Eye swapping temporally modulates potency of continuous flash suppression

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Continuous flash suppression (CFS) refers to a technique to render a monocular stimulus invisible by presenting a dynamic series of high-contrast patterns (such as Mondrian patterns) to the other eye. Despite its popularity as a tool to suppress stimulus from awareness, the suppression mechanisms underlying CFS remain not well understood. To further elucidate the suppression mechanisms, this study investigated the effects of eye swapping on CFS suppression by manipulating the eye of presentation of the suppressor and the target. Results showed that eye swapping of the suppressor and the target significantly reduced the strength of CFS suppression when swapping frequency was higher (3.5 Hz). However, strong suppression persisted at lower swapping frequency (1.2 Hz). Investigation of the time course of suppression revealed that suppression was weaker just after eye swapping but that it quickly regained strength over the monocular presentation period of the suppressor. However, this buildup seemed to not be fast enough to closely follow eye swapping at higher frequency. These findings can be better understood by the contribution of monocular processes to CFS suppression. They imply that interocular suppression caused by competition between monocular processes can mediate phenomenal suppression over multiple eye swaps when swapping frequency is low. The significance of the findings is discussed in relation to binocular rivalry and binocular switch suppression.

Introduction

Continuous flash suppression (CFS) refers to a technique used to render invisible visual stimulus presented to one eye, that is, a target stimulus, by presenting a dynamic series of high-contrast contour-rich patterns to the other eye (Tsuchiya & Koch, 2005). Frequently used as suppressing stimulation are Mondrian patterns, which are composed of rectangles of different sizes and colors that are typically refreshed at a rate of approximately 10 Hz. Because CFS is very potent and can suppress an otherwise clearly visible monocular stimulus from awareness for an extended period of time, it has emerged as a popular technique for investigating visual processing outside of conscious awareness.

Nevertheless, despite its popularity, the suppression mechanisms underlying CFS are not well understood. Indeed, recent studies have revealed several important spatiotemporal characteristics of suppression in CFS. These studies provide converging evidence that the suppression in CFS is feature-specific. For example, Yang and Blake (2012) showed that Mondrian displays generally have strong spectral power at both low spatial frequencies and cardinal orientations, and thus they strongly suppress stimulus components of these spatial features. In a temporal domain, several studies have shown that with manipulating update frequency of Mondrian patterns the optimal frequency for suppression depends on the temporal properties of the target. With a brief target (24 msec) stronger suppression could be found for higher updating frequencies up to 28.5 Hz (Kaunitz, Fracasso, Skujevskis, & Melcher, 2014), whereas with a prolonged target whose contrast gradually increased over several seconds the maximum suppression was found to be approximately 6 Hz (Zhu, Drewes, & Melcher, 2016; Drewes, Zhu, & Melcher, 2018). Moreover, Han, Lunghi, and Alais (2016) revealed that dynamic Mondrian patterns have high temporal energy at low temporal frequencies even when Mondrian patterns were updated at a typical rate of 10 Hz. Consistently, they also found that, using spatiotemporally filtered noise as a suppressor, temporal tuning of CFS suppression for a long target peaks at approximately 1 Hz. Subsequent studies further showed that CFS suppression is temporally

Citation: Shimizu, M. & Kimura, E. (2020). Eye swapping temporally modulates potency of continuous flash suppression. *Journal of Vision*, *20*(3):1, 1–10, https://doi.org/10.1167/jov.20.3.1.

https://doi.org/10.1167/jov.20.3.1 Received January 18, 2019; published March 17, 2020 ISSN 1534-7362

selective (Han, Blake, & Alais, 2018; Han & Alais, 2018). Some of these studies indicated similarities in feature selectivity of the suppression between CFS and binocular rivalry (Han et al., 2016; Han et al., 2018; Han & Alais, 2018), and argued that CFS and rivalry share suppression mechanisms, although binocular rivalry typically involves two static, rather than dynamic, images presented dichoptically.

The present study extended the investigation of the suppression mechanisms underlying CFS and investigated the effects of eye of presentation on CFS. Specifically, we investigated whether CFS suppression takes place with visual representations of the stimulus images tagged with eye-of-origin information. The effects of eye of presentation have been studied in binocular rivalry studies using an eye-swapping paradigm, and it appears to play an important role in understanding what mechanisms are responsible for binocular rivalry; that is, rivalry may involve a competition between stimulus representations without regard to their eye of origin (i.e., stimulus rivalry), or it could involve interactions between incompatible monocular representations (i.e., eye rivalry). Blake, Westendorf, and Overton (1980) swapped vertical and horizontal gratings between the eyes after one of the images (e.g., vertical grating) became exclusively dominant. Thereafter observers reported seeing the other image (horizontal grating). This finding supported eye rivalry and indicated that what dominates during rivalry is the region of the eye on which the vertical grating was first presented. However, Logothetis, Leopold, and Sheinberg (1996) introduced a variant of the eye-swapping technique called a flicker-and-swap paradigm, in which dichoptic images were flickered at 18 Hz and swapped between the eyes three times per second. They found that one of the images could become dominant for a few seconds over multiple eye swaps. This finding indicated that the perceptual dominance can be mediated by stimulus rivalry that relies on competition at binocular processing stages. Subsequently, these apparently discrepant views have been integrated into a hybrid model, which assumes that rivalry entails both eye and stimulus rivalry and these are mediated by competitions at different neural sites (e.g., Blake & Logothetis, 2002; Tong, Meng, & Blake, 2006).

