



Continuous flash suppression operates in local spatial zones: Effects of mask size and contrast



Shui'Er Han^{*,1}, Raphael Lukaszewski¹, David Alais

University of Sydney, School of Psychology, NSW 2006, Australia

ARTICLE INFO

Number of reviewers = 2

Keywords:

Continuous flash suppression
Binocular rivalry
Surround suppression
Unconscious visual processing

ABSTRACT

Continuous flash suppression (CFS) is a technique in which presenting one eye with a dynamic Mondrian sequence prevents a low-contrast target in the other eye from being perceived for many seconds. Frequently used to study unconscious visual processing, CFS bears many similarities with binocular rivalry (BR), another popular dichoptic stimulation technique. It is therefore puzzling that the effect of mask size and contrast seem to differ between CFS and BR. To resolve this discrepancy, we conducted a systematic investigation on the effects of mask size and contrast in CFS. Also, building on findings from BR, we asked if the collinearity of the contours in the Mondrian masker play a role in CFS suppression. Our results showed a robust effect of mask contrast on suppression durations, and an effect of mask size that depended on collinearity. Specifically, higher mask contrasts produced longer suppression regardless of collinearity and mask size. Mask size, on the other hand, had little effect on suppression when collinearity was low and it weakened suppression when collinearity is high. These observations parallel prior findings in BR, further substantiating the close link between the two paradigms and demonstrating the usefulness of a shared explanatory framework describing both phenomena.

1. Introduction

Our world is full of rich visual information. Due to limited cognitive resources, only a small amount of the incoming information is processed into our conscious experience, placing emphasis on cues that would determine behavioural success (e.g., Tsao & Livingstone, 2008; Batty, Cave, & Pauli, 2005). This raises questions regarding the state of unperceived information, and for decades, studies have sought to uncover the extent to which unconscious stimuli influence behaviour. Among the arsenal of tools used to suppress visual awareness, continuous flash suppression (CFS) has emerged as a popular and effective technique. Similar to binocular rivalry (BR), it involves the presentation of irreconcilable images to both eyes, with the exception that one of the images is a high-contrast, dynamic sequence of Mondrian patterns and the other a low-contrast static target. Observers typically report the mask as being perceptually dominant initially, and it may take up to 20 s or more before the target becomes perceptually visible. This allows easy study of unconscious processes in the suppressed eye and has seen the widespread use of CFS in studies of unconscious visual processing (Jiang, Costello, & He, 2007; Stein, Sterzer, & Peelen, 2012; Gobbin et al., 2013; Heyman & Moors, 2014).

Studies examining the underlying mechanisms of CFS revealed

similarities with BR. For instance, rather than a complete and non-selective attenuation, suppression in both paradigms has been shown to be feature-selective for attributes such as orientation (Stuit, Cass, Paffen, & Alais, 2009; Stuit, Paffen, van der Smagt, & Verstraten, 2011; Yang & Blake, 2012; Han & Alais, 2018) and motion (Stuit et al., 2011; Moors, Wagemans, & de-Wit, 2014; but see Ananyev, Penney, & Hsieh, 2017). These feature-selective processes also appeared to operate independently. In BR, sensitivity to spatial information remained intact during motion rivalry and *vice versa* (Alais & Parker, 2006). Likewise, CFS suppression worked better on spatial form than on temporal information, and this dissociation increased with higher temporal frequencies (Zadbood, Lee, & Blake, 2011). Other similarities included the preference for parvocellular-biased stimuli (i.e., high contrast, low temporal frequency and high spatial frequency), which produced stronger interocular suppression in both BR and CFS (He, Carlson, & Chen, 2005; Han, Lungchi, & Alais, 2016). Stimuli that did not elicit parvocellular responses readily were more likely to produce weak rivalry or even binocular fusion (He, Carlson, & Chen, 2005).

Given the similarities between BR and CFS, it is puzzling that the effects of stimulus size and contrast seem to differ between the two paradigms. In CFS, increasing mask contrast typically enhances suppression (Tsuchiya & Koch, 2005; Han et al., 2016) whereas the effect of

* Corresponding author at: University of Sydney, School of Psychology, Griffith Taylor Building (A19), NSW 2044, Australia.

E-mail address: han.shuier@gmail.com (S. Han).

¹ Both authors contributed equally to this work.

Table 1

Mask (M) and Target (T) Size Comparison for a Sample of CFS Studies Stimulus sizes are measured in degrees of visual angle. The list presented CFS empirical studies taken from the first 30 Google Scholar search results, including stimulus sizes used in our previous work.

Study	M Size	T Size	M/T ratio
Tsuchiya and Koch (2005)	6° × 6°	6° × 6°	1
Tsuchiya, Koch, Gilroy, and Blake (2006)	1.6° × 1.6°	1.6° × 1.6°	1
Almeida, Mahon, Nakayama, and Caramazza (2008)	7° × 7°	7° × 7°	1
Sterzer, Jalkanen, and Rees (2009)	2.8° × 4°	2.8° × 4°	1
Yuval-Greenberg and Heeger (2013)	3° radius	2.9° radius	1.1
Gayet, Paffen, Belopolsky, Theeuwes, and Stigchel (2016)	2.2° × 2.2°	1.2° radius	1.1
Stein and Sterzer (2011)	8.4° × 8.4° – 10° × 10°	6.6° × 8° – 8.3° × 10°	1.2–1.3
Zhu, Drewes, and Melcher (2016)	9.9° × 12.4°	Face: 7.9° × 9.9° Geometric: 7.9° × 7.9°	1.6 2
Yamada and Kawabe (2011)	14.2° × 14.2°	9° × 12°	1.9
Stein, Senju, Peelen, and Sterzer (2011)	9° × 9°	3.3° × 4.6°	2
Faivre, Berthet, and Kouider (2012)	8° × 6°	3.2° × 3.9°	3.8
Tsuchiya, Moradi, Felsen, Yamazaki, and Adolphs (2009)	16° × 16°	8° × 8°	4
Mudrik, Breska, Lamy, and Deouell (2011)	5.26° × 5.26°	2.83° × 2.03°	4.8
Yang and Blake (2012)	2° × 2° & 4° × 4°	Gabor: 1° radius Face: 2° × 1.5°	1.3 5.3
Costello, Jiang, Baartman, McGlennen, and He (2009)	10.7° × 10.7°	5° × 4°	5.7
Han, Blake, and Alais (2018)	5.5° × 5.5°	1.3° radius	5.7
Adams, Gray, Garner, and Graf (2010)	7.2° × 8.8°	4° × 2.7°	5.9
Van Opstal, De Loof, Verguts, and Cleeremans (2016)	8.8° × 8.8°	3.6° × 3.6°	6
Salomon, Lim, Herbelin, Hesselmann, and Blanke (2013)	48° × 36°	16° × 18°	6
Han et al. (2016)	5.4° × 5.4°	2° × 2°	7.3
Rabovsky, Stein, and Abdel Rahman (2016)	10.4° × 10.4°	3.1° × 4.7°	7.4
Zhou, Jiang, He, and Chen (2010)	11.3° × 11.3°	3.6° × 4.6°	7.7
Moors, Boelens, Overwalle, and Wagemans (2016)	Range from 5.26° × 5.26° – 6.76° × 6.76°	2.86° × 2.03°	4.8–7.9
Stein and Sterzer (2012)	6° × 6°	1.7° × 2.3°	9.2
Yang et al. (2007)	3.7° × 3.7°	Face: 1.9° × 1.9° Eye: 0.5° × 1.8°	3.8 15.2
Jiang et al. (2007)	10.7° × 10.7°	2.1° × 2.6°	16.9
Stein, Hebart et al. (2011)	10° × 10°	2.1° × 2.6°	18.3
Han and Alais (2018)	5.4° × 5.4°	Experiment 1: 0.5° × 1° Experiment 2: 1.5° × 1.5°	4.1–18.6
Heyman and Moors (2014)	10° × 10°	0.92° – 4.35° × 0.92°	25–18.1
Hesselmann, Darcy, Ludwig, and Sterzer (2015)	8.11° × 8.11°	0.40°– 0.81° radius	31.9–130.8
Stein et al. (2012)	8.4° × 8.4° – 12° × 12°	Faces: 3.2° × 4.5° – 5.2° Bodies: 1.5° – 4.3° × 4.5° – 6.9° Inanimate: 1.8°–4.3° × 4.8° Animate: 1.7°–4.4° × 2.3° – 5.3°	5.7–36.8
Moors, Wagemans, and de-Wit (2014)	5.5° × 5.5°	0.23° radius	182

mask size is less apparent, ranging from a 1:1 ratio to more than ten times the size of the target in previous studies (summarised in Table 1). BR, on the other hand, is known to have a higher incidence of piecemeal suppression with increasing stimulus size (Blake, O'Shea, & Mueller, 1992). Stimulus size also interacted with contrast in BR, characterised by a positive relationship between contrast and suppression strength when the stimuli were small (i.e., 0.8° by 0.8°), and a null effect of contrast when stimuli size increased (Kang, 2009). The interaction between stimulus size and contrast in BR has been attributed to local spatial suppressive processes (Kang, 2009), which trigger perceptual switches in neighbouring spatial zones (Blake, 2001) when these local spatial zones shared properties such as structure (Paffen, Alais, & Verstraten, 2005), motion (Paffen, te Pas, Kanai, van der Smagt, & Verstraten, 2004), and collinearity (Alais, Lorenceau, Arrighi, & Cass, 2006). Since the rivaling gratings in Kang (2009) contained proximal collinear spatial zones, any effect of contrast may be negated by the greater amount of spatial zone interactions in larger gratings. Similarly, if we assume that both interocular suppression paradigms share a common mechanism, then the discrepancy between CFS and BR could be explained by the low structural similarity within each randomly configured Mondrian pattern (Fig. 1a). With low structural similarity, perceptual switches from interactions among local spatial zones are probably less likely, causing mask size to be less of a concern in CFS.

