

1 Individual variation in inter-ocular suppression and sensory eye
2 dominance
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5 Mengxin Wang, Paul McGraw and Timothy Ledgeway
6
7 School of Psychology
8 University of Nottingham
9 Nottingham
10 NG7 2RD
11 United Kingdom
12

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13 Abstract

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

35

36 1. Introduction

37 When the relative differences between the two eyes' images become too large, they
38 compete for awareness and the brain must adopt a strategy to prevent the unwanted
39 consequences of confusion and diplopia. It has long been recognised that one possible
40 solution is to alternate visual awareness between the two images (binocular rivalry) but
41 another strategy is to simply suppress one image (inter-ocular suppression), so that the
42 other one dominates perception (e.g. Alais, 2012; Blake & Logothetis, 2002; Tsuchiya &
43 Koch, 2005). An understanding of how these processes operate is fundamentally
44 important not only for explaining binocular vision in the normal visual system, but also
45 for situations when it is disrupted during development (e.g. Barrett, Bradley, & McGraw,
46 2004).

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

66 Over the last decade or so, our understanding of BR and CFS has advanced significantly,
67 but we still have little understanding of the relationship between these two processes.
68 For example, an important unresolved issue concerns whether CFS is merely an
69 enhanced version of BR (i.e. quantitatively different), or if they rely on distinct
70 mechanisms (i.e. qualitatively different). It has been suggested that CFS is not a special
71 form of BR, based on the observation that one of Levelt's (1965) propositions of BR—
72 that increasing the strength of one rivalrous stimulus only shortens the phase duration
73 of the other stimulus—does not apply in the case of CFS (Tsuchiya & Koch, 2005).
74 However the generality of Levelt's original proposition has subsequently been
75 questioned (Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006) and thus its bearing
76 on the relationship between BR and CFS remains equivocal. Furthermore Baker and
77 Graf (2009) have shown that depth of suppression measured using dichoptic masking is
78 positively associated with longer phase durations during BR, suggesting that both
79 phenomena may share a common mechanism.

80 Studies that have examined the effects of low-level stimulus properties on the depth of
81 suppression evoked by either BR or CFS, are also relevant to this issue. For example, it is
82 well established that the degree of suppression under BR, indicated by either a change
83 in sensitivity or relative percept dominance, can be modulated by basic attributes such
84 as the orientations and spatial frequencies of the stimuli (Fahle, 1982; Kakizaki, 1960;
85 Song & Yao, 2009; Stuit, Cass, Paffen, & Alais, 2009; Whittle, 1965). Similarly, it is known
86 that in CFS the spatiotemporal properties of both the dynamic flashing stimulus and the
87 target stimulus can influence the efficacy of suppression (S. Han, Blake, & Alais, 2018; S.
88 Han, Lunghi, & Alais, 2016; Yang & Blake, 2012; Zhan, Engelen, & de Gelder, 2018; Zhu,
89 Drewes, & Melcher, 2016). However, some studies that have investigated how the same
90 low-level stimulus properties affect CFS and BR suggest that they may be mediated, at
91 least in part, by distinct mechanisms. For instance we have recently reported that CFS is
92 not an “all-or-nothing” phenomenon and its potency as measured by the depth of
93 suppression of a target stimulus depends critically both on the contrast and the
94 luminance of the dynamic noise pattern inducing the suppression (Gao et al., 2016,
95 2018; Ledgeway, McGraw, & Thompson, 2013). This clearly suggests that CFS may
96 engage different inhibitory mechanisms to BR, as for the latter suppression depth (but

97 not rivalry dynamics) is supposedly independent of the contrast and luminance of the
98 inducing stimulus (Holopigian, 1989).

99 The suppression evoked by CFS and BR are often assumed to reflect the same
100 underlying process and many studies have adopted CFS as an alternative technique to
101 BR to render a stimulus invisible (e.g. Hong & Blake, 2009; Moors, Wagemans, & De-Wit,
102 2014; Sterzer, Jalkanen, & Rees, 2009; Yamashiro et al., 2014; Zadbood, Lee, & Blake,
103 2011). However, as substantial methodological differences between studies exist, this
104 necessarily limit the conclusions that can be currently drawn. Thus there is a need to
105 meaningfully compare the depth of suppression evoked by BR and CFS, under directly
106 comparable conditions using the same set of participants, in order to better understand
107 their relationship. Investigating the relationship between BR and CFS may be crucial for
108 understanding the role of temporal transient components in the modulation of
109 suppression.

110 Individual differences in susceptibility to laboratory-induced suppression, and rivalry,
111 are present in subjects with normal binocular vision. For example, in the literature on
112 binocular rivalry, individual differences in the temporal dynamics of the perceptual
113 tracking task have been frequently noted, with respect to phase duration (Bosten et al.,
114 2015; Carter & Pettigrew, 2003; Dieter, Sy, & Blake, 2017a; Law, Miller, & Ngo, 2017;
115 Patel, Stuit, & Blake, 2015; van Loon et al., 2013), alternation rate (Carter & Pettigrew,
116 2003; Dieter et al., 2017a; Fesi & Mendola, 2015; Hancock, Gareze, Findlay, & Andrews,
117 2012; Kleinschmidt, Sterzer, & Rees, 2012; Law et al., 2017; Miller et al., 2010), and local
118 biases in the visual field (Dieter, Sy, & Blake, 2017b). These individual differences in BR
119 appear to be associated with other aspects of visual and cortical functioning including
120 cortical surface area (Genç, Bergmann, Singer, & Kohler, 2013), gamma-amino-butyric
121 acid (GABA) concentration (van Loon et al., 2013), peak frequency of Gamma activity in
122 visual cortex (Fesi & Mendola, 2015), frequency of saccadic eye movements (Hancock et
123 al., 2012), dynamics of other perceptual rivalry paradigms (Carter & Pettigrew, 2003;
124 Patel et al., 2015), and genetic factors (Miller et al., 2010). Importantly the high intra-
125 individual reliability of some of these measurements indicates that they are unlikely to
126 be measurement error (Genç et al., 2013; Miller et al., 2010).

