Strength of continuous flash suppression is optimal when target and masker modulation rates are matched

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Continuous flash suppression (CFS) is a popular technique whereby a dynamic sequence of Mondrian patterns is presented to one eye in order to suppress a static target presented to the other eye. Although the effectiveness of CFS is generally assumed to increase with the flicker rate of the Mondrian masker, a recent study has shown that suppression is optimal at very low masker rates for sustained targets, but higher rates may be necessary for transient targets. Here we vary the modulation rates of the masker and target using temporally filtered dynamic noise, which allowed us to examine the relationship between target and masker frequency and its effect on suppression strength. Using these carefully controlled, temporally narrowband stimuli, we demonstrate a pattern of results showing that suppression is greatest when target and masker modulate at similar frequencies. This finding indicates the involvement of early temporal-frequency-tuned filters underlying CFS and is consistent with many existing findings in the CFS literature. We also find that these temporally selective processes are orientation selective, which points to an early cortical substrate such as neurons in primary visual cortex. Overall, our study reveals that CFS suppression can be maximized by carefully matching the masker and target in temporal frequency and orientation. More generally, we show the importance of using carefully controlled stimuli for elucidating the underlying mechanisms of CFS. This approach is important at a theoretical level, as it will enable comparison of CFS with existing models of binocular rivalry and interocular suppression and facilitate a unified explanatory framework.

Introduction

Our sensory system is flooded with information from the external environment, yet only a small proportion constitutes our conscious experience. Several techniques have been developed to render visual images invisible to allow investigation of the functional and processing status of nonperceived input (Breitmeyer, Ogmen, & Chen, 2004; Kim & Blake, 2005; Tsuchiya & Koch, 2005). Continuous flash suppression (CFS) is one of the most widely used of these techniques. In the CFS paradigm, a dynamic sequence of random Mondrian patterns is viewed in one eye while a static target is presented to the other eye. This generally produces effective and long-lasting suppression, especially when low-contrast targets are used—which is generally the case (Tsuchiya & Koch, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006). Unlike in binocular rivalry, the first visual percept in CFS is reliably that of the dynamic Mondrian sequence, meaning the suppressed target can be conveniently studied from the outset (Yang, Brascamp, Kang, & Blake, 2014). This, coupled with long suppression times, has seen CFS become a widely adopted technique (e.g., Fang & He, 2005; Moors & Wagemans, 2015; Yang, Zald, & Blake, 2007).

Mondrian refresh rates of 10 Hz or higher are typically adopted in CFS studies (e.g., Xu, Zhang, & Geng, 2011; Yuval-Greenberg & Heeger, 2013), as it is widely assumed that one of the keys to CFS's strong suppression is the rapid pattern changes in the masking eye (Tsuchiya et al., 2006; Tsuchiya & Koch, 2005). Existing evidence, however, suggests that the optimal refresh rate for the masker may differ depending on the nature of the target to be suppressed. One study using brief static targets found that the optimal masker required a flicker rate of up to 28.5 Hz (Kaunitz, Fracasso, Skujevskis, & Melcher, 2014), while another using prolonged static targets found that suppression peaked at around 6 Hz (Zhu, Drewes, & Melcher, 2015). Both of these studies varied the update rate of independent static images, meaning the luminance changes were abrupt and the temporal frequency content was therefore broadband.

A recent study was the first to control the temporal frequency of the masking stimulus in narrow passbands (Han, Lunghi, & Alais, 2016). In this study, where the image undergoes smooth and continuous modulation rather than discrete transient changes, the masking frequency giving greatest suppression of prolonged static targets was very low, at ~1 Hz. Although it may not be obvious at first glance, using the image update rate to manipulate temporal frequency produces broadband temporal content with a strong bias to very low temporal frequencies. This is best exemplified by the pixel timeline, where the 100-ms presentation time of each pattern and the central tendency of luminance changes jointly produce a slow-modulating, stepped waveform (for more details, see Supplementary Text S1, Supplementary Figure S1 and Han et al., 2016). Increasing the update rate does not change the low temporal bias; however, the proportion of high temporal-frequency energy increases (Figure 1a). Therefore, one consistent interpretation of these studies, despite their different temporal manipulations, is that prolonged static targets are best produced by very low temporal frequencies.

Psychophysical studies of temporal processing conclude that the entire temporal dimension in vision is encoded by a broad low-pass channel with a cutoff around 4 Hz (Anderson & Burr, 1985; Cass & Alais, 2006; Snowden, Hess, & Waught, 1995) and one or perhaps two higher, bandpass channels (Cass & Alais, 2006; Hess & Snowden, 1992; Johnston & Clifford, 1995). By this account, stimuli that are static or slowly modulating will activate the low-pass temporal-frequency channel, whereas rapidly modulating, transient stimuli would stimulate the high-frequency, bandpass channel. Detection of a static target thus becomes more difficult with low masker modulation or update rates (Han et al., 2016; Zhu et al., 2015), as target and masker will both activate the same channel. Likewise, higher Mondrian update rates are better suppressors of transient targets (Kaunitz et al., 2014) because the increased high-temporal-frequency content drives the same channel as the transient target. Physiologically, these channels may correspond to parvocellular and magnocellular neurons, which are, respectively, more responsive to slower modulating and transient visual stimuli (Derrington & Lennie, 1984).

Several studies have shown that CFS is feature selective. For instance, similarities in target and masker spatial frequency (Maehara, Huang, & Hess, 2009; Yang & Blake, 2012) and speeds (Moors, Wagemans, & De-Wit, 2014) have been shown to enhance suppression. It is therefore likely that CFS would involve suppression processes that are selective in the temporal dimension. However, because Mondrian maskers are temporally broadband and CFS studies typically use static targets (but see Ananyev, Penney, & Hsieh, 2017;

Kaunitz et al., 2014; Moors et al., 2014), the proposition has not been specifically addressed. In this study, we measured the temporal selectivity of CFS by comparing 2- and 10-Hz narrowband noise maskers on targets modulating at a range of temporal frequencies. We predict that, regardless of masker temporal frequency, enhanced suppression will be observed when target and masker frequencies are similar. In contrast, suppression will be reduced for any target–masker combination that activates different channels. We quantify this using two dependent measures: suppression duration and contrast sensitivity threshold. Measured using the commonly used breaking-CFS (b-CFS) paradigm, suppression durations reflect the time to visibility and are more susceptible to nonperceptual factors such as participant decisional criteria in determining target visibility (Yang et al., 2014). Including a more objective measure such as contrast sensitivity threshold allows us to compare both measures and better understand the general trend. In addition, measuring contrast sensitivity will facilitate comparisons with binocular-rivalry studies, which often measure contrast sensitivity in suppression (Alais, 2012; Stuit, Cass, Paffen, & Alais, 2009).