Alternatively, mask contrast and size may have similar effects on CFS and BR, but these effects have yet to be explored. Since CFS is

generally used to render images invisible (e.g., Yang, Zald, & Blake, 2007; Heyman & Moors, 2014), and it does that very effectively, the relationship between mask size and contrast has not been studied. Presented at a higher contrast than the target, the Mondrian pattern structure is also rich in randomly arranged contours that are updated in a rapid, unpredictable manner. In addition, the temporal and spatial frequency spectrums of the Mondrian mask have a 1/f broadband profile (Yang & Blake, 2012; Han et al., 2016). Collectively, these properties produce a large imbalance of neural activity linked to the masker compared to the target, providing suppression that is sufficiently effective for the needs of the CFS experiment. To evaluate both possibilities, we conducted systematic investigations on the independent effects of Mondrian mask size and contrast in Experiments 1 and 2, respectively, using the breaking-CFS (b-CFS) paradigm (Jiang et al., 2007; Stein, Hebart & Sterzer, 2011), which measures the time required for a target to reach visual awareness.

2. Experiments 1–2: establishing the effect of mask size and contrast

2.1. Materials and methods

2.1.1. Participants

Participants for Experiments 1 & 2 were drawn from a pool of undergraduate psychology students who had signed up to participate in perception experiments. Each was reimbursed \$20 AUD per hour for

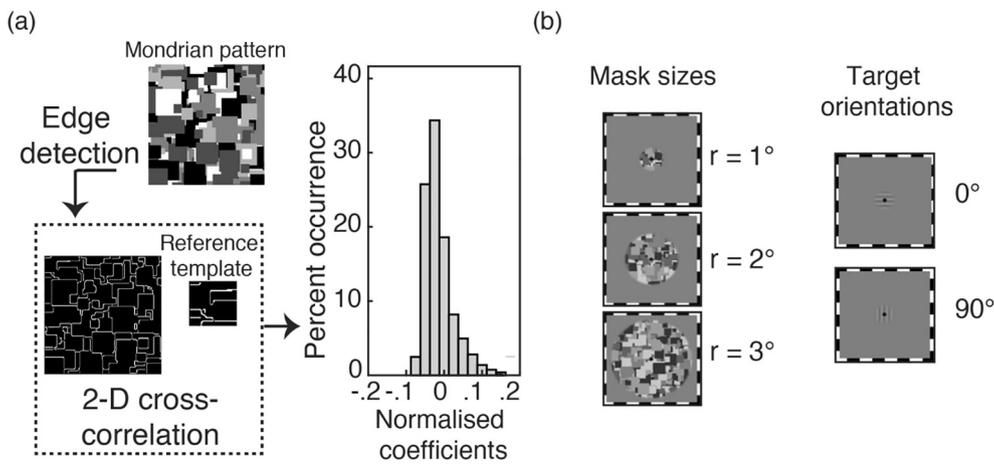


Fig. 1. Spatial properties of the Mondrian sequences used in Experiments 1–4: (a) The random configuration of the Mondrian pattern produces featurally uncorrelated local spatial zones. To illustrate, we first extracted the edges of a 200 by 200 pixels Mondrian pattern using the Canny method (Canny, 1986). Then, using a reference template (50 by 50 pixels) extracted from the image, we performed a two-dimensional cross-correlation on the image's pattern edges. The resultant histogram of the normalised cross-correlation coefficients revealed a bias towards very low ($< |0.2|$) normalised correlation coefficients. (b) To vary the size of the Mondrian mask, each pattern was windowed with a circular mask of a specific radius (i.e., 1° , 2° , 3°). The circular mask was chosen because it allows non-overlapping

areas around the target to be equal in area. Targets were vertically (90°) or horizontally (0°) oriented sinusoidal gratings with a spatial frequency of 3 cycles per degree. Similar to the mask stimuli, each target was windowed with a circular mask of a specific radius (i.e., 1°).

their time. We determined the sample size based on previous work, where effect sizes of $\eta_p^2 = 0.55$ to $\eta_p^2 = 0.84$ were obtained with seven to eleven participants (Han et al., 2016). We recruited ten students (3 females, Mean age = 23.5, $SD = 3.26$) in Experiment 1, and another 11 students (3 females, Mean age = 22.91, $SD = 3.0$) participated in Experiment 2. All participants were naïve to the purpose of the experiment and had normal or corrected-to-normal eyesight. Participants also tested normal for stereovision, assessed using the Fly Stereo Acuity Test (Stereo Optical Company Inc., Chicago, IL). Experiments were performed with the approval of the Human Research Ethics Committee, University of Sydney (Ref: 2016/662) and in accordance to the principles outlined in the Declaration of Helsinki. Informed consent was obtained from all participants.

2.1.2. Stimuli

For both experiments, the Mondrian mask was a 10 Hz sequence of patterns each composed of 265 squares set to 0, 30, 50, 70, or 100% luminance and randomly generated sizes within 0.52° – 1.3° in length. As the use of square patterns would produce a concentration of spectral power in the vertical and horizontal orientations (Yang & Blake, 2012), the target stimuli were horizontally or vertically oriented sinusoidal gratings. The spatial frequency of all target stimuli was 3 cycles per degree (cpd). Both target and mask stimuli were windowed with a circular, raised cosine function (0.29° width ramp) that smoothed the edges of the mask into the background. This allowed us to control the size of the visual stimuli and to avoid afterimages from the hard edges. The target had a radius of 1° of visual angle in both experiments. Mask sizes were 1° , 2° , and 3° radius (Fig. 1b, top panel) in Experiment 1. As the results of Experiment 1 revealed stronger suppression with larger mask sizes, we adopted the 3° radius in Experiment 2 to maximise the possible range for suppression durations. All visual stimuli were normalised to mean luminance.

During the experimental task, the visual stimuli were presented within a square (6.2° length) with a black and white checked fusion frame (0.29° width) to facilitate binocular fusion (see Fig. 1). Each Mondrian sequence was set to 15% RMS contrast in Experiment 1, and in Experiment 2 the Mondrian RMS contrast levels were 6.6%, 13.2%, and 29.8%. To reduce between-subject variability, the target RMS was first set to 10 times the monocular contrast thresholds recorded for each participant in Experiment 1. However, due to the low variability in contrast thresholds across participants and comparable thresholds across both eyes in Experiment 1 (see Results and Fig. 2), target RMS was later set to 6.6% in Experiment 2, 10 times the median threshold in Experiment 1. The phase of target grating was jittered across trials in both experiments to minimise local adaptation. Stimuli were presented

on a linearized Mitsubishi Diamond Pro 2070SB CRT monitor (100 Hz refresh rate) that was connected to a DATAPixx data acquisition system (Vpixx Technologies, Saint-Bruno, Quebec) to allow for millisecond precision and 16-bit contrast resolution.

2.1.3. Procedure

Prior to the experimental tasks, participants' demographic data such as gender and handedness were recorded. Sighting dominance was assessed using the standard Porta's test in which participants aligned their finger with a distant object, first with both eyes then alternately with each eye. The open eye with the least displacement in perceived alignment was designated as the dominant eye. Participants then began the experimental tasks, during which the stimuli were viewed through a mirror stereoscope, placed 50 cm in front of the monitor (57 cm total viewing distance) and adjusted to achieve stable fusion for each individual. Participants were instructed to fixate at the central, black fixation dot (0.1° radius) at all times during the experiment.

Contrast sensitivity may differ across participants and between eyes. As such, monocular contrast thresholds were first measured in Experiment 1. The target was presented to each eye separately, and its contrast was adjusted with a QUEST adaptive staircase procedure (Watson & Pelli, 1983). Participants judged the orientation of the target ('horizontal or vertical') for each trial, and completed a total of 40 trials for each staircase. The threshold was set to 75% accuracy for each eye, estimated by fitting a psychometric function with a Maximum likelihood procedure. Participants then proceeded to complete three blocks of the b-CFS task, during which the target was presented at 10 times the threshold value for each eye. As in the threshold measurement task, participants identified the orientation of the target as quickly and accurately as possible. Each block consisted of 24 trials that interleaved different target orientations, mask sizes and masking eye (total of 24 trials per mask size, 12 each eye). In both the threshold measurement and b-CFS tasks, one second of dichoptic static noise (6° square) was presented at the end of each trial to reduce afterimages and adaptation.

Apart from the contrast threshold measurement task, similar procedures were used in Experiment 2. Participants completed three blocks of the b-CFS, each consisting of 24 trials. The different masking eye, levels of mask contrast and target orientations were interleaved within each block, resulting in 24 trials per mask contrast (12 trials per eye). To familiarise participants with the demands of the b-CFS task, participants completed 5–10 practice trials with a higher target contrast (e.g., 15 times measured thresholds in Experiment 1). Data from these practice trials were not included in subsequent analyses.

