Depth of interocular suppression associated with continuous flash suppression, flash suppression, and binocular rivalry

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When conflicting images are presented to the corresponding regions of the two eyes, only one image may be consciously perceived. In binocular rivalry (BR), two images alternate in phenomenal visibility; even a salient image is eventually suppressed by an image of low saliency. Recently, N. Tsuchiya and C. Koch (2005) reported a technique called continuous flash suppression (CFS), extending the suppression duration more than 10-fold. Here, we investigated the depth of this prolonged form of interocular suppression as well as conventional BR and flash suppression (FS) using a probe detection task. Compared to monocular viewing condition, CFS elevated detection thresholds more than 20-fold, whereas BR did so by 3-fold. In subsequent experiments, we dissected CFS into several components. By manipulating the number and timing of flashes with respect to the probe, we found that the stronger suppression in CFS is not due to summation between BR and FS but is caused by the summation of the suppression due to multiple flashes. Our results support the view that CFS is not a stronger version of BR but is due to the accumulated suppressive effects of multiple flashes.

Keywords: binocular rivalry, flash suppression, continuous flash suppression, interocular, depth of suppression, contrast sensitivity, awareness, consciousness

Introduction

The search for neural concomitants of conscious visual awareness has become a central theme in contemporary cognitive neuroscience (Koch, 2004). Among the arsenal of tools available for implementing this search is binocular rivalry (BR), the alternation in visual awareness between two dissimilar stimuli imaged on corresponding regions of the two eyes (Blake & Logothetis, 2002). Rivalry entails a beguiling dissociation between physical stimulation and visual perception, and the occurrence of rivalry implies the existence of fluctuating patterns of neural activity producing these alternations in perceptual dominance between one stimulus and the other. Inspired by this implication, a number of investigators have attempted to use rivalry to identify stages in visual processing at which neural activity is correlated with fluctuations in perceptual state (Haynes, Deichmann, & Rees, 2005; Haynes & Rees, 2005; Leopold & Logothetis, 1996; Logothetis & Schall, 1989; Lumer, Friston, & Rees, 1998; Lumer & Rees, 1999; Polonsky, Blake, Braun, & Heeger, 2000; Sheinberg & Logothetis, 1997; Tong & Engel, 2001; Tong, Nakayama, Vaughan, & Kanwisher, 1998; Wunderlich, Schneider, & Kastner, 2005).

As a tool for exploring neural concomitants of awareness, however, rivalry has some limitations (Kim & Blake, 2005). For one thing, the periods of perceptual dominance typically last only a few seconds, meaning that a given stimulus remains suppressed for a relatively short period of time (Levelt, 1965). It is true that suppression durations in rivalry can be lengthened somewhat by varying the relative strengths of the two competing monocular stimuli (Fox & Rasche, 1969) or by explicitly directing attention to the dominant stimulus (Chong & Blake, 2006; Helmholtz, 1924; Meng & Tong, 2004). Still, it is impossible to predict when switches in dominance will occur because the individual durations of dominance and suppression vary randomly from period to period (Fox & Herrmann, 1967). For this reason, it is challenging to extract deterministic, causal events from ever-changing stochastic perceptual states.

Some of these limitations of BR can be overcome, however, using any one of several other interocular suppression

techniques. One such technique, called flash suppression (FS), has proven useful for reliably establishing the initial perceptual dominance of one stimulus for a short period of time (Wolfe, 1984). In FS, the to-be-suppressed stimulus is first presented to one eye (the other eye is temporarily unstimulated), followed shortly thereafter by the abrupt presentation of a rival stimulus to the other eye. With this sequence of events, the most recently presented stimulus typically achieves immediate dominance, with the first stimulus being suppressed from vision (FS differs from dichoptic backward masking (Breitmeyer, 1984) in that, with FS, the two rival stimuli remain on for an extended duration and are not briefly flashed as they are with conventional masking). This procedure effectively eliminates uncertainty about the dominance of a given stimulus for the first several seconds following onset of dichoptic stimulation. On the downside, however, FS has no control over the subsequent dynamics of rivalry, which remain stochastic (Blake, Westendorf, & Fox, 1990). The randomness of rivalry can be minimized using a new technique called continuous flash suppression (CFS), which combines the potency of BR and FS (Tsuchiya & Koch, 2005). With CFS, a series of different, contour-rich patterns is continuously flashed to one eye at a steady rate of ∼10 Hz. With this dynamic, complex stimulus presented to one eye, a highly salient image (e.g., the picture of an angry face) presented to the other eye may be reliably suppressed throughout an entire viewing period, sometimes longer than 3 min. Other studies also exploited the combination of FS and BR and/or use of dynamic stimuli to extend otherwise brief dominance periods (Gilroy & Blake, 2005; Moradi, Koch, & Shimojo, 2005; Pasley, Mayes, & Schultz, 2004). The CFS technique, which virtually eliminates the uncertainty about changes in perceptual state, has been used to study the ability of a suppressed stimulus to generate high-level visual aftereffects (Moradi et al., 2005) as well as low-level visual afterimages (Gilroy & Blake, 2005; Tsuchiya & Koch, 2005). As well, the technique has been used to demonstrate that ordinarily salient, erotic pictures can direct visual attention to a given location in the visual field even when those pictures are erased from visual awareness by CFS (Jiang, Fang, Huang, & He, 2005). In addition, CFS has been used in brain imaging studies to identify brain regions that respond to visual stimuli falling outside of conscious awareness (Fang & He, 2005; Pasley et al., 2004).

