). These individual differences in BR appear to be associated with other aspects of visual and cortical functioning including cortical surface area (Genç, Bergmann, Singer, & Kohler, 2013), gamma-amino-butyric acid (GABA) concentration (van Loon et al., 2013), peak frequency of Gamma activity in visual cortex (Fesi & Mendola, 2015), frequency of saccadic eye movements (Hancock et al., 2012), dynamics of other perceptual rivalry paradigms (Carter & Pettigrew, 2003; Patel et al., 2015), and genetic factors (Miller et al., 2010). Importantly the high intra-individual reliability of some of these measurements indicates that they are unlikely to be measurement error (Genç et al., 2013; Miller et al., 2010).

In terms of individual differences in CFS, researchers have observed that the duration of suppression ranges from a few seconds to minutes for different participants (Yamashiro et al., 2014, 2009), and others report considerable variability in threshold elevations evoked by CFS across individuals (Hong & Blake, 2009). Similarly we have recently noted marked individual differences, in a relatively small sample of 8 participants, using a conventional CFS paradigm (Ledgeway et al., 2013). Detection thresholds for a probe grating presented to one eye were measured for each of a range of dynamic noise contrasts (0–0.8) presented to the other eye. Results showed that the depth of suppression increased strongly (by up to a factor of 25) with the contrast of the dynamic noise. The threshold versus noise contrast function was characterised by a straight line, on linear-log axes, but crucially the slope of this line (an index of suppression gain) differed substantially between observers. Neuroimaging studies have also sought to identify the neural substrates associated with individual susceptibility to CFS and suppression depth has been shown to be correlated with an individual's fMRI activity in both early (striate cortex) and later cortical visual areas (Yamashiro et al., 2014, 2009).

Tasks of inter-ocular suppression such as BR and, more recently, CFS have also been used to assess sensory eye dominance, under the assumption that the dominant eye is somewhat less susceptible to suppression. However not only are there considerable individual differences in sensory eye dominance measured using each of these techniques, there is little consistency between tasks in terms of the eye which is dominant (e.g. Dieter et al., 2017a; Han, He, & Ooi, 2018; Yang, Blake, & McDonald, 2010). Moreover, many studies that have sought to compare BR and CFS in the laboratory have averaged measurements of suppression between eyes, or have chosen to examine only the eye that elicits the higher level of suppression, which may obscure asymmetries between the two eyes' susceptibility to suppress or be suppressed.

In the present study we sought to measure the depth of inter-ocular suppression evoked by both BR and CFS, using comparable stimuli and procedures in the same set of participants, to elucidate the relationship between these two processes. In addition, pooling data across individuals and eyes risks masking substantial variations in binocular vision that exist in the general population. Therefore we also aimed to establish the pattern of individual differences in susceptibility to BR and CFS in a representative sample of participants, with normal binocular vision. Finally, we addressed the role of sensory eye dominance in inter-ocular suppression, by assessing potential asymmetries between the eyes with respect to BR and CFS.

2. Experiment 1: individual differences and eye dominance associated with CFS and BR

2.1. Methods

2.1.1. Participants

Twenty-five subjects participated in Experiment 1 (age range: 21–49 years, 10 females and 15 males), including the three authors (S1, S7 and S8). The participants all had normal or corrected-to-normal vision and no history of ocular disease. All had stereopsis (range: 15–120 arcsec) as assessed by the TNO test (*Laméris Ootech*, Nieuwegein, The Netherlands). The study was conducted with the approval of University of Nottingham, School of Psychology Ethics Committee and all participants gave informed consent. All participants practised the tasks before any formal data collection.

2.1.2. Apparatus and stimuli

Stimuli were grey scale images, computer generated using an *Apple*

Macintosh running custom software written in the C programing language and were presented on a pair of identical LCD monitors (22 in. *Samsung Sync-Master 2233RZ*; 1024 × 768-pixel resolution; 60 Hz refresh rate; 318 cd/m^2 maximum luminance). The spatial characteristics, timing and luminance properties of these displays, for use in vision experiments, have been well documented (Wang & Nikolic, 2011). The two monitors were temporally synchronised with each other (driven by the dual outputs of the same video card) and calibrated such that output luminance was a linear function of the digital representation of the image. For precise control of luminance contrast the number of intensity levels available on each display was increased using the noisy-bit method, which was applied to each colour channel separately (Allard & Faubert, 2008).

Participants viewed the stimuli dichoptically through a Wheatstone mirror stereoscope, producing an effective (optical) viewing distance of 231.5 cm, in an otherwise dark room. Although the angle of the pair of full-silvered mirrors was nominally ± 45°, with respect to the median plane of the head, it was adjusted if needed for individual observers to ensure that stable fusion was achieved. The stimuli were presented against a uniform "grey" background (159 cd/m^2) within a central square region of each display which was surrounded by a high contrast, checkered fusion frame (2.21° × 2.21°), along with a pair of vertically and horizontally oriented Nonius lines, to assist stable binocular fusion. A binocular fixation cross was presented at the centre of the displays between trials and a chin rest was employed to stabilise head position when performing the tasks.