127 In terms of individual differences in CFS, researchers have observed that the duration of
128 suppression ranges from a few seconds to minutes for different participants (Yamashiro
129 et al., 2014, 2009), and others report considerable variability in threshold elevations
130 evoked by CFS across individuals (Hong & Blake, 2009). Similarly we have recently
131 noted marked individual differences, in a relatively small sample of 8 participants, using
132 a conventional CFS paradigm (Ledgeway et al., 2013). Detection thresholds for a probe
133 grating presented to one eye were measured for each of a range of dynamic noise
134 contrasts (0-0.8) presented to the other eye. Results showed that the depth of
135 suppression increased strongly (by up to a factor of 25) with the contrast of the
136 dynamic noise. The threshold versus noise contrast function was characterised by a
137 straight line, on linear-log axes, but crucially the slope of this line (an index of
138 suppression gain) differed substantially between observers. Neuroimaging studies have
139 also sought to identify the neural substrates associated with individual susceptibility to
140 CFS and suppression depth has been shown to be correlated with an individual's fMRI
141 activity in both early (striate cortex) and later cortical visual areas (Yamashiro et al.,
142 2014, 2009).

143 Tasks of inter-ocular suppression such as BR and, more recently, CFS have also been
144 used to assess sensory eye dominance, under the assumption that the dominant eye is
145 somewhat less susceptible to suppression. However not only are there considerable
146 individual differences in sensory eye dominance measured using each of these
147 techniques, there is little consistency between tasks in terms of the eye which is
148 dominant (e.g. Dieter et al., 2017a; C. Han, He, & Ooi, 2018; Yang, Blake, & McDonald,
149 2010). Moreover, many studies that have sought to compare BR and CFS in the
150 laboratory have averaged measurements of suppression between eyes, or have chosen
151 to examine only the eye that elicits the higher level of suppression, which may obscure
152 asymmetries between the two eyes' susceptibility to suppress or be suppressed.

153 In the present study we sought to measure the depth of inter-ocular suppression
154 evoked by both BR and CFS, using comparable stimuli and procedures in the same set of
155 participants, to elucidate the relationship between these two processes. In addition,
156 pooling data across individuals and eyes risks masking substantial variations in
157 binocular vision that exist in the general population. Therefore we also aimed to

158 establish the pattern of individual differences in susceptibility to BR and CFS in a
159 representative sample of participants, with normal binocular vision. Finally, we
160 addressed the role of sensory eye dominance in inter-ocular suppression, by assessing
161 potential asymmetries between the eyes with respect to BR and CFS.

162 2. Experiment 1: Individual differences and eye dominance 163 associated with CFS and BR

164 2.1. Methods

165 2.1.1. *Participants*

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

174 2.1.2. *Apparatus and Stimuli*

175 Stimuli were grey scale images, computer generated using an *Apple Macintosh* running
176 custom software written in the C programming language and were presented on a pair of
177 identical LCD monitors (22 inch *Samsung Sync-Master 2233RZ*; 1024 x 768-pixel
178 resolution; 60 Hz refresh rate; 318 cd/m² maximum luminance). The spatial
179 characteristics, timing and luminance properties of these displays, for use in vision
180 experiments, have been well documented (P. Wang & Nikolic, 2011). The two monitors
181 were temporally synchronised with each other (driven by the dual outputs of the same
182 video card) and calibrated such that output luminance was a linear function of the
183 digital representation of the image. For precise control of luminance contrast the
184 number of intensity levels available on each display was increased using the noisy-bit
185 method, which was applied to each colour channel separately (Allard & Faubert, 2008).

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

197 The pair of conflicting monocular stimuli used to trigger CFS or BR consisted of a
198 spatially two-dimensional noise pattern composed of square elements ($0.128^\circ \times 0.128^\circ$),
199 and a horizontally-oriented sinusoidal grating (spatial frequency 1.8 cpd). For the noise
200 pattern, the luminance of each element was assigned by random sampling with
201 replacement, from a uniform probability distribution spanning a range determined by a
202 Michelson contrast of 20%. For the CFS protocol, the noise pattern was updated with a
203 new stochastic sample every 100 ms (10 Hz) to create a stream of dynamic visual noise.
204 This stimulus sequence was presented to one eye, and the grating was presented to the
205 other eye. The phase of the grating was always 0° (i.e. \pm sine phase) with respect to the
206 horizontal midline and each half of the square display window contained an integer
207 number of cycles, preventing luminance artefacts. The Michelson contrast of the grating
208 was 20%. For BR, the stimuli were identical to the CFS task, except that the noise
209 pattern was static.