Experiment 1

Methods

Masker stimuli

Spatiotemporally narrowband maskers were generated by filtering 205 randomly generated noise images (each 128×128 pixels, approximately $5.4° \times 5.4°$, 15% RMS contrast and normalized to mean luminance). These noise images were first converted to the frequency domain using a three-dimensional fast Fourier transform and then filtered spatially and temporally using narrowband, log-Gaussian filters. The spatial filter had a center frequency of 3 c/° and the temporal filter had a center frequency of 2 or 10 Hz. All filters had a full bandwidth at half height of one octave. Masker images were then back-transformed and normalized to maximum contrast (15% RMS) and to space-averaged mean luminance. Maskers were then presented at 95% of maximum contrast (see examples of masker stimuli in Figure 1b and Supplementary Movies S1 and S2).

Target stimuli

Targets were dynamic filtered noise images made from the same spatiotemporal filtering process as the masker images but using independent noise images. They were generated with the same RMS contrast and
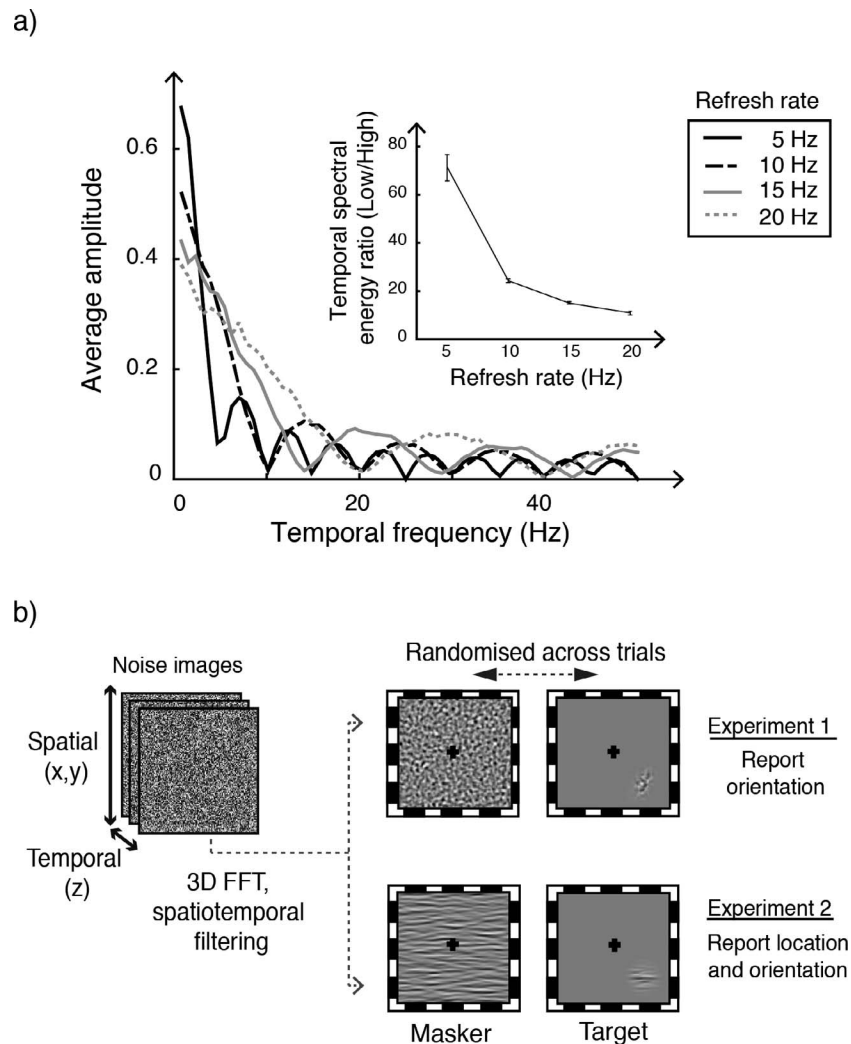
Figure 1. (a) Effect of Mondrian refresh rate on temporal-frequency content. Two-dimensional Fourier analyses show that the Mondrian masker has a strongly low-biased temporal-frequency amplitude spectrum across different refresh rates. Although the trend becomes more broadband with faster flicker rates, the low-frequency bias remains. These differences were quantified by comparing the power spectral densities of low (<4 Hz) and high (≥4 Hz) temporal frequencies for Mondrian maskers at 5, 10, 15, and 20 Hz (inset). Five maskers were independently generated for each masker refresh rate. Twenty-five pixels were then randomly sampled from each of these five maskers and their timelines analyzed. (b) Stimuli used in the current experiments. To generate masker and target stimuli, a three-dimensional Fourier transform was first performed on a stack of 205 randomly generated noise images, before narrowband log-Gaussian filters were applied to the temporal (2, 3, 5, 7.5, and 10 Hz) and spatial dimensions (3 c/°). Targets were also spatially windowed with an elliptical Gaussian mask in Experiment 1 and a circular Gaussian mask in Experiment 2. To reduce retinotopic adaptation, the presentation of maskers and targets were randomized between the eyes across trials. Checkerboard frames were used to enclose both maskers and targets to ensure stable fusion. Participants were instructed to report the target's orientation in Experiment 1 (tilted left or right) and its location (which quadrant) and orientation (horizontal or vertical) in Experiment 2.

center spatial frequency, could take a range of temporal frequencies (2, 3, 5, 7.5, or 10 Hz), and were windowed in the space domain by a small Gaussian mask of either $SD_{xy} = 10$ pixels for monocular threshold measurements or $SD_x = 4.5$ pixels and $SD_y = 7.5$ pixels for all CFS tasks. Targets thus measured approximately $1° \times 1°$ at half height for monocular threshold measurements and $0.5° \times 1°$ at half height for all CFS tasks.

Both targets and maskers were enclosed by a 0.5°-thick checkerboard frame ($5.9° \times 5.9°$ externally and $5.4° \times 5.4°$ internally; see Figure 1) to encourage stable fusion. All visual stimuli were presented on a Mitsubishi Diamond Pro 2070SB CRT monitor (screen refresh rate of 100 Hz) connected to a DATAPixx data-acquisition system (Vpixx Technologies, Saint-Bruno, Canada), which allowed millisecond precision and a 16-bit contrast resolution. The presentation order of the

target and masker between the eyes was randomized between dominant and nondominant eyes to mitigate adaptation effects.

Participants

In Experiment 1, suppression durations and visual contrast thresholds were recorded for five participants who were unaware of the purposes of the experiment (four women, one man; age range: 19–24 years, $SD =$ 1.82). Another three participants who were unaware of the purposes of the experiment (two women, one man; age range: 21–30 years, $SD = 5.2$) completed only the b-CFS task, whereas threshold measurements were conducted for author SH and four participants (four women; age range: 20–29 years, $SD = 4.93$). All participants had normal or corrected-to-normal visual acuity. Participants also had normal stereovision, assessed using the Fly Stereo Acuity test. All experiments were performed with the approval of the institutional review board at the University of Sydney and according to the principles of the Declaration of Helsinki. Informed consent was obtained for all participants and participants were reimbursed 20 AUD per hour for their participation.