But how do these various techniques for inducing interocular suppression—BR, FS, and CFS—relate to one another? Tsuchiya and Koch (2005) reckoned that CFS is not simply a stronger version of BR but rather represents a continuous version of FS (hence the term CFS). Their conclusion was based on two properties of CFS. First, the total dominance duration of CFS is critically dependent on the flash rate, reaching its peak at ∼3–10 Hz, resembling in this respect the effectiveness of FS as a function of pre-adaptation (Wilke, Logothetis, & Leopold, 2003; Wolfe,

1984). Second, the observed increase of the total dominance time is accompanied by an *increase* of the mean dominance period of the dominant stimulus and not by a *decrease* in the mean dominance period of the suppressed figure. This latter observation stands in contrast to the behavior of dominance and suppression durations in BR (Fox & Rasche, 1969; Levelt, 1965). These two properties were explained by a phenomenal model which asserted CFS as an accumulation of FS (Tsuchiya & Koch, 2005).

Tsuchiya and Koch (2005) characterized the durations of phenomenal suppression in CFS by instructing observers to indicate, via key press, which one of two competing stimuli was currently visible. Although this tracking procedure adequately documents the dynamics of CFS, it does not provide a quantitative index of the strength of CFS. For that purpose, measures of sensitivity, such as detection thresholds obtained by an objective forced-choice procedure, are superior. Toward that end, we have investigated the inhibitory nature of CFS by characterizing the "depth of suppression" using a probe detection task, which has been extensively employed in BR (Blake & Camisa, 1979; Fox & Check, 1972; Nguyen, Freeman, & Alais, 2003; Nguyen, Freeman, & Wenderoth, 2001; Norman, Norman, & Bilotta, 2000; Ooi & Loop, 1994; Wales & Fox, 1970; Watanabe, Paik, & Blake, 2004). With this technique, a monocular probe target is briefly superimposed on a rival stimulus while that stimulus is dominant and, on other trials, while it is suppressed (probe presentations are triggered contingent on the observer's reported perceptual states of rivalry); following each presentation, observers make a psychophysical judgment, typically forced-choice, about some aspect of the probe target. Results consistently show that probe thresholds are elevated approximately 0.50 $\log_{10}$-units during suppression phases compared to dominance; dominance thresholds are equivalent to those measured during nonrivalry, monocular viewing. The depth of suppression, indexed by threshold elevation, remains constant even when suppressing stimuli are made "stronger" (i.e., higher luminance or higher contrast) (Blake & Camisa, 1979; Hollins & Bailey, 1981), and the depth of suppression remains constant throughout an individual suppression phase (Fox & Check, 1972; Norman et al., 2000). For FS, the depth of suppression in chromatic channels is different from that for BR (Ooi & Loop, 1994). Other than that, the depth of suppression in FS has not been characterized with regard to the depth of suppression in BR.

We here demonstrate that the depth of CFS is much deeper than that of BR. Furthermore, we show that the depth of a single episode of FS critically depends on the timing of the flash relative to the onset of probe. Interestingly, the occurrence of peak suppression is not altered even when FS is combined with BR. A final experiment reveals that multiple flashes synergistically summate to yield suppression equivalent to that measured using CFS. Based on these results, we conclude that CFS is a "continuous" version of FS.

Experiment 1: Depth of CFS

Methods

Two of the authors (NT, LG) and two naive but experienced observers gave informed consent to participate in the experiments. One of the naive observers participated only in Experiments 1 and 3. All had normal or corrected to normal eyesight, and all had normal stereo vision. All experiments were performed with the approval of the Institutional Review Board, Vanderbilt University.

The observer viewed grayscale, dichoptic images on a video monitor through a mirror stereoscope in an otherwise dark room. The viewing distance from the eyes to the display was 92 cm. To stabilize fixation, we employed a head and a chin rest. All displays and trial-related events were controlled using Matlab 5.2.1 and the Psychophysics Toolbox (Brainard, 1997) running under Mac OS 9.2.2. The monitor (100 Hz refresh rate) was calibrated using a color-bit stealing technique that provided an effective resolution of 10 bits after linearization (Tyler, 1997).

To compare results obtained using CFS with those measured using BR, we used rather small stimuli (1.6° × 1.6°) to facilitate exclusive dominance (Blake, O'Shea, & Mueller, 1992). Forty different Mondrian patterns, consisting of many random-sized squares of white (58 cd/m^2), gray (29 cd/m^2), and black were created before each block. A red fixation cross and a black/white checkered border surrounding the square rival targets promoted stable binocular fusion (Figure 1a).