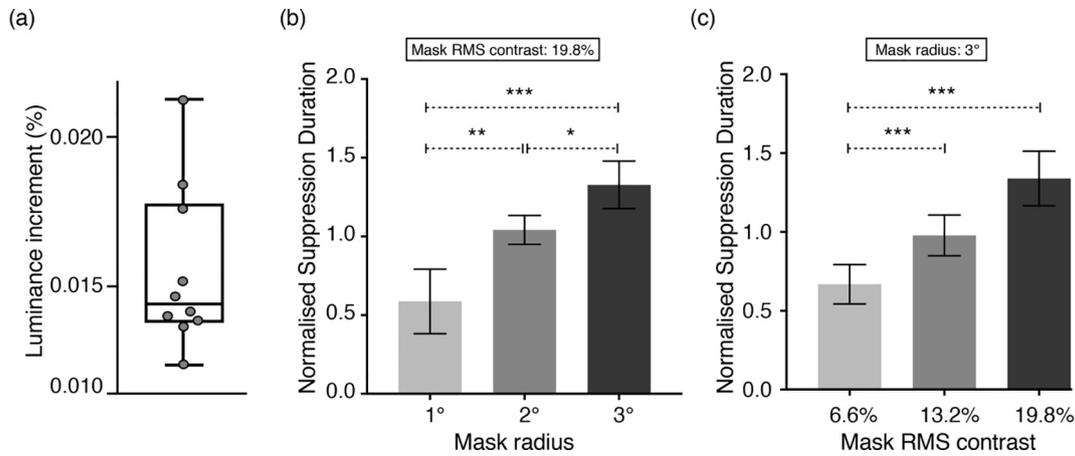


Fig. 2. Experiments 1 and 2: (a) Contrast sensitivity was determined in Experiment 1 by measuring the amount of luminance increment required to judge the orientation of a grating target with 75% accuracy. The distribution of luminance increments was comparable across participants, ranging approximately 0.011%. (b) The effect of mask size was assessed in Experiment 1. Significant increases in normalised suppression durations were found as the mask radius increased from 1° to 2°, and 2° to 3°. (c) The effect of mask contrast was assessed in Experiment 2. Levels of higher mask contrasts (RMS = 13.2% and 19.8%) performed comparably, only producing significantly longer suppression durations than the lowest mask contrast (RMS = 6.6%). Asterisks represent statistical significance after Bonferroni correction (*: $p < .05$, **: $p < .01$, ***: $p < .001$). Error bars represent 95% confidence intervals.

2.1.4. Data normalisation

Time to visibility measures in the b-CFS paradigm are affected by factors such as individual differences in interocular suppression durations, response times and subjective criteria (Gayet, Van der Stigchel, & Paffen, 2014; Yang, Brascamp, Kang, & Blake, 2014). In addition, CFS does not work with equal effectiveness for all participants, with up to 50% of participants exhibiting insufficient depth of CFS suppression in Stein et al. (2012). Thus, upon completion of the data collection, the dataset was first screened to identify participants with ceiling or chance performances. This resulted in the exclusion of two participants’ data from Experiment 1, as their data revealed no signs of effective suppression (e.g., suppression durations of just 800 ms). One participant’s data was excluded from Experiment 2, as the recorded accuracy was found to be at chance level. We then normalised the data to reduce between-subject variability, described as follows. Following the exclusion of ceiling and chance performing datasets, incorrect responses and outlier response times were then removed from each individual’s data. Outliers were defined as trials where the response time was greater than three median absolute deviations (or MADs, see Eq. (1)) from each participant’s median suppression duration for each experimental condition. Collapsed across all conditions recorded for each participant, incorrect trials made up 1% of all trials and outlier data made up 10% of all trials in Experiment 1. Similarly, incorrect trials made up 1% of all trials and outliers constituted 11% of all trials in Experiment 2. From these remaining data, normalised suppression durations were calculated for each trial by dividing the response time by the participant’s overall mean response time across all conditions for that experiment (Eq. (2)). This normalisation procedure was performed to reduce inter-subject variability and Type II error (but see normalisation methods discussed in Gayet & Stein, 2017). Means for experiment conditions were calculated from these normalised suppression durations across all participants. Statistical significance was then assessed on these normalised data.

$$MAD = \text{median}(|\text{SuppressionDuration}_{\text{Trial}} - \text{median}(\text{SuppressionDuration}_{\text{Trial}})|) \tag{1}$$

$$\text{Normalised Suppression Duration}_{\text{Trial}} = \frac{\text{SuppressionDuration}_{\text{Trial}}}{\text{OverallMean}_{\text{Participant}}} \tag{2}$$

2.2. Results of experiments 1–2

2.2.1. Contrast thresholds

To determine if the use of contrast threshold measurements was a practical approach in reducing variability in the b-CFS data, we examined the contrast threshold dataset collected in Experiment 1 for any systematic differences between non-dominant and dominant eyes. There was no significant difference in contrast threshold values between the non-dominant and dominant eye, $t(9) = 2.06, p = .07$. We then collapsed the data and examined the amount of variability in thresholds across participants. As described in Fig. 2a, contrast sensitivity was comparable across participants, with a very narrow range of approximately 1%.

2.2.2. Effect of mask size

To examine the relationship between sighting dominance and mask size, a two-way repeated-measures (rm-) ANOVA (mask size \times masking eye) was conducted. The results showed no significant main effect for sighting dominance, $F(1,7) = 2.28, p = .175$, and no interaction with mask size, $F(2,14) = 0.82, p = .461$. The data was then collapsed across eyes and analysed with a one-way rm-ANOVA. Fig. 2b shows the mean normalised suppression duration for the three size conditions in Experiment 1, collapsed across masking eye. The results revealed a significant effect of mask size, $F(2,7) = 21.6, p < .001, \eta_p^2 = 0.42$. Correcting for Type I error using Bonferroni-adjustments showed that the 2° and 3° masks produced significantly longer suppression durations than the 1° mask, $t(7) = 4.13, p = .01$ and $t(7) = 5.08, p = .004$. The 3° mask also performed better than the 2° mask, $t(7) = 3.91, p = .02$.

2.2.3. Mask contrast

A two-way rm-ANOVA looking at the effects of contrast and masking eye found no significant main effect for sighting dominance, $F(1,9) = 0.19, p = .672$, nor a significant interaction with contrast, $F(2,18) = 0.04, p = .959$. The data was then collapsed across masking eyes and assessed with a one-way rm-ANOVA. As expected from previous research (e.g., Tsuchiya & Koch, 2005), contrast had a significant main effect on suppression durations, $F(2,18) = 18.69, p < .001, \eta_p^2 = 0.675$. Bonferroni-corrected pairwise comparisons showed that the high contrast mask (19.8% RMS) and the medium contrast mask (13.2% RMS) produced significantly longer suppression durations than the low contrast mask (6.6% RMS), $t(9) = 5.31, p = .002$ and $t(9) = 4.32, p = .005$. Both high and medium contrast masks performed

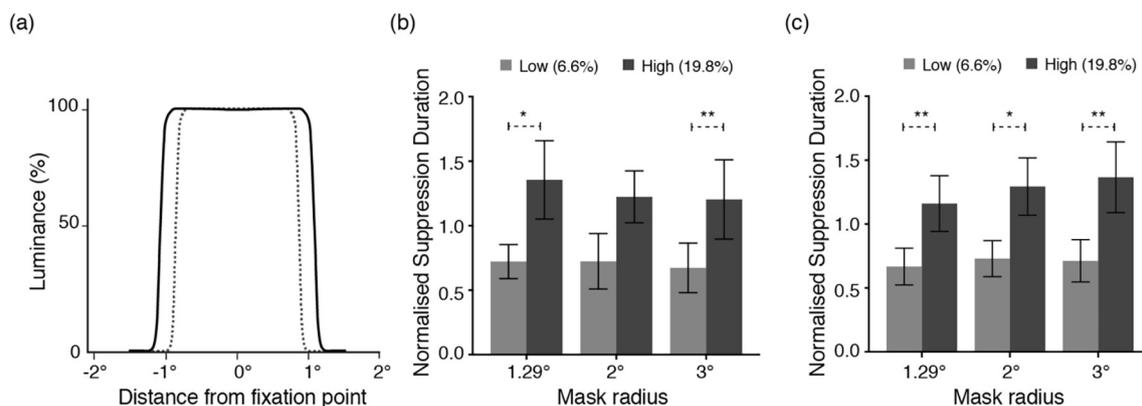


Fig. 3. Experiments 3 and 4: (a) Spatial luminance profile of target used in Experiments 3–4. To ensure that the mask remained at maximum luminance over the entire area of the target (dashed grey line), a slightly larger mask size was used (radius = 1.29°, black line). (b) The effect of mask size and contrast in a randomised presentation design. Apart from a main effect of mask contrast, there was neither a significant interaction between the two variables nor a significant main effect of mask size. (c) The effect of mask size and contrast in a blocked design, sorted by mask contrast. Similar to the randomised presentation, there was no significant interaction between mask size and contrast and there was no significant main effect of mask size either. Asterisks represent statistical significance after Bonferroni correction (*: $p < .05$, **: $p < .01$). Error bars represent 95% confidence intervals.

comparably $t(9) = 2.94$, $p = .05$. These results were summarised in Fig. 2c.

2.3. Discussion for experiments 1–2

The effects of mask size and contrast on CFS are an understudied topic. Assessments are surprisingly rare – only few studies have looked at the effect of mask contrast on suppression strength (Han et al., 2016; Ludwig, Sterzer, Kathmann, & Hesselmann, 2016; Tsuchiya & Koch, 2005). As such, the goal of Experiments 1–2 was to establish the independent effects of mask size and contrast respectively. Three mask sizes (i.e., 1°, 2°, and 3° radius) and three contrast levels (i.e., 6.6%, 13.2% and 29.8% RMS) were tested, and the dependent measure was the time to target visibility. Our results revealed significant effects of mask size and contrast, producing significantly longer suppression durations as the mask size or contrast increases. Sighting dominance did not influence the results of both experiments, and it was unlikely that differences in contrast sensitivity could have driven the pattern of results, as contrast thresholds were comparable between eyes and across participants in Experiment 1.