In view of these findings in binocular rivalry studies, if CFS suppression is mostly mediated by monocular processes that are responsible for eye rivalry, it is expected that repetitive eye swaps during CFS would disrupt suppression, and thus a target would be easily detected. By contrast, if binocular processes (or processes indifferent to the eye of presentation) that mediate stimulus rivalry contribute substantially to CFS suppression, the suppression could be stable and potent even with repetitive eye swaps. Moreover, a third possibility can be conceived, namely that eye swapping may result in stronger suppression, if we take into consideration another type of perceptual suppression termed binocular switch suppression (BSS) (Arnold, Law, & Wallis, 2008). Initially, Arnold, Grove, and Wallis (2007) found that during binocular rivalry a better focused image on one eye became perceptually dominant relative to a conflicting blurred image on the other eye. They also found that persistent suppression can be achieved even when two images are swapped between the eyes. Subsequently, Arnold et al. (2008) extended this finding and demonstrated BSS, in which a high-contrast white noise produced stable and potent suppression over a low-contrast image by simply repeatedly switching the two conflicting images between the eyes. The strength of BSS was greatest at a switching rate of approximately 1 Hz. Arnold et al. (2008) discussed that BSS is mediated by predominantly perturbing neural adaptation within monocular neurons at early stages of visual processing. Moreover, they argued that BSS and CFS are mediated by different neural mechanisms, mainly because the optimal rate of stimulus changes was different for the two types of suppression. If this is true, additional suppressive effects due to eye swapping could be observed in CFS suppression. In fact, this prediction was tested by Arnold et al. (2008) (their experiment 3), although the results did not show beneficial effects of combining BSS and CFS. However, because Arnold et al. (2008) used a white noise as their suppressor and this type of stimulus has been demonstrated to be a much weaker suppressor for CFS than Mondrian patterns (Drewes et al., 2018), such effects of the eye of presentation should be investigated using typical Mondrian patterns.

To further elucidate suppression mechanisms underlying CFS, we investigated these possible effects of eye swapping on CFS suppression by manipulating the eye of presentation of the suppressor and the target during CFS.

Experiment 1

Experiment 1 aimed to investigate the effects of eye swapping on the strength of CFS suppression. Accordingly, we measured the time required for target detection in different eye-of-presentation conditions. Two swapping frequencies, 1.2 and 3.5 Hz, were used; the former was close to the optimal frequency for BSS (Arnold et al., 2008), whereas the latter was to that for stimulus rivalry in a flicker-and-swap paradigm (Lee & Blake, 1999).