Eye-dominance assessment

Eye dominance was determined using the "hole in the hand" test, a variation on the Miles test (Miles, 1930). Participants were first seated a distance away (~150 cm) from an object placed at eye level. They were instructed to view the object through a small hole created by both hands, first with both eyes and then alternately with each eye. The eye with less displacement in perceived object location was designated as the dominant eye.

Procedure for b-CFS

Targets were first subjectively equated by measuring contrast detection thresholds for each target frequency. To do this, a two-alternative forced-choice (2AFC) QUEST adaptive procedure was adopted for each target frequency, and each staircase consisted of 24 trials. No maskers were presented in the threshold-determination task. Participants judged the location of the target, situated 1.3° to the left or right of a central fixation cross. Each trial lasted for 2 s, followed by 300 ms of dynamic visual white noise. Thresholds were defined at 75% accuracy and were estimated by fitting a cumulative Gaussian psychometric function with the maximum-likelihood estimation procedure. Targets were then presented five times above the respective thresholds for the b-CFS task. To avoid abrupt onsets, maskers and targets were also ramped in contrast

during the initial 1,000 ms of each trial, with the masker leading 50 ms (five frames) before the target to accumulate suppressive effects (Tsuchiya et al., 2006). Predictability and local adaptation were reduced by randomly presenting targets at different points from trial to trial chosen from a circle with a radius of ~1.2° around the fixation cross. Targets were oriented ±45° and participants indicated the orientation of the target (tilted left or right) as soon as it became visible. The time required for each response was recorded, followed by 5 s of dynamic visual white noise. Ten trials per target frequency were collected, the order of which was presented in randomized blocks for each participant. Only trials with correctly located targets and suppression durations that were not more than three times the median absolute deviation were included for analysis. These trials were then sorted according to the dominant eye and averaged for each target temporal frequency. Each participant's data were then normalized to their respective average suppression durations across the 2- and 10-Hz conditions.

Procedure for CFS threshold measurements

Separate 2AFC QUEST adaptive staircases were adopted for each target frequency and each eye. Similar to the b-CFS task, participants were asked to judge the orientation of targets, which were oriented ±45° at random positions along a circle of radius ~1.2° centered on the fixation cross. Each trial lasted for 2 s, followed by 300 ms of dynamic visual white noise. Similar to the b-CFS task, target temporal frequencies were blocked in a randomized order, whereas the order of masker frequency was presented in counterbalanced blocks. Similar to Experiment 1, the eye of origin was randomized within each block. Each staircase consisted of 22 trials, resulting in a total of 220 trials per masker frequency. Thresholds were estimated by fitting a cumulative Gaussian psychometric with the maximum-likelihood estimation procedure. Each participant's estimated thresholds were then normalized to the participant's individual average threshold across the 2- and 10-Hz conditions.

Results

Normalized suppression durations

The effects of masker and target temporal frequencies on suppression durations are summarized in Figure 2a. We first tested the effect of eye dominance on suppression durations using separate 2×5 (eye dominance $\times$ target temporal frequency) repeated-measures ANOVAs for each masker temporal frequency. There was no evidence of eye-dominance effects for either masker frequency—2 Hz: $F(1, 7) < 1$;
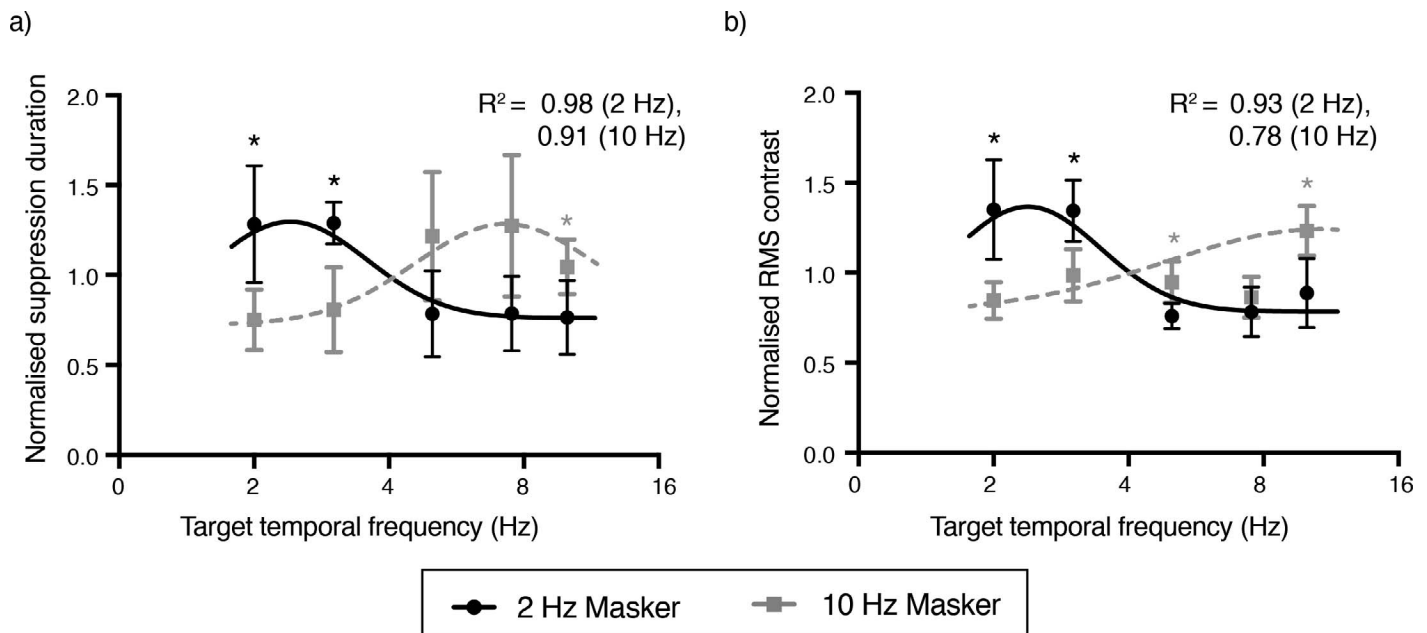
a)

b)

Figure 2. (a) Data from Experiment 1 showing the effect of masker and target rates on normalized suppression durations, with target frequency plotted as a logarithmic scale. The data show that CFS suppression duration is strongly dependent on masker–target similarity, increasing with target temporal frequency when the 10-Hz masker was presented and showing a reverse trend when the 2-Hz masker was presented. Group means were described by normal Gaussian functions centered at 1.27 octaves for the 2-Hz masker and 3.25 octaves for the 10-Hz masker. (b) Data from Experiment 1 showing the effect of masker and target rates on contrast thresholds, with target frequency plotted on a logarithmic scale. Gaussian functions were fitted to the group averages and revealed a very similar pattern to the suppression-duration data: a mean frequency of 1.25 octaves for the 2-Hz masker and 3.39 octaves for the 10-Hz masker. All error bars represent 95% confidence intervals, and asterisks indicate significant pairwise comparisons after Holm–Bonferroni correction. Black asterisks indicate that the 2-Hz masker performed better than the 10-Hz masker, and gray asterisks indicate that the 10-Hz masker performed better than the 2-Hz masker.