A bigger and brighter stimulus is generally more salient than a smaller, dimmer stimulus. It is possible that the increased salience might have contributed to suppression through attentional capture, especially towards the end of the Mondrian's dominance period (see influence of attention on BR dynamics in Dieter, Melnick, & Tadin, 2015), when interocular suppression is the weakest (Alais, Cass, O'Shea, & Blake, 2010). However, the contribution of attentional capture is unlikely to be substantial, as the task required participants to identify the orientation of the target. With repeated testing, selective attention to a task-relevant stimulus has been shown to increase its visibility during BR (Dieter, Melnick, & Tadin, 2016). As a result, any suppressive advantage gained from attentional capture might be counteracted by the increase in target visibility over time. Moreover, properties that could contribute to the Mondrian mask's salience are also associated with greater suppressive strength, e.g., high contrast (Blake, 1989; Brascamp, Klink, & Levelt, 2015), abundant high spatial frequency edges (Baker & Graf, 2009) and rapid update changes (Wolfe, 1984). Low-level mechanisms have been thought to underlie the suppressive advantage of these properties, such as the greater V1 response to spatial edges (Perna, Tosetti, Montanaro, & Morrone, 2008). Thus, while we do not deny the influence of attentional capture, it is unclear how it alone could drive the mask contrast and size effects in Experiments 1–2.

Increasing the contrast of the CFS mask decreases the neural decodability of stimulus-related information in the ventral and superior

dorsal regions (Ludwig et al., 2016), presumably via gain modulation (Yuval-Greenberg & Heeger, 2013). Thus one interpretation is that the effectiveness of the CFS mask varies with the amount of global activation. Larger masks would stimulate more retinotopic neural populations and higher mask contrasts are expected to trigger greater neuronal responses (e.g., monotonic S-shaped function of V1 neuronal responses; Carandini, Heeger, & Movshon, 1997). The resulting greater global activation may trigger greater suppression of target-related activity, explaining the mask size and contrast effects observed in Experiments 1–2. To test this possibility, we examine the relationship between mask size and contrast in Experiments 3–4.

3. Experiments 3–4: evaluating the global activation hypothesis

In Experiments 1 and 2, suppression durations increased as mask size and contrast increased. These effects could be attributed to the increased global activation produced by larger and brighter masks. Based on the idea that simultaneous increases in mask size and contrast would generate a lot more global activation than increases in either parameter, we re-examined the effect of mask size (i.e., 1.29°, 2°, and 3° radius) at two levels of mask contrast (i.e., 6.6% and 29.8% RMS). If a global activation mechanism underlay CFS suppression, mask size would have a greater effect on suppression durations when the mask is also presented at high contrast.

Experiments 3–4 also served to test the robustness of the mask size effect. Several participants in Experiment 1 reported seeing the target break suppression along the edges of the mask, which may be a consequence of the raised cosine function used to soften the mask edges. As illustrated in Fig. 3a, the function produces a lower level of contrast around the mask edges, weakening suppression and increasing the probability of target breakthrough. Imperfect fusion of the same-sized targets and masks could also facilitate target breakthroughs. We thus enlarged the small mask slightly, ensuring that the mask remained at full luminance across the full area of the target (Fig. 3a). The effect of mask size was also evaluated with randomised (Experiment 3) and blocked stimulus presentations (Experiment 4). Randomised presentations are useful for controlling order effects, but this form of presentation might be problematic for b-CFS, as it is susceptible to participants' criteria for target visibility (Yang et al., 2014). When presented with a mix of potentially easy and difficult trials, participants might find it difficult to come a stable decision threshold (Heekeren & Marrett, 2008) or adjust their response in accordance to the stimulus presented on the preceding trial (Los, 1996). On the other hand, participants may adopt different strategies for each block in blocked presentations, due

to familiarity with the stimuli content (Stein, Hebart et al., 2011; Los, 1996). It would be interesting to see if the effect of mask size varies in magnitude with presentation type. As manipulating mask contrast is the most straightforward way to vary CFS effectiveness (e.g., Tsuchiya & Koch, 2005), we sorted trials according to mask contrast.

3.1. Materials and methods

3.1.1. Participants

12 students (8 females, Mean age = 21.0, SD = 2.77) participated in Experiment 3, whereas 17 students (14 females, Mean age = 22.12, SD = 3.25) were recruited in Experiment 4. All were naïve to the purpose of the experiment and had normal or corrected-to-normal vision, and normal stereovision. Informed consent was obtained from all participants.

3.1.2. Stimuli

The same target stimulus from Experiments 1–2 was used in Experiments 3–4. The mask RMS contrast levels were 6.6% (same contrast as the target) and 29.8% (three times that of the target), whereas the mask sizes were 1.29°, 2°, 3° in radius. The diameter of the smallest mask size condition was 12 pixels (0.29° DVA) wider than the small condition in Experiment 1 to ensure the mask remained at maximum luminance over the entire area of the target (Fig. 3a).

3.1.3. Procedure

The same experimental procedures from previous experiments were followed in Experiments 3–4, with the exception that in Experiments 3 and 4 the stimulus presentation sequences were determined differently. Specifically, in Experiment 3, mask sizes and contrast levels were randomly interleaved within each block, producing a fully randomised presentation design. In Experiment 4, low- and high-contrast masks were presented in separate blocks, whereas the different mask sizes were randomised in each block. In Experiment 3, all but one participant completed three blocks of 48 trials. The remaining participant completed four blocks of 48 trials. Experiment 4's participants completed four blocks of 48 trials. In both experiments, the masking eye was randomised across trials.

3.1.4. Data normalisation

The same normalisation procedure from previous experiments was used. A total of seven participants were excluded, including two from Experiment 3. One participant could not perform the task (Experiment 3), whereas the remaining six found the task too easy and showed no signs of effective CFS suppression. The remaining datasets were then examined for outliers and incorrect trials. Collapsed across all conditions tested for each individual participant, incorrect trials made up 1% of all trials in both experiments and outliers constituted 14% in Experiment 3 and 15% in Experiment 4. As in previous experiments, the remaining data were normalised for each participant across all conditions.

3.2. Results

3.2.1. Randomised presentation

Fig. 3b summarises the trends obtained with the randomised presentation. The effect of sighting dominance was tested with a three-way rm-ANOVA (mask size, contrast and masking eye). Results showed that sighting dominance did not have a significant main effect $F(1,9) = 4.38, p = .07$, and there were no significant interactions with mask size and contrast, $F(1,9) = 2, p = .16$ and $F(1,9) = 1.27, p = .29$, respectively. The three-way interaction among mask size, contrast and masking eye was also not significant, $F(1,9) = 0.33, p = .72$.

The data was then collapsed across eyes and re-analysed with a two-way rm-ANOVA (mask size and contrast). The results showed a significant main effect for contrast $F(1,9) = 19.62, p = .002, \eta_p^2 = 0.746$,

where higher contrast conditions produced significantly longer suppression than lower contrast conditions. There was neither a significant main effect for size, $F(2,18) = 0.46, p = .639$, nor a significant interaction between size and contrast, $F(2,18) = 0.28, p = .757$.

3.2.2. Blocked presentation

We conducted a three-way rm-ANOVA (mask size, contrast, and masking eye) to evaluate the effect of sighting dominance. Sighting dominance did not have a significant effect on suppression durations, $F(1,11) = 0.76, p = .401$, and did not interact with mask size and contrast, $F(2,11) = 0.25, p = .78$ and $F(1,11) = 0.05, p = .84$ respectively. There was also no significant three-way interaction among mask size, contrast and masking eye, $F(2,11) = 1.34, p = .28$.

Fig. 3c shows the mean suppression durations for the six conditions in Experiment 4, collapsed across masking eye. Similar to the randomised presentation, there was a significant main effect for contrast, such that high-contrast masks produced significantly more suppression than low-contrast masks, $F(1,11) = 24.6, p < .011, \eta_p^2 = 0.798$. Mask size also did not affect suppression significantly, $F(2,22) = 0.926, p = .411$, and did not interact with mask contrast, $F(2,22) = 0.58, p = .57$.

3.3. Discussion

In Experiments 3–4, we asked if CFS suppression operates over global spatial zones. We employed a factorial design, which tested three mask sizes (i.e., 1.29°, 2°, 3° radius) and two mask contrast levels (i.e., 6.6% and 29.8% RMS). By using a larger small mask size condition (1.29° versus 1° in Experiments 1–2) and by comparing the effect of randomised and blocked stimulus presentations, these experiments also tested the reliability and robustness of the mask size effect. Given that simultaneous increases in mask size and contrast should result in a greater increase in global activity than either parameter, we expected mask size to not only have a significant effect on suppression durations, but to also increase in magnitude when the mask is presented at high contrast. Contrary to our predictions, the results consistently showed a significant effect of mask contrast but not mask size. As in the previous experiments, sighting dominance did not drive these trends. Thus, the effect of mask size was not robust and did not depend the ease of developing a stable decision criterion, which could have been reduced in the more variable, randomised presentation (Heekeren & Marrett, 2008).

Perhaps by using enlarging the smallest mask size and reducing the range of mask sizes as a result, we decreased the sensitivity of our mask size manipulation. This was unlikely, as the radius of the smallest mask size was only 0.29° wider than that in Experiment 1. In addition, the current mask size range would have resulted in five-fold difference in area between the largest and smallest masks. This ratio was similar to mask contrast, which had a ratio of four between the highest and lowest mask contrast used. Assuming that a broader range was required for a reliable effect of mask size, it would suggest a stronger impact of mask contrast on suppression. This would be inconsistent with a global activation account, as there was no reason for either parameter to have a greater influence if the resultant global activity drove suppression. Instead, it seemed more likely that the effect of mask size observed in Experiment 1 was a consequence of presenting equally sized target and mask in the smallest mask condition. As all mask edges were softened with a raised cosine function, the equal sized mask would produce weaker suppression around the target edges, facilitating target breakthroughs. Imperfect fusion between the equally sized target and mask could also reduce the suppression duration of the target (see BR example in Moutoussis & Zeki, 2002), though eye-tracking data would be required to determine the fusion quality of the smallest mask condition.