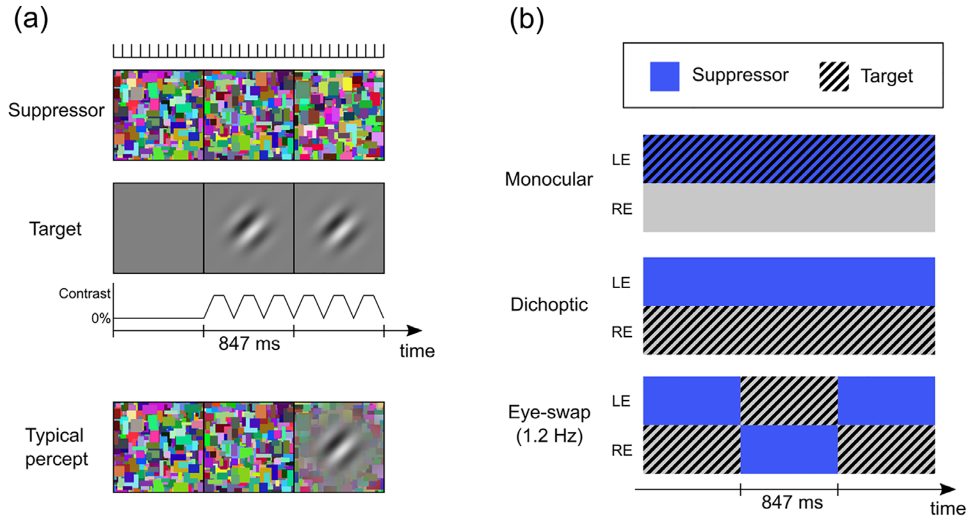

Figure 1. Stimulus sequence (a) and the eye-of-presentation conditions (b) in Experiment 1. (a) The suppressor (top row) was a dynamic Mondrian pattern; it was refreshed every 94 msec, as illustrated above the suppressor image. The target (second row) was presented a few seconds after the onset of the suppressor and also temporally modulated, as illustrated below the target image. The bottom row illustrate a typical percept. (b) In the monocular condition (top row), both the suppressor (represented by blue color) and the target (hatched pattern) were presented to the same eye, whereas only the background was presented to the other eye (no interocular competition). In the dichoptic condition (middle row), the two stimuli were presented to different eyes and the eye of presentation was fixed during the trial. In the eye-swapping condition, the two stimuli were dichoptically presented and repeatedly exchanged between the eyes every 847 msec (1.2 Hz) or 282 msec (3.5 Hz). LE and RE represent the left eye and the right eye, respectively.

Methods

Observers

Twelve observers, including one of the authors, participated in Experiment 1. They had normal or corrected-to-normal visual acuity and normal color vision. All observers except for the author were naive regarding the purpose of the experiment. Prior to the experiment, the observers who participated in this and following experiments provided written informed consent after thorough explanation of the procedures. The experiments were conducted in accordance with the Declaration of Helsinki.

Apparatus

Stimuli were generated using MATLAB (The MathWorks Inc., Natick, MA) and Psychophysics Toolbox 3 (Brainard, 1997; Pelli, 1997; Kleiner, Brainard, & Pelli, 2007). The stimuli for the left and the right eye were presented side-by-side on a 19-in. color CRT monitor (EIZO T766, EIZO Corporation, Ishikawa, Japan) with a pixel resolution of 1280 × 1024 pixels and a refresh rate of 85 Hz. The intensity of each phosphor was varied with 8-bit resolution. Spectroradiometric calibration was performed on three phosphors of the monitor with a CS-1000 spectroradiometer and an LS-100 luminance meter (KONIKA MINOLTA, Inc., Tokyo, Japan). Observers viewed the stimuli through a mirror stereoscope placed in front of their eyes, so that the left-side stimulus on the monitor was projected to the left eye and the right-side stimulus to the right eye, respectively. The observer's head was stabilized by a chin rest to maintain the viewing distance of 105 cm. The experiments were conducted in a dark room.

Stimuli and conditions

The suppressor was a dynamic Mondrian composed of a series of Mondrian patterns refreshed every 94 msec (Figure 1a). Each Mondrian pattern subtended 1.62 × 1.62 degrees and was created by superimposing numerous chromatic rectangles of variable height and width (0.16–0.63 degrees). The color of each rectangle was randomly determined by independently choosing red, green, blue values ranging from 0.15 to 0.85. The target stimulus was an achromatic Gabor patch ($\sigma = 0.22$ degrees, 2.5 cpd) of 40% Michelson contrast. It was tilted 45 degrees to the left or right from vertical (clockwise [CW] or counter-clockwise [CCW]) and its spatial phase was randomly determined on each trial.

Both the suppressor and the target were presented in the center of a uniform circular background (18 cd/m^2) subtending 4.6 degrees in diameter, presented on the left and the right side of the monitor. The background was always presented to each eye to help binocular fusion, and observers were instructed to fixate at its center during the trial. Binocular fusion was further facilitated by a fixation pattern composed of four black crosses (0.5 × 0.5 degrees), each of which was located at 1.2 degrees away from the center of the background in the left, right, upper, and lower directions. Between the trials a central fixation cross (0.5 × 0.5 degrees) was also presented on the left and the right backgrounds to indicate that the next trial was ready to begin.

We manipulated the eye of presentation of the stimuli in four conditions (Figure 1b). In the dichoptic condition (Figure 1b, middle), which followed the ordinary CFS procedure, the suppressor was presented to the observer's dominant eye and the target to the nondominant eye. There were two eye-swapping conditions (Figure 1b, bottom) in which the suppressor and the target were dichoptically presented as in the dichoptic condition, but the eye of presentation was repeatedly swapped at either 1.2 or 3.5 Hz (exact swapping rates were 1.18 and 3.54 Hz, respectively, and thus the latter was three times as high as the former). The fourth condition was the monocular condition in which the suppressor and the target were monocularly superimposed (Figure 1b, top). This condition was included to confirm that interocular conflict was necessary to produce strong and stable suppression in CFS. As the manipulation of the eye of presentation changed how and to which eye the target was presented, the detection time of the target was also measured without the suppressor. Before the main experiment, the observer's dominant eye was determined by measuring perceptual dominance time during conventional binocular rivalry (rivalry of 1 minute with orthogonal Gabor patches, tested on five trials), although a recent study recommended to use the same task as in the main experiment to determine eye dominance (Ding, Naber, Gayet, Van der Stigchel, & Paffen, 2018).