210 *2.1.3. Procedure*

211 A typical trial is illustrated in Figure 1. To directly compare the depth of suppression
212 evoked by BR with that evoked by CFS, a two-alternative forced choice (2-AFC) probe
213 detection paradigm was used to quantify the contrast increment required to break the
214 suppression (Fox & Check, 1968, 1972; Tsuchiya et al., 2006). At the beginning of each
215 trial the participant was required to view the binocular fixation cross and wait until the

216 noise pattern completely dominated perception (i.e. it was exclusively perceived). This
217 ensured that the grating was being suppressed by the noise. The participant then
218 pressed a key that triggered the presentation of the probe stimulus. The probe stimulus
219 consisted of a contrast increment applied to either the top or bottom half of the grating,
220 chosen at random on each trial. The probe lasted for 500 ms, with a smooth temporal
221 onset and offset modulated by a Gaussian envelope (SD 100 ms). Following the offset of
222 the probe, the dynamic noise stopped updating for the CFS task or the noise remained
223 stationary for the BR task, and a response was expected at this point. Participants were
224 required to judge the probe's spatial location (top vs. bottom). Following this response,
225 the noise and grating were replaced with a blank interior within the fusion border and
226 then the fixation cross was presented for 1000 ms before the next trial began.

227 **Insert Figure 1 about here**

228 The probe contrast increment threshold for each observer was measured using a three-
229 down-one-up adaptive staircase tracking the 79% correct response level. For the
230 staircase a proportional step size of 30% was used before the fourth reversal and was
231 15% thereafter. The staircase terminated after 12 reversals and the geometric mean of
232 the last four reversals was used to calculate the threshold for that particular set of trials.

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

242 2.2. Results

243 The overall group mean probe increment thresholds measured under CFS, BR, and the
244 baseline condition (averaged across both eyes, and then across all subjects) are shown
245 in Figure 2. These data are plotted in the same manner as Tsuchiya et al. (2006) and
246 despite some differences in the methodologies employed (e.g. the base contrast of the
247 grating; isotropic noise vs. random Mondrians) they exhibit a similar pattern of results,
248 validating our testing protocol. Both BR and CFS elicited considerable inter-ocular
249 suppression, indicated by the elevated mean probe thresholds compared to that
250 measured in the baseline (monocular sensitivity) condition. However the depth of
251 suppression elicited by CFS was approximately three times greater.

252 **Insert Figure 2 about here**

253 To reveal the individual differences within our sample of participants, and also any
254 potential asymmetries between the two eyes with respect to baseline sensitivity, BR
255 and CFS, the right eye's thresholds are plotted against the left eye's thresholds
256 separately for every observer in Figure 3. Considerable individual variation in
257 thresholds is evident in all three conditions, whereby the mean probe thresholds,
258 averaged across eyes, ranged from 1.94 to 7.19% for the baseline condition, 2.22 to
259 20.06% for BR and 5.53 to 53.48% for CFS. That is, there is almost an order of
260 magnitude difference between the lowest and highest thresholds obtained for each
261 condition. Indeed the coefficient of variance (ratio of the *SD* to the mean) shows that the
262 relative variability is comparable for thresholds measured under CFS (51.56%) and BR
263 (51.91%), while baseline thresholds are much less variable (35.70%).

264 In term of sensory eye dominance in inter-ocular suppression, it is clear from Figure 3
265 that although the thresholds for the two eyes are in general similar (i.e. fall close to a
266 diagonal line with unity slope), for many individuals they are not necessarily the same.
267 To quantify the potential asymmetries between the two eyes with respect to baseline
268 sensitivity, BR and CFS, the Spearman rank-order correlation coefficient was calculated
269 for each condition (a non-parametric test was used due to the violation of the
270 assumption of normality assessed by the Shapiro-Wilk test). This showed (see Figure 3)

271 that in the sample we tested, for all tasks, one eye's threshold is significantly predictable
272 from the other eye's threshold (although r_s never exceeds 0.84). Nonetheless, inspection
273 of Figure 3b and 3c shows that for BR and CFS tasks there is an overall bias towards
274 right eye dominance in our sample, in that the right eye is less susceptible to
275 suppression than the left eye, and is most evident for CFS.

276 **Insert Figure 3 about here**

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

292 **Insert Figure 4 about here**

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

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

296 where *Suppression* denotes the mean threshold measured when the participant was
 297 undergoing either the CFS or BR task, and *Baseline* represents the mean threshold
 298 measured in the absence of the noise. This index allows us to directly quantify for each
 299 task and observer, the degree of asymmetry between the two eyes' susceptibility to
 300 suppress or be suppressed, whilst discounting any potential baseline differences in
 301 monocular sensitivity. Positive and negative values indicate right and left eye
 302 dominance¹, respectively. Whilst zero signifies perfectly balanced suppression between
 303 the eyes, higher absolute values of the *Asymmetry Index* suggest a greater degree of bias.

304 Figure 5 plots the asymmetry indices calculated for both BR and CFS (see figure legend).
 305 Asymmetric suppression between the eyes can be seen in both tasks. One participant
 306 (S15) showed no suppression under BR when the grating was presented to her right
 307 eye, so it was not possible to compute a meaningful asymmetry index in this case and
 308 this participant's data was excluded from further statistical analysis. While many points
 309 cluster around zero for both axes (i.e. the centre point) the rest of the points can be
 310 found in nearly every quadrant. Spearman rank-order correlations showed that there
 311 was no significant association between the indices measured on the two tasks. A Bayes
 312 factor was then computed to quantify the evidence for the null hypothesis (i.e. no
 313 relationship between the asymmetry indices obtained on the two tasks), based on the
 314 method proposed by Wetzels and Wagenmakers (2012). Since the method is designed
 315 for parametric tests, for the sake of simplicity² the data for one other participant (S1,
 316 the most extreme outlier) were excluded from this analysis, such that the remaining
 317 data became normally distributed. A Bayes factor of 0.24 (N=23) was obtained,
 318 suggesting substantial to strong evidence for the null hypothesis, according to the
 319 categories defined by Jeffreys (1961), that there is no relationship between the
 320 asymmetries observed in the CFS and BR tasks.

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.