10 Hz: $F(1, 7) = 1.53$, $p = 0.26$, $\eta_p^2 = 0.18$. Eye dominance also did not interact with target temporal frequency—2 Hz: $F(4, 28) < 1$; 10 Hz: $F(4, 28) = 1.46$, $p = 0.27$ (Greenhouse–Geisser corrected), $\eta_p^2 = 0.17$. In contrast, target temporal frequency had a significant main effect with both types of maskers—2 Hz: $F(1, 7) = 9.55$, $p < 0.001$, $\eta_p^2 = 0.57$; 10 Hz: $F(1, 7) = 2.72$, $p < 0.05$, $\eta_p^2 = 0.28$. Having established that there were no eye-dominance effects, we pooled the raw suppression-duration data and recompiled a normalized data set without sorting the data according to the dominant eye. This increased the number of data points per target temporal frequency, and allowed us to better estimate individual means for each target frequency. Responses that were inaccurate or more than three times the median absolute deviation were excluded.

Using the pooled data, we conducted a 2 × 5 (masker × target temporal frequency) repeated-measures ANOVA. Due to violations of sphericity, statistical significance was assessed with Greenhouse–Geisser correction. Neither masker frequency, $F(1, 7) < 1$, nor target frequency, $F(4, 28) < 1$, had a significant effect on suppression duration, but they interacted significantly, $F(4, 28) = 9.32$, $p < 0.01$, $\eta_p^2 = 0.57$. Shorter normalized durations were produced at higher target

frequencies when the 2-Hz masker was presented, and the reverse was true when the masker modulated at 10 Hz. These differences between the two masker frequencies were verified by Holm–Bonferroni-corrected paired-samples t tests. Specifically, as plotted in Figure 2a, the 2-Hz masker produced significantly longer normalized durations than the 10-Hz masker when the targets modulated at 2 Hz, $t(7) = 3.65$, $p < 0.05$, and 3 Hz, $t(7) = 4.13$, $p < 0.05$. In contrast, the 10-Hz masker produced significantly longer normalized durations than the 2-Hz masker when the target modulated at 10 Hz, $t(7) = 3.56$, $p < 0.05$.

To further characterize the trends observed, we fitted normal Gaussian functions to each individual's data, with target temporal frequency plotted on a binary logarithmic scale as in Figure 2. Using Holm–Bonferroni-corrected paired-samples t tests to compare the group mean fit parameters, we determined that normalized durations peaked at 1.41 octaves ($SD = 0.48$) when the 2-Hz masker was presented—significantly lower than the peak duration obtained with the 10-Hz masker, which was located at 2.96 octaves ($SD = 0.35$), $t(7) = 7.56$, $p < 0.001$. Although estimated standard deviations were on average wider with the 10-Hz masker than the 2-Hz masker—1.79 octaves ($SD = $

0.82) and 1.46 octaves ($SD = 0.238$), respectively—this difference did not reach statistical significance, $t(7) = 1.25$, $p = 0.25$. There was no significant difference between the amplitudes of the 2- and 10-Hz maskers, $t(7) = 0.12$ $p = 0.91$. These results for the estimated parameters were not driven by the quality of function fits, as R^2 values were comparable between the two masker frequencies, $R_2{}^2 = 0.78$ ($SD = 0.07$) and $R_{10}{}^2 = 0.74$ ($SD = 0.17$).

Normalized contrast thresholds

The threshold results for Experiment 1 are summarized in Figure 2b. The effect of eye dominance on thresholds was first examined using separate 2×5 repeated-measures ANOVAs (eye dominance $\times$ target temporal frequency) for each masker frequency. Target temporal frequency had a significant main effect in both instances—2 Hz: $F(4, 36) = 12.16$, $p < 0.01$ (Greenhouse–Geisser corrected), $\eta_p{}^2 = 0.58$; 10 Hz: $F(4, 36) = 8.03$, $p < 0.001$, $\eta_p{}^2 = 0.47$. These results were not influenced by eye-specific trends, as eye dominance had no significant effect on thresholds—2 Hz: $F(1, 9) = 3.10$, $p = 0.11$, $\eta_p{}^2 = 0.26$; 10 Hz: $F(1, 9) < 1$—and did not interact significantly with target temporal frequency—2 Hz: $F(4, 36) < 1$; 10 Hz: $F(4, 36) = 1.87$, $p = 0.14$, $\eta_p{}^2 = 0.17$. The data were therefore collapsed across both eyes and reanalyzed with a 2×5 repeated-measures ANOVA (masker $\times$ target temporal frequency). Our results showed that target temporal frequency had a significant effect on thresholds, $F(4, 36) = 8.22$, $p < 0.001$, $\eta_p{}^2 = 0.48$, but masker frequency did not, $F(1, 9) < 1$. Similar to the suppression-duration data, both factors interacted strongly, $F(4, 36) = 14.32$, $p < 0.001$, $\eta_p{}^2 = 0.61$, increasing in magnitude as the difference between target and masker frequencies decreases. These differences were verified by Holm–Bonferroni-corrected paired-samples t tests. This showed that the 2-Hz masker produced significantly higher thresholds than the 10-Hz masker when the target modulated at 2 and 3 Hz—$t(9) = 3.60$, $p < 0.05$, and $t(9) = 3.23$, $p < 0.05$, respectively—and that the 10-Hz masker produced significantly higher thresholds when the target modulated at 5 and 10 Hz—$t(9) = 3.93$, $p < 0.05$, and $t(9) = 3.07$, $p < 0.05$, respectively.

As with normalized durations, normal Gaussian functions were fitted to each individual's threshold data. Fits for two participants were excluded from the group analysis due to poor-quality fits (e.g., R^2 value of 0.15). Estimated parameters from the remaining individual's fits were compared using Holm–Bonferroni-corrected paired-samples t tests. Similar to normalized durations, peak threshold elevation produced by the 2-Hz masker occurred at 1.36 octaves ($SD = 0.74$), significantly lower than the 10-Hz masker's 3.02 octaves ($SD = 0.74$), $t(7) = 22.1$, $p < 0.001$. There were

no significant differences in estimated amplitude, $t(7) = 2.20$, $p = 0.19$, or standard deviation, $t(7) = 0.06$, $p = 0.95$. Similar to normalized durations, both the 2- and 10-Hz masker frequencies had comparable quality of fit, $R_2{}^2 = 0.70$ ($SD = 0.18$) and $R_{10}{}^2 = 0.71$ ($SD = 0.10$), $t(7) = 0.22$, $p = 0.83$.