To strictly control the eye of presentation, several precautions were taken. First, we used a frame interleaving technique for stimulus presentation (e.g., Watanabe et al., 2011). The suppressor and the target were drawn separately and presented on alternative pages at the 85-Hz frame rate. This technique allowed us to flexibly manipulate the eye of presentation of the suppressor and the target without any display-device-based interaction between them, although it reduced both the effective stimulus contrast and the refresh rate of the stimulus images in half. Second, the contrast of the target was also temporally modulated at 3.5 Hz. It was ramped up to the maximum over 94 msec, kept at that value for 94 msec, and then ramped down over 94 msec. This modulation was repeated during target presentation and eye swapping was synchronous with the target modulation. This procedure was used to minimize transients at eye exchanges and to keep the time course of the target presentation identical across different eye-of-presentation conditions. Eye swapping necessarily introduces a temporal change in target presentation, which might affect the detectability of the target in the eye-swapping conditions relative to that in the dichoptic condition.

Procedure

On each trial, the observer's key press initiated the stimulus sequence. After a blank period of 500 msec, the suppressor was presented alone to establish its perceptual dominance. The target was then introduced with a delay of 2 to 4 seconds (in 1-second step). The target presentation with both variable delay and contrast ramp was intended to prevent observers from predicting its onset. The eye of presentation of the two stimuli was manipulated depending on the stimulus condition (Figure 1b). The observer's task was to indicate the orientation of the target (CW or CCW) as soon as possible. The suppressor and the target were presented until observers made a response or 10 seconds passed after the target onset. An auditory feedback was provided on every trial to indicate whether the correct response was given or not. At the end of the trial, a dynamic random noise (1.62 × 1.62 degrees) was presented for 1 second to reduce carryover effects such as afterimages.

At the beginning of the experiment, observers dark-adapted for at least 5 minutes and then preadapted to the circular background for 2 minutes. All eight stimulus conditions (four eye-of-presentation conditions × two suppressor conditions [with and without the suppressor]) were tested 10 times in a pseudorandom order for each observer. Observers could have as many practice trials as they wanted to familiarize themselves with the stimulus and the task before the main experiment.

Results

Prior to the analysis, the trials on which the response was incorrect (3.2%) and the detection time was shorter than 100 msec (0.1%) were discarded. The mean detection time was calculated in different eye-of-presentation conditions for each observer and then averaged across different observers (Figure 2). The detection time was analyzed by using a two-way repeated-measures analysis of variance (ANOVA) with the suppressor (absent/present) and the eye of presentation as factors. We observed significant main effects for the presence/absence of suppressor, $F(1, 11) = 106.11$, $p < 0.001$, $\eta_p^2 = 0.91$, and the eye-of-presentation, $F(3, 33) = 51.37$, $p < 0.001$, $\eta_p^2 = 0.82$. An interaction was also significant, $F(3, 33) = 49.53$, $p < 0.001$, $\eta_p^2 = 0.82$. This significant interaction

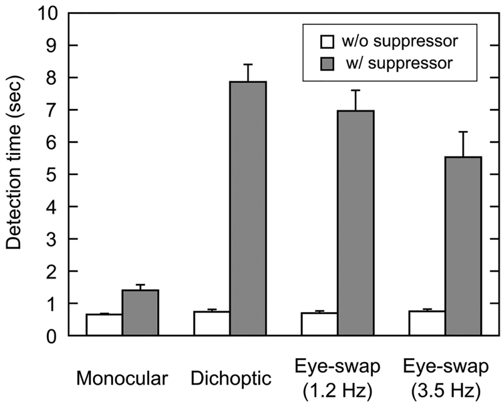

Figure 2. Results of Experiment 1. Detection time in the monocular, dichoptic, and two eye-swapping conditions. For each condition, the white bar shows the detection time without the suppressor, whereas the gray bar shows the time with the suppressor. Error bars indicate +1 *SEM* across observers.

reflected differential effects of the eye of presentation; the detection time was significantly modulated when the suppressor was presented (gray bars in Figure 2), $F(3, 33) = 50.83$, $p < 0.001$, $\eta_p^2 = 0.82$, whereas it was not when the suppressor was absent (white bars in Figure 2), $F(3, 33) = 1.45$, $p = 0.245$, $\eta_p^2 = 0.12$. Furthermore, post hoc analysis with Bonferroni correction ($\alpha = 0.05/6$) revealed that when the suppressor was present, the detection time in the 3.5-Hz eye-swapping condition was shorter than that in the dichoptic and the 1.2-Hz eye-swapping conditions, $t(11) = 3.39$, $p = 0.006$, and $t(11) = 4.13$, $p = 0.002$, respectively, whereas it was longer than that in the monocular condition, $t(11) = 5.76$, $p < 0.001$. The analysis of the simple main effect of the suppressor revealed that the detection time was significantly increased with the suppressor in all eye-of-presentation conditions, $F(1, 11) = 22.43$, $p < 0.001$; $F(1, 11) = 180.51$, $p < 0.001$; $F(1, 11) = 92.83$, $p < 0.001$; and $F(1, 11) = 38.14$, $p < 0.001$, for the monocular, dichoptic, 1.2-Hz, and 3.5-Hz eye-swapping conditions, respectively.