The pair of conflicting monocular stimuli used to trigger CFS or BR consisted of a spatially two-dimensional noise pattern composed of square elements (0.128° × 0.128°), and a horizontally-oriented sinusoidal grating (spatial frequency 1.8 cpd). 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%. For the CFS protocol, the noise pattern was updated with a new stochastic sample every 100 ms (10 Hz) to create a stream of dynamic visual noise. This stimulus sequence was presented to one eye, and the grating was presented to the other eye. The phase of the grating was always 0° (i.e. ± sine phase) with respect to the horizontal midline and each half of the square display window contained an integer number of cycles, preventing luminance artefacts. The Michelson contrast of the grating was 20%. For BR, the stimuli were identical to the CFS task, except that the noise pattern was static.

2.1.3. *Procedure*

A typical trial is illustrated in Fig. 1. To directly compare the depth of suppression evoked by BR with that evoked by CFS, a two-alternative forced choice (2-AFC) probe detection paradigm was used to quantify the contrast increment required to break the suppression (Fox & Check, 1968, 1972; Tsuchiya et al., 2006). At the beginning of each trial the participant was required to view the binocular fixation cross and wait until the noise pattern completely dominated perception (i.e. it was exclusively perceived). This ensured that the grating was being suppressed by the noise. The participant then pressed a key that triggered the presentation of the probe stimulus. The probe stimulus consisted of a contrast increment applied to either the top or bottom half of the grating, chosen at random on each trial. The probe lasted for 500 ms, with a smooth temporal onset and offset modulated by a Gaussian envelope (*SD* 100 ms). Following the offset of the probe, the dynamic noise stopped updating for the CFS task or the noise remained stationary for the BR task, and a response was expected at this point. Participants were required to judge the probe's spatial location (top vs. bottom). Following this response, the noise and grating were replaced with a blank interior within the fusion border and then the fixation cross was presented for 1000 ms before the next trial began.

The probe contrast increment threshold for each observer was measured using a three-down-one-up adaptive staircase tracking the 79% correct response level. For the staircase a proportional step size of 30% was used before the fourth reversal and was 15% thereafter. The staircase terminated after 12 reversals and the geometric mean of the last four reversals was used to calculate the threshold for that particular set of trials.

To assess potential asymmetries between the two eyes with respect to BR and CFS, thresholds were measured with both configurations of eye of presentation. That is, in half the conditions tested, the grating was always presented to the left eye and the noise to the right eye, and for the remaining trials the converse was true. Baseline probe thresholds were also obtained using an identical procedure, but in the absence of the noise stimulus. Participants completed a minimum of five staircases for each condition tested, in a pseudorandom order and the final threshold for each condition was calculated as the arithmetic mean of these values (the standard error of the mean, SEM, was also calculated).

2.2. *Results*

The overall group mean probe increment thresholds measured under CFS, BR, and the baseline condition (averaged across both eyes, and then across all subjects) are shown in Fig. 2. These data are plotted in the same manner as Tsuchiya et al. (2006) and despite some differences in the methodologies employed (e.g. the base contrast of the grating; isotropic noise vs. random Mondrians) they exhibit a similar pattern of results, validating our testing protocol. Both BR and CFS elicited considerable inter-ocular suppression, indicated by the elevated

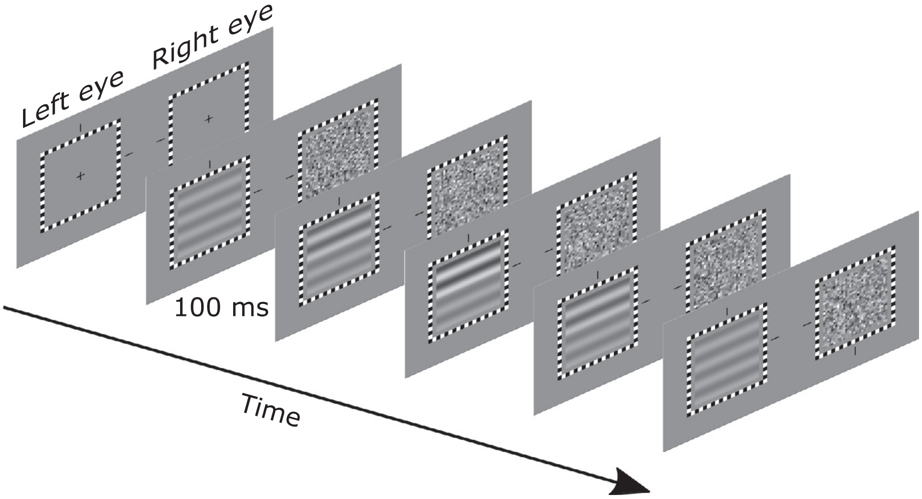

Fig. 1. Schematic representation of a single trial. After the initiation of the trial, a noise pattern (either dynamic in the case of CFS or static in the case of BR) was presented to one eye (right eye in this example) and a sinusoidal grating was simultaneously presented to the other eye. For CFS the noise image was replaced with a new sample every 100 ms (i.e. at 10 Hz). A probe (contrast increment) was presented randomly to either the top or bottom half of the grating. The location of the probe was judged after its offset.

