



Detecting contrast changes in invisible patterns during binocular rivalry

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ABSTRACT

When dissimilar images are presented to the two eyes, the human visual system lapses into binocular rivalry, a unique perceptual state characterized by stochastic alternations in dominance of one of the two source images over the other. Probe targets delivered to an eye during suppression phases are more difficult to detect than probes delivered during dominance phases. Nearly all probe studies have involved presenting new stimulation (e.g., a spot of light) either superimposed on or replacing the suppressed stimulus. Here, we ask whether observers can detect a reduction in the contrast of the suppressed stimulus itself. In other words, can observers detect a probe that should make an already invisible stimulus even weaker? Specifically, we compared observers' ability to detect contrast increments and contrast decrements introduced within a rival pattern during dominance and suppression. Contrast increment thresholds were elevated across all pedestal contrasts when the increment was introduced during suppression compared to during dominance, replicating previous results. Contrast decrement thresholds measured during suppression were elevated to an even greater extent, but the fact that they were obtained at all establishes that observers were able to detect probes that should make an already invisible target even more difficult to perceive. In a second experiment, we found a similar pattern of results for contrast change detection in complex images of faces as well. Based on the resulting threshold-vs.-contrast functions, we suggest that, regardless of the complexity of the image, rivalry suppression modulates the neural contrast response function through a mixture of reduced overall response gain and a shift in the contrast gain.

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1. Introduction

The phenomenon of binocular rivalry implies that the brain is intolerant of visual conflict. Instead of melding into a stable binocular composite, incompatible stimuli presented to the two eyes rival for perceptual dominance, producing alternating periods during which one of two ordinarily visible stimuli disappears from visual awareness for several seconds at a time (Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006; Kim & Blake, 2005; Leopold & Logothetis, 1999; van Boxtel, van Ee, & Erkelens, 2007; Wheatstone, 1838). These temporary periods of perceptual blindness to an otherwise clearly visible stimulus would seem to suggest that rivalry suppression involves potent inhibitory neural events. But contrary to this intuition, a suppressed stimulus retains at least some of its effectiveness, evidenced by the capacity of a suppressed stimulus to induce visual aftereffects (Blake & He, 2005), to contribute in disparity processing (Harrad, McKee, Blake, & Yang, 1994; Su, He, & Ooi, 2009; Treisman, 1962), and to bias the perceptual appearance of the currently dominant stimulus (Andrews & Blake-

more, 2002; Pearson & Clifford, 2005). Moreover, during suppression phases of rivalry, visual sensitivity is depressed only a fraction of a log unit on simple tasks involving detection of light flashes or contrast increments (Blake & Camisa, 1979; Ling & Blake, 2009; Makous & Sanders, 1978; Nguyen, Freeman, & Wenderoth, 2001; Norman, Norman, & Bilotta, 2000; Wales & Fox, 1970; Watanabe, Paik, & Blake 2004; Westendorf, Blake, Sloane, & Chambers, 1982). This evidence suggests that the profound phenomenological invisibility of a suppressed stimulus is actually caused by only relatively modest changes in neural activity.

Up to this point, nearly all of the published experiments probing visual sensitivity during rivalry suppression have involved tasks in which either a new stimulus is introduced during suppression (e.g., the picture of a face is briefly superimposed on the suppressed rival target) or the suppressed stimulus itself is replaced with another stimulus (e.g., incoherently moving dots are replaced with coherently moving dots). But what would happen if the probe were simply some manipulation of a fundamental characteristic of the suppressed stimulus itself, one that actually weakened that stimulus further? For example, how well can an observer detect a reduction in the contrast of a rival pattern that was already invisible during suppression phases? We know that contrast decrements

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are easily detected when discrimination thresholds are measured under non-rivalry conditions (e.g., Wolfson & Graham, 2001), but is that true when the decrement occurs within a pattern that is already invisible?

That simple question motivated the experiments described in this paper, where we employed methods very similar to those used in a previous study by Watanabe et al. (2004). Specifically, we measured detectability of contrast increments and contrast decrements during both dominance and suppression phases of binocular rivalry, with the background pattern against which contrast increments or decrements were presented (the pedestal) being one of the two rivaling patterns. In the first experiment, the rivaling patterns were a grating in one eye and a checkerboard stimulus in the other. In the second experiment, the rivaling patterns were more complex: a face in one eye and a house in the other. By measuring change thresholds for a number of different pedestal contrast values, we were able to obtain functions describing how contrast change detection depends on the contrast of background pattern, for both simple and complex rival stimuli. Those resulting functions lead to interesting speculations about the influence of interocular suppression on the underlying neural contrast response function.