Discussion

Short detection time in the monocular condition confirmed that dichoptic presentation of the suppressor and the target was necessary to produce a strong and stable suppression in CFS that was demonstrated in the dichoptic condition. This finding indicates that interocular suppression caused by competition between monocular processes was essential for CFS suppression. However, although interocular suppression predicted that eye swaps would have led to target detection, the strong suppression persisted in the 1.2-Hz eye-swapping condition. More frequent eye swaps at 3.5 Hz significantly reduced the potency of CFS. In any case, eye swapping did not result in stronger suppression; this finding is not consistent with the prediction based on BSS (Arnold et al., 2008).

Eye swapping at very high frequency can completely abolish the suppression and produce the appearance of the suppressor and the target being superimposed on each other in a semitransparent manner. However, this transparent appearance did not seem obvious in the 3.5-Hz eye-swapping condition. When asked, the observers could not discriminate different eye-of-presentation conditions based on the appearance of the stimulus. We selected the higher swapping frequency (3.5 Hz) based on previous findings that, around this swapping frequency, stimulus rivalry has been consistently observed (Logothetis et al., 1996; Lee & Blake, 1999). In accord with these findings, we found significantly stronger suppression in the 3.5-Hz eye-swapping condition than in the monocular condition (Figure 2). The eye swaps at the higher frequency still produced much stronger disruptive effects than monocular superimposition of the target on the suppressor. Overall, it seems reasonable to assume that the suppression persisted even in the 3.5-Hz eye-swapping condition.

How can the effects of eye swapping on CFS suppression be accounted for in view of the contribution of monocular and binocular processes? A possible explanation assumes the contribution of both monocular and binocular processes to CFS suppression. That is, eye swapping disrupted the suppression mediated by monocular processes in both the 1.2- and 3.5-Hz eye-swapping conditions. However, the suppression by binocular processes persisted and was weaker at higher swapping frequency. Alternatively, it is also possible that the suppression was mainly mediated by monocular processes and the rise (buildup) of suppression was sufficiently fast. The suppression was regained soon after eye swapping, and thus persisted when the swapping frequency was low. However, the process failed to fully follow faster eye swapping, which shortened the target detection time. These two accounts were further tested in Experiment 2.

Experiment 2

The main objective of Experiment 2 was to investigate the time course of suppression in the 1.2-Hz eye-swapping condition. We measured the strength of suppression at different timings of the presentation cycle of the suppressor, just before or after eye swapping. If the suppression is mediated by a purely binocular process, then the strength of suppression should not vary relative to the timing of eye swapping. By contrast, if the suppression is mediated

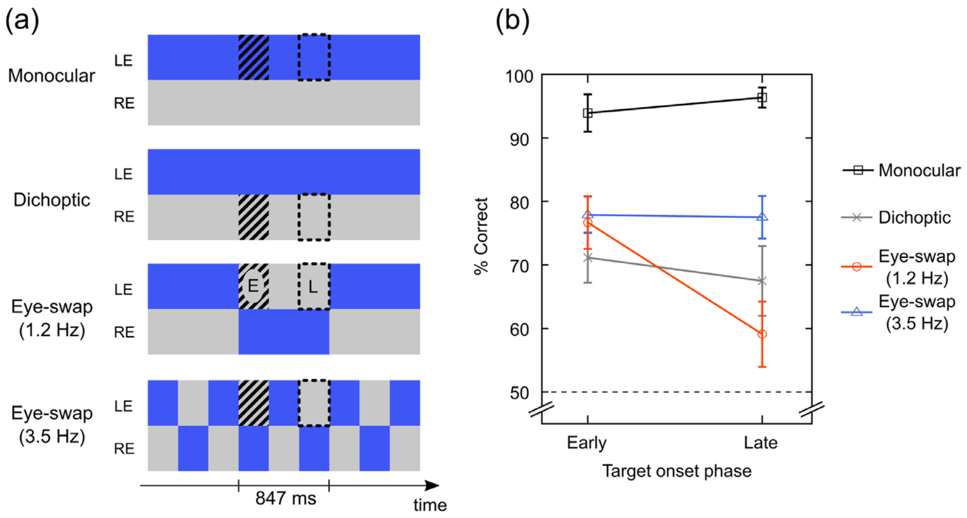

Figure 3. Stimulus conditions and results of Experiment 2. (a) Schematic illustration of the target presentation in different eye-of-presentation conditions. The format of the illustration is the same as that of Figure 1(b). A brief target was presented either at an early (depicted by "E") or a late phase ("L") of the suppressor presentation half-cycle in the 1.2-Hz eye-swapping condition (third row). The target was presented at the corresponding timing in the other conditions. (b) Percent correct performance of the target detection task was plotted as a function of target onset phase. Different symbols represent different eye-of-presentation conditions. Error bars indicate ±1 *SEM* across observers. The dashed line designates the chance level of the task (50%). LE and RE represent the left eye and the right eye, respectively.

by a monocular process and builds up quickly after eye swapping, then suppression should be weak just after swapping and become stronger near the end of the presentation. To test these predictions, we changed the experimental task and measured detectability of a briefly presented target at different points in time.