321 **Insert Figure 5 about here**

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

329 3. Experiment 2: Does the inter-ocular asymmetry in 330 suppression vary with noise refresh rate?

331 The importance of the transient (constantly changing) nature of the suppressing
332 stimulus (e.g. noise) for evoking the potent and robust inter-ocular suppression found
333 in CFS, compared to other techniques, has been realised since its inception. Tsuchiya et
334 al. (2006), for example, observed that the depth of suppression evoked by CFS
335 depended on the number of updates (i.e. flashes) of the dynamic Mondrian sequence.
336 They found that suppression increased with an increasing number of flashes and
337 reached a maximum with 5 flashes, each separated by 100 ms, equivalent to an image
338 update rate of 10 Hz. A number of later studies have also investigated this issue
339 although there is some variation in what is reported to be the optimal rate that triggers
340 the strongest suppression effect (S. Han et al., 2016; Zhan et al., 2018; Zhu et al., 2016).
341 Nonetheless these findings highlight the crucial role played by transient components in
342 eliciting the relatively high degree of suppression found with CFS compared to BR.

343 The results of Experiment 1 indicate that even in two tasks designed to assess the depth
344 of inter-ocular suppression, sensory eye dominance is task dependent. The paradigms
345 used to quantify suppression under CFS and BR differed only in terms of the temporal
346 properties of the noise stimulus: Dynamic noise refreshing at 10 Hz was used to trigger
347 suppression for the former, whilst a stationary noise pattern was used for the latter.
348 This raises the possibility that the differential patterns of sensory eye dominance,
349 observed in the same individuals across the two tasks, may in fact be indicative of

350 differences in low-level temporal properties (i.e. temporal tuning or temporal
351 sensitivity) of the two eyes in response to binocular stimulation. If this is the case, it is
352 reasonable to expect that varying the refresh rate of the dynamic noise pattern in a CFS
353 task will systematically influence the magnitude of any asymmetry observed between
354 the eyes with respect to suppression depth. The aim of the present experiment was to
355 test this hypothesis.

356 3.1. Methods

357 3.1.1. Participants

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

360 3.1.2. Apparatus and Stimuli

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

364 3.1.3. Procedure

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

369 3.2. Results

370 Figure 6 shows the contrast increment thresholds for each participant measured as a
371 function of the refresh rate of the noise serving as the suppressing stimulus. Generally,
372 suppression depth tends to increase as the noise refresh rate increases, consistent with
373 the findings of Tsuchiya et al. (2006). However participant S1, who showed the least
374 suppression, seems to exhibit a ceiling effect in that suppression depth appears to
375 increase little for refresh rates > 2.5 Hz. For observers S2 and S16, although the
376 suppression increased with the noise refresh rate when the probe stimulus was

377 presented to the left eye, thresholds remained relatively constant when the probe
378 stimulus was presented to the right eye under all CFS conditions. Nevertheless, when
379 averaged across both eyes, a mixed-effects model analysis incorporating a random
380 effect of individuals, shows a significant fixed effect of the noise refresh rate ($b = 1.97$,
381 $t_{(26)} = 4.47$, $p < 0.001$). Thus despite the discrepancies in thresholds between the eyes of
382 some participants, the overall susceptibility to suppression for a given individual
383 increases as the noise rate is increased.

384 **Insert Figure 6 about here**

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

399 4. General discussion

400 A common view is that inter-ocular suppression arises when the two eyes are
401 stimulated with incompatible images and is mediated by mechanisms that encode
402 binocular differences (Katyal, Engel, He & He, 2016; Katyal, Vergeer, He, He & Engel,
403 2018; Said & Heeger, 2013). However evidence from modeling studies suggests that
404 inter-ocular suppression might operate under a much broader range of conditions, even
405 when the inputs to the two eyes are identical (e.g. Baker & Wade, 2017; Meese,

406 Georgeson & Baker, 2006). Therefore exactly what instantiates inter-ocular suppression
407 is not yet firmly established. CFS and BR are two representative examples but their
408 precise relationship remains unclear. The results of Experiment 1 revealed significant
409 correlations between the suppression measured in the two tasks, for both directions of
410 inter-ocular suppression (i.e. from left eye to right eye and *vice versa*). This suggests
411 that a common underlying mechanism is likely to be responsible, at least in part, for
412 evoking the inter-ocular suppression under CFS and BR. Similarly, Baker and Graf (2009)
413 reported that greater depth of suppression under dichoptic masking was associated
414 with longer phase durations during BR. In addition, BR elicits comparable patterns of
415 suppression depth to those evoked by another type of inter-ocular suppression termed
416 permanent suppression (Ooi & Loop, 1994). These findings collectively suggest
417 considerable overlap in these inter-ocular suppression phenomena.

418 We sought to address the role of sensory eye dominance in inter-ocular suppression, by
419 assessing potential asymmetries between the eyes with respect to BR and CFS. Sensory
420 eye dominance has previously been reported on a variety of binocular tasks including
421 BR and CFS (e.g. Bossi, Hamm, Dahlmann-Noor, & Dakin, 2018; Dieter et al., 2017a; Yang
422 et al., 2010). In the present study, utilising an objective measure of suppression, we also
423 found that the thresholds measured in BR and CFS tasks exhibited notable variation
424 (asymmetry) between many of our participant's eyes. Interestingly when we computed
425 an asymmetry index, to quantify the sign and magnitude of each participant's eye
426 dominance on each task, whilst discounting baseline differences in monocular
427 sensitivity, there was no significant association between the indices measured on the
428 two tasks. Indeed for half of our participants for which a meaningful asymmetry index
429 could be computed, the sign of the index was different for BR and CFS. That is, for one
430 task a participant's right eye was dominant (less susceptible to inter-ocular suppression)
431 and for the other task the left eye was dominant. This finding could be important in the
432 sense that it might imply some degree of task-dependence for sensory eye dominance.
433 This clearly suggests that although CFS and BR may share one, or more, stages of visual
434 processing, they are not necessarily one and the same (c.f. Holopigian, 1989). However,
435 those that showed changes in sensory eye dominance between the two tasks had
436 considerably smaller absolute asymmetry indices (mean = 3.68 ± 1.20 for BR and $3.00 \pm$
437 0.93 for CFS) than those that did not switch (mean = 5.52 ± 1.99 for BR and 4.80 ± 1.38