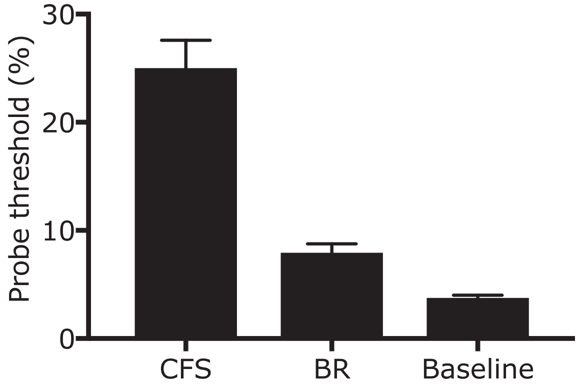

Fig. 2. Mean contrast increment thresholds (N = 25) measured under CFS, BR and the baseline condition. Error bars represent SEM across individuals.

mean probe thresholds compared to that measured in the baseline (monocular sensitivity) condition. However the depth of suppression elicited by CFS was approximately three times greater.

To reveal the individual differences within our sample of participants, and also any potential asymmetries between the two eyes with respect to baseline sensitivity, BR and CFS, the right eye's thresholds are plotted against the left eye's thresholds separately for every observer in Fig. 3. Considerable individual variation in thresholds is evident in all three conditions, whereby the mean probe thresholds, averaged across eyes, ranged from 1.94 to 7.19% for the baseline condition, 2.22 to 20.06% for BR and 5.53 to 53.48% for CFS. That is, there is almost an order of magnitude difference between the lowest and highest thresholds obtained for each condition. Indeed the coefficient of variance (ratio of the *SD* to the mean) shows that the relative variability is comparable for thresholds measured under CFS (51.56%) and BR (51.91%), while baseline thresholds are much less variable (35.70%).

In terms of sensory eye dominance in inter-ocular suppression, it is clear from Fig. 3 that although the thresholds for the two eyes are in general similar (i.e. fall close to a diagonal line with unity slope), for many individuals they are not necessarily the same. To quantify the potential asymmetries between the two eyes with respect to baseline sensitivity, BR and CFS, the Spearman rank-order correlation coefficient was calculated for each condition (a non-parametric test was used due to the violation of the assumption of normality assessed by the Shapiro-Wilk test). This showed (see Fig. 3) that in the sample we tested, for all tasks, one eye's threshold is significantly predictable from the other eye's threshold (although r_s never exceeds 0.84). Nonetheless, inspection of Fig. 3b and c shows that for BR and CFS tasks there is an overall bias towards right eye dominance in our sample, in that the right eye is less susceptible to suppression than the left eye, and is most evident for CFS.

To investigate the relationship between the degree of suppression evoked by CFS and BR, Spearman rank-order correlations were also conducted between the thresholds measured under the two tasks. To control for the baseline variations in monocular sensitivity, partial correlation was used to reveal the relationship between the magnitude of suppression elicited by each task. Fig. 4 illustrates the residuals of the thresholds measured under CFS versus those for BR, separately for each eye, after partitioning out the variance accounted for by the baseline thresholds. It is evident that performance on the two tasks are significantly associated, although it is worth noting that the correlation for right eye suppression was much weaker than that for the left eye (r_s of 0.437 vs. 0.729, respectively). This latter result implies that the direction and degree of asymmetric suppression between the two eyes is to some extent task dependent. That is, (as indicated in Fig. 3b and c) the right eye bias in our sample is much more marked for thresholds measured under CFS than those under BR. Therefore, an additional analysis was conducted to explore the relationship between inter-ocular variations in CFS and BR.

To quantify the eye dominance associated with inter-ocular suppression on each task, a signed asymmetry index was calculated for each participant using the following equation:

$$Asymmetry\ Index = 20 \times \log_{10}\left(\frac{Suppression_{lefteye} - Baseline_{lefteye}}{Suppression_{righteye} - Baseline_{righteye}}\right), \tag{1}$$

where *Suppression* denotes the mean threshold measured when the participant was undergoing either the CFS or BR task, and *Baseline* represents the mean threshold measured in the absence of the noise. This index allows us to directly quantify for each task and observer, the degree of asymmetry between the two eyes' susceptibility to suppress or be suppressed, whilst discounting any potential baseline differences in monocular sensitivity. Positive and negative values indicate right and left eye dominance,[1] respectively. Whilst zero signifies perfectly balanced suppression between the eyes, higher absolute values of the *Asymmetry Index* suggest a greater degree of bias.

Fig. 5 plots the asymmetry indices calculated for both BR and CFS (see figure legend). Asymmetric suppression between the eyes can be seen in both tasks. One participant (S15) showed no suppression under BR when the grating was presented to her right eye, so it was not possible to compute a meaningful asymmetry index in this case and this participant's data was excluded from further statistical analysis. While many points cluster around zero for both axes (i.e. the centre point) the rest of the points can be found in nearly every quadrant. Spearman rank-order correlations showed that there was no significant association between the indices measured on the two tasks. A Bayes factor was then computed to quantify the evidence for the null hypothesis (i.e. no relationship between the asymmetry indices obtained on the two tasks), based on the method proposed by Wetzels and Wagenmakers (2012). Since the method is designed for parametric tests, for the sake of simplicity[2] the data for one other participant (S1, the most extreme outlier) were excluded from this analysis, such that the remaining data became normally distributed. A Bayes factor of 0.24 (N = 23) was obtained, suggesting substantial to strong evidence for the null hypothesis, according to the categories defined by Jeffreys (1961), that there is no relationship between the asymmetries observed in the CFS and BR tasks.