Another objective of Experiment 2 was to investigate the effects of eye of presentation using a more objective dependent measure than target detection time, used in Experiment 1. It has been argued that the target detection time is susceptible to differences in decisional criterion (Stein, Hebart, & Sterzer, 2011; Stein & Sterzer, 2014; Yang, Brascamp, Kang, & Blake, 2014). Accordingly, we used a more objective sensitivity measure of target detectability to investigate whether a pattern of results similar to those found in Experiment 1 could also be demonstrated; that is, both the persistence of suppression at lower swapping frequency and the significant reduction in the magnitude of suppression at higher frequency. For this objective, all of the four eye-of-presentation conditions were tested in Experiment 2.

Methods

Observers

Ten naive observers participated in Experiment 2. Five of them had also participated in Experiment 1. They had normal or corrected-to-normal visual acuity and normal color vision.

Stimuli and procedure

The eye of presentation was manipulated in the same way as in Experiment 1, that is, in the monocular, dichoptic, 1.2-Hz, and 3.5-Hz eye-swapping conditions. Of all four conditions, the most critical one was the 1.2-Hz eye-swapping condition in which the presentation timing of the target was manipulated relative to the suppressor presentation (Figure 3a). The target was presented at either one of the two timings: (1) at an "early" phase that corresponded to just after eye swapping, that is, at the timing when the suppressor has been just switched from one eye to the other, and (2) at a "late" phase that corresponded to just before the next eye swapping, that is, after the suppressor had been on one eye and just before it would be switched to the other eye. The duration of the target was 282 msec. The target contrast was ramped up for 94 msec, kept at its maximum for 94 msec, and ramped down for 94 msec. In the other eye-of-presentation conditions, the target was also presented at the corresponding timing to equate the onset latency of the target relative to the onset of the suppressor (Figure 3a). In these conditions, the "early" and "late" phases did not have any special meaning with respect to the time course of suppression. The maximum target contrast was varied in one of three levels (0.00, –0.25, and –0.50 in log unit) to make the trial-by-trial variability in target detectability larger and the appearance of the target less predictable. However, because target detectability was expected to be low for lower contrasts and this could make the possible effects of the timing of target presentation difficult to detect (i.e., floor effect), our main analysis will focus on the results with the target contrast of 0 log unit. The results for all contrast levels (0.00, –0.25, and –0.50 log unit) were reported in supplementary materials (Supplementary Figure S1).

The observer's task was a two-alternative forced choice to indicate the orientation of the target (CW or CCW) after the stimulus presentation. No mask was presented following the stimulus. Auditory feedback was provided on every trial to indicate whether the observer's response was correct or wrong. All combinations of the eye of presentation (four conditions) and the target contrast (three levels) were repeated 50 times. In each condition, the timing of target presentation (early vs. late) was randomly chosen. All other aspects of the method were the same as those in Experiment 1.

Results and discussion

The percentage of trials on which the orientation of the target of 0 log unit contrast was correctly identified is shown in Figure 3b. A two-way repeated-measures ANOVA showed a significant main effect of the eye of presentation, $F(3, 27) = 18.57$, $p < 0.001$, $\eta_p^2 = 0.67$, and of the timing of target presentation, $F(1, 9) = 6.52$, $p = 0.031$, $\eta_p^2 = 0.42$. The interaction was also significant, $F(3, 27) = 8.43$, $p < 0.001$, $\eta_p^2 = 0.48$. Multiple comparisons for the significant effect of the eye of presentation with Bonferroni correction ($\alpha = 0.05/6$) showed mostly consistent results with those of the detection time in Experiment 1 (Figure 2). The percentage of correct responses was significantly higher in the monocular condition than in the other three conditions [$t(9) = 5.12$, $p < 0.001$ (vs. dichoptic); $t(9) = 5.74$, $p < 0.001$ (vs. 1.2-Hz eye swapping); $t(9) = 5.58$, $p < 0.001$ (vs. 3.5-Hz eye swapping)]. The percentage of correct responses in the 1.2-Hz eye-swapping condition was not significantly different from that in the dichoptic condition, $t(9) = 0.30$, $p = 0.773$, but it was significantly lower than that observed in the 3.5-Hz eye-swapping condition, $t(9) = 4.26$, $p = 0.002$. However, unlike results in Experiment 1, the difference between the dichoptic and the 3.5-Hz eye-swapping condition in Experiment 2 did not reach statistical significance, $t(9) = 2.14$, $p = 0.061$. Supplementary materials (Supplementary Figure S1) show the results for all contrast levels (0.00, –0.25, and –0.50 log unit).