The observer initiated each trial by pressing a button. In CFS, a 10-Hz stream of Mondrian patterns was presented to one eye, and a horizontal sinusoidal grating of 10% contrast and 1.8 cpd was presented to the other eye (Figure 1a). After insuring that no part of the grating was visible, the observer pressed a button that increased the luminance contrast of either the upper or the lower half of the grating (which from here on we shall refer to as the background grating). The first frame of this increment was synchronized with the nearest Mondrian flash. The phase of the background grating was 0° at the horizontal center to avoid an artifactual edge. The luminance contrast was smoothly varied (Gaussian onset/offset with a standard deviation of 100 ms; see Figure 1a) for an extent of 500 ms to avoid abrupt onset/offset transients. Immediately following the offset of this contrast increment probe, a brief sound alerted the observer to press one of two computer keys to report which half of the background grating—upper vs. lower—contained the contrast increment (2-AFC). CFS and the background grating remained present until the observer responded; error feedback was not provided. After two consecutive correct responses, the magnitude of the contrast increment was reduced by 30% of the current increment, and after each error it was increased by 30% (a two-down-one-up staircase strategy converging to 71% correct performance; Levitt, 1971). After four reversals, the contrast
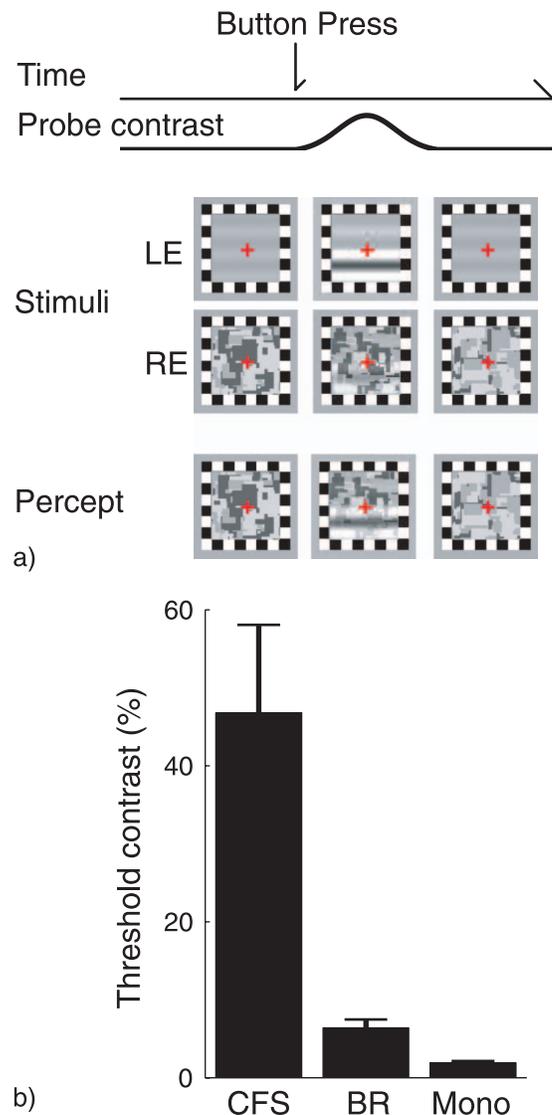

Figure 1. Depth of suppression in CFS. (a) Physical stimuli to the two eyes (upper two rows) and typical percept (lower row) for CFS. The observer viewed a constant 10% contrast grating (the "background") in one eye (in this example, left eye; LE) and a 10-Hz stream of black/white/grey Mondrians in the other eye (right eye; RE). Upon button press, either the upper or the lower half of the background grating increased its contrast gradually over 500 ms. The observer judged which field contained the probe (2-AFC). In BR, the stimulus to the other eye was a stationary Mondrian. In the monocular-viewing (Mono) condition, a blank field was presented to the unprobed eye and contrast increment started 500 ms after the button press. (b) Contrast increment thresholds (mean + *SEM*) for the three conditions for $n = 4$ observers.

adjustment was reduced to 15%. One block terminated after 12 reversals, and the threshold was estimated by taking the geometric mean of the contrast values of the last 10 reversals.

In BR, a single stationary Mondrian pattern was randomly chosen from 40 patterns for presentation on each trial. After

initiating a trial, the observer waited until the stationary Mondrian dominated perception completely, at which time the observer pressed a key that immediately triggered a contrast increment of the upper or lower half of the background grating. In the monocular-viewing condition, a blank field was presented to the eye that otherwise would have viewed the Mondrian. In this case, a contrast increment was induced 500 ms after the key press; until then the observer saw the 10% contrast background grating. Everything else was the same as during CFS.

During one block of the staircase, the same eye was used for probe detection, and the suppression protocol (monocular viewing, BR, or CFS) was held constant. Observer NT used one eye as the probe eye throughout; the other observers used both eyes in a balanced manner. Measurements were repeated two to six times for each condition.

Results and discussion

Figure 1b compares the depth of suppression for the three conditions. As expected, under nonrival, monocular viewing without suppression, the contrast increment threshold was very low (1.9 ± 0.2%, mean ± *SEM*). Measured during BR, the contrast increment threshold measured in the suppressed eye averaged 6.2 ± 0.9%, a value approximately 0.5 log-units higher than that measured under nonrivalry conditions. This modest but significant increase in threshold during suppression is consistent with previous results showing elevated thresholds during suppression phases of rivalry (Nguyen et al., 2001; Watanabe et al., 2004). Measured during CFS, increment thresholds averaged 44.7 ± 10.3%, a 1.4 log-unit increase in threshold relative to the nonrival, dominance condition. Obviously, CFS produces considerably deeper suppression than does BR, which dovetails with the potency of CFS to produce considerably longer durations of exclusive dominance compared to dominance durations produced by BR (Tsuchiya & Koch, 2005). The enhancement of the depth of suppression also argues against an idea that CFS is a stronger version of BR because the depth of BR suppression is constant regardless of the strength of suppressing figures (Blake & Camisa, 1979; Hollins & Bailey, 1981). The results presented here were obtained with a particular set of probe target values of spatial frequency and temporal onset/offset; in other experiments, we have replicated this pattern of results using lower spatial frequencies and more abrupt probe presentations (see Auxiliary Files).

