

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 ($1.6^\circ \times 1.6^\circ$) 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

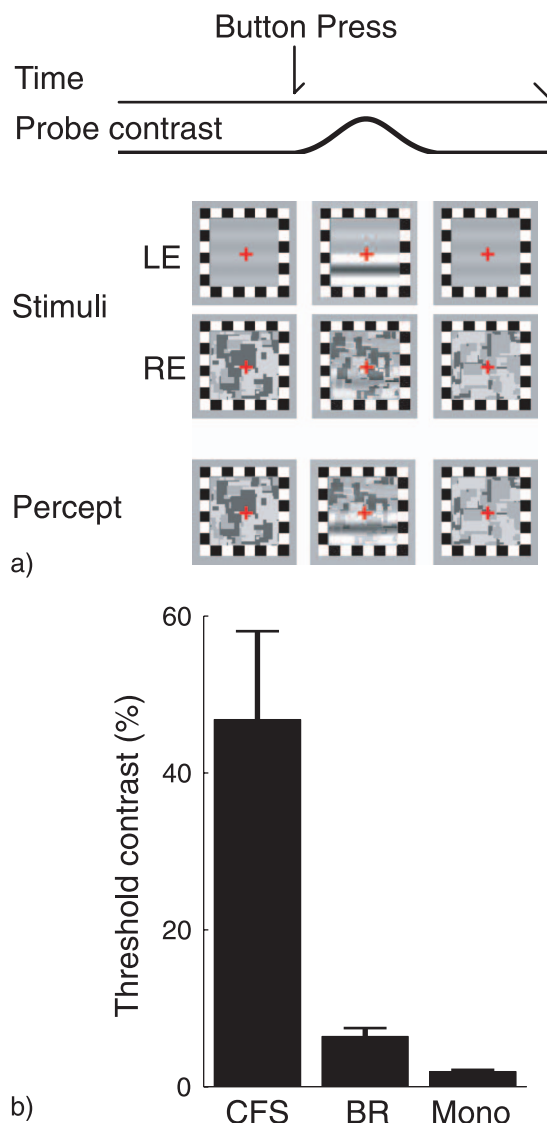


Figure 1. Depth of suppression in CFS. (a) Physical stimuli to the two eyes (upper two rows) and typical percept (lower row) for CFS. The observer viewed a constant 10% contrast grating (the “background”) in one eye (in this example, left eye; LE) and a 10-Hz stream of black/white/grey Mondrians in the 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

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

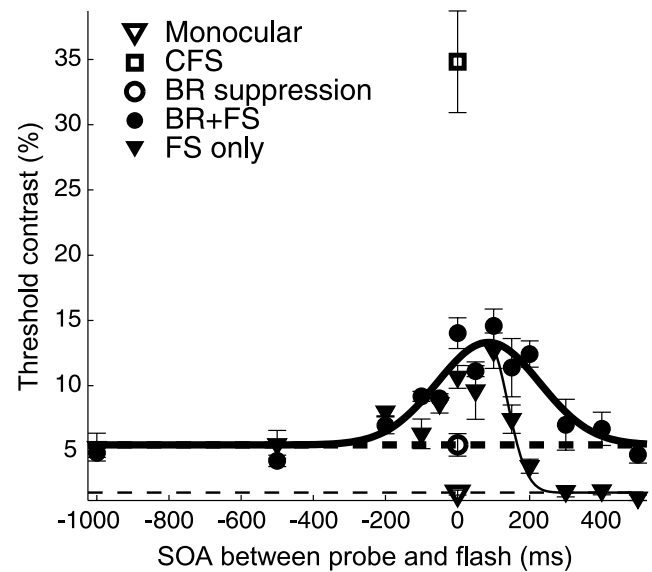


Figure 2. Does a single FS summate with rivalry suppression? Contrast increment thresholds as a function of SOA between the onset of the probe and the Mondrian flash. For comparison, the results in [Experiment 1](#) are replotted here with empty symbols (monocular, CFS, and BR suppression). Filled symbols 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