Discussion

Experiment 1 asked if CFS suppression strength depended on the temporal-frequency difference between target and masker. Using temporally narrow-band filtered-noise maskers, we measured the effect of masker temporal frequency at 2 and 10 Hz on the suppression durations and contrast sensitivity thresholds of targets modulating at 2, 3, 5, 7.5, and 10 Hz. Although the suppression-duration data were more variable than contrast thresholds (see confidence intervals in Figure 2a and 2b), in general, greater suppression durations and contrast thresholds were obtained with increasingly similar target and masker temporal frequencies. This was true regardless of masker frequency, and suggested a strong effect of temporal-frequency selectivity in CFS suppression for both dependent measures. Similar conclusions are supported by analyses of data from individual participants. Specifically, normal Gaussian functions fitted to individual data showed significantly lower estimated means for the 2-Hz masker, but there were no differences in estimated standard deviations and amplitudes. Thus, neither masker frequency was more sensitive to differences in target temporal frequency than the other, nor had a suppressive advantage as has been previously suggested from studies using static targets (Han et al., 2016; Kaunitz et al., 2014; Zhu et al., 2015). What counted in the present experiment, regardless of masker frequency, was the relative difference between target and masker temporal frequency, with maximum suppression occurring for small frequency differences. These results were also not linked to eye dominance, as it neither had an effect on contrast thresholds nor interacted significantly with target temporal frequency.

These observations offer an explanation of the different optimal Mondrian update rates reported in the literature. Nevertheless, the findings are not entirely surprising. As mentioned earlier, high and low temporal frequencies have been shown to elicit responses in different neuronal populations. Specifically, greater parvocellular responses are recorded at low temporal frequencies and greater magnocellular responses are recorded at higher frequencies (Alitto, Moore, Rathbun, & Usrey, 2011; Derrington & Lennie, 1984; Livingstone & Hubel, 1988). Although the magnocellular and parvocellular pathways are reported to

interact (Ferrera, Nealey & Maunsell, 1994; Nealey & Maunsell, 1994; Sawatari & Callaway, 1996), we would expect greater interference, and thereby longer suppression of the target, when targets and maskers engage similar neuronal populations, as the masker is effectively noise in the same channel as the target, with the masker dominating the output because of its much higher contrast.

Neurophysiological studies have shown that activity triggered by higher temporal frequencies is capable of suppressing lower frequencies in the lateral geniculate nucleus, whereas lower frequencies have not been found to inhibit higher frequencies (Fawcett, Barnes, Hillebrand, & Singh, 2004; Freeman, Durand, Kiper, & Carandini, 2002; Hawken, Shapley, & Grosof, 1996; Reid & Alonso, 1996; Shou & Leventhal, 1989; Yen, Fukuda, & Kim, 2012). Similar asymmetrical observations have been reported in a human psychophysical study, with binocularly viewed high-temporal-frequency stimuli (>4 Hz) found to mask low frequencies but not vice versa (Cass & Alais, 2006). These trends were not observed in our data, suggesting that the underlying mechanisms might be cortical in origin. Nevertheless, we did not view the lack of asymmetry as precluding precortical contributions, as interocular competition could occur at multiple levels (Pearson & Clifford, 2006). For instance, although monocular inputs to the lateral geniculate nucleus are largely segregated in separate layers (Meissirel, Wikler, Chalupa, & Rakic, 1997), feedback signals from V1 may produce fluctuations in lateral geniculate nucleus activity that correlate with rivalry alternations (Haynes, Deichmann, & Rees, 2005; Wunderlich, Schneider, & Kastner, 2006).

Experiment 2

In Experiment 1, normalized suppression durations and target contrast thresholds increased as target and masker temporal frequencies became similar. Neither masker frequency had a suppressive advantage over the other, producing comparable amplitudes and spreads of normalized durations and thresholds. These results suggested dominant cortical influences, and the goal of Experiment 2 was to evaluate this idea. To do so, we asked if the effect of target orientation on suppression durations and contrast thresholds differs between 2- and 10-Hz maskers. The reasoning behind this approach is as follows. Precortical regions are poorly tuned to orientation (Reid & Alonso, 1996; Shou & Leventhal, 1989) and are more responsive to higher temporal frequencies (Hawken et al., 1996). These properties have been linked to cross-oriented masking in V1 (Freeman et al., 2002), where effective target

suppression is produced by fast-modulating, orthogonally oriented maskers (Alitto et al., 2011; Cass & Alais, 2006). Comparing the effect of orientation between 2- and 10-Hz maskers thus allows us to infer the relative contributions of precortical and cortical influences. If CFS suppression were underpinned by substantial precortical influences, the 10-Hz masker would produce a less orientation-specific effect than the 2-Hz masker. In contrast, a more dominant cortical influence in CFS would produce comparable orientation effects on target suppression for both masker frequencies and suppression.

Materials and methods

Visual stimuli

All targets and masker stimuli were generated with the same spatiotemporal filtering technique as in Experiment 1 (3 c/° spatially and 2 or 10 Hz temporally), with the addition that these stimuli were also spatially filtered in frequency space using a Gaussian orientation filter with an orientation bandwidth of $\pm 10°$. See examples of masker stimuli in Figure 1b and Supplementary Movies S3 and S4. Targets and maskers always had the same temporal frequency in this experiment—either both 2 Hz or both 10 Hz—and were either iso- or cross-oriented, making a 2×2 factorial combination. Targets and maskers were normalized to maximum contrast (15% RMS) and set to mean luminance. Maskers were approximately $5.4° \times 5.4°$ in dimensions (128×128 pixels), whereas targets, measuring $1.5° \times 1.5°$ in diameter, were generated by windowing the spatiotemporally filtered noise images with a small Gaussian mask ($SD_{xy} = 8.8$ pixels). Both targets and maskers were enclosed in a 0.5°-thick checkerboard frame ($5.9° \times 5.9°$ externally and $5.4° \times 5.4°$ internally). Maskers were presented at 95% of maximum contrast and spanned the entire $5.4° \times 5.4°$ area.

Participants

Suppression durations and thresholds were measured for two participants (both female; age range: 19–20 years). Another eight participants (six women, two men; age range: 19–24 years, $SD = 1.64$) completed the b-CFS task, and threshold measurements were recorded for another six participants (two women, four men; age range: 19–30 years, $SD = 3.9$). All participants had normal or corrected-to-normal visual acuity. Participants also had normal stereovision, assessed using the Fly Stereo Acuity test. All experiments were performed with the approval of the institutional review board of the University of Sydney, and according to the principles of the Declaration of Helsinki. Informed

consent was obtained from all participants. Participants were reimbursed 20 AUD per hour for their participation.

Eye-dominance assessment

Eye dominance was assessed with the same test from Experiment 1.