Having demonstrated that CFS is not simply a version of BR suppression, we next performed several experiments in an attempt to dissect CFS into components using the probe technique. Starting with Experiment 2, we measured the depth of suppression produced by a single flash (like that associated with FS) as a function of the timing between the flash and the test probe used to index suppression depth, and we also assessed that flash's interaction with BR.

Experiment 2: Depth of single FS

In Experiment 2, we first decomposed CFS into a series of discrete, individual flashes. Our aim was to learn whether FS elevates the detection threshold more than does BR and, if so, how the magnitude of that elevation in threshold depends on the time between flash onset and probe onset. Previous studies of FS (Wilke et al., 2003; Wolfe, 1984) showed a tight relation between the effectiveness of perceptual suppression and flash timing, but those studies did not assess the relation between the depth of suppression and flash timing. Second, we asked if suppression following a single flash becomes stronger when BR suppression is already present. In other words, do the effects of FS and BR suppression combine to yield suppression in excess of that produced by FS or BR on their own?

Methods

Three observers from Experiment 1 participated in the experiment. The equipment, stimuli (Mondrians and probes), and the basic procedure used to estimate thresholds (2-AFC and staircase) were identical to those used in Experiment 1.

For flash suppression (FS-only), the observer initiated a trial by pressing a button, which triggered a baseline dichoptic display for 500 ms, consisting of a fusion frame with a blank interior presented to one eye and the 10% contrast, background grating within the fusion frame viewed by the other eye. The blank field was replaced by a single Mondrian pattern (not rapid, successive exposures) at time T_M, and this single pattern remained present until the trial was terminated by the observer's response. A 500-ms contrast increment probe was superimposed on either the top- or the bottom-half of the background grating starting from time T_C. Across blocks, we varied the stimulus onset asynchrony (SOA) between the onset of the probe and the onset of the Mondrian (SOA = $T_C - T_M$). For negative SOA values (SOA < 0: Mondrian flash preceded the probe), the actual sequence of events on a trial was (1) button press by the observer that triggered presentation of the background grating for 500 ms, (2) replacement of the blank field by the Mondrian pattern at T_M, then (3) presentation of the contrast increment probe. For nonnegative SOA values (SOA ≥ 0), the order of events 2 and 3 was reversed; that is, the probe preceded presentation of the Mondrian or the two were coincident in time.

For the FS plus BR condition, the observer initially viewed a stationary Mondrian with one eye and the background grating with the other, that is, dichoptic stimulation producing the conventional BR. When the stationary Mondrian was exclusively dominant in rivalry, the observer pressed a button which triggered the FS sequence. For SOA < 0, the Mondrian pattern was replaced shortly before the contrast probe. For SOA > 0, the contrast probe occurred shortly

before the Mondrian was replaced. For SOA = 0, the contrast probe was coincident with replacement of the Mondrian. For each condition, the observer judged whether the probe appeared in the upper or the lower half of the background grating. For each trial, Mondrian patterns were chosen randomly from the 40 patterns created before each block of trials.

Results and discussion

Using a paradigm similar to that used in Experiment 1, we characterized the depth of single FS by measuring contrast increment thresholds while manipulating the SOA between the onset of a probe and a Mondrian flash. SOA ranged from −1000 to +500 ms, where negative SOA values imply that the Mondrian flash occurred before the probe. Filled triangles in Figure 2 show the thresholds for the single flash suppression (FS-only) condition (error bars are SEM). Single FS elevated probe thresholds only within a narrow time window, with the peak threshold elevation occurring at SOA = 100 ms. Relative to the monocular condition, thresholds measured using the single FS procedure were elevated 0.8 log-units, a depth of suppression index considerably smaller than that associated with CFS (which yielded a 1.26 log-unit increase for these three observers in Experiment 1) but considerably larger than that associated with BR (0.46 log-unit elevation for these three observers). The contrast of the probe was modulated in a Gaussian manner with its peak at SOA = 250 ms. In other words, a single flash suppressed the probe most strongly when it was presented to the other eye 150 ms before the contrast of the probe became maximal. For SOA longer than 150 ms, the effect of single flash diminished dramatically, and with SOA > 300 ms, its effect was nil (i.e., probe sensitivity was equivalent to that measured for monocular-viewing condition). For SOA < −100 ms, the effects were comparable to that of BR in Experiment 1 (thick broken line and empty circle).

Next consider probe thresholds measured when FS is paired with BR (filled circles in Figure 2). Over much of the range of SOA values, probe thresholds for FS + BR are no more elevated than they are for the FS condition alone. The notable exception is when SOA exceeds 100 ms, at which point the combination of BR and FS produce threshold elevation in excess of that produced by either procedure alone. Even within this regime where the two interact, their summed effect is less than that predicted based on linear summation of the two inhibitor effects (predicted elevation is 1.28 log-units; measured elevation is 0.82 log-units).