4. Experiment 5: evaluating the role of local suppressive processes

The previous experiments showed that suppression duration was significantly influenced by mask contrast but not mask size. These results argued against a robust mask size effect. In Experiment 5, we tested the idea that CFS suppression depended on local spatial interactions documented in BR (Paffen et al., 2004; Paffen et al., 2005; Alais et al., 2006). Specifically in BR, the dominance duration of a high contrast central rivalry stimulus decreased when surrounded by a high-contrast annulus grating of the same orientation or direction of motion (Paffen et al., 2004; Paffen et al., 2005). The effect was observed when the annulus was presented in the same or different eye from the central stimulus (Paffen et al., 2004; Paffen et al., 2005), and was thought to be due to iso-orientation surround suppression in the primary visual cortex (Fries, Albus, & Creutzfeldt, 1977; Knierim & van Essen, 1992). If CFS operates through similar mechanisms to BR, we would expect collinear surrounds to weaken the suppressive strength of the central mask, reducing suppression durations as a result. In addition, we would expect results similar to those of Kang (2009). That is, when collinearity is low, mask contrast would have a greater effect on the strength of suppression. In contrast, when collinearity is high, changing the mask contrast would have a smaller effect on suppression strength.

4.1. Materials and methods

4.1.1. Participants

Eleven female students (Mean age = 20.8, $SD = 2.6$) participated in Experiment 5. All were naïve to the purpose of the experiment and had normal or corrected-to-normal vision and normal stereovision. Informed consent was obtained from all participants.

Stimuli. The target stimulus was a 3 cpd sinusoidal grating tilted 6° to the left or right. The generation of the mask stimuli was designed to create a Mondrian-like stimulus composed only of hard vertical edges. We first computed five sets of 20 vertically oriented square wave gratings, as this allowed us to test the effect of collinearity and to produce hard edges. The same duty cycle was used for each set of gratings, but varied from 39% to 44% across the five sets of gratings to avoid adaptation to the same duty cycle. Given the feature selectivity of CFS (e.g., Yang & Blake, 2012), the range was also specifically chosen to resemble the spatial properties of the target. To mimic the stochastic alignment of contours of a 10 Hz Mondrian, each of these gratings were phase-jittered between $-\pi$ and π . As the monitor had a screen rate of 100 Hz, the gratings were then replicated 10 times to form a stepped presentation profile. The luminance timeline of each vertical bar in

each grating was then replaced with a randomly sampled timeline extracted from a 10 Hz Mondrian. As in the previous experiments, target stimuli and mask sequences were windowed with a circular, raised cosine function (0.29° width ramp). This produced a target radius of 1° and central mask radius of 1.29° . Collinear mask annuli were generated from the same grating sequences as the central mask, and had an external radius of 3.2° and internal radius of 1.38° . Orthogonal annuli had the same dimensions, but were rotated 90° from the vertical. Suppression with the grating sequences was weaker than the regular Mondrian, presumably because spatial energy was concentrated along the vertical, leaving the tilted target slightly incompatible with the mask stimuli. As such, target RMS contrast was set at 2%, a lower value than previous experiments. Mask RMS contrast levels were set at 2% (same contrast as the target) for the low contrast condition, and 20% (ten times that of the target) for the high contrast condition. A total of six experimental conditions were generated with these stimuli, and they were masks presented without an annulus, a collinear or orthogonal annulus (henceforth NA, NCA, CA), each at high or low contrast.

4.1.2. Procedure

The same experimental procedures from previous experiments were followed in Experiment 5. Low and high contrast masks were presented in separate blocks that interleaved the NA, NCA and CA conditions. All participants completed four blocks of 36 trials each, during which the masker was randomised between the eyes, across trials.

4.1.3. Data normalisation

Outliers and incorrect trials were excluded from the dataset. Collapsed across all conditions tested for each participant, incorrect trials made up 1% of all trials and outliers constituted 14%. The remaining data were then normalised for each participant with the same normalisation procedure from previous experiments.

4.2. Results

We first conducted a three-way rm-ANOVA (mask type, contrast, and masking eye) to evaluate the effect of sighting dominance. Sighting dominance did not have a significant effect on suppression durations, $F(1,10) = 0.25$, $p = .63$, $\eta_p^2 = 0.02$, and did not interact with contrast and mask type, $F(1,10) = 0.07$, $p = .80$, $\eta_p^2 = 0.01$ and $F(1,10) = 2.11$, $p = .15$, $\eta_p^2 = 0.17$, respectively. There was also no significant three-way interaction among mask type, contrast and masking eye, $F(2,20) = 2.01$, $p = .16$, $\eta_p^2 = 0.17$. The data were then collapsed across

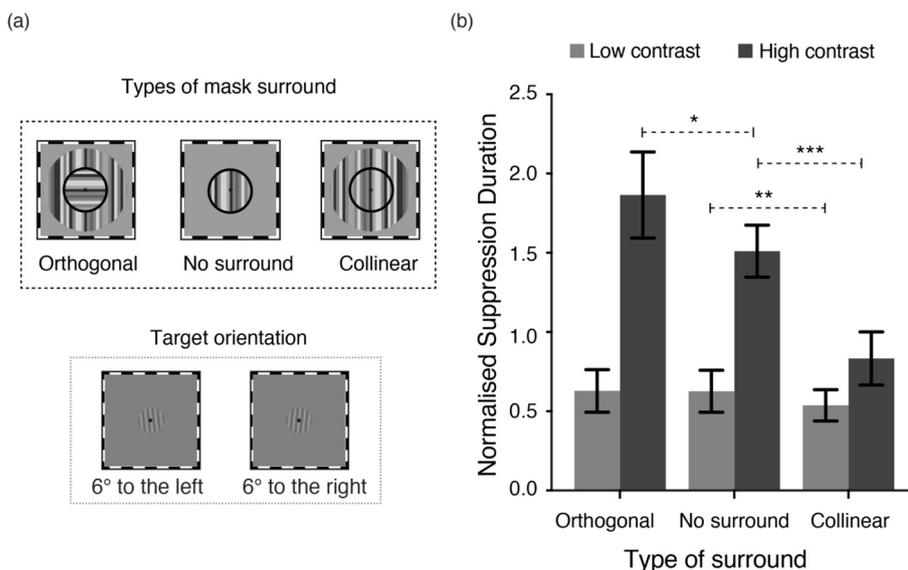


Fig. 4. Experiment 5: (a) Mask and target stimuli used in Experiment 5. Three types of mask surround conditions were presented, namely, surrounds with contours orthogonal to the central mask, surrounds with collinear contours and no surround. The target was a 3 cpd sinusoidal grating tilted 6° to the left or right. (b) The effect of mask type and contrast on suppression durations. We found a significant interaction between the two independent variables: higher mask contrasts produced longer suppression, but the magnitude of increase was dependent on the type of mask (see left panel for example surround). Compared to the no-surround condition, increasing mask size with a orthogonal surround produced an increase in suppression durations whereas the use of a collinear surround weakened suppression. These results suggest the role of local spatial interactions in CFS, and could explain the unreliable mask size effect observed in Experiments 1, 3 and 4. Asterisks represent statistical significance after Bonferroni correction (*: $p < .05$, **: $p < .01$, ***: $p < .001$). Error bars represent 95% confidence intervals.

masking eye (Fig. 4) and re-analysed with a two-way rm-ANOVA (mask size and contrast). We found significant main effects of mask contrast and mask type, $F(1,10) = 57.6$, $p < .001$. $\eta_p^2 = 0.85$, and $F(1,10) = 40.4$, $p < .001$. $\eta_p^2 = 0.80$, respectively. Mask contrast and mask type also interacted significantly, $F(2,20) = 20.4$, $p < .001$, $\eta_p^2 = 0.67$, characterised by a weaker effect of mask surround in the low mask contrast condition (Fig. 4).

To comprehend this interaction, we first plotted individual raw suppression durations (Fig. S6, panel a). We observed that the low mask contrast conditions produced a concentration of data points around 1–2 s, suggesting that a floor effect might be contributing to the interaction between mask contrast and surround. Further analyses with Bonferroni-corrected paired-samples t-tests showed that the use of the collinear surround decreased suppression duration significantly for both low and high mask contrasts, $t(10) = 4.08$, $p = .009$ and $t(10) = 5.61$, $p < .001$ respectively. In contrast, the orthogonal surround increased suppression duration, but only when mask contrast was high, $t(10) = 3.07$, $p = .048$. Adding an orthogonal surround did not significantly vary suppression durations when mask contrast was low, $t(10) = 0.35$, $p = 1.0$. Interestingly, orthogonal surrounds produced a larger effect of mask contrast than collinear surrounds, $t(10) = 5.28$, $p < .001$. Similarly, masks without surrounds also had a larger contrast effect than masks with collinear surrounds, $t(10) = 4.05$, $p = .005$.

5. General discussion

Previous studies have demonstrated several similarities between BR and CFS, raising the possibility of a shared theoretical framework. It is thus puzzling that the effects of mask size and contrast seem to differ between BR and CFS. Specifically, while BR suppression has been reported to weaken with larger mask sizes (Blake, 2001), it is unclear why a wide variety of mask sizes have been used in CFS studies (Table 1). In addition, while mask contrast has been shown to increase CFS suppression (Tsuchiya & Koch, 2005; Han et al., 2016), Kang (2009) showed that mask contrast had a greater effect on BR suppression when the mask size was small. Here, we conducted a systematic investigation into the effects of mask size and contrast on CFS, measuring the time to visibility with the b-CFS paradigm. To our best knowledge, the effects of mask size and contrast have not been studied in CFS. We thus verified the existence of the discrepancy between CFS and BR by studying the independent effects of mask size and contrast in Experiments 1–2, before proceeding to examine the relationship between mask size and contrast in randomised and blocked presentations in Experiments 3–4. As lateral interactions among local, collinear spatial zones have been observed in BR (e.g., Alais et al., 2006), a final experiment was conducted to examine the influence of collinearity on CFS.