438 for CFS). Thus the change in sign is likely to be a noisy result and is consistent with
439 some previous reports on eye dominance (e.g. Li et al., 2010).

440 Whilst the data show that the range of the asymmetry index values is somewhat wider
441 in BR than in CFS (see Figure 5), this may be due in part to the way the index is
442 calculated. That is, it uses four measurements (see Equation 1) to obtain the final value
443 and the error terms are not taken into account. Consequently errors in the individual
444 threshold values measured will have a multiplicative impact on the final ratio that is
445 computed. With relatively small values in particular, as typically found in the case of BR,
446 the errors may yield spuriously large asymmetry scores. This is likely to be the case for
447 some of the observers, such as S1³. Consequently further research is needed to address
448 the reliability of this finding.

449 Phenomenally CFS appears distinct from BR, in terms of the persistent unilateral inter-
450 ocular suppression compared to the stochastic perceptual alternations that are
451 characteristic of BR. However, the stimuli triggering the two processes, only differ in
452 terms of the presence or absence of transient components in the noise used for CFS and
453 BR, respectively. It is therefore possible that CFS is just an extreme, but more stable,
454 version of binocular rivalry such that the switches of perceptual dominance are
455 minimised by the temporal characteristics of the noise. Commensurate with this
456 suggestion, there is evidence that neural adaptation may be the mechanism
457 underpinning perceptual alternations in BR (Alais, 2012; Alais, Cass, O'Shea, & Blake,
458 2010; Kang & Blake, 2010; Laing & Chow, 2002; Lankheet, 2006; Shimaoka & Kaneko,
459 2011; Wilson, 2003). If this is the case, the transient nature of the suppressing stimulus
460 (e.g. noise) used to evoke CFS might serve to preclude or reduce adaptation of the
461 mechanism encoding the noise, compared with the mechanism encoding the persistent
462 static image presented to the other eye, such that it can dominate perception for a
463 relatively prolonged period of time.

464 We found in Experiment 2 that the depth of suppression increased when the noise was
465 updated at a faster rate, up to a value of 10 Hz that is conventionally used in

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

466 experiments employing a CFS task (Tsuchiya & Koch, 2005; Tsuchiya et al., 2006; Yang
467 & Blake, 2012). Although the optimal refresh rate to trigger inter-ocular suppression is
468 still under debate (S. Han et al., 2016; Zhan et al., 2018; Zhu et al., 2016), our finding
469 that the depth of suppression systematically varied with flicker rate, underscores the
470 crucial role of temporal transient energy in the modulation of suppression evoked by
471 CFS.

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

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

492 It is tempting to speculate that clinical suppression, typically found in strabismus and
493 amblyopia, is mediated by the same mechanism as laboratory-induced suppression (e.g.
494 BR). Some research has provided evidence that the suppression in amblyopia exhibited

495 similar time course as rivalry suppression (Wolfe, 1986). Where their time courses
496 differ, they can be equated, in amblyopia and normal subjects, using neutral density
497 filters (Leonards & Sireteanu, 1993). However, strabismic suppression is not tuned to
498 wavelength as is typically the case in BR (Ooi & Loop, 1994; Smith III, Levi, Harwerth, &
499 White, 1982; Smith III, Levi, Manny, Harwerth, & White, 1985). This finding may
500 provide useful insight for future investigations into the relationship between
501 laboratory-induced inter-ocular suppression, and clinical suppression that is
502 pathologically present in atypical visual development.

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

515

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723

724

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

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

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

743 Figure 4: Suppression depth measured under CFS versus that measured under BR when
744 the probe stimulus was presented to the (a) left eye and (b) right eye, for twenty-five
745 subjects. The axes show adjusted thresholds (note the difference in scales for the
746 ordinates and abscissae), which are the residuals left after accounting for the variance
747 arising from the monocular baseline thresholds. The results of Spearman partial
748 correlations are shown on each plot (see text for further details).

749 Figure 5: The asymmetry index (Equation 1) in the depth of suppression between the
750 two eyes for BR and CFS. (a) The index for every individual is plotted for CFS (ordinate)
751 against that for BR (abscissa). The vertical and horizontal dashed lines indicate
752 symmetric suppression under BR and CFS, respectively. The dotted diagonal line (unity

753 slope) indicates matched asymmetries on the two tasks, in terms of both magnitude and
754 direction. *S15 showed no suppression under BR when the grating was presented to her
755 right eye, so it was not possible to compute a meaningful asymmetry value for this
756 participant and it was therefore conservatively assigned to be zero. The Spearman rank-
757 order correlation coefficient between the indices measured on the two tasks (excluding
758 S15's data) is shown on the plot. (b) The same data are summarised in a violin plot,
759 allowing a direct comparison between the distributions of asymmetry indices for BR
760 and CFS along the same axis.