One interpretation is that FS may be a combination of transient inhibition, which exerts its action within a narrow time window, and BR suppression, which is sustained and constant throughout a suppression phase (Fox & Check, 1972; Norman et al., 2000). In particular, Norman et al. showed that the depth of suppression quickly reaches at
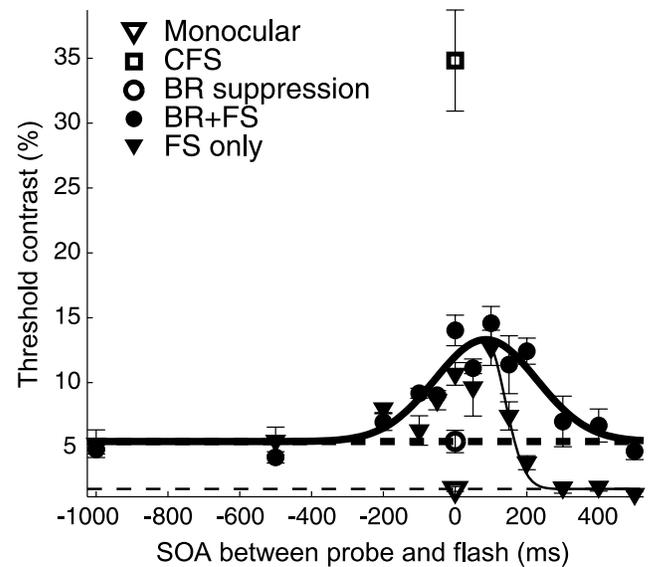

Figure 2. Does a single FS summate with rivalry suppression? Contrast increment thresholds as a function of SOA between the onset of the probe and the Mondrian flash. For comparison, the results in Experiment 1 are replotted here with empty symbols (monocular, CFS, and BR suppression). Filled symbols show the results in the single FS (FS-only, triangles) and the FS combined with BR suppression (FS + BR, circles) conditions, respectively (error bars are SEM). The solid curves were the least-square-fit Gaussian functions to the FS + BR (thick) and FS-only (thin) conditions, respectively. The dashed lines are the asymptotic values for the Gaussian, taken from the thresholds for the BR suppression (thick) and the monocular-viewing (thin) conditions, respectively. For SOA < 0, a Mondrian flash precedes the probe. For both the FS-only and FS + BR conditions, the peak suppression occurred around an SOA of 100 ms, where the thresholds were higher than BR but lower than CFS. The FS-only and the FS + BR conditions did not show a clear difference when SOA < 100 ms, but showed clear differences in tuning width when SOA > 150 ms; n = 3 observers.

maximal strength just after the onset of suppression (20 ms after the initiation of complete dominance) and remains constant up to 1000 ms after the onset of suppression. When SOA < −100 ms, the transient component may have already dissipated such that the measured thresholds reflect the sustained BR inhibition for both FS and BR conditions. When SOA is near +100 ms, the transient inhibition effectively coincides with the peak of probe contrast to elevate thresholds maximally. When SOA > 100 ms, in the FS-only condition, the transient inhibition does not elevate the threshold because the initial rise of the probe contrast is sufficient to signal its location. On the other hand, this initial rise is effectively masked by the moderate, sustained BR inhibition in the FS + BR condition, resulting in the observed broad temporal tuning curve. This would explain why the latencies to the peak of inhibition were comparable in both the FS-only and FS + BR conditions, with both

reflecting the latency for the transient FS-specific inhibition. Further, it would also explain why the amplitudes of the peak were comparable, with both mainly reflecting the effect of transient FS inhibition.

Inspection of Figure 2 reveals three notable characteristics. First, when a Mondrian flash occurred well in advance of the probe event (SOA < −100 ms), contrast increment thresholds were comparable to those measured for the BR condition (5.5%) alone. At SOA = 500 ms, the threshold was also similar to BR in the FS + BR condition. Second, the thresholds in the FS-only condition seem to agree well with those in the FS + BR condition for SOA < 100 ms. Third, for SOA > 150 ms, the thresholds for the FS-only condition dropped quickly to the thresholds in the monocular-viewing condition.

Considering these characteristics, we used a least squares method to fit two Gaussian curves to the data. For the FS + BR condition, we fitted the thresholds with a Gaussian function with an asymptote value being the threshold of the BR contrast increment threshold of Experiment 1:

$$y = a \times \exp\left(-\left(\frac{x-b}{c}\right)^2\right) + 5.5,$$

where y is the threshold, x is SOA, a is the peak threshold, b is the SOA at the peak, c is the width of the tuning, and 5.5% is the threshold in the BR condition. Using 13 points (the means of 3 observers), we obtained the best fit, shown as a thick line in Figure 2 (df = 10, a = 7.9%, b = 85.5 ms, c = 201.0 ms, and R^2 = .85). As the thresholds for the rising part in the FS-only condition (SOA < 50 ms) was well captured by such a Gaussian fit, we made no attempt to fit the data here. Next, we fitted the thresholds in the falling part of the FS-only condition (for SOA ≥ 50 ms) with a second Gaussian with an asymptote value defined by the monocular-viewing condition in Experiment 1, fixing a to 7.9% and b to 85.5 ms and changing the asymptote value to the monocular-viewing threshold (1.8%). We obtained the best fit for c to be 74.9 ms with R^2 = .97 (df = 6). Thus, when FS was combined with BR, the temporal tuning of suppression was broadened from 74.9 to 201.0 ms.