Measured independently, we found that mask size and contrast had significant main effects on normalised suppression durations, producing longer suppression of the target as mask size and contrast increased. However, only the effect of mask contrast was replicated in Experiments 3–4. Not only were there no significant effects of mask size in both experiments, mask size and contrast did not interact significantly. As similar trends were obtained for both randomised (Experiment 3) and blocked presentations (Experiment 4), the results cannot be chalked up to participant decisional factors, such as the difficulty to settle on a stable decision criteria when conditions of varying levels of difficulty (i.e., low and high contrast) are interleaved together (Hecker & Marrett, 2008). Instead, it seemed more likely that the mask size effect observed in Experiment 1 was unreliable and probably driven by the smallest mask size condition. Matched with the target's size, factors such as imperfect fusion and weaker suppression around the target edges could have reduced suppression durations in the smallest mask size condition, thereby driving the size effect observed. In Experiment 5, surrounding the central mask with a collinear surround weakens target suppression, producing lower suppression

durations than the no-surround and orthogonal surround conditions. This was reminiscent of the surround suppression effects reported by Paffen et al. (2005), where the stimulus strength of the central stimulus was weakened by the presence of an iso-oriented surround. Although following the same general trend, the effect of collinearity seemed to be weaker at low mask contrast. Specifically, the orthogonal surround condition was as effective as the no-surround condition at low mask contrast, but was more effective at high mask contrast. The collinear surround condition was consistently weaker than the no-surround and orthogonal surround conditions at both levels of mask contrast, but the magnitude of change was noticeably smaller. We acknowledge that the magnitude differences in trend were probably driven by a floor effect, where the differences between conditions were obscured by factors such as subjective criteria and response times (Yang et al., 2014). More interestingly, mask contrast effects were smaller in the collinear surround condition, suggesting that the interaction between mask size and contrast in Kang (2009) might be explained by collinearity. Finally, we did not find a significant effect of sighting dominance, a finding that was consistent over five experiments.

The implications of these observations are as follows. Firstly, the effect of collinearity in Experiment 5 showed that both CFS and BR involve local suppressive processes, reminiscent of surround suppression. Surround suppression is a phenomenon in which the response to a central visual stimulus is inhibited by the presence of neighbouring stimuli (Chubb, Sperling, & Solomon, 1989; Yu, Klein, & Levi, 2001). It could operate in interocular, monocular and binocular presentations (Chubb et al., 1989; Paffen & Pas, te, S. F., Kanai, R., van der Smagt, M. J., & Verstraten, F. A. J., 2004; Paffen et al., 2005). In our study, monocular inhibition from the collinear surround could have suppressed the neural activity associated with the central mask, reducing its potency for interocular suppression. This could explain the results of Kang (2009), who found no effect of stimulus contrast in BR when large rivaling gratings were presented. Similar to the collinear surround condition in Experiment 5, the large rivaling gratings in Kang (2009) were similar susceptible to surround suppression, explaining the absence of contrast effects in BR and the smaller contrast effect for collinear surrounds in Experiment 5. It follows that collinearity could influence the adherence to or deviation from Levelt's second law of rivalry, which states that the average dominance of a stimulus remains comparable regardless of its stimulus strength (Brascamp et al., 2015). Thus raising stimulus contrast would be a good way to increase the effectiveness of interocular suppression in both paradigms, if and only if the manipulated stimulus has low collinearity.

Secondly, the demonstration of surround suppression in CFS raises important implications for clinical research. For example, studies have adopted the technique to examine the unconscious processing of eye gaze (Seymour, Rhodes, Stein, & Langdon, 2016), affective faces (Kring, Siegel, & Barrett, 2014) and interpersonal interactions (Zhu et al., 2015) in schizophrenic patients. As schizophrenic patients have been found to exhibit weaker surround suppression for stimuli defined by size, contrast (Tibber et al., 2013) and orientation (Yoon et al., 2009; Seymour et al., 2013), it is curious if and how the organisation of mask contours contributes to CFS suppression. Assuming surround suppression is less of a concern for producing effective CFS suppression in schizophrenia, one implication is that the spatial predictability of the mask contours may not have the same effect on suppression as normal participants (Han, Alais, and Blake (2018)). It would also be interesting to see if performance on CFS tasks could be related to differences in surround suppression between individuals with and without schizophrenia. Given the increasing popularity of the technique, understanding the relationship between known differences in clinical and normal populations (e.g., surround suppression) and CFS performance is unlikely to be trivial. Not only does it increase our comprehension of the results, but it also affords the opportunity to improve the use of CFS in clinical research.

Thirdly, the lack of sighting dominance effects in our study parallels

with an earlier study by Han and Alais (2018). These results contrast with the eye-specific effects reported in previous binocular rivalry studies (e.g., Blake, Westendorf, & Overton, 1980; Lee & Blake, 2004), but we raise caution in drawing this distinction prematurely. This is because effects of eye dominance have been shown in previous CFS research (Yang, Blake, & McDonald, 2010), and the evidence linking sighting dominance and interocular suppression have been mixed (Bosten et al., 2015; Dieter, Sy, & Blake, 2017; Ding, Naber, Gayet, Van der Stigchel, & Paffen, 2018). Instead, we question if our randomised visual presentation might have contributed to the apparent lack of eye-specific effects. To elaborate, the presentation of the mask was randomised between the eyes in all five experiments. Performed to reduce neural adaptation and to maintain suppressive effectiveness, this procedure might have disrupted or weakened any eye-specific processes. Support for this conclusion comes from Moors, Stein, Wagemans, and van Ee (2015), who previously reported that serial correlations of suppression durations were weaker with variable eye presentations than fixed eye presentations in CFS. Note that such serial correlations were not exclusive to CFS, as similar correlations have been observed in BR (Mamassian & Goutcher, 2005).

An account based solely on local suppressive processes in CFS would suggest that the use of an orthogonal surround would produce comparable suppression to having no surround. In Experiment 5, however, we discovered that suppression was more effective with an orthogonal surround than without a surround. As adding a surround does increase the overall activation in the masking eye, the result might be indicative of global activation mechanisms. One may even postulate possible global activation mechanisms, such as gain modulation on early visual processes (Klink, van Ee, Nijs, & Brouwer, 2008) and attentional capture at late dominance periods (Dieter et al., 2015). Yet, it is noteworthy that the masks presented in Experiments 1–4 had low collinearity within each pattern update, and any substantial effect of global activation would have been evident in those experiments. Although we do not have a clear understanding of this result, we speculate that it might be related to differences in individuals' criteria for target visibility (Yang et al., 2014), a common limitation of the b-CFS paradigm. We remain open to the possibility that global activity could have a subtle influence on CFS suppression strength, but more objective measures are required to verify the validity of this claim. Given the evidence presented in this study and in previous research, we believe there is no need to assume a distinct neural mechanism for CFS and BR. In fact, our findings showed that the use of a shared framework could be feasible and useful for the study of both paradigms.

Author contributions

S.H., R.L. and D.A. designed the research. S.H. programmed the visual stimuli.

R.L. and S.H. collected and analysed the data. S.H., R.L. and D.A. wrote the paper.

Statement of competing interests

The authors declare no competing financial interests.

Acknowledgements

This research was supported by the Australian Research Council, Discovery Project DP130102336.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.visres.2018.11.006>.