Procedure for b-CFS

Targets were presented at a fixed contrast of 5% RMS, modulating at the same rate as the masker temporal frequency. The order of temporal frequency was blocked in a counterbalanced manner. Orientation was also randomized within each block, such that the difference in orientation between targets and maskers in a given trial was either 0° or 90°. This gave rise to a total of four conditions per eye: 2 Hz iso-oriented, 2 Hz cross-oriented, 10 Hz iso-oriented, and 10 Hz cross-oriented. Participants were asked to report, as accurately as possible, the location (which quadrant) and orientation (horizontal or vertical) of the target as soon as it became visible. As in Experiment 1, maskers and targets were ramped in contrast during the initial 1,000 ms of each trial, with the masker presented 50 ms (five frames) before the target. Local adaptation was also reduced by presenting each target in one of four quadrants, with its location randomly chosen from a circle with a radius of 1° around the fixation cross. After each response, 5 s of dynamic white noise was presented to both eyes and the time required for the target to reach visibility was recorded. Twenty trials were recorded for each condition, giving rise to 10 trials per eye and a total of 80 trials per participant. Accurate trials were sorted according to eye dominance, and durations longer than three times the median absolute deviation from the median were identified and removed from each condition. Suppression durations were then normalized to the average duration for each subject across all conditions.

Procedure for CFS threshold measurements

For each participant, masker temporal frequencies were presented in counterbalanced blocks, whereas target orientation and eye of origin were randomized within each block. The stimuli were presented on the screen for a total of 2,000 ms, immediately followed by 1,000 ms of dynamic visual white noise. Participants then judged the location of the target, which was presented in one of the four quadrants. The target contrast was varied with a 4AFC QUEST adaptive staircase procedure, and separate staircases were used for each eye and each orientation. These were interleaved within each block and consisted of 25 trials each.

Thresholds were estimated by fitting the resulting experimental data with a cumulative Gaussian psychometric function using the maximum-likelihood estimation procedure. As this was a 4AFC task, thresholds were defined as the level of RMS contrast at which accuracy was 62.5%. The estimated thresholds for each participant were then normalized to the participant's average threshold across all conditions (i.e., masker temporal frequency, eye of origin, and orientation).

Results

Normalized suppression durations

Prior to comparing the size of orientation effects between the 2- and 10-Hz maskers, we determined whether there were eye-dominance effects by conducting separate 2×5 repeated-measures ANOVAs (eye dominance $\times$ orientation) for each masker frequency. Orientation had a strong effect on normalized durations produced by 2- and 10-Hz maskers—$F(1, 9) = 30.2$, $p < 0.001$, $\eta_p^2 = 0.77$, and $F(1, 9) = 28.8$, $p < 0.001$, $\eta_p^2 = 0.76$, respectively. Performance of neither masker was affected by eye dominance—2 Hz: $F(1, 9) = 1.56$, $p = 0.24$, $\eta_p^2 = 0.15$; 10 Hz: $F(1, 9) < 1$. Similarly, the effect of orientation was not dependent on eye dominance—2 Hz: $F(1, 9) = 1.50$, $p = 0.25$, $\eta_p^2 = 0.14$; 10 Hz: $F(1, 9) < 1$.

Having established that there was no effect of eye dominance, we pooled across both eyes and processed raw suppression-duration data with the same exclusion criteria (i.e., accurate trial, no more than three times the median absolute deviation). We then conducted a 2×2 (masker temporal frequency $\times$ orientation) repeated-measures ANOVA. The results are plotted in Figure 3a. There were significant main effects of masker temporal frequency, $F(1, 9) = 9.91$, $p < 0.05$, $\eta_p^2 = 0.52$, and target orientation, $F(1, 9) = 53.86$, $p < 0.0001$, $\eta_p^2 = 0.86$. These factors interacted significantly, $F(1, 9) = 8.08$, $p < 0.05$, $\eta_p^2 = 0.47$, and we examined this interaction more closely with Holm–Bonferroni-corrected paired-samples t tests. In general, iso-oriented target–masker combinations produced significantly longer normalized durations—2 Hz: $t(9) = 5.24$, $p < 0.01$; 10 Hz: $t(9) = 5.32$, $p < 0.01$. As shown in Figure 3b, this difference was significantly larger for the 2-Hz masker, $t(9) = 2.84$, $p < 0.05$, and was driven by the significantly longer durations for the 2-Hz iso-orientation condition, $t(9) = 3.01$, $p < 0.05$.

Normalized contrast thresholds

To examine the effect of eye dominance, the data were first analyzed with separate 2×2 repeated-measures ANOVAs (eye dominance $\times$ orientation) for each masker temporal frequency. Similar to Experiment 1, eye
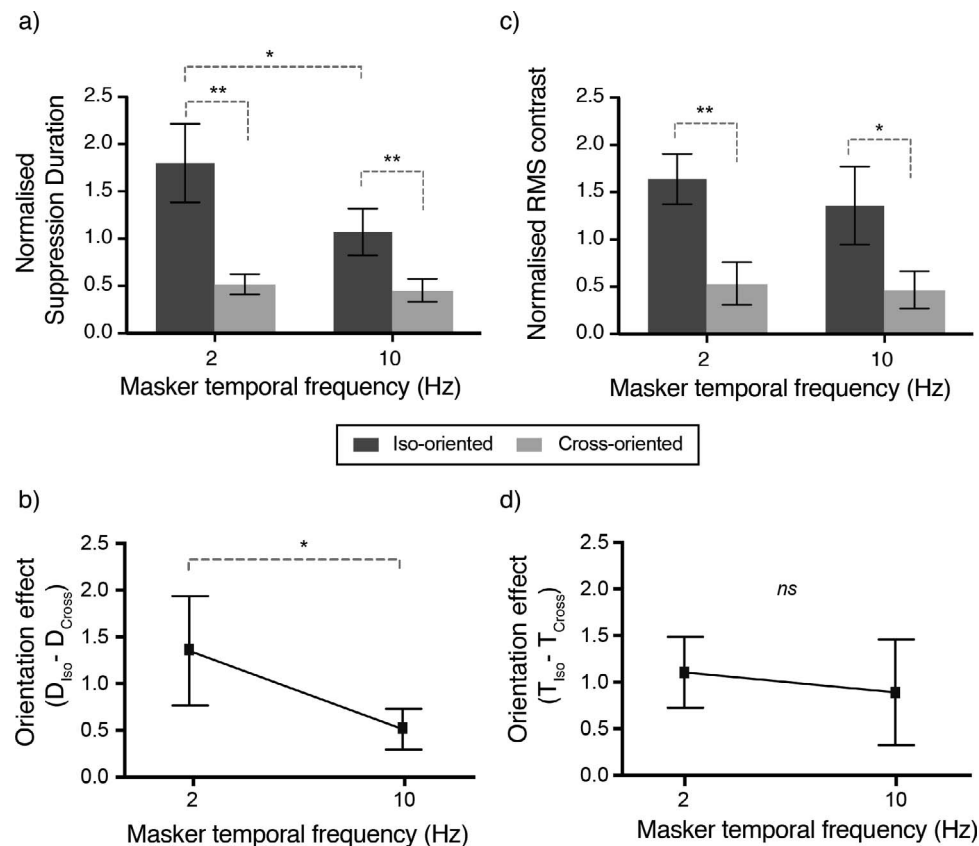
Figure 3. (a) Data from Experiment 2 showing the effect of orientation and masker rates on target suppression durations. Suppressed targets were narrowband spatially filtered noise temporally modulating at either 2 or 10 Hz and were orientationally filtered to have the same or orthogonal orientation as the masker (i.e., iso-oriented and cross-oriented). Iso-oriented targets remained suppressed for longer durations, and this increase was larger with the 2-Hz masker than the 10-Hz masker. (b) Data from the same experiment showing the effect of masker rates on the size of orientation effects in normalized durations. Changes in normalized durations were larger for the 2-Hz masker compared to the 10-Hz masker, demonstrating a stronger orientation selectivity in the 2-Hz maskers. (c) Data from the same experiment showing the effect of orientation and masker rates on target contrast sensitivity thresholds. Similar to target suppression durations, thresholds were raised when the target and masker shared the same orientation, and this was true regardless of masker temporal frequency. However, we do not observe the same suppressive advantage in the 2-Hz iso-orientation condition. (d) Data from the same experiment showing the effect of masker rates on the size of orientation effects in normalized thresholds. Unlike suppression durations, orientation had a comparable effect on normalized thresholds for 2- and 10-Hz maskers. Asterisks denote statistical significance after Holm–Bonferroni-corrected paired-samples t tests (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$), and all error bars represent 95% confidence intervals.