2. Experiment 1

2.1. Methods

2.1.1. Participants

Participants were four adult males; all had normal or corrected-to-normal acuity and excellent depth perception as verified by the standardized tests included in the StereoOptical Vision Tester. Three of the four participants were naïve to the purpose of the investigation and one was the first author (S1).

2.1.2. Apparatus

Dichoptic visual stimuli were generated on the left and right halves of a gamma-corrected, 22-in. CRT monitor (Mitsubishi Diamond Pro 2020u; 1800 × 1440 at 85 Hz frame-rate). For controlling contrast, we employed a software-implemented “bit-stealing” technique that provides an effective contrast resolution of 10 bits (Tyler, 1997). The two rival patterns (a radial checkerboard pattern 1.5° in diameter and a 6.7 cycles/° and a horizontal sine-wave grating with smoothed edges, 1.5° in diameter) were viewed through a mirror stereoscope, with the monitor’s mean luminance (29 cd/m²) providing the only source of illumination in an otherwise dark testing chamber. All aspects of the experiment – display generation, trial sequences, and staircase procedure – were controlled using Matlab and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) running on a Macintosh G5 computer.

2.1.3. Procedure

The experiment comprised blocks of trials each administered as a 2-alternative, spatial forced-choice staircase procedure. Within a given block of trials constituting a staircase, the contrast of the horizontal grating (the pedestal) was fixed at one of four values (15%, 22.5%, 33.8%, or 50.6% Michelson contrast), and within a given staircase contrast probes were presented only during dominance phases of the pedestal or only during suppression phases of the pedestal. For a given block of trials, the polarity of the contrast probe (increment vs. decrement) remained the same, with the magnitude of this probe varying over trials according to a staircase procedure.

Before each block of trials comprising a staircase, the observer adjusted the mirrors of the stereoscope to achieve stable binocular alignment of sample fusion frames and rival targets. Next began a

series of discrete trials, each following the sequence shown schematically in Fig. 1. On each trial, the observer monitored the rivalry state of the pedestal and pressed the spacebar to indicate when it had achieved the appropriate state for that block of trials (i.e., horizontal grating dominant or horizontal grating suppressed). Tapping the spacebar in this way triggered a change in the contrast of either the top half or the bottom half of the pedestal. In some blocks of trials, the probe comprised an increase in contrast (contrast increment) and in other blocks the probe comprised a decrease in contrast (contrast decrement); the observer always knew which probe condition was being tested. Observers were instructed to always wait at least one complete cycle of rivalry before initiating a probe and to never trigger trials when experiencing a mixture of the two rival targets. To avoid abrupt onset transients, the change in contrast was ramped to its full magnitude using a half-Gaussian temporal window spanning 680 ms ($\sigma = 190$ ms). Additionally, to preclude introduction of a sharp contrast edge in the middle of the horizontal grating, the contrast increment (or decrement) was spatially aligned so that its zero crossing coincided exactly with the horizontal center of the entire grating.

Because we were interested in comparing detectability of decrements to that of increments, we did not use the standard contrast “pulse” procedure whereby an “increment” (or a “decrement”) appears briefly before a return to the original baseline contrast. With this procedure an “increment” actually consists of an increment *and* a decrement (or vice versa for a “decrement”). To more precisely measure the detectability of pure increments and pure decrements, we instead introduced the contrast change in the upper or lower half of the horizontal grating and left that new contrast level present for 340 ms. At the end this brief time, the two rival targets disappeared simultaneously, leaving only the fusion borders visible. The observer used the up and down arrows on the keyboard to indicate whether the change in contrast occurred in the top or bottom half of the grating, guessing if necessary.

Within a given block of trials, the magnitude of the contrast increment (or decrement) was varied according to a 3:1 staircase procedure that targeted the ~80% correct level of performance on this 2AFC task. At the start of each staircase, changes in contrast were initially relatively large (starting at 50% of pedestal contrast), and were then reduced as the staircase converged onto the threshold estimate (The step size reduced by 30% for the first three reversals, and 15% for the rest of the reversals). The staircase was terminated following 12 reversals and the average contrast increment or decrement over the last six reversals constituted the threshold estimate for that block of trials. Three thresholds were obtained per each condition.