In summary, profound individual differences are evident in our measures of inter-ocular suppression under both CFS and BR. Whilst the significant correlations between the suppression produced by CFS and BR are at least suggestive of a similar mechanism mediating both phenomena, the finding that sensory eye dominance is task dependent (i.e. can be different for BR and CFS in the same individual) indicates that they might each also engage distinct mechanisms at some stage of binocular processing. This important issue will be explored further in the next experiment.

3. Experiment 2: does the inter-ocular asymmetry in suppression vary with noise refresh rate?

The importance of the transient (constantly changing) nature of the suppressing stimulus (e.g. noise) for evoking the potent and robust inter-ocular suppression found in CFS, compared to other techniques, has been realised since its inception. Tsuchiya et al. (2006), for example, observed that the depth of suppression evoked by CFS depended

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[1] Positive values of the index indicate greater suppression of the probe stimulus when it is viewed by the left eye than the right eye, and therefore indicate right eye dominance.

[2] The results of the Shapiro-Wilk test showed that the asymmetry indices for CFS were normally distributed but this was not the case for BR. Excluding one extreme case, the outlier S1, made the asymmetry indices for BR also normally distributed.

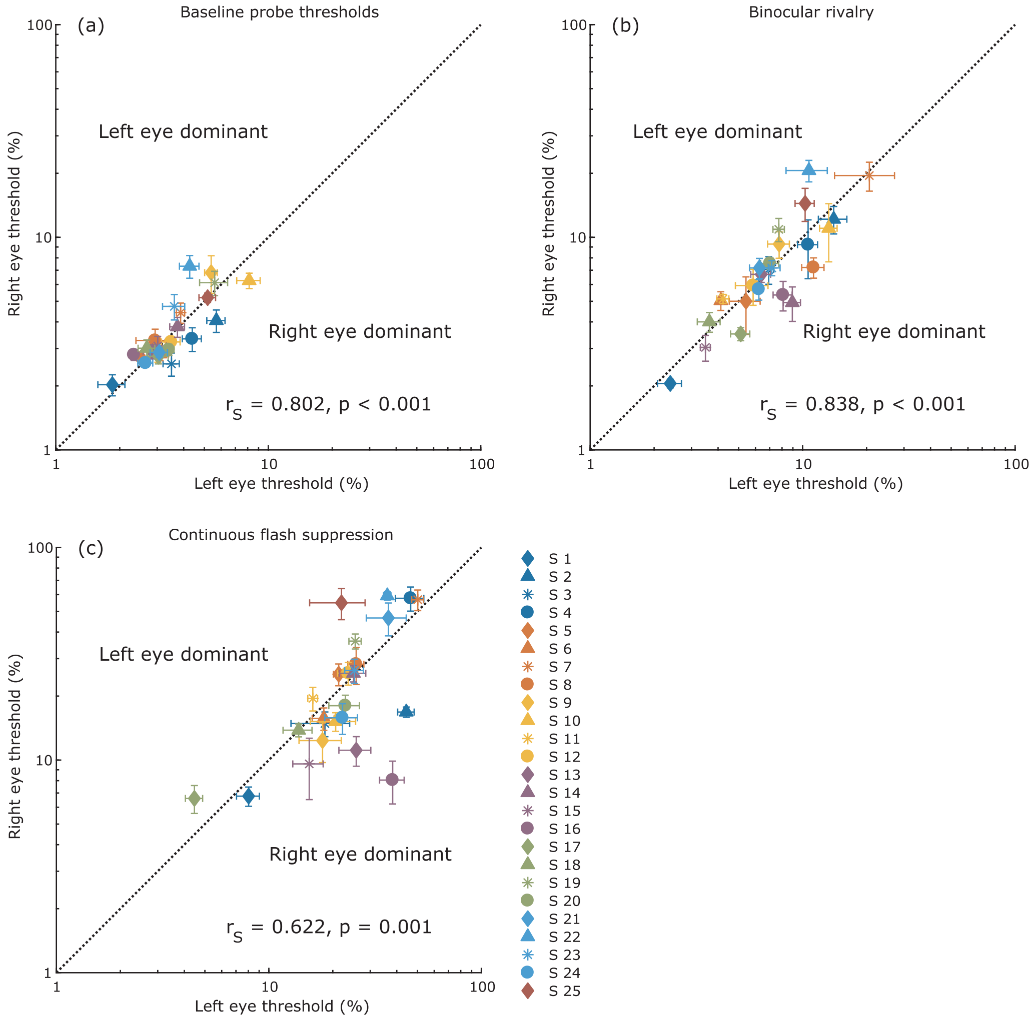

Fig. 3. Right eye thresholds plotted against left eye thresholds for all twenty-five individuals, measured (a) when there was no suppressing noise (baseline condition), (b) under suppression during BR and (c) under CFS. The diagonal dotted line (of unity slope) on each plot indicates where thresholds would fall if both eyes were equally sensitive to the probe stimulus. Points above the line show higher right eye thresholds than left eye thresholds (left eye dominance), whereas those below the line indicate the converse. Horizontal and vertical error bars represent the SEM calculated across repetitions of the task for each individual. The Spearman rank-order correlation coefficient between the two eyes' thresholds is also shown on each plot.