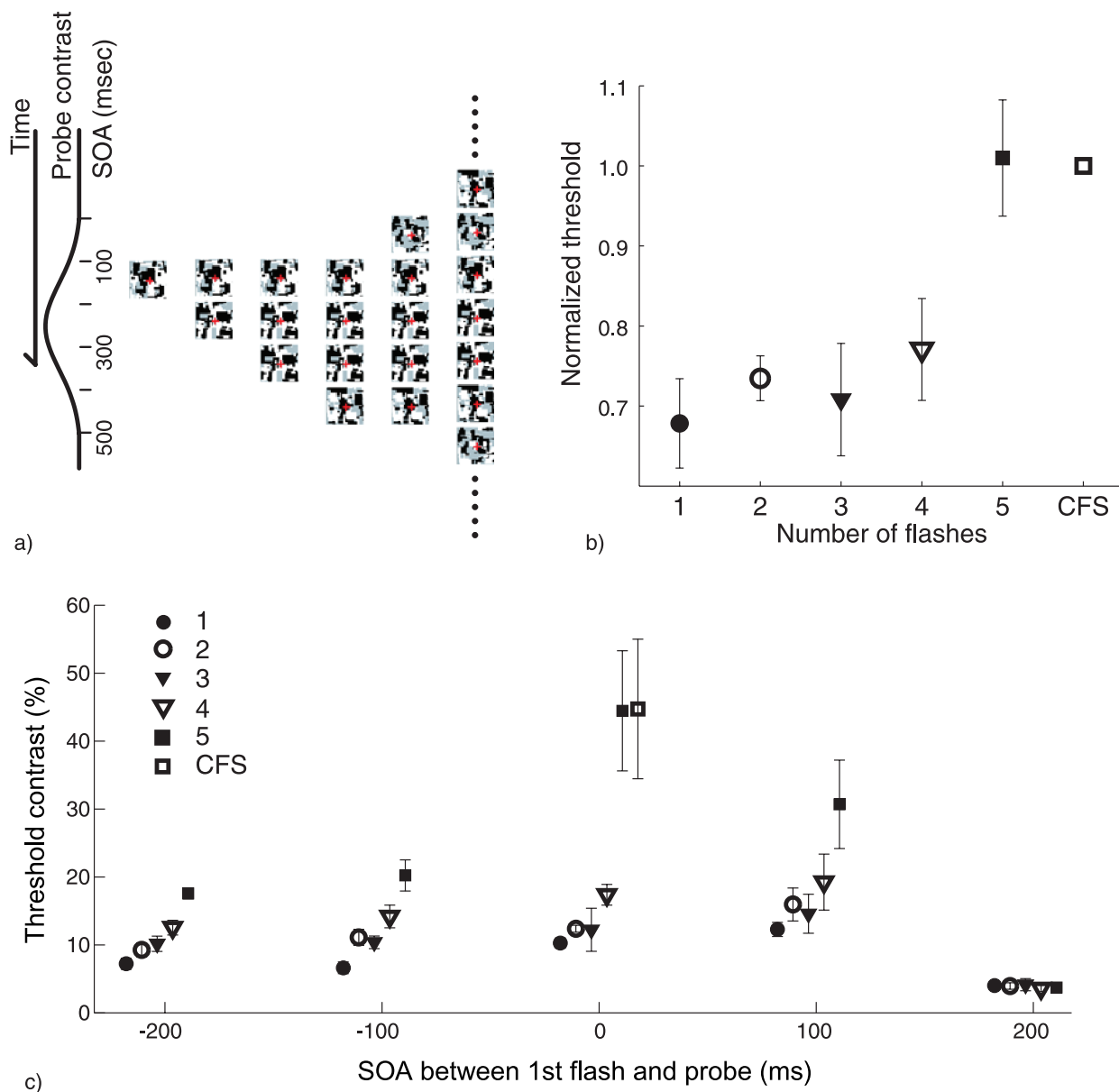


Figure 3. How many flashes are necessary to attain the depth of CFS? (a) Probe detection thresholds for multiple FS. Each flash is followed 100 ms later by another flash. The timing of the first flash was varied from -200 to $+200$ ms (in a vertical axis) relative to the onset of the probe (in the schematic 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 \pm *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)

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