The number of trials in a given block varied depending on the observer’s performance, but block durations averaged 8 min. Observers were free to rest between trials if they desired, and data were collected for no more than 1 h at a time. Each observer completed three staircases for the dominance and suppression conditions with the four pedestal contrasts and two probe types, generating a total of 60 threshold estimates across 20 unique condition combinations. Observers were given substantial practice on the tasks before formal data collection began.

2.2. Results

Increment and decrement threshold results for all conditions are shown in Fig. 2a. All four observers produced qualitatively similar results; both contrast increments and contrast decrements were detected across all pedestal contrasts, even under rivalry suppression. The pedestal contrasts tested captured the rising portion of the full threshold-vs.-contrast (TvC) curve, evidenced by the positive linear slopes found in all four conditions (Watanabe et al.,

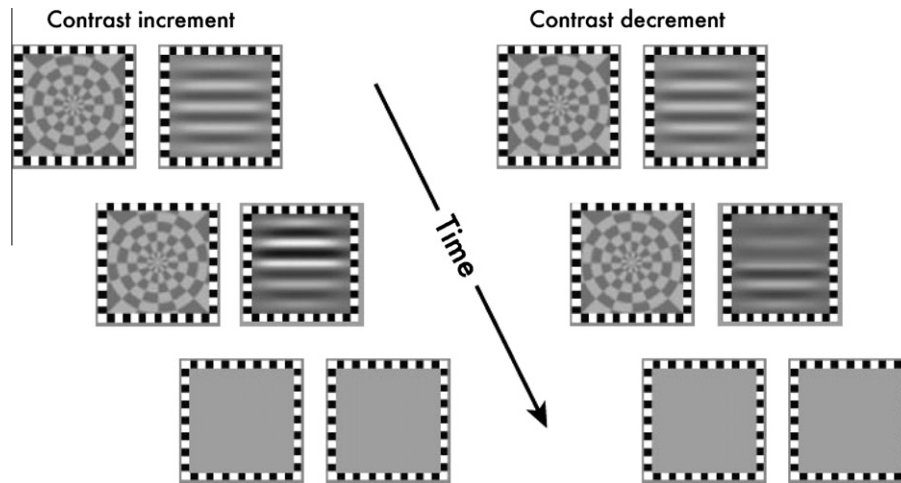


Fig. 1. Schematic of stimulus conditions and trial sequence in Experiment 1. On the left is a condition where the probe was an increment in the contrast of the upper part of the horizontal grating. On the right is a condition where the probe was a decrement in the contrast of the upper part of the horizontal grating. In the actual experiment, probes occurred either within the top half or the bottom half of the grating, and following each trial the observer indicated the probe location. The probe remained present for 680 ms, after which both rival targets disappeared. Probes were presented when the horizontal grating was exclusively visible in rivalry (dominance) or when the radial checkerboard was exclusively visible (suppression).