761 Figure 6: Contrast increment thresholds as a function of noise refresh rate. Red squares
762 show thresholds measured when the probe stimulus was presented to the left eye and
763 the noise to the right eye. Black circles represent the converse configuration. Red
764 dashed lines and black dotted lines mark the baseline thresholds for the left and right
765 eye, respectively. Error bars represent the *SEM* calculated across repetitions of the task
766 for each individual. The results of the TNO test for each individual are also shown, as an
767 assessment of the quality of binocular vision.

Figure 1

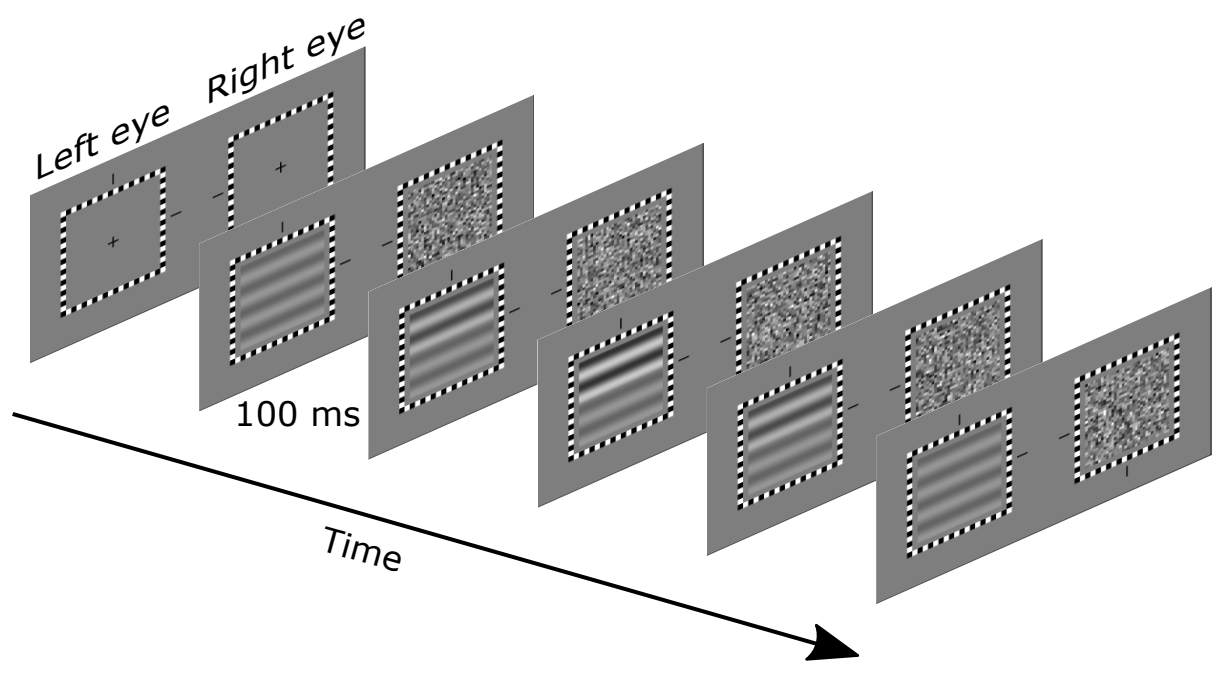


Figure 2

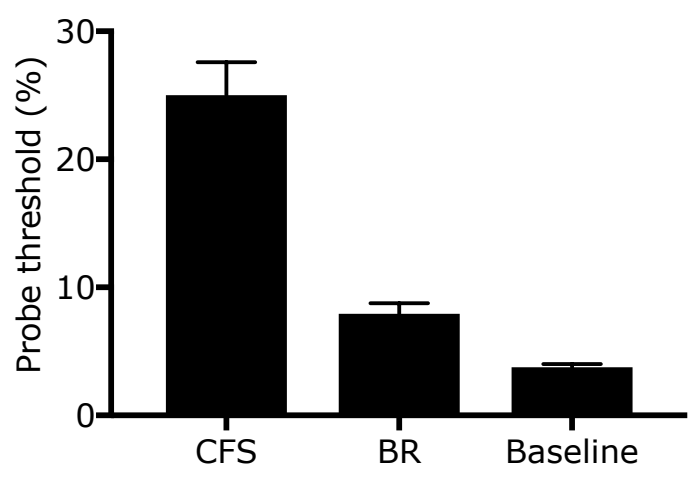


Figure 3

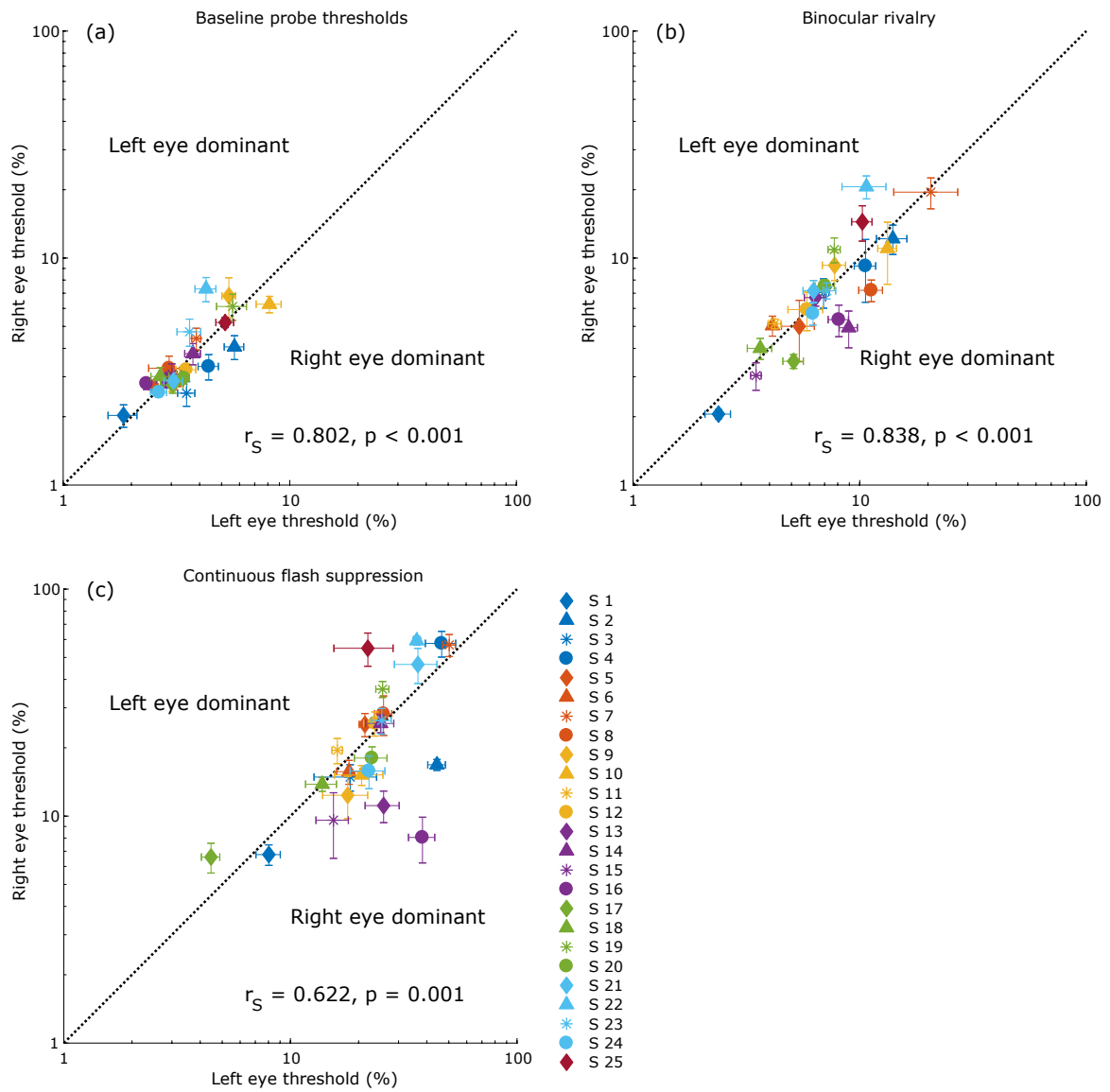


Figure 4

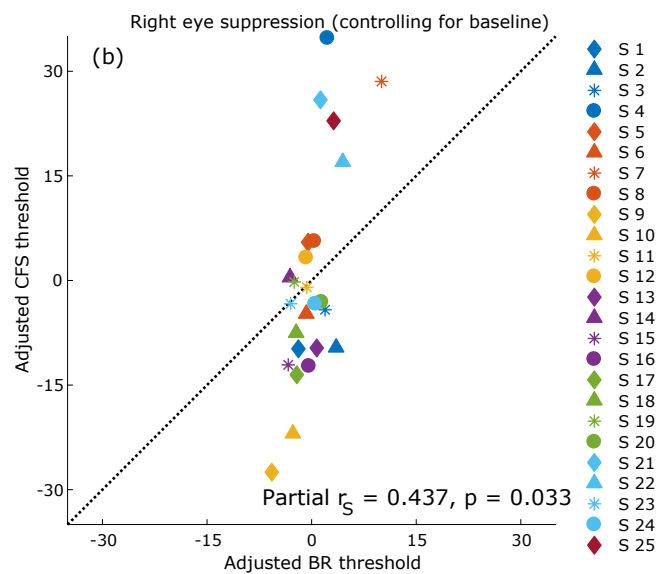
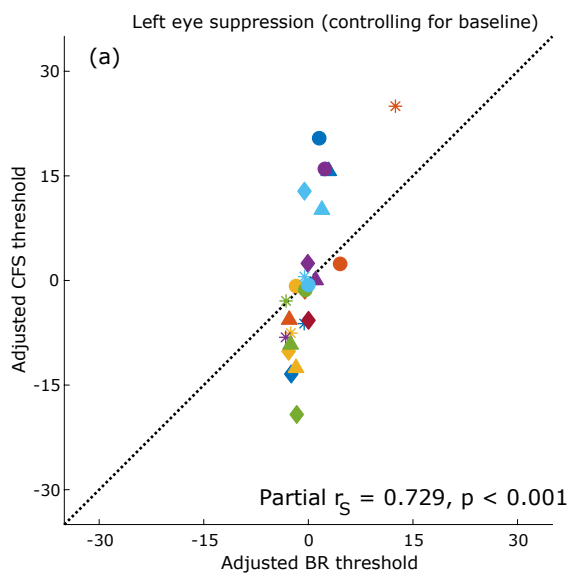