We draw three conclusions from this experiment. First, although much weaker than CFS, single FS impaired the probe detection more than did BR, but only within a narrow time window, peaking at SOA = 85.5 ms. This time dependency contrasts sharply with the constant depth of suppression characteristic of BR (Fox & Check, 1972; Norman et al., 2000), thereby providing further evidence that FS and BR involve different mechanisms for inhibition. Second, the maximal suppression for FS was not enhanced when combined with BR suppression, suggesting that the peak of the inhibition in both of the conditions mainly reflects the peak of transient FS inhibition. Third, threshold elevation in the FS-only condition dropped to the monocular-

viewing level with a tuning width of 74.9 ms, yet it synergistically interacted with BR suppression to broaden the temporal tuning curve (201.0 ms), leading to more profound suppression. These results suggest that the very robust depth of suppression accompanying CFS may arise from the cooperative inhibition among multiple flashes, a hypothesis we explore in our third experiment.

Experiment 3: How many flashes constitute CFS?

In Experiment 2, a single flash never elevated the thresholds by an amount approaching the depth of suppression measured using CFS. Further, we found that FS combined with BR suppression did not change the depth of suppression (although temporal tuning was altered). To account for the deep suppression in CFS (Experiment 1), we hypothesize that a single flash *cooperates* with neighboring flashes to enhance inhibition. In Experiment 3, we test this hypothesis by varying the number of flashes and the SOA between the onsets of the first flash and the probe. Although it is evident that many flashes must eventually amplify suppression cooperatively to produce CFS, it is difficult to predict exactly what happens for intermediate number of flashes.

When a target is inhibited by a first masker, a second masker can inhibit the first masker to recover the visibility of the target (*disinhibition*) (Breitmeyer, Rudd, & Dunn, 1981; Dember & Purcell, 1967; Robinson, 1966). In other cases, multiple maskers can enhance inhibition cooperatively (Macknik & Livingstone, 1998; Macknik & Martinez-Conde, 2004; Macknik, Martinez-Conde, & Haglund, 2000). Which effects are observed depends on the precise spatiotemporal arrangement of the stimuli. With that in mind, we investigated timing of a sequence of flashes comprising a short burst of CFS.

Methods

The same four observers tested in Experiment 1 participated in this experiment. The equipment, stimuli, and basic procedure were the same as those used for the FS-only condition in Experiment 2. The number of flashes was varied from one to five and, at the same time the SOA was varied between the onsets of the probe and the first Mondrian flash; across blocks, SOA values were varied from −200 to 200 ms according to a staircase procedure (Figure 3a).

The observer initiated a trial by a button press, which triggered a 500-ms presentation of 10% contrast background grating to one eye and a blank interior within the fusion border presented to the other eye. With an appropriate SOA (see Methods for Experiment 2), the probe and the first of
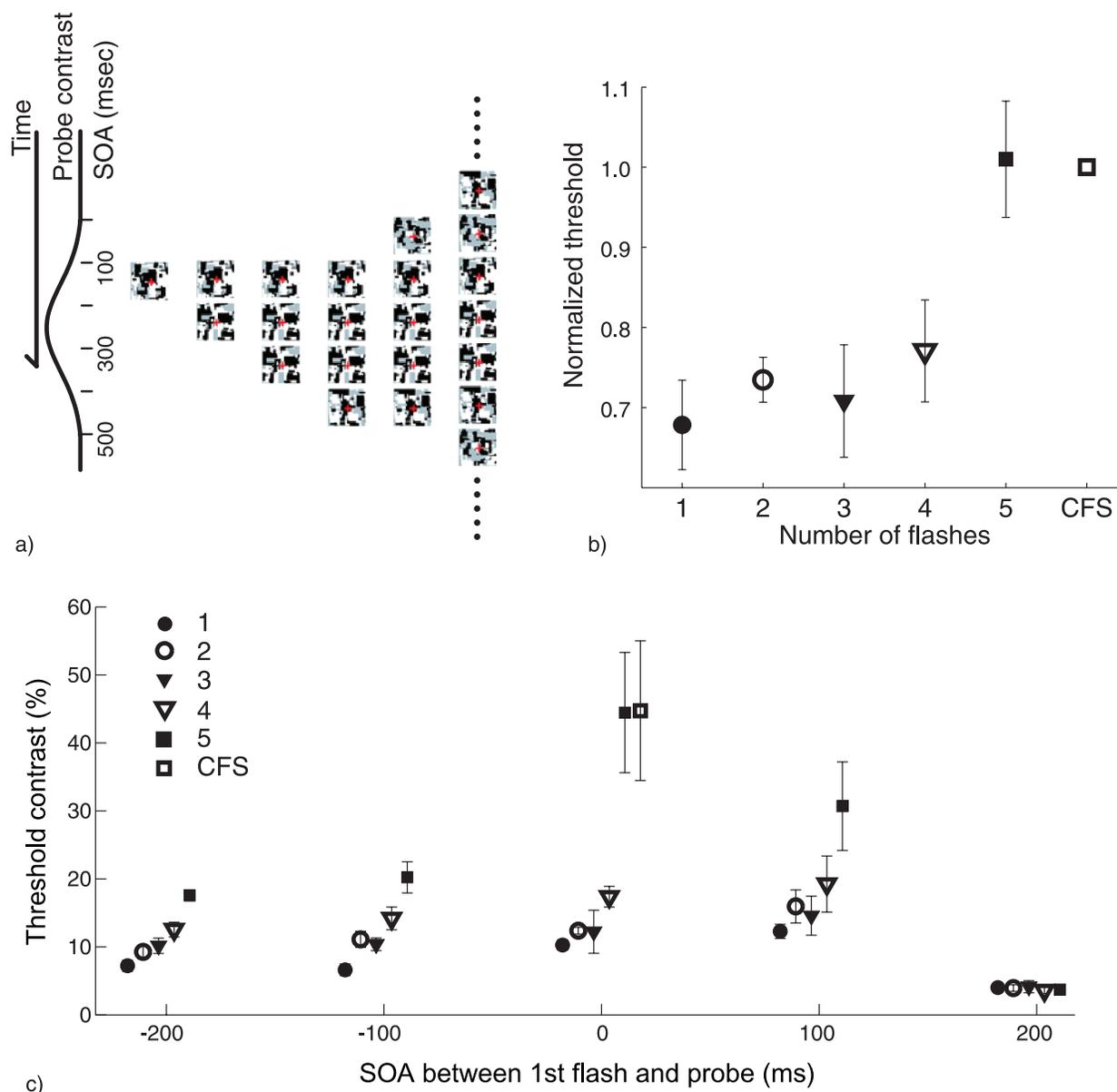
Figure 3. How many flashes are necessary to attain the depth of CFS? (a) Probe detection thresholds for multiple FS. Each flash is followed 100 ms later by another flash. The timing of the first flash was varied from −200 to +200 ms (in a vertical axis) relative to the onset of the probe (in the schematic figure here, vertical positions of the Mondrians indicate the timing of flashes). The contrast of the 500-ms probe was modulated in a Gaussian manner, with its peak at 250 ms. (b) Normalized thresholds as a function of the number of flashes (error bars for *SEM*). The highest thresholds among the five SOAs were log-transformed and divided by the thresholds for the CFS condition (for 1–4 flashes, the chosen SOA was +100 ms, and for 5 flashes it was 0 ms). The thresholds in the 5-FS were comparable to the CFS condition. Single FS did not differ much from 2-, 3-, and 4-FS. (c) Thresholds (mean ± *SEM*) as a function of all the tested SOAs (in a horizontal axis). Symbols: filled circles, 1 flash; empty circles, 2 flashes; filled triangles, 3 flashes; empty triangles, 4 flashes; filled triangles, 5 flashes; an empty square, CFS; *n* = 4 observers.