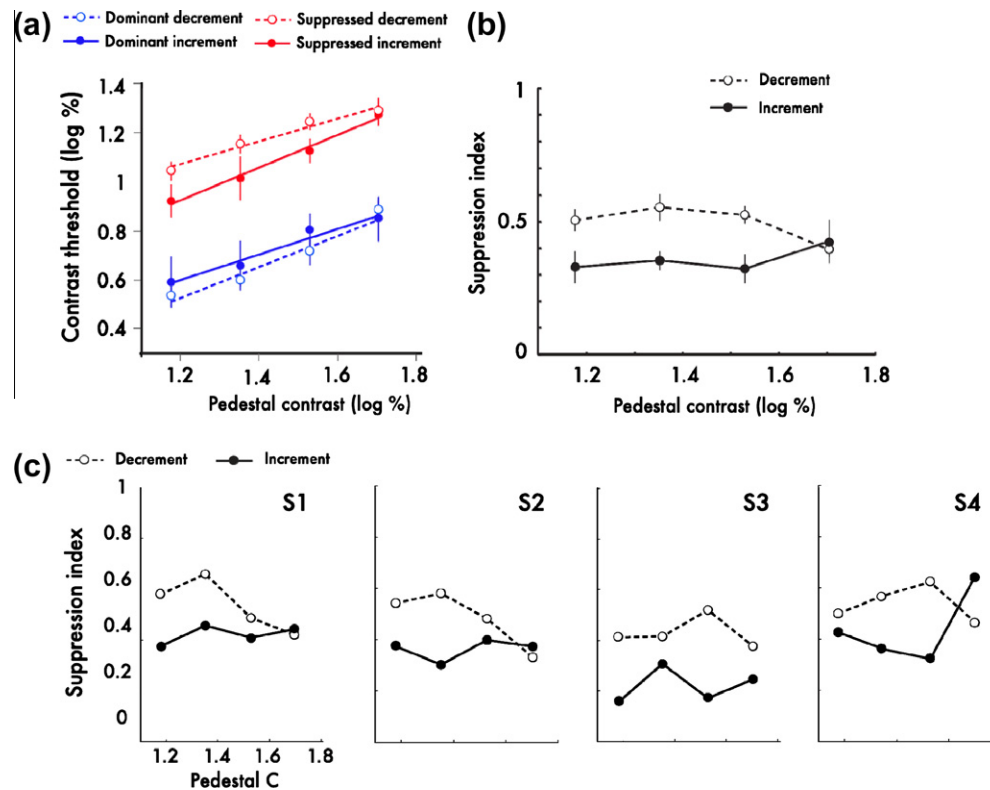


Fig. 2. Data from Experiment 1. (a) Contrast thresholds for detection of probes comprising either increments (filled symbols) or decrements (open symbols) as a function of the contrast of the pedestal grating against which the probes appeared. Probes were presented either when the pedestal grating was dominant in rivalry (blue) or was suppressed in rivalry (red). Data points are averages over four observers. Error bars correspond to ± 1.96 C.I. Lines correspond to best-fit linear regression. (b) Magnitude of suppression (dominance thresholds – suppression thresholds) as a function of pedestal contrasts, for increments and decrements, averaged across observers. (c) Magnitude of suppression plots for individual observers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2004). We did not observe the “dipper” portion to the TvC curve because we were unable to measure contrast discrimination at very low pedestal contrast levels, because the horizontal grating rarely achieved exclusive dominance when its contrast was less than 5%. In a separate pilot study, however, we confirmed that these points fell on the rising portion of the TvC curve under monocular viewing, with the dipper occurring at lower contrasts than were tested here (Fig. 3).

As found in all other binocular rivalry probe studies, thresholds measured during suppression were elevated relative to those measured during dominance, evidenced here by the significant vertical shifts of both the increment and the decrement curves measured under suppression. A nested *F*-test (Lu & Doshier, 2000) revealed significant differences between the suppressed and dominant conditions (increments: $F(4, 8) = 7.05$, $p < .01$; decrements: $F(4, 8) = 7.29$, $p < .01$). The difference between thresholds for dominance and

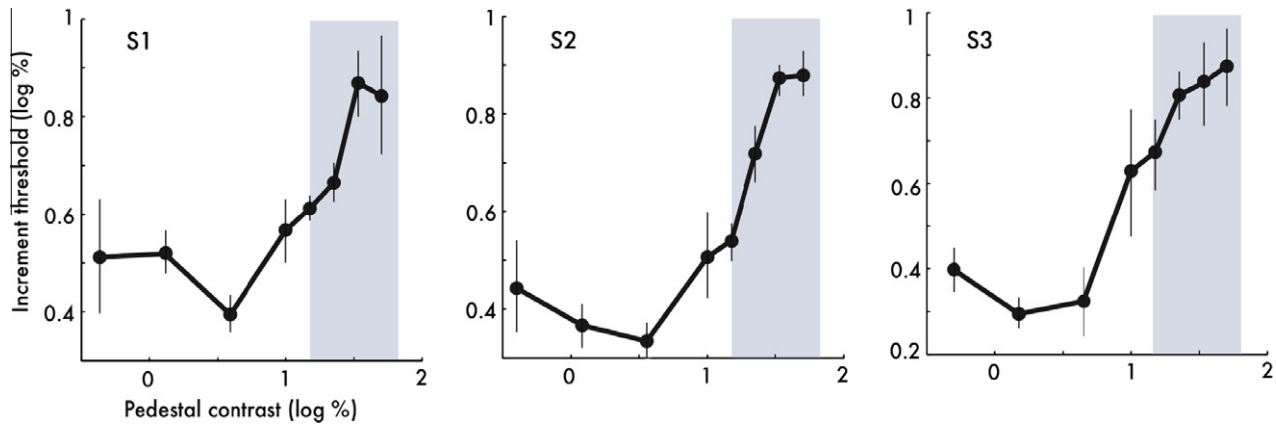


Fig. 3. Pilot TvC Curves. To ensure that the pedestal contrasts tested fell on the rising portion of the TvC curve, full TvC functions were collected for three of the four observers under monocular viewing. As can clearly be seen, the range of pedestal contrasts tested in Experiment 1 (those falling within the grayed box) fell substantially to the right of the dipper function. Error bars correspond to ± 1.96 C.I.