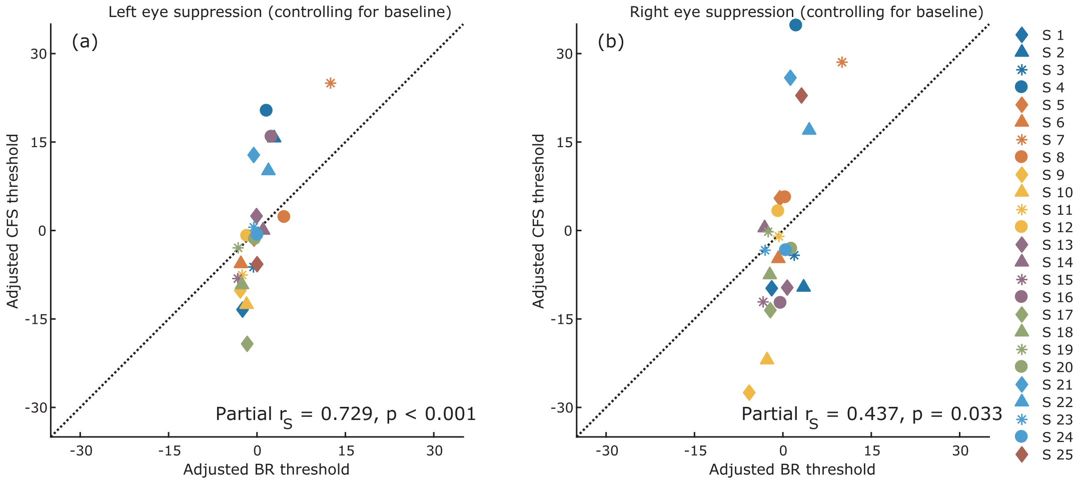

Fig. 4. Suppression depth measured under CFS versus that measured under BR when the probe stimulus was presented to the (a) left eye and (b) right eye, for twenty-five subjects. The axes show adjusted thresholds , which are the residuals left after accounting for the variance arising from the monocular baseline thresholds. Note the striking difference between the suppression depth produced by CFS and BR, indicated by the range of the data points on the ordinates and abscissae of identical scales. The results of Spearman partial correlations are shown on each plot (see text for further details).

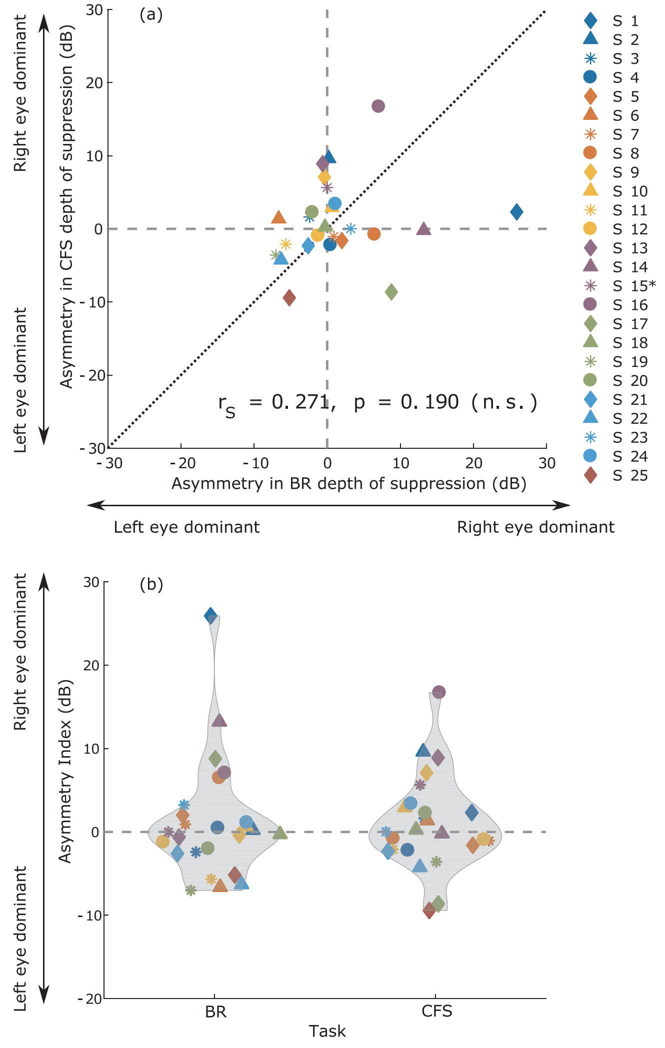

Fig. 5. The asymmetry index (Eq. (1)) in the depth of suppression between the two eyes for BR and CFS. (a) The index for every individual is plotted for CFS (ordinate) against that for BR (abscissa). The vertical and horizontal dashed lines indicate symmetric suppression under BR and CFS, respectively. The dotted diagonal line (unity slope) indicates matched asymmetries on the two tasks, in terms of both magnitude and direction. *S15 showed no suppression under BR when the grating was presented to her right eye, so it was not possible to compute a meaningful asymmetry value for this participant and it was therefore conservatively assigned to be zero. The Spearman rank-order correlation coefficient between the indices measured on the two tasks (excluding S15's data) is shown on the plot. (b) The same data are summarised in a violin plot, allowing a direct comparison between the distributions of asymmetry indices for BR and CFS along the same axis.

on the number of updates (i.e. flashes) of the dynamic Mondrian sequence. They found that suppression increased with an increasing number of flashes and reached a maximum with 5 flashes, each separated by 100 ms, equivalent to an image update rate of 10 Hz. A number of later studies have also investigated this issue although there is some variation in what is reported to be the optimal rate that triggers the strongest suppression effect (Han et al., 2016; Zhan et al., 2018; Zhu et al., 2016). Nonetheless these findings highlight the crucial role played by transient components in eliciting the relatively high degree of suppression found with CFS compared to BR.