multiple Mondrian patterns were presented. Until the observer made a response, the last Mondrian pattern and the baseline grating remained on the display to avoid transients at the offset of the displays. Except for the last Mondrian pattern, each Mondrian pattern was replaced with another one every 100 ms (with no blank period between successive Mondrians).

Results and discussion

How many flashes are necessary to attain the depth of suppression associated with CFS? To answer this question, we computed the thresholds at the SOA that gave the strongest suppression for a specific number of flashes. The thresholds were then log-transformed (for equal variance)

and divided by the log-transformed threshold in CFS condition. Figure 3b shows the normalized thresholds as a function of the number of flashes. Notably, the threshold for the five-flash condition was comparable to the threshold for CFS (paired *t* test, *p* > .9). However, the thresholds for the conditions using two to four flashes were comparable in magnitude to those measured using a single flash (see also Figure 2), a depth of suppression considerably less than that associated with CFS. One-way ANOVA resulted in significant difference (*p* = .0103) among one to five flashes. After correcting for multiple comparisons with Tukey's honestly significant difference criterion, 5-FS was found to be significantly different from one to three flashes at *p* < .05.

Figure 3c plots all measured thresholds as a function of SOA. For SOA < 200 ms, the thresholds for the 5-FS (filled squares) were higher than those for the 4-FS (empty triangles), which in turn were higher than those for the rest of conditions. At SOA = 200 ms, thresholds for all conditions dropped below the level of the BR condition in Experiment 1. Thus, at least one flash must be presented no later than 200 ms after the onset of the probe for effective multiple FS to occur. The thresholds in the 5-FS condition were much higher at SOA = 0 ms. Such strong SOA dependency was not apparent in the conditions that involved one to four flashes.

Detailed examination of Figure 3c reveals that the threshold was 44.4 ± 8.8% for the 5-FS at SOA = 0 ms (1.37 log-unit elevation in threshold relative to monocular testing), very close to the threshold for the CFS condition (44.7%). Remarkably, the potency of a multiple flash sequence is substantially reduced simply by removing the first flash (four-flash, SOA = 100 ms) or the last flash (four-flash, SOA = 0 ms) from this five-flash sequence. Removal of one flash reduces threshold elevation from 1.37 log-units to approximately 1 log-unit. Moreover, adding one flash to the 4-FS at the "wrong" time also dampens the efficacy of a five-flash sequence; the thresholds were 20.2 ± 2.3% for 5 flashes at SOA = −100 ms and 30.7 ± 6.5% for 5 flashes starting at 100 ms. This kind of highly nonlinear interaction can be observed in other data points as well. For example, although the 3-FS starting at SOA = 200 ms did not elevate thresholds at all on their own (4.1 ± 0.9%), combined with the 2-FS starting at SOA = 0 ms, whose threshold was 9.3 ± 1.0%, they amounted to the strongest 5-FS.

The depth of suppression produced by CFS can be achieved when at least five flashes are presented in succession. As for intermediate number of flashes, they neither facilitated suppression nor disinhibited the suppressed target (Breitmeyer et al., 1981; Dember & Purcell, 1967; Robinson, 1966). It is possible that each additional flash acts as a masker for the immediately following or preceding flash, canceling its suppressive effect. Why, then, does the inhibition become suddenly strong when there are five flashes? One possibility is that disinhibition may be strong only for the flash at the onset or the offset of a set of multiple flashes, that is, the first or last flash. When there are

five flashes, disinhibition from the first or last flash may not be able to disinhibit the third flash, resulting in strong threshold elevation (Macknik & Livingstone, 1998; Macknik & Martinez-Conde, 2004; Macknik et al., 2000).