suppression averaged ~ 0.43 log units, a value just a bit higher than that reported by Watanabe et al. (2004) for increments. Interestingly, during suppression, decrements were significantly harder to detect than were increments (Fig. 2b; $F(4, 8) = 6.36$, $p < .01$), something not found in the dominance thresholds, where increments were harder to detect than decrements ($F(4, 8) = 5.88$, $p < .01$). This pattern was consistent for all observers, with a greater average suppression index for decrements than increments (Mean suppression indices for decrements vs. increments: S1 = 0.54 vs. 0.42; S2 = 0.48 vs. 0.36 = S3, 0.43 vs. 0.21; S4 = 0.54 vs. 0.44). Suppression indices for individual observers are shown in Fig. 2c. While there is some inter-subject variability in magnitude of suppression, this could be due to different levels of contrast sensitivity, which in turn captures different parts of the rising portion of the TvC.

2.3. Discussion

Our data may shed light on an interesting, relatively unexplored aspect of binocular rivalry: the impact that dominance and suppression have on the neural response to the rivalry targets. TvC functions are often used to infer the underlying contrast response function (CRF), which expresses the relationship between the contrast of a given stimulus and the neural response generated by that stimulus. The CRF for neurons in early visual areas is characteristically sigmoidal in shape, with an expansive nonlinearity at relatively low contrasts followed by a compressive nonlinearity at higher contrasts. These expansive and compressive regions of the CRF are widely believed to translate to particular regions on the TvC curve (e.g., Boynton, Demb, Glover, & Heeger, 1999; Legge & Foley, 1980; Morrone, Denti, & Spinelli, 2004). In lower-contrast regions of the CRF, where the slope accelerates, neural sensitivity to changes in contrast heightens with increasing pedestal contrasts. Thus, at lower-contrast levels, contrast discrimination performance is facilitated with increasing pedestal contrasts. On the TvC curve, this corresponds to the leftmost portion of the 'dipper function' (the part we were unable to access in our study). However, in higher-contrast regions of the CRF, where the slope decelerates, sensitivity to contrast changes is depressed as a function of pedestal contrast. Thus, at higher-contrast levels, contrast discrimination is impaired with increasing pedestal contrasts; on the TvC curve, this corresponds to the rightmost portion of the 'dipper function'. In summary, the TvC curve can be considered proportional to the inverse of the slope of the CRF (e.g., Boynton et al., 1999; Huang & Dobkins, 2005; Legge & Foley, 1980; Morrone et al., 2004; see Appendix A).

What potential changes might the CRF undergo during rivalry suppression? Two prominent models have been proposed for how the CRF can be affected: contrast gain and response gain (see Appendix A; Huang & Dobkins, 2005; Ling & Carrasco, 2006; Martinez-Trujillo & Treue, 2002; Reynolds & Heeger, 2009; Williford & Maunsell, 2006). Response gain models predict a constant multiplicative decrease in the overall neural responsivity to a suppressed stimulus, such that the greatest suppression modulation occurs at the highest stimulus contrasts. Translated to TvC curves, response gain modulation manifests itself as a vertical shift in the function, constant across all pedestal contrasts (Fig. 4a, bottom panel). Contrast gain models propose that when a stimulus is suppressed, the CRF shifts its sensitivity towards higher contrasts, such that more physical contrast is needed to attain a given neural response, compared to when that stimulus was dominant. This modulation predicts the largest changes in the CRF at mid-contrasts, tapering off at low and high contrasts. Translated to TvC curves, contrast gain modulation manifests itself as a lateral displacement of the dipper function (Fig. 4b, bottom panel).

Although our data do not capture the entire 'dipper' portion of the TvC curve, these functions may still provide some insight into the altered state of the CRF under rivalry suppression. Given that the pedestal contrasts tested were relatively high (15–50%), and that we observed positive slopes in all conditions, it is likely that our data correspond to the rightward region of the TvC function, corresponding to the compressive portion of the CRF. Indeed, prior to the main experiment, we collected pilot data where TvC curves were measured for contrast increments under monocular viewing, confirming that these points did in fact fall to the right of the dipper function (Fig. 3). Our results revealed an upward shift in contrast thresholds across all pedestal contrasts, which is the signature of a response gain attenuation of the CRF.