The results of Experiment 1 indicate that even in two tasks designed to assess the depth of inter-ocular suppression, sensory eye dominance is task dependent. The paradigms used to quantify suppression under CFS and BR differed only in terms of the temporal properties of the noise stimulus: Dynamic noise refreshing at 10 Hz was used to trigger suppression for the former, whilst a stationary noise pattern was used for the latter. This raises the possibility that the differential patterns of sensory eye dominance, observed in the same individuals across the two tasks, may in fact be indicative of differences in low-level temporal properties (i.e. temporal tuning or temporal sensitivity) of the two eyes in response to binocular stimulation. If this is the case, it is reasonable to expect that varying the refresh rate of the dynamic noise pattern in a CFS task will systematically influence the magnitude of any asymmetry observed between the eyes with respect to suppression depth. The aim of the present experiment was to test this hypothesis.

3.1. Methods

3.1.1. Participants

Seven representative participants (S1, S2, S4, S7, S8, S13 and S16) that took part in Experiment 1, also participated in Experiment 2.

3.1.2. Apparatus and stimuli

The apparatus and stimuli were identical to those used in Experiment 1 with the exception that performance was measured for each of a range of noise refresh rates. Four values of refresh rate were tested—0 (i.e. BR with static noise), 2.5, 5 and 10 Hz.

3.1.3. Procedure

The procedure was identical to that used in Experiment 1. All conditions were repeated at least five times in a pseudorandom order. The data reported for thresholds measured under the baseline condition, noise refresh rate of 0 Hz and 10 Hz are those from Experiment 1.

3.2. Results

Fig. 6 shows the contrast increment thresholds for each participant measured as a function of the refresh rate of the noise serving as the suppressing stimulus. Generally, suppression depth tends to increase as the noise refresh rate increases, consistent with the findings of Tsuchiya et al. (2006). However participant S1, who showed the least suppression, seems to exhibit a ceiling effect in that suppression depth appears to increase little for refresh rates > 2.5 Hz. For observers S2 and S16, although the suppression increased with the noise refresh rate when the probe stimulus was presented to the left eye, thresholds remained relatively constant when the probe stimulus was presented to the right eye under all CFS conditions. Nevertheless, when averaged across both eyes, a mixed-effects model analysis incorporating a random effect of individuals, shows a significant fixed effect of the noise refresh rate ($b = 1.97$, $t_{(26)} = 4.47$, $p < 0.001$). Thus despite the discrepancies in thresholds between the eyes of some participants, the overall susceptibility to suppression for a given individual increases as the noise rate is increased.

Despite all participants showing relatively similar baseline monocular sensitivities for the two eyes, there are some discrepancies between individuals when the thresholds were measured with noise presented simultaneously to the other eye. First, participants S1, S4, S7 and S8 exhibit little asymmetry between the two eyes with respect to suppression depth, regardless of the refresh rate of the suppressing noise pattern. In contrast S2, S13 and S16 exhibit marked asymmetries between their eyes, the magnitude of which increases as noise refresh rate is increased. In all cases there is little difference between eyes in the BR condition. These results confirm that asymmetric suppression only exists in some observers, rather than being a universal phenomenon, since not every participant showed different degrees of suppression for the two eyes in one or more conditions. For those observers that did show asymmetric suppression, its magnitude depended strongly on the flicker rate of the noise. Notably, the magnitude of asymmetry is not predictable from the individual's stereo vision (see Fig. 6 for results of the TNO test).