References

- Adams, W. J., Gray, K. L. H., Garner, M., & Graf, E. W. (2010). High-level face adaptation without awareness. *Psychological Science*, 21(2), 205–210. <https://doi.org/10.1177/0956797609359508>.
- Alais, D., & Parker, A. (2006). Independent binocular rivalry processes for motion and form. *Vision Research*, 52(5), 911–920. <https://doi.org/10.1016/j.visres.2006.10.027>.
- Alais, D., Cass, J., O'Shea, R. P., & Blake, R. (2010). Visual sensitivity underlying changes in visual consciousness. *Current Biology*, 20(15), 1362–1367. <https://doi.org/10.1016/j.cub.2010.06.015>.
- Alais, D., Lorenceau, J., Arrighi, R., & Cass, J. (2006). Contour interactions between pairs of Gabors engaged in binocular rivalry reveal a map of the association field. *Vision Research*, 46(8–9), 1473–1487. <https://doi.org/10.1016/j.visres.2005.09.029>.
- Almeida, J., Mahon, B. Z., Nakayama, K., & Caramazza, A. (2008). Unconscious processing dissociates along categorical lines. *Proceedings of the National Academy of Sciences USA*, 105(39), 15214–15218. <https://doi.org/10.1073/pnas.0805867105>.
- Ananyev, E., Penney, T. B., & Hsieh, P. B. (2017). Separate requirements for detection and perceptual stability of motion in interocular suppression. *Scientific Reports*, 7(7230), 1–10. <https://doi.org/10.1038/s41598-017-07805-5>.
- Baker, D. H., & Graf, E. W. (2009). Natural images dominate in binocular rivalry. *Proceedings of the National Academy of Sciences*, 106(13), 5436–5441.
- Batty, M. J., Cave, K. R., & Pauli, P. (2005). Abstract stimuli associated with threat through conditioning cannot be detected preattentively. *Emotion*, 5(4), 418–430. <https://doi.org/10.1037/1528-3542.5.4.418>.
- Blake, R. (1989). A neural theory of binocular rivalry. *Psychological Review*, 96(1), 145–167. <https://doi.org/10.1037/0033-295X.96.1.145>.
- Blake, R. (2001). A primer on binocular rivalry, including current controversies. *Brain and Mind*. <https://doi.org/10.1023/A:1017925416289>.
- Blake, R., O'Shea, R. P., & Mueller, T. J. (1992). Spatial zones of binocular rivalry in central and peripheral vision. *Visual Neuroscience*, 8(5), 469–478. <https://doi.org/10.1017/S0952523800004971>.
- Blake, R., Westendorf, D. H., & Overton, R. C. (1980). What is suppressed during binocular rivalry? *Perception*, 9(2), 223–231. <https://doi.org/10.1068/p090223>.
- Bosten, J. M., Goodbourn, P. T., Lawrance-Owen, A. J., Bargary, G., Hogg, R. E., & Mollon, J. D. (2015). A population study of binocular function. *Vision Research*, 110(Part A), 34–50. <https://doi.org/10.1016/j.visres.2015.02.017>.
- Brascamp, J. W., Klink, P. C., & Levelt, W. J. M. (2015). The 'laws' of binocular rivalry: 50 years of Levelt's propositions. *Vision Research*, 109, 20–37. <https://doi.org/10.1016/j.visres.2015.02.019>.
- Canny, J. (1986). A computational approach to edge detection. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, PAMI-8(6), 679–698.
- Carandini, M., Heeger, D. J., & Movshon, J. A. (1997). Linearity and normalization of simple cells of the macaque primary visual cortex. *Journal of Neuroscience*, 17, 8621–8644.
- Chubb, C., Sperling, G., & Solomon, J. A. (1989). Texture interactions determine perceived contrast. *Proceedings of the National Academy of Science, USA*, 86, 9631–9635.
- Costello, P., Jiang, Y., Baartman, B., McGlennen, K., & He, S. (2009). Semantic and subword priming during binocular suppression. *Consciousness and Cognition*, 18(2), 375–382. <https://doi.org/10.1016/j.concog.2009.02.003>.
- Dieter, K. C., Melnick, M. D., & Tadin, D. (2015). When can attention influence binocular rivalry? *Attention, Perception, & Psychophysics*, 77(6), 1908–1918. <https://doi.org/10.3758/s13414-015-0905-6>.
- Dieter, K. C., Sy, J. L., & Blake, R. (2017). Individual differences in sensory eye dominance reflected in the dynamics of binocular rivalry. *Vision Research*, 141, 40–50. <https://doi.org/10.1016/j.visres.2016.09.014>.
- Dieter, K. C., Melnick, M. D., & Tadin, D. (2016). Perceptual training profoundly alters binocular rivalry through both sensory and attentional enhancements. *Proceedings of the National Academy of Sciences USA*, 113(45), 12874–12879. <https://doi.org/10.1073/pnas.1602722113>.
- Ding, Y., Naber, M., Gayet, S., Van der Stigchel, S., & Paffen, C. L. E. (2018). Assessing the generalizability of eye dominance across binocular rivalry, onset rivalry, and continuous flash suppression. *Journal of Vision*, 18(6), 1–13. <https://doi.org/10.1167/18.6.6>.
- Faivre, N., Berthet, V., & Kouider, S. (2012). Nonconscious influences from emotional faces: A comparison of visual crowding, masking, and continuous flash suppression. *Frontiers in Psychology*, 3(129), 1–13. <https://doi.org/10.3389/fpsyg.2012.00129>.
- Fries, W., Albus, K., & Creutzfeldt, O. D. (1977). Effects of interacting visual patterns on single cell responses in cat's striate cortex. *Vision Research*, 17, 1001–1008.
- Gayet, S., Paffen, C. L. E., Belopolsky, A. V., Theeuwes, J., & Stigchel, S. V. (2016). Visual input signalling threat gains preferential access to awareness in a breaking continuous flash suppression paradigm. *Cognition*, 149, 77–83. <https://doi.org/10.1016/j.cognition.2016.01.009>.
- Gayet, S., & Stein, T. (2017). Between-subject variability in the breaking continuous flash suppression paradigm: Potential causes, consequences, and solutions. *Frontiers in Psychology*, 8, 1362–1411. <https://doi.org/10.3389/fpsyg.2017.00437>.
- Gayet, S., Van der Stigchel, S., & Paffen, C. L. E. (2014). Breaking continuous flash suppression: Competing for consciousness on the pre-semantic battlefield. *Frontiers in Psychology*, 5(475), 423–510. <https://doi.org/10.3389/fpsyg.2014.00460>.
- Gobbini, M. I., Gors, J. D., Halchenko, Y. O., Rogers, C., Guntupalli, J. S., Hughes, H., & Cipolli, C. (2013). Prioritized detection of personally familiar faces. *PLoS One*, 8(6), e66620. <https://doi.org/10.1371/journal.pone.0066620>.
- Han, S., & Alais, D. (2018). Strength of continuous flash suppression is optimal when target and masker modulation rates are matched. *Journal of Vision*, 18(3), 1–14. <https://doi.org/10.1167/18.3.3>.