At first glance, then, it would then appear that a response gain model underlies rivalry suppression. However, a pure response gain reduction fails to account for another important aspect of our data: the magnitude of threshold elevation under suppression was larger for contrast decrements than for contrast increments. Increments and decrements have different thresholds, depending on where the pedestal contrast lands on the CRF. For a pedestal contrast falling within the expansive region of the CRF (Fig. 4a, top panel, blue portion of CRF), contrast increments elicit larger changes in neural response than equivalent contrast decrements, whereas for a stimulus falling within the compressive region (Fig. 4a, top panel, red portion of CRF), contrast decrements elicit larger changes. In fact, increments and decrements only generate similar changes in neural response when the pedestal contrast

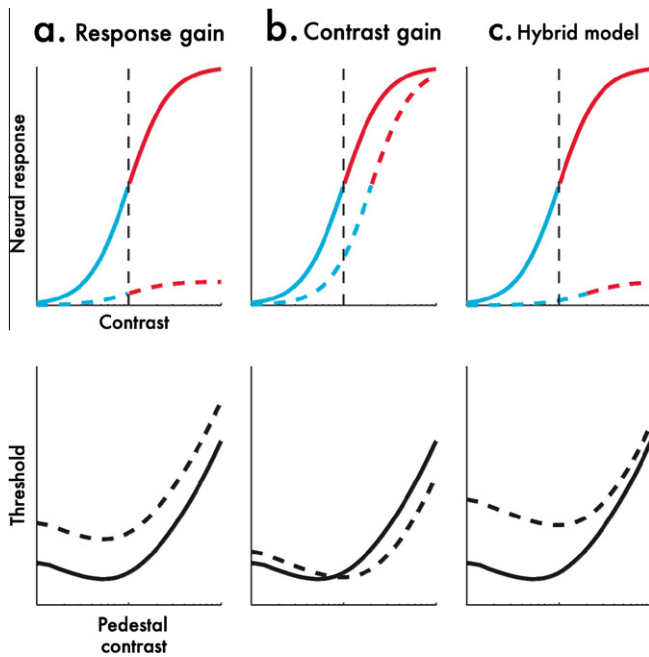


Fig. 4. Hypothetical changes in the contrast response functions (CRFs, top panel), and their corresponding changes in behavioral threshold-vs.-contrast curves (TvCs, bottom panel), during dominance (solid lines) and suppression (dotted lines). See Appendix A for equations. (a) The top panel depicts a response gain change in the CRF. The red portion of the curves indicates the compressive region of the CRF, where sensitivity is higher for contrast decrements. The blue portion indicates the expansive region of the CRF, where sensitivity is higher for contrast increments. Note that under a strict response gain modulation, the contrast at which CRF transitions from expansive to compressive (inflection point) is the same for dominance and suppression. This behavior predicts the TvC curves depicted in the bottom panel. (b) Contrast gain shifts the CRF to the right, such that higher contrast are needed to achieve a given level of neural activity. Under contrast gain, the relationship between increment and decrement sensitivity shifts in favor of contrast increments. (c) A hybrid model would decrease both the responsiveness of the CRF and its contrast sensitivity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

straddles the inflection point of the CRF (Fig. 4a, top panel, dotted vertical line). Had any of the pedestal contrasts we tested fallen on the expanding portion of the CRF (to the left of the dipper), we would have observed a reversal of the differences between increments and decrements, as the points tested would then have fallen on the accelerating portion of the TvC, causing increment sensitivity to be worse than decrements – which we did not observe in the data. Thus, we are certain that the pedestal contrasts tested fell on the compressive portion of the CRF. Given the shape of the CRF and the relatively high pedestal contrast values used here, we would expect contrast decrements to produce lower detection thresholds than increments during dominance, which we did observe in our data.

What impact would different gain changes have on increment and decrement thresholds? Fig. 4a illustrates an example of a large reduction in response gain of the CRF (dashed line). Although the overall neural response is considerably weakened, the relation between contrast increments and contrast decrements should remain unaltered under suppression if only response gain were operating. The identical inflection points with and without the response gain reduction illustrate this principle (Fig. 4a, top panel, dotted line). Thus, in terms of TvC curves, the response gain model predicts no difference in suppression magnitude between increments and decrements. Clearly, this prediction alone cannot explain our results.

A contrast gain modulation of the CRF, however, would shift the balance between contrast increments and decrements. For instance, if the CRF underwent a contrast gain modulation during

suppression, the contrast level that originally corresponded to the inflection point under dominance (Fig. 4b, top panel, dotted line), where increments and decrements elicit balanced changes in neural activity, would subsequently fall in a region where increments were more easily detectable compared to decrements (Fig. 4b, top panel, blue portion of dashed line). In terms of TvC curves, the contrast gain model predicts stronger suppression for contrast decrements than increments. And, indeed, these two probe conditions did produce significantly different thresholds during suppression, with detection thresholds for contrast decrements suffering more during suppression than thresholds for detecting contrast increments ($p < .005$).