dominance did not influence thresholds—2 Hz: $F(1, 7) < 1$; 10 Hz: $F(1, 7) = 1.2$, $p = 0.31$, $\eta_p^2 = 0.15$—nor interact significantly with orientation at either frequency—2 Hz: $F(1, 7) < 1$; 10 Hz: $F(1, 7) = 2.08$, $p = 0.19$, $\eta_p^2 = 0.23$. In contrast, orientation strongly affected thresholds—2 Hz: $F(1, 7) = 47.4$, $p < 0.001$, $\eta_p^2 = 0.87$; 10 Hz: $F(1, 7) = 13.8$, $p < 0.01$, $\eta_p^2 = 0.66$. The data were therefore collapsed across both eyes and analyzed in a 2×2 repeated-measures ANOVA, with masker frequency and orientation as independent variables. The results are summarized in Figure 3c. Holm–Bonferroni-corrected paired-samples t tests were also conducted to evaluate the results of the ANOVA. Similar to the b-CFS results, there was a strong effect of orientation, $F(1, 7) = 36$, $p < 0.001$, $\eta_p^2 = 0.84$. There was, however, no effect of masker frequency, $F(1,$

$7) = 1.75$, $p = 0.23$, $\eta_p^2 = 0.20$, and no significant interaction between masker frequency and orientation, $F(1, 7) < 1$. As with suppression durations, we found significantly higher thresholds for the 2- and 10-Hz iso-orientation conditions—$t(7) = 6.89$, $p < 0.001$, and $t(7) = 3.71$, $p < 0.05$, respectively. However, there was no significant difference between the change in normalized thresholds for 2 and 10 Hz, $t(7) = 0.91$, $p = 0.40$.

General discussion

Despite the widespread use of CFS in studies of unconscious processing and awareness, work elucidating its underlying mechanisms is still incomplete. For

example, faster masker refresh rates have generally been associated with greater interocular suppression (e.g., Xu et al., 2011), but recent studies show that this view is simplistic. Prolonged, static target presentations are more effectively suppressed by slower Mondrian update rates, for example, ~6 Hz (Zhu et al., 2015), whereas rates up to 28.5 Hz are required for brief target presentation times (Kaunitz et al., 2014). The disparity in trends could be attributed to temporal-frequency selectivity, as the Mondrian masker contains more low-frequency energy at slow refresh rates and more high-frequency energy at faster update rates (Figure 1a). To test this idea, we presented a range of combinations of target and masker temporal frequency (i.e., 2- and 10-Hz maskers; targets at 2, 3, 5, 7.5, and 10 Hz). Two dependent measures were recorded—suppression duration and target contrast thresholds—as this allowed us to verify results obtained with the b-CFS paradigm. Since the b-CFS paradigm relies on subjective reports of visibility, measuring contrast thresholds provides a second, more objective dependent measure that allows us to rule out nonperceptual effects such as differences in participant criteria (Yang et al., 2014).

Consistent with our hypothesis, Experiment 1 showed that suppression in CFS is temporal-frequency selective. Normalized durations and thresholds increased as the difference between target and masker temporal frequencies decreased, regardless of masker frequency. Gaussian approximations of the tuning functions also revealed that, apart from differences in estimated mean frequency, no significant differences in the estimated amplitudes and bandwidth were obtained for either dependent measure. In Experiment 2, clear increases were obtained in both dependent measures when iso-oriented targets and maskers were presented, regardless of masker frequency. We also compared the sizes of orientation effects between the 2- and 10-Hz maskers, and found a significantly larger orientation effect with the 2-Hz masker when suppression durations were recorded, although this effect was not replicated with contrast thresholds. Presenting the masker in the dominant eye has been shown to produce greater interocular suppression (Yang, Blake, & McDonald, 2010), but this was not observed in our study. No significant effect of eye dominance was obtained, regardless of dependent measure. This might be related to the use of sighting dominance as an eye-dominance assessment, as the current evidence linking sighting dominance and interocular suppression is mixed (Bosten et al., 2015; Dieter, Sy, & Blake, 2017). Nevertheless, the results did consistently reveal strong selectivity for orientation and temporal frequency in both dependent measures, suggesting that any effect of eye dominance would not have resulted in a drastic change in trend.

We discuss the implications of the findings as follows. First, the b-CFS paradigm is often criticized for its susceptibility to nonperceptual effects such as participant decisional criteria (Yang et al., 2014). To account for these influences, a control where the target stimulus is presented in the masking eye is typically included and compared with the CFS condition (e.g., Jiang, Costello, & He, 2007). Unfortunately, this comparison has been shown to be inappropriate (Stein, Hebart, & Sterzer, 2011), leading to the proposal that b-CFS observations are better interpreted as evidence for differences in mere stimulus detectability (Stein & Sterzer, 2014). Similar trends between suppression durations and contrast thresholds were obtained in this study, suggesting that normalized duration could provide an excellent proxy for the more objective measure of contrast elevation. One exception was the size of orientation effects for the 2- and 10-Hz conditions; the suppression-duration data revealed a significantly larger effect of orientation in the 2-Hz condition, but this was not replicated with contrast thresholds. We do not have a firm understanding of this result, though given the inconsistent results and variability in the data (Figure 3b through 3d), it might be driven by differences in stimulus detectability and participant decisional criteria in the b-CFS task. The longer exposure period in b-CFS might also have a stronger adaptation effect on the 10-Hz masker (see Solomon, Peirce, Dhruv, & Lennie, 2004), thereby weakening its orientation effect. Note that these results contrast with those of Cass and Alais (2006), who observed clear asymmetric inhibition of low frequencies and cross-oriented masking by high temporal frequencies. Obtaining these differences might be dependent on the type of visual presentation, as Cass and Alais (2006) used binocularly viewed maskers and targets.