Critically, post hoc analysis of the significant interaction revealed that the simple main effect of the timing of target presentation was only significant in the 1.2-Hz eye-swapping condition, $F(1, 9) = 24.92$, $p < 0.001$, $\eta_p^2 = 0.73$. In the other conditions, the timing did not significantly affect the target detectability as expected. Multiple comparisons for the eye of presentation at the early phase with Bonferroni correction ($\alpha = 0.05/6$) showed that the percentage of correct responses was higher in the monocular condition than in the dichoptic and the 3.5-Hz eye-swapping condition, $t(9) = 4.20$, $p = 0.002$; $t(9) = 3.85$, $p = 0.004$, respectively. Multiple comparison at the late phase with Bonferroni correction ($\alpha = 0.05/6$) showed that the percentage in the monocular condition was higher than in the other three conditions [$t(9) = 4.97$, $p < 0.001$ (vs. dichoptic); $t(9) = 7.83$, $p < 0.001$ (vs. 1.2-Hz eye swapping); $t(9) = 6.15$, $p < 0.001$ (vs. 3.5-Hz eye swapping)]. Moreover, the percentage in the 1.2-Hz eye-swapping condition was lower than in the 3.5-Hz eye-swapping condition, $t(9) = 6.13$, $p < 0.001$.

The significant effect of the timing of target presentation found in the 1.2-Hz eye-swapping condition clearly demonstrated that the strength of interocular suppression varied as a function of the time after eye swapping. The suppression was relatively weak just after eye swapping, but then it became stronger by the time of the next eye swap (Figure 3b). This finding suggested that the suppression was quickly building up after eye swapping over the monocular presentation period of the suppressor. The stronger suppression at the late phase cannot be easily explained by monocular backward masking from an immediately following Mondrian pattern. If that were the case, then the stronger suppression would have also been found in the 3.5-Hz eye-swapping condition, because the target in that condition was also followed by a Mondrian pattern. Moreover, if the contribution of monocular masking were substantial, stronger suppression would have been found in the 3.5-Hz eye-swapping condition. This is because, as shown in Figure 3a, the target in the 3.5-Hz eye-swapping condition was sandwiched between a preceding and a following Mondrian pattern, and thus target detection could be disrupted by both forward and backward masking (see also Macknik & Livingstone, 1998). Therefore interocular suppression is more likely the cause of the observed differences in suppression between the 1.2- and the 3.5-Hz eye-swapping conditions. Overall, the present findings are consistent with the hypothesis that CFS suppression is mainly mediated by competition between monocular processes that can produce a quickly rising interocular suppression.

General discussion

To further elucidate visual mechanisms underlying CFS, the present study investigated the effects of eye of presentation on CFS suppression using an eye-swapping paradigm. Results confirmed that dichoptic presentation was essential for strong CFS suppression using both detection time (Experiment 1) and detectability of the target (Experiment 2) as respective dependent measures. Moreover, the most persistent and strongest CFS suppression was found in the dichoptic condition (Figure 2), in which the eye of presentation was fixed during CFS. The results also revealed that the effects of eye swapping of the suppressor and the target depended on the swapping frequency. When the swapping frequency was low (1.2 Hz), the strong suppression as found in the dichoptic condition persisted. However, the suppression was significantly reduced in magnitude at a higher swapping frequency (3.5 Hz). Experiment 2 indicated that this dependency on swapping frequency of CFS suppression can be accounted for by the contribution of monocular processes to CFS suppression. In this experiment, a brief flash was presented at different timing relative to eye swapping; we found that CFS suppression was weaker just after eye swapping but this suppression quickly regained its strength over the monocular presentation period of the suppressor when the swapping frequency was low (Figure 3b). However, this buildup of suppression did not seem to be fast enough to closely follow 3.5-Hz eye swapping, although significant CFS suppression was found even with this frequent eye swapping. Overall, these results indicated that CFS suppression is mainly mediated by interocular competition between monocular processes (i.e., eye rivalry).

This strong contribution of monocular processes to CFS suppression is consistent with the view that CFS and binocular rivalry share interocular suppression mechanisms (Han et al., 2016; Han et al., 2018; Han & Alais, 2018). The argument in the previous studies was based on the findings of similarities in spatiotemporal characteristics of the suppression between CFS and binocular rivalry; the suppressions observed in CFS and in binocular rivalry were selective in both spatial and temporal domains (see also Hong & Blake, 2009; Maehara, Huang, & Hess, 2009; Yang & Blake, 2012). As feature selectivity of suppression has generally been associated with stimulus rivalry that can be mediated by binocular processes indifferent to the eye of origin, it may seem contradictory to the contribution of monocular processes found in the present study. However, feature selectivities implicated in CFS suppression are the ones that can be found at early stages of visual processing, such as in V1 or even in the precortical parvo/magno pathways (Hong & Blake, 2009; Han et al., 2016; Han & Alais, 2018). Moreover, a recent study showed that monocular processes can mediate stimulus rivalry (Brascamp, Sohn, Lee, & Blake, 2013). Therefore it is not implausible to assume that both selectivity to spatiotemporal features and specificity to eye of origin coexist in single visual processes.