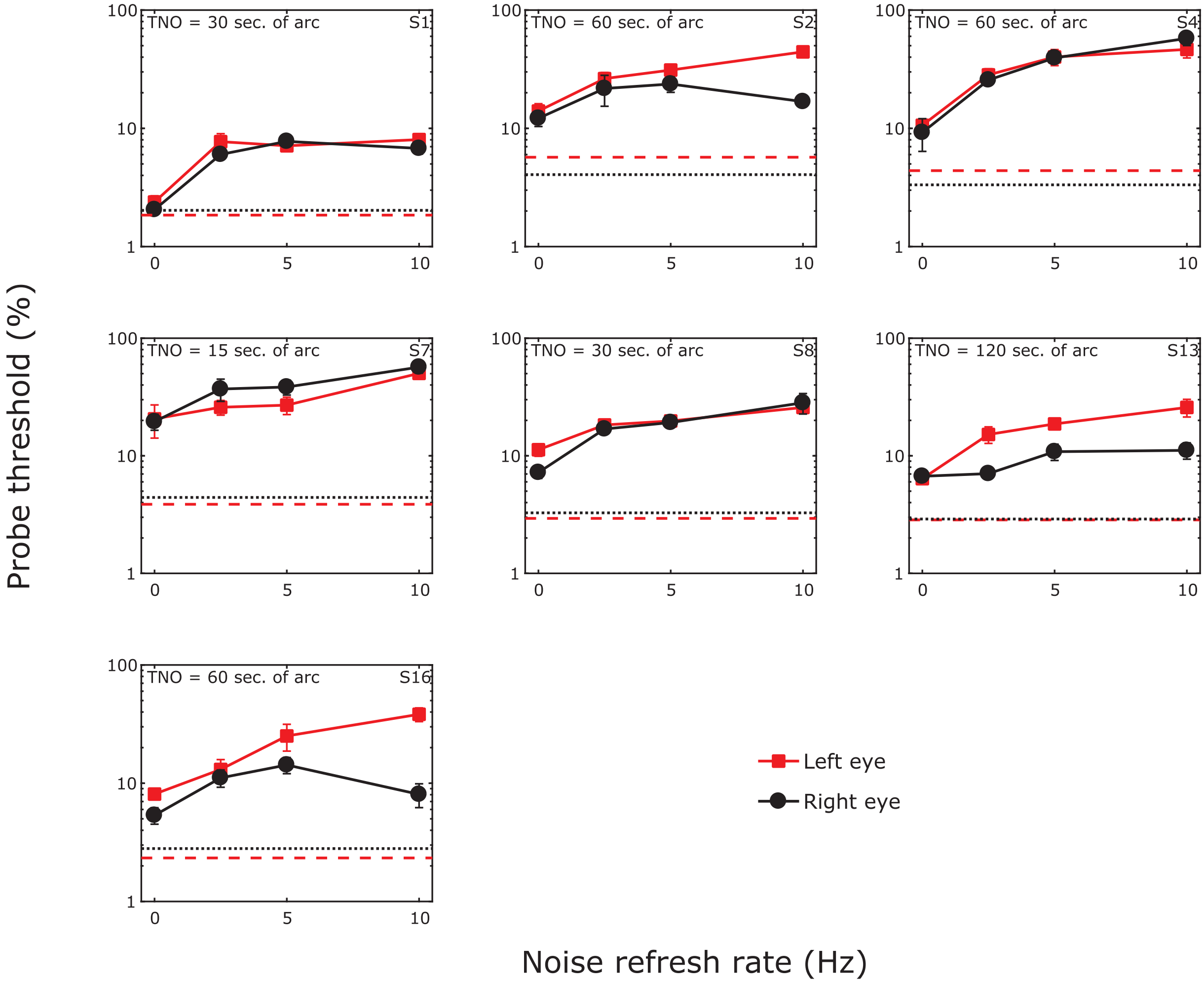

Fig. 6. Contrast increment thresholds as a function of noise refresh rate. Red squares show thresholds measured when the probe stimulus was presented to the left eye and the noise to the right eye. Black circles represent the converse configuration. Red dashed lines and black dotted lines mark the baseline thresholds for the left and right eye, respectively. Error bars represent the SEM calculated across repetitions of the task for each individual. The results of the TNO test for each individual are also shown, as an assessment of the quality of binocular vision. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. General discussion

A common view is that inter-ocular suppression arises when the two eyes are stimulated with incompatible images and is mediated by mechanisms that encode binocular differences (Katyal, Engel, He, & He, 2016; Katyal, Vergeer, He, He, & Engel, 2018; Said & Heeger, 2013). However evidence from modeling studies suggests that inter-ocular suppression might operate under a much broader range of conditions, even when the inputs to the two eyes are identical (e.g. Baker & Wade, 2017; Meese, Georgeson, & Baker, 2006). Therefore exactly what instantiates inter-ocular suppression is not yet firmly established. CFS and BR are two representative examples but their precise relationship remains unclear. The results of Experiment 1 revealed significant correlations between the suppression measured in the two tasks, for both directions of inter-ocular suppression (i.e. from left eye to right eye and *vice versa*). This suggests that a common underlying mechanism is likely to be responsible, at least in part, for evoking the inter-ocular suppression under CFS and BR. Similarly, Baker and Graf (2009) reported that greater depth of suppression under dichoptic masking was associated with longer phase durations during BR. In addition, BR elicits comparable patterns of suppression depth to those evoked by another type of inter-ocular suppression termed permanent suppression (Ooi & Loop, 1994). These findings collectively suggest considerable overlap in these inter-ocular suppression phenomena.

We sought to address the role of sensory eye dominance in inter-ocular suppression, by assessing potential asymmetries between the eyes with respect to BR and CFS. Sensory eye dominance has previously been reported on a variety of binocular tasks including BR and CFS (e.g. Bossi, Hamm, Dahlmann-Noor, & Dakin, 2018; Dieter et al., 2017a; Yang et al., 2010). In the present study, utilising an objective measure of suppression, we also found that the thresholds measured in BR and CFS tasks exhibited notable variation (asymmetry) between many of our participant's eyes. Interestingly when we computed an asymmetry index, to quantify the sign and magnitude of each participant's eye dominance on each task, whilst discounting baseline differences in monocular sensitivity, there was no significant association between the indices measured on the two tasks. Indeed for half of our participants for which a meaningful asymmetry index could be computed, the sign of the index was different for BR and CFS. That is, for one task a participant's right eye was dominant (less susceptible to inter-ocular suppression) and for the other task the left eye was dominant. This finding could be important in the sense that it might imply some degree of task-dependence for sensory eye dominance. This clearly suggests that although CFS and BR may share one, or more, stages of visual processing, they are not necessarily one and the same (c.f. Holopigian, 1989). However, those that showed changes in sensory eye dominance between the two tasks had considerably smaller absolute asymmetry indices (mean = 3.68 ± 1.20 for BR and 3.00 ± 0.93 for CFS) than those that did not switch (mean = 5.52 ± 1.99 for BR and 4.80 ± 1.38 for CFS). Thus the change in sign is likely to be a noisy result and is consistent with some previous reports on eye dominance (e.g. Li et al., 2010).