Taken together, the elevation of difference thresholds under suppression implicates a response gain reduction of the CRF with rivalry, and the larger magnitude of suppression with contrast decrements implicate a contrast gain shift. How do we reconcile these seemingly incompatible conclusions? Contrast gain and response gain modulations of the CRF are not mutually exclusive; in the visual attention literature, hybrid models involving some degree of both have been shown to best account for particular instances of attentional modulation (Ling & Carrasco, 2006; Reynolds & Heeger, 2009; Williford & Maunsell, 2006). Could a hybrid gain model best describe the influence of rivalry suppression on the CRF? Our simulations show this could be the case: both aforementioned characteristics of our data can be captured by a model incorporating both a large decrease in response gain, and a small shift in the contrast gain of the CRF (Fig. 4c).

3. Experiment 2

To what extent does rivalry suppression depend on the type of stimulus being suppressed? The current prevailing view of binocular rivalry states that rivalry alternations arise from neural events distributed throughout the visual hierarchy (Tong, Meng, & Blake, 2006). According to some (Alais & Melcher, 2007), the locus of those neural events is determined by the complexity of the rival stimuli. For example, rival gratings might tap visual processes earlier in the hierarchy than those tapped by more “meaningful” objects such as houses and faces. It is reasonable to ask, therefore, whether suppression of complex stimuli would evoke similar changes to the CRF as with simple stimuli, particularly given the existence of results showing that suppression has minimal effect on some high-level tasks (Li, Freeman, & Alais, 2005).

The nature of rivalry suppression could indeed differ substantially with stimulus complexity. For instance, it has been suggested that the strength of suppression amplifies along the visual hierarchy (Tong et al., 2006), impairing sensitivity to a greater extent for suppressed complex stimuli and tasks that recruit higher-level areas (Alais & Melcher, 2007; Nguyen, Freeman, & Alais, 2003). There is also evidence that CRFs change as one ascends the visual hierarchy, in a way that promotes contrast invariance at higher stages of visual processing (Avidan et al., 2001; Rolls & Baylis, 1986; Sclar, Maunsell, & Lennie, 1990). We felt it worthwhile, therefore, to repeat our increment and decrement threshold measurements using a complex image as the pedestal background upon which those changes appeared. To accomplish this, instead of using simple gratings as the rivalry targets, we used images of faces and houses.

3.1. Methods

3.1.1. Participants

Four adult males participated in Experiment 2, three of which were naïve to the purpose of the investigation while the other was the first author (S1).

3.1.2. Procedure

The design was similar to Experiment 1, except that the rivaling stimuli were images of a face and a house. The faces were of neutral-affect males and females, sampled from the Pictures of Facial Affect series (Ekman & Friesen, 1976), and the houses were taken from a private set (30% RMS contrast). Like in Experiment 1, contrast increment and decrement thresholds were measured under rivalry suppression and dominance, with the face here acting as the pedestal image. While in Experiment 1 contrast changes occurred in either the top or bottom half of the pedestal image, here they occurred in either the left or right half of it (Fig. 5). Observers performed a 2AFC task, reporting in which side of the face image the change occurred. To avoid sharp discontinuities in contrast, the boundary between the pedestal and the side of the face that changed contrast was smoothed with a sigmoidal ramp. To obtain TvC curves, thresholds were acquired at 81% accuracy for the face at four pedestal RMS contrasts (3.1%, 6.3%, 12.5% or 25%), using an adaptive staircase procedure (QUEST; Watson & Pelli, 1983). These pedestal contrasts have previously been shown to fall to the right of the dipper function for TvC curves measured with natural images (Bex, Mareschal, & Dakin, 2007).