Additionally, we would like to point out that the present findings do not rule out the contribution of feature-selective binocular processes to CFS suppression. Previous studies on binocular rivalry have provided converging evidence for the contribution of both eye and stimulus rivalry (Brascamp, Knapen, Kanai, van Ee, & van den Berg, 2007; Bartels & Logothetis, 2010; Abe, Kimura, & Goryo, 2011; Stuit, Paffen, van der Smagt, & Verstraten, 2011). Moreover, it has also been demonstrated that manipulating stimulus properties, such as spatiotemporal characteristics and complexity of rivaling images, can change the nature of suppression (e.g., Lee & Blake, 1999; Sandberg, Bahrami, Lindeløv, Overgaard, & Rees, 2011). For example, Lee and Blake (1999) showed that the contribution of eye and stimulus rivalry can change with the spatial and temporal frequencies of rivaling grating stimuli. Furthermore, other studies have shown that interocular competition of different stimulus types, for example, simple stimuli such as orthogonal gratings or high-level complex stimuli such as face and house images, can be mediated by different types of rivalry (Sandberg et al., 2011). Thus with different types of rivaling stimuli, a stronger contribution of binocular processes might be found in the CFS paradigm.

Although we did not find an increase in the strength of suppression by eye swapping, these results may not be inconsistent with the involvement of BSS (Arnold et al., 2008). In fact, it is possible that the suppression at the early phase (Experiment 2) was mediated by similar mechanisms underlying BSS. It is because the suppression was caused by eye swapping of two conflicting stimuli, one of which was stronger than the other as in BSS. The swapping frequency dependency of the suppression was also similar to that found in BSS; the frequency of approximately 1 Hz produced stronger effects (Figures 2 and 3b). A discrepancy between the previous and the present findings lies in the relative strength of BSS to CFS. The present study shows that the suppression produced by eye swapping of Mondrian patterns (BSS) was weaker than the built-up interocular suppression caused by repetitively updating Mondrian patterns (CFS) (Figure 3b). Arnold et al. (2008) found that BSS is superior to CFS in terms of the depth and the duration of suppression. This apparent discrepancy may be accounted for by the fact that Arnold et al. (2008) used a white noise as the suppressor; this has been shown to be a much weaker suppressor than Mondrian patterns for CFS (Drewes et al., 2018). Low spatial-frequency components in Mondrian patterns play a critical role in producing strong and persistent suppression in CFS (Yang & Blake, 2012).

Considering the findings in recent CFS studies together with the present findings, the visual mechanisms underlying BSS and CFS may not be very different. The previous CFS studies showed that even when Mondrian patterns are updated at 10 Hz, strong energy lies in low temporal frequency range (Han et al., 2016). Moreover, temporal tuning of CFS suppression peaks at approximately 1 Hz when tested with a suppressor composed of spatiotemporally filtered noise (Han et al., 2018; Han & Alais, 2018). Thus the optimal effective rate of stimulus change for BSS and CFS can be very similar. Overall, BSS and CFS may be accounted for as follows. When two conflicting stimuli are presented dichoptically and one is much stronger than the other, then the stronger stimulus becomes perceptually dominant, presumably through competition between monocular processes. If the two stimuli are static, relative stimulus strength can change because of neural adaptation to the stronger stimulus in a monocular process, and thus the percept would eventually vary over time as in binocular rivalry. However, if the eye of presentation of the two stimuli is swapped as in BSS, or the stronger stimulus is temporally updated as in CFS, the neural adaptation can be mitigated, and thus the dominance of the stronger stimulus can persist over an extended period of time. The relative effectiveness of eye swapping and repetitive updating in mitigating neural adaptation may vary with stimulus properties, such as spatiotemporal components.

Conclusion

The present study revealed that phenomenal suppression mediated by interocular competition between monocular processes can persist even when the eye of presentation of rivaling stimuli is repetitively switched. Thus phenomenal continuation of the suppression over several eye swaps may not be conclusive evidence for the contribution of binocular and/or feature-selective processes to suppression, particularly when the suppressor is much stronger than the target as in the CFS paradigm.

Keywords: continuous flash suppression, eye of origin, interocular suppression

Acknowledgments

This work was partly supported by Grants-in-Aids for Scientific Research from the Japan Society for the Promotion of Science to EK (Nos. 26285162, 25285197, and 18K18686). We are grateful to two anonymous reviewers for their helpful comments and suggestions for the earlier versions of the manuscript.

Commercial relationships: none.

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