Whilst the data show that the range of the asymmetry index values is somewhat wider in BR than in CFS (see Fig. 5), this may be due in part to the way the index is calculated. That is, it uses four measurements (see Eq. (1)) to obtain the final value and the error terms are not taken into account. Consequently errors in the individual threshold values measured will have a multiplicative impact on the final ratio that is computed. With relatively small values in particular, as typically found in the case of BR, the errors may yield spuriously large asymmetry scores. This is likely to be the case for some of the observers, such as S1.[3] Consequently further research is needed to address the reliability of this finding.

Phenomenally CFS appears distinct from BR, in terms of the persistent unilateral inter-ocular suppression compared to the stochastic perceptual alternations that are characteristic of BR. However, the stimuli triggering the two processes, only differ in terms of the presence or absence of transient components in the noise used for CFS and BR, respectively. It is therefore possible that CFS is just an extreme, but more stable, version of binocular rivalry such that the switches of perceptual dominance are minimised by the temporal characteristics of the noise. Commensurate with this suggestion, there is evidence that neural adaptation may be the mechanism underpinning perceptual alternations in BR (Alais, 2012; Alais, Cass, O'Shea, & Blake, 2010; Kang & Blake, 2010; Laing & Chow, 2002; Lankheet, 2006; Shimaoka & Kaneko, 2011; Wilson, 2003). If this is the case, the transient nature of the suppressing stimulus (e.g. noise) used to evoke CFS might serve to preclude or reduce adaptation of the mechanism encoding the noise, compared with the mechanism encoding the persistent static image presented to the other eye, such that it can dominate perception for a relatively prolonged period of time.

We found in Experiment 2 that the depth of suppression increased when the noise was updated at a faster rate, up to a value of 10 Hz that is conventionally used in experiments employing a CFS task (Tsuchiya & Koch, 2005; Tsuchiya et al., 2006; Yang & Blake, 2012). Although the optimal refresh rate to trigger inter-ocular suppression is still under debate (Han et al., 2016; Zhan et al., 2018; Zhu et al., 2016), our finding that the depth of suppression systematically varied with flicker rate, underscores the crucial role of temporal transient energy in the modulation of suppression evoked by CFS.

Our results revealed that asymmetric inter-ocular suppression, present in a subset of our participants, whilst modest in the case of BR, increased when the noise was flashed and as its rate was increased. Furthermore, that the lack of obvious asymmetry in the thresholds measured in our baseline condition, implies that monocular sensitivity cannot be the origin of the asymmetry in thresholds measured under suppression. Instead, the asymmetry occurs at a stage where the inputs from both eyes interact. Consistent with this finding, Han et al. (2018) have shown that the imbalance in sensory eye dominance cannot be fully accounted for by a discrepancy in monocular contrast thresholds and that at least some degree of the asymmetry must be purely binocularly driven.

The seemingly contradictory conclusion, that a common mechanism might underpin CFS and BR whilst they differ in terms of sensory eye dominance, may be reconciled in the following sense. Our results are in line with the suggestion that the differential patterns of sensory eye dominance, observed in some individuals across BR and CFS tasks, arise due to differences in the temporal response properties of the two eyes under conditions of inter-ocular suppression. This suggests that the nature of the inter-ocular suppression underlying the two processes is likely to be the same, but the introduction of temporal transient energy in the stimulus viewed by one eye in CFS may reveal intrinsic differences between the eyes, in some individuals (even with normal binocular vision), associated with the visual processing of those components.

It is tempting to speculate that clinical suppression, typically found in strabismus and amblyopia, is mediated by the same mechanism as laboratory-induced suppression (e.g. BR). Some research has provided evidence that the suppression in amblyopia exhibited similar time course as rivalry suppression (Wolfe, 1986). Where their time courses differ, they can be equated, in amblyopia and normal subjects, using neutral density filters (Leonards & Sireteanu, 1993). However, strabismic suppression is not tuned to wavelength as is typically the case in BR (Ooi & Loop, 1994; Smith, Levi, Harwerth, & White, 1982; Smith, Levi, Manny, Harwerth, & White, 1985). This finding may provide useful insight for future investigations into the relationship between laboratory-induced inter-ocular suppression, and clinical suppression that is pathologically present in atypical visual development.

In summary, individual differences in suppression depth measured using CFS are likely to be commonplace in the general population, and are predictive of performance on an analogous BR task. However sensory eye dominance is task dependent and can be different for BR and CFS in the same individual. This latter finding may have important practical implications, when using tests of inter-ocular suppression to assess eye dominance, both in the general population and in clinical cases. We have also demonstrated that asymmetries in suppression for the two eyes depend critically and systematically on the temporal properties (flicker rate) of the noise stimulus inducing that suppression. We speculate that a possible explanation is that differences in temporal processing arising between the two eyes, under conditions of sensory conflict, can lead to marked asymmetries in the efficacy of inter-ocular suppression. This is an important area for further research, which we are currently exploring in our laboratory.

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[3] The range of individual asymmetry indices revealed with BR becomes narrower than that with CFS if excluding this subject's data (see Fig. 5b).

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