- Han, S., Blake, R., & Alais, D. (2018). Slow and steady, not fast and furious: Slow modulations drive continuous flash suppression best. *Consciousness and Cognition*, 58, 10–19. <https://doi.org/10.1016/j.concog.2017.12.007>.
- Han, S., Lunghi, C., & Alais, D. (2016). The temporal frequency tuning of continuous flash suppression reveals peak suppression at very low frequencies. *Scientific Reports*, 6(1), 1. <https://doi.org/10.1038/srep35723>.
- Han, S., Alais, D., & Blake, R. (2018). Battle of the Mondrians: Investigating the role of unpredictability in continuous flash suppression. *i-Perception*, 9(4), 1–21. <https://doi.org/10.1177/2041669518792930>.
- He, S., Carlson, T., & Chen, X. C. (2005). Parallel pathways and temporal dynamics in binocular rivalry. In D. Alais, & R. Blake (Eds.). *Binocular Rivalry* (pp. 81–100). Cambridge, Massachusetts: The MIT Press.
- Heekeren, H. R., & Marrett, S. (2008). The neural systems that mediate human perceptual decision making. *Nature Reviews Neuroscience*, 9(6), 467–479. <https://doi.org/10.1038/nrn2374>.
- Hesselmans, G., Darcy, N., Sterzer, P., & Knops, A. (2015). Exploring the boundary conditions of unconscious numerical priming effects with continuous flash suppression. *Consciousness and Cognition*, 31, 60–72. <https://doi.org/10.1016/j.concog.2014.10.009>.
- Heyman, T., & Moors, P. (2014). Frequent words do not break continuous flash suppression differently from infrequent or nonexistent words: Implications for semantic processing of words in the absence of awareness. *PLoS One*, 9(8), e104719. <https://doi.org/10.1371/journal.pone.0104719>.
- Jiang, Y., Costello, P., & He, S. (2007). Processing of invisible stimuli: Advantage of upright faces and recognizable words in overcoming interocular suppression. *Psychological Science*, 18(4), 349–355. <https://doi.org/10.1111/j.1467-9280.2007.01902.x>.
- Kang, M. S. (2009). Size matters: A study of binocular rivalry dynamics. *Journal of Vision*, 9(1), <https://doi.org/10.1167/9.1.17>.
- Klink, P. C., van Ee, R., Nijs, M. M., & Brouwer, G. J. (2008). Early interactions between neuronal adaptation and voluntary control determine perceptual choices in bistable vision. *Journal of Vision*. <https://doi.org/10.1167/8.5.16>.
- Knierim, J. J., & van Essen, D. C. (1992). Neuronal responses to static texture patterns in area V1 of the alert macaque monkey. *Journal of neurophysiology*, 67(4), 961–980.
- Kring, A. M., Siegel, E. H., & Barrett, L. F. (2014). Unseen affective faces influence person perception judgments in schizophrenia. *Clinical Psychology Science*, 2(4), 443–454. <https://doi.org/10.1177/2167702614536161>.
- Lee, S. H., & Blake, R. (2004). A fresh look at interocular grouping during binocular rivalry. *Vision Research*, 44, 983–991.
- Los, S. A. (1996). On the origin of mixing costs: Exploring information processing in pure and mixed blocks of trials. *Acta Psychologica*, 94, 145–188. [https://doi.org/10.1016/0001-6918\(95\)00050-X](https://doi.org/10.1016/0001-6918(95)00050-X).
- Ludwig, K., Sterzer, P., Kathmann, N., & Hesselmann, G. (2016). Differential modulation of visual object processing in dorsal and ventral stream by stimulus visibility. *Cortex*, 83, 113–123. <https://doi.org/10.1016/j.cortex.2016.07.002>.
- Mamassian, P., & Goutcher, R. (2005). Temporal dynamics in bistable perception. *Journal of Vision*, 5(4), 361–375. <https://doi.org/10.1167/5.4.7>.
- Moors, P., Stein, T., Wagemans, J., & van Ee, R. (2015). Serial correlations in continuous flash suppression. *Neuroscience of Consciousness*, 1(1), 1–10. <https://doi.org/10.1093/nc/niv010>.
- Moutoussis, K., & Zeki, S. (2002). The relationship between cortical activation and perception investigated with invisible stimuli. *Proceedings of the National Academy of Sciences USA*, 99(14), 9527–9532. <https://doi.org/10.1073/pnas.142305699>.
- Moors, P., Boelens, D., Overwalle, J., & Wagemans, J. (2016). Scene integration without awareness: Conclusive evidence for processing scene congruency during continuous flash suppression. *Psychological Science*, 27, 945–956. <https://doi.org/10.1177/0956797616642525>.
- Moors, P., Wagemans, J., & de Wit, L. (2014). Moving stimuli are less effectively masked using traditional continuous flash suppression (CFS) compared to a moving Mondrian mask (MMM): A test case for feature-selective suppression and retinotopic adaptation. *PLoS One*, 9(5), e98298–e98310. <https://doi.org/10.1371/journal.pone.0098298>.
- Mudrik, L., Breska, A., Lamy, D., & Deouell, L. Y. (2011). Integration without awareness: Expanding the limits of unconscious processing. *Psychological Science*, 22(6), 764–770. <https://doi.org/10.1177/0956797611408736>.
- Paffen, C. L. E., Alais, D., & Verstraten, F. A. J. (2005). Center-surround inhibition deepens binocular rivalry suppression. *Vision Research*, 45(20), 2642–2649. <https://doi.org/10.1016/j.visres.2005.04.018>.
- Paffen, C. L., te Pas, S. F., Kanai, R., van der Smagt, M. J., & Verstraten, F. A. J. (2004). Center-surround interactions in visual motion processing during binocular rivalry. *Vision Research*, 44(14), 1635–1639. <https://doi.org/10.1016/j.visres.2004.02.007>.
- Perna, A., Tosetti, M., Montanaro, D., & Morrone, M. C. (2008). Bold response to spatial phase congruency in human brain. *Journal of Vision*, 8(10), 1–15.
- Rabovsky, M., Stein, T., & Abdel Rahman, R. (2016). Access to awareness for faces during continuous flash suppression is not modulated by affective knowledge. *PLoS One*, 11(4), e0150931. <https://doi.org/10.1371/journal.pone.0150931>.
- Salomon, R., Lim, M., Herbelin, B., Hesselmann, G., & Blanke, O. (2013). Posing for awareness: Proprioception modulates access to visual consciousness in a continuous flash suppression task. *Journal of Vision*, 13(2), 1–8. <https://doi.org/10.1167/13.7.2>.
- Seymour, K., Stein, R., Sanders, L. L., Guggenmos, M., Theophil, I., & Sterzer, P. (2013). Altered contextual modulation of primary visual cortex responses in schizophrenia. *Neuropsychopharmacology*, 38(13), 2607–2612. <https://doi.org/10.1038/npp.2013.168>.
- Seymour, K., Rhodes, G., Stein, T., & Langdon, R. (2016). Intact unconscious processing of eye contact in schizophrenia. *Schizophrenia Research: Cognition*, 3, 15–19. <https://doi.org/10.1016/j.sch.2015.11.001>.
- Stein, T., & Sterzer, P. (2011). High-level face shape adaptation depends on visual awareness: Evidence from continuous flash suppression. *Journal of Vision*, 11(5), 1–14. <https://doi.org/10.1167/11.8.5>.
- Stein, T., & Sterzer, P. (2012). Not just another face in the crowd: Detecting emotional schematic faces during continuous flash suppression. *Emotion*, 12(5), 988–996. <https://doi.org/10.1037/a0026944>.
- Stein, T., Hebart, M. N., & Sterzer, P. (2011). Breaking continuous flash suppression: A new measure of unconscious processing during interocular suppression. *Frontiers in Human Neuroscience*, 5. <https://doi.org/10.3389/fnhum.2011.00167>.
- Stein, T., Senju, A., Peelen, M. V., & Sterzer, P. (2011). Eye contact facilitates awareness of faces during interocular suppression. *Cognition*, 119, 307–311. <https://doi.org/10.1016/j.cognition.2011.01.008>.
- Stein, T., Sterzer, P., & Peelen, M. V. (2012). Privileged detection of conspecifics: Evidence from inversion effects during continuous flash suppression. *Cognition*, 125(1), 64–79. <https://doi.org/10.1016/j.cognition.2012.06.005>.
- Sterzer, P., Jalkanen, L., & Rees, G. (2009). Electromagnetic responses to invisible face stimuli during binocular suppression. *NeuroImage*, 46(3), 803–808. <https://doi.org/10.1016/j.neuroimage.2009.02.046>.
- Stuit, S. M., Cass, J., Paffen, C. L. E., & Alais, D. (2009). Orientation-tuned suppression in binocular rivalry reveals general and specific components of rivalry suppression. *Journal of Vision*, 9(11), 17. <https://doi.org/10.1167/9.11.17>.
- Stuit, S. M., Paffen, C. L. E., van der Smagt, M. J., & Verstraten, F. A. J. (2011). Suppressed images selectively affect the dominant percept during binocular rivalry. *Journal of Vision*, 11(10), 7. <https://doi.org/10.1167/11.10.7>.
- Tibber, M. S., Anderson, E. J., Bobin, T., Antonova, E., Seabright, A., Wright, B., ... Dakin, S. C. (2013). Visual surround suppression in schizophrenia. *Frontiers in Psychology*, 4(88), 1–13. <https://doi.org/10.3389/fpsyg.2013.00088>.
- Tsao, D. Y., & Livingstone, M. S. (2008). Mechanisms of face perception. *Annual Review of Neuroscience*, 31, 411–437. <https://doi.org/10.1146/annurev.neuro.30.051606.094238>.
- Tsuchiya, N., & Koch, C. (2005). Continuous flash suppression reduces negative afterimages. *Nature Neuroscience*, 8(8), 1096–1101. <https://doi.org/10.1038/nn1500>.
- Tsuchiya, N., Koch, C., Gilroy, L. A., & Blake, R. (2006). Depth of interocular suppression associated with continuous flash suppression, flash suppression, and binocular rivalry. *Journal of Vision*, 6(10), 6–11. <https://doi.org/10.1167/6.10.6>.
- Tsuchiya, N., Moradi, F., Felsen, C., Yamazaki, M., & Adolphs, R. (2009). Intact rapid detection of fearful faces in the absence of the amygdala. *Nature Neuroscience*, 12(10), 1224–1225. <https://doi.org/10.1038/nn.2380>.
- Van Opstal, F., De Loof, E., Verguts, T., & Cleeremans, A. (2016). Spontaneous eyeblinks during breaking continuous flash suppression are associated with increased detection times. *Journal of Vision*, 16(14), 1–10. <https://doi.org/10.1167/16.14.21>.
- Watson, A. B., & Pelli, D. G. (1983). Quest: A Bayesian adaptive psychometric method. *Perception & Psychophysics*, 33(2), 113–120. <https://doi.org/10.3758/BF03202828>.
- Wolfe, J. M. (1984). Reversing ocular dominance and suppression in a single flash. *Vision Research*, 24(5), 471–478. [https://doi.org/10.1016/0042-6989\(84\)90044-0](https://doi.org/10.1016/0042-6989(84)90044-0).
- Yamada, Y., & Kawabe, T. (2011). Emotion colors time perception unconsciously. *Consciousness and Cognition*, 24(4), 1835–1841. <https://doi.org/10.1016/j.concog.2011.06.016>.
- Yang, E., & Blake, R. (2012). Deconstructing continuous flash suppression. *Journal of Vision*, 12(3), 8. <https://doi.org/10.1167/12.3.8>.
- Yuval-Greenberg, S., & Heeger, D. J. (2013). Continuous flash suppression modulates cortical activity in early visual cortex. *Journal of Neuroscience*, 33(23), 9635–9643. <https://doi.org/10.1523/JNEUROSCI.4612-12.2013>.
- Zhu, W., Drewes, J., & Melcher, D. (2016). Time for awareness: The influence of temporal properties of the mask on continuous flash suppression effectiveness. *PLoS One*, 11(7), e0159206–e159215. <https://doi.org/10.1371/journal.pone.0159206>.
- Yang, E., Blake, R., & McDonald, J. E. (2010). A new interocular suppression technique for measuring sensory eye dominance. *Investigative Ophthalmology and Visual Science*, 51(1), 588–593. <https://doi.org/10.1167/iovs.08-3076>.
- Yang, E., Brascamp, J., Kang, M., & Blake, R. (2014). On the use of continuous flash suppression for the study of visual processing outside of awareness. *Frontiers in Psychology*, 5, 1–17. <https://doi.org/10.3389/fpsyg.2014.00724>.
- Yang, E., Zald, D. H., & Blake, R. (2007). Fearful expressions gain preferential access to awareness during continuous flash suppression. *Emotion*, 7(4), 882–886. <https://doi.org/10.1037/1528-3542.7.4.882>.
- Yoon, J. H., Rokem, A. S., Silver, M. A., Ursu, S., Ragland, J. D., & Carter, C. S. (2009). Diminished orientation-specific surround suppression of visual processing in schizophrenia. *Schizophrenia Bulletin*, 35(6), 1078–1084. <https://doi.org/10.1093/schbul/sbp064>.
- Yu, C., Klein, S. A., & Levi, D. M. (2001). Surround modulation of perceived contrast and the role of brightness induction. *Journal of Vision*, 1(1), 18–31. <https://doi.org/10.1167/1.1.3>.
- Zadbood, A., Lee, S., & Blake, R. (2011). Stimulus fractionation by interocular suppression. *Frontiers in Human Neuroscience*, 5, 1–9. <https://doi.org/10.3389/fnhum.2011.00135>.
- Zhou, W., Jiang, Y., He, S., & Chen, D. (2010). Olfaction modulates visual perception in binocular rivalry. *Current Biology*, 20(15), 1356–1358. <https://doi.org/10.1016/j.cub.2010.05.059>.
- Zhu, Y., Yang, Z., Zhao, J., Li, T., Wang, M., Qian, J., Jiang, Y., Wang, J., Weng, X., Yu, D., & Li, C. (2015). Can interpersonal hypersensitivity under subconscious condition explain paranoid symptom in schizophrenia? *Asia-Pacific Psychiatry*, 9(2017), e12221. <https://doi.org/10.1111/appy.12221>.