Second, by demonstrating that the suppression of temporal information is frequency selective and sensitive to orientation, we extend the work of previous CFS studies (Moors et al., 2014; Yang & Blake, 2012), contributing to an emerging theme that CFS suppression may be inherently feature specific. Contradictory evidence does exist in the literature, but our view is that in the absence of spatiotemporal control with narrow-band stimuli, it is difficult to determine the extent to which feature selectivity influences CFS suppression. For example, Ananyev et al. (2017) found that regardless of target speed, slow-moving Mondrian patterns (1°/s–2°/s) were most effective in suppressing a moving circular disk. Barring more complicated processes, basic spatiotemporal attributes of the stimuli could offer an explanation. As both the target and the masker patterns were composed of shapes with sharp spatial edges and uniform luminance, the spatial profiles would be broadband and $1/f^n$. Mathematically, temporal frequency is the product of spatial frequency

and velocity, meaning that the stimuli would be biased toward low temporal frequencies. It therefore seems probable that the low-pass tuning observed in the study by Ananyev et al. might be a consequence of temporal-frequency selectivity. Such specificity is reminiscent of early visual cortical regions such as V1, where neurons exhibit narrow tuning functions to stimulus dimensions such as orientation, spatial frequency, and temporal frequency. Indeed, studies interested in the neural substrates of CFS suppression have implicated early visual areas (Maier et al., 2008; Watanabe et al., 2011; Yuval-Greenberg & Heeger, 2013). Robust activity reduction in higher visual areas has also been reported (Fang & He, 2005; Hesselmann & Malach, 2011; Jiang & He, 2006), and it is possible that the use of spatiotemporally controlled stimuli like the ones used in the current study might shed some light on how these areas influence each other during CFS suppression.

Third, temporal-frequency selectivity could offer possible explanations for phenomena such as stimulus fractionation in CFS (Moors, Hesselmann, Wagemans, & van Ee, 2017; Zadbood, Lee, & Blake, 2011). Bearing resemblance to independent form- and motion-suppressive processes in rivalry (Alais & Parker, 2006), CFS suppression was reportedly more effective on the form of the target than its temporal information. Visibility of temporal modulations increases with temporal rate but not target form, which remained suppressed (Zadbood et al., 2011). Since the Mondrian masker is biased toward low frequencies (Figure 1), temporally selective processes cannot exert substantial suppression on higher target frequencies. This is important, as it explains the increased dissociation between form and temporal information at higher target-modulation rates. Similarly, the low temporal dominance of the Mondrian masker could explain the preservation of dorsal-stream activity in CFS (Fang & He, 2005). Low temporal frequencies are more likely to elicit parvocellular responses (Derrington & Lennie, 1984) that feed into the ventral stream (Merigan & Maunsell, 1993). As a result, dorsal activity that is elicited by target attributes such as high temporal frequencies (Derrington & Lennie, 1984; Merigan & Maunsell, 1993) and elongated shapes (Sakuraba, Sakai, Yamanaka, Yokosawa, & Hirayama, 2009) is inevitably spared. As pointed out by Ludwig and Hesselmann (2015), differences in the extent of dorsal preservation (see Fogelson, Kohler, Miller, Granger, & Tse, 2014; Hesselmann & Malach, 2011) would then depend on the low-level characteristics of the target and masker presented and the method of presentation used.

Last, our findings can be distinguished from those of Alais and Parker (2012), who used spatiotemporally filtered stimuli similar to ours in a binocular-rivalry paradigm. Their competing stimuli were matched for size, contrast, spatial frequency, and orientation content, so that the only difference between them was temporal frequency, which was carefully manipulated. Rivalry alternations were only reliably reported when modulation rates differed by about two octaves (a fourfold difference), proving that interocular suppression can arise from temporal-frequency differences alone. This result differs from the temporally selective suppression observed in the present CFS study, but so too do the stimulus conditions. Here, spatially similar stimuli differ interocularly in size and contrast, whereas in the rivalry example only the temporal frequency differed (without which the images would fuse). Therefore, the two studies and their conclusions are not directly comparable. However, because rivalry and CFS paradigms both involve interocular suppression, we speculate that differences between the two studies may be related to the size disparity between masker and target in CFS. It is known in binocular rivalry that surrounding one rival image with a spatially similar annulus (e.g., same orientation) enhances suppression of the competing image—regardless of which eye receives the surround (Paffen, Alais, & Verstraten, 2006)—and thus the use of the large maskers and spatially similar targets in our study may contribute additional suppression in CFS.

The feature-selective nature of CFS suppression has very important consequences. In particular, care should be taken when pairing targets and maskers to ensure that their stimulus properties overlap, to make sure the stimulus attributes of the target are appropriately suppressed by the masker. Spatiotemporally controlled stimuli like the ones we have used here and elsewhere (Han et al., 2016) afford a high degree of stimulus control so that targets and maskers can be well matched. This is difficult with the commonly used dynamic Mondrian masker, as its amplitude spectrum, both temporally and spatially, is pink—that is, low frequencies dominate and high frequencies are only weakly present (Han et al., 2016; Yang & Blake, 2012). This means that there is the potential for some target attributes to escape interocular suppression, and this may lead to misleading reports of targets being processed in the absence of awareness. Our view is that careful matching of masker and target properties is very important in CFS research, both for elucidating the specific underlying mechanisms and for providing a more rigorous test for claims of processing without awareness.

Conclusions

This study mapped the temporal tuning of CFS suppression with temporally narrowband maskers and targets and found strong evidence of feature selectivity

for temporal frequency. Two dependent measures, target suppression duration and target contrast threshold, both increased as the temporal-frequency difference between target and masker decreased. This pattern held for low- and high-frequency maskers, with consistent patterns for both measures showing that the two dependent variables are highly correlated. These findings add to evidence demonstrating feature selectivity in both binocular rivalry and CFS (Maehara et al., 2009; Moors et al., 2014; Yang & Blake, 2012) and suggest that a single model of interocular suppression could explain both paradigms. Finally, feature specificity has important implications for choosing CFS stimuli, as poorly matched maskers and targets may lead to particular target attributes escaping significant suppression and leading to spurious claims of processing without awareness.

Keywords: continuous flash suppression, binocular rivalry, feature selectivity, temporal frequency

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