Figure 5

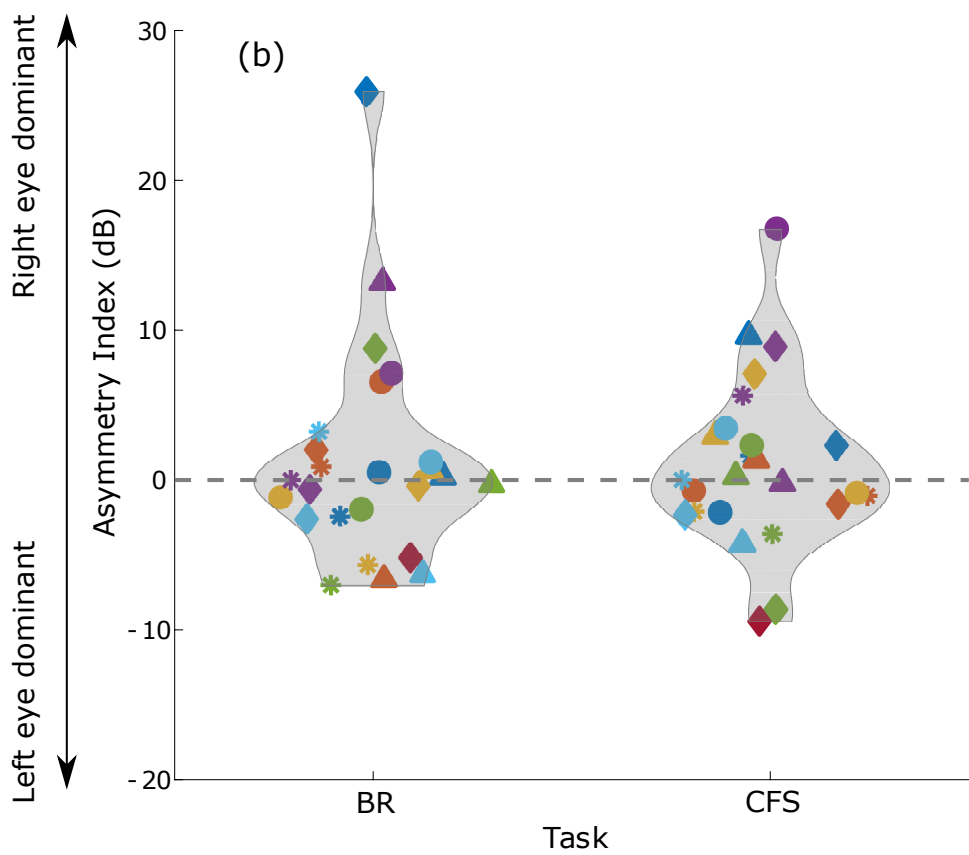
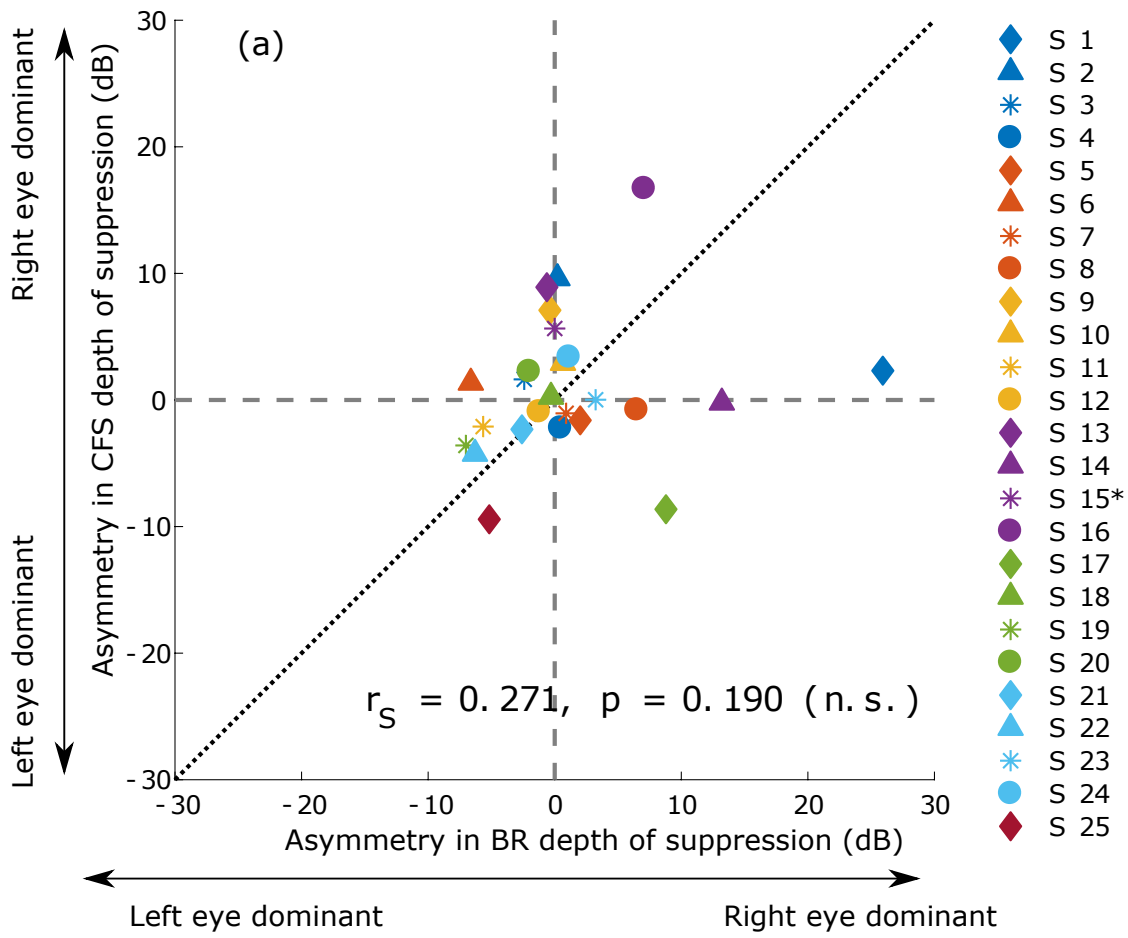


Figure 6