General discussion

We used a probe detection paradigm to compare the depth of suppression associated with three, procedurally distinct, techniques for producing interocular suppression. Although all three can effectively abolish perceptual awareness of a stimulus, our results clearly show that CSF, FS, and BR yield different magnitudes of suppression, ranging from the modest suppression depth associated with BR (0.5 log-units) through the intermediate depth of suppression found with FS (0.8 log-units) to the deep suppression produced by CFS (1.4 log-units). Particularly paradoxical is the pronounced difference in suppression strength between CFS and BR, both procedures capable of producing the same phenomenological state: invisibility of a normally visible stimulus. It is true, however, that invisibility durations produced by CFS can last an order of magnitude longer than invisibility durations characteristic of BR suppression. We imagine that the enduring effectiveness of CFS arises from its relative immunity to adaptation owing to the repeated presentation of a new stimulus. With BR, in contrast, the dominant stimulus remains constant and therefore more susceptible to the weakening effect of adaptation. Indeed, neural adaptation is a standard component in contemporary models of rivalry (Laing & Chow, 2002; Lankheet, 2006; Wilson, 2003).

But why is the depth of suppression so much greater with CFS compared to BR? One possibility is that distinct neuronal mechanisms underlie CFS and BR, mechanisms incorporating different inhibitory circuits. This possibility is not far-fetched, for we know that monoptic and dichoptic masking are mediated by different neuronal circuits (Macknik & Martinez-Conde, 2004; Tse, Martinez-Conde, Schlegel, & Macknik, 2005) capable of producing the same perceptual outcome (Macknik & Martinez-Conde, 2004; Schiller, 1965). Alternatively, CFS and BR may arise from the same neural mechanisms, with the differences in stimulus conditions inducing differences in the magnitude of inhibition arising within those mechanisms. From other work, it is known that neural discharges at the onset and at the offset of a stimulus are particularly important for visibility of that stimulus (Macknik & Livingstone, 1998) and moreover are especially potent generators of inhibition signals by that stimulus (Macknik et al., 2000). With CFS, the visual system is receiving a steady, continuous stream of onset/offset transients generated by one eye's stimulus, stimulus conditions absent from BR stimulation. In this respect, CFS resembles the novel form of backward masking called "standing wave of invisibility" (Macknik & Livingstone,

1998). Here, an observer repeatedly views a pair of briefly presented stimuli in close temporal proximity; under these conditions, one stimulus (the "target") can be rendered invisible for extended durations by the other stimulus (the "mask"), just like what is observed using CFS.

Our results also establish a conceptual linkage between CFS and FS, a third technique for producing interocular suppression. Specifically, we believe that FS is a scaled-down variant of CFS, comprising a single suppressive event that, when repeated several times, graduates to CFS. Again, the major difference between FS and CFS concerns the durations of phenomenal invisibility of the stimulus viewed by the other eye: a single FS episode produces suppression durations comparable in duration to those measured during BR, whereas CFS can suppress a stimulus for much longer durations. It is almost certainly the sustained barrage of transients contained in CFS that endows this technique with its potency to sustain suppression for so long.

As for the comparison between FS and BR, previous studies have shown that these two techniques have different suppressive effects on color sensitivity (Ooi & Loop, 1994) and that they are differentially susceptible to the modulatory effect of selective attention (Chong & Blake, 2006; Meng & Tong, 2004; Mitchell, Stoner, & Reynolds, 2004; Ooi & He, 1999; Sasaki & Gyoba, 2002). Our results show that FS and BR generate different depths of suppression and, of course, that FS is limited to a narrow window of time centered around presentation of the dichoptic stimulus presented to the other eye. All things considered, we conclude that FS involves a temporary bursts of inhibition associated with the onset of the FS stimulus; BR, on the other hand, does not critically rely on stimulus-generated transients but instead presumably results from sustained inhibition associated with perceptual conflict.

Using brain imaging techniques, several research groups have explored neural responses to dominant and suppressed stimuli during BR (Haynes et al., 2005; Haynes & Rees, 2005; Lee & Blake, 2002; Lumer et al., 1998; Lumer & Rees, 1999; Polonsky et al., 2000; Tong & Engel, 2001; Tong et al., 1998; Williams, Morris, McGlone, Abbott, & Mattingley, 2004; Wunderlich et al., 2005), during FS (Lee, Blake, & Heeger, 2005) and during CFS (Fang & He, 2005; Pasley et al., 2004) (and He and Jiang, 2006 VSS). Procedural differences among these various experiments, however, make it impossible to compare those results in a meaningful way. The time is ripe, it would seem, for a systematic comparison of neural responses associated with BR, CFS, and FS, using procedures more like those employed in our psychophysical experiments. Such comparisons may shed light on the nature and loci of neural events supporting these distinct forms of interocular suppression.

As a final note, what can be said about the relative merits of these procedures as tools for studying visual perception? If prolonged invisibility is the aim without concern for long volleys of transient events, CFS represents the preferred method. If, however, one is interested in perceptual bistability and its underlying neural dynamics, BR should be favored. If discrete trials involving brief presentations are required, FS fills the bill.

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