3.2. Results

All four observers produced qualitatively similar results: the pedestal contrasts captured the rising portion of the full TvC curve, and both contrast increments and contrast decrements were detected across all face pedestal contrasts, even under rivalry suppression (Fig. 6). As in Experiment 1, thresholds measured during suppression were significantly elevated relative to those measured during dominance (increment: $F(4, 8) = 6.81, p < .01$; decrement: $F(4, 8) = 6.86, p < .01$). The difference between thresholds for dominance and suppression averaged ~ 0.49 log units – roughly the same elevation in threshold that we observed in Experiment 1 using simple gratings. Contrast decrements were easiest to detect in dominant stimuli (Fig. 5b; $F(4, 8) = 6.16, p < .01$), and most difficult to detect with suppressed stimuli ($F(4, 8) = 6.00, p < .01$). This pattern was consistent for all observers, with a greater average suppression index for decrements than increments (Mean suppression indices for decrements vs. increments: S1 = 0.58 vs. 0.35; S2 = 0.66 vs. 0.34; S3 = 0.65 vs. 0.42; S4 = 0.57 vs. 0.47). Importantly, this pattern of results bears a striking resemblance to those of Experiment 1, suggesting that regardless of the complexity of

the stimulus, rivalry suppression operates on that stimulus representation in a constant fashion.

4. General discussion

This experiment introduced a novel probe type for examining sensitivity during suppression phases of binocular rivalry, namely contrast decrements that actually decrease the overall visibility of a rivalry pattern. From a strictly phenomenological perspective, it seems remarkable that decrements can be detected at all during periods when the pedestal grating is suppressed, since the observer has no perceptual awareness of the pattern in which the decrement occurs. How can one detect a reduction in visibility of a pattern if that pattern is invisible in the first place? This outcome is not surprising, however, when we stop to realize that neural representations of the suppressed pattern are maintained to some degree at least within early stages of visual processing during periods of rivalry suppression. This is supported by a number of psychophysical and brain imaging studies in humans showing that, during binocular rivalry, traces of neural signals evoked by a suppressed stimulus can be found within the thalamus and the early visual cortex (see review by Tong et al., 2006). Single-unit studies in alert monkeys trained to monitor states of rivalry point to the same conclusion (see review by Leopold & Logothetis, 1999). We thus can envision a situation where detection of contrast increments and contrast decrements are mediated, at least in part, by transient activity in distinct ON and OFF channels of the sort known to exist in early stages of the visual pathways (e.g., Schiller, Sandell, & Maunsell, 1986). This conjecture comports with observers' reports of what they experienced when detecting decrements in a suppressed pattern: they described having a sense of something disappearing even though what they were seeing – the radial pattern (Experiment 1) or the house (Experiment 2) – remained visible. Indeed, the partial survival of a suppressed signal is perhaps a necessity for the oscillatory nature of binocular rivalry to arise: were the neural representation of a suppressed signal in one eye completely abolished, there would no longer be any competition between the two eyes, and the signal in the dominant eye would remain visible indefinitely.

The modulatory effects of suppression have previously been shown to depend critically on the complexity of a stimulus. Suppression depth (i.e., the magnitude of the elevation in thresholds

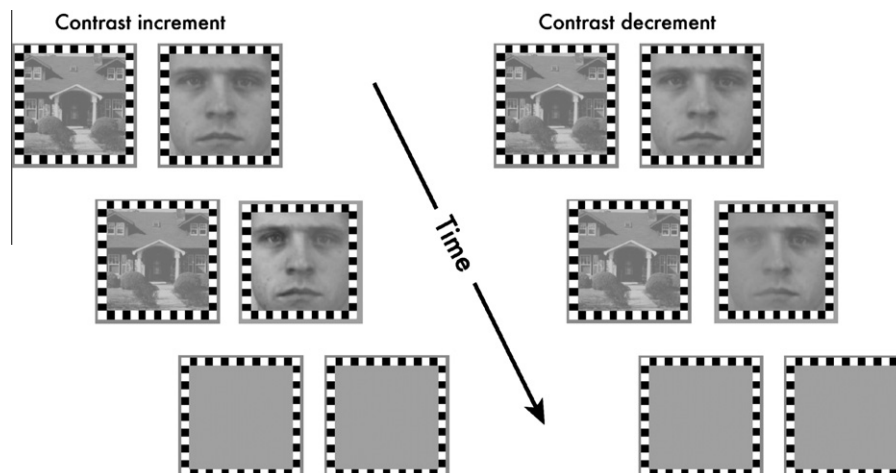


Fig. 5. Schematic of stimulus conditions and trial sequence for Experiment 2. The design was identical to Experiment 1, excepting that the rivaling stimuli here were images of faces and houses. On the left is a condition where the probe was an increment in the RMS contrast of the left part of the face pedestal. On the right is a condition where the probe was a decrement in the RMS contrast of the left part of the face pedestal. Probes were presented when the face was exclusively visible in rivalry (dominance) or when the house was exclusively visible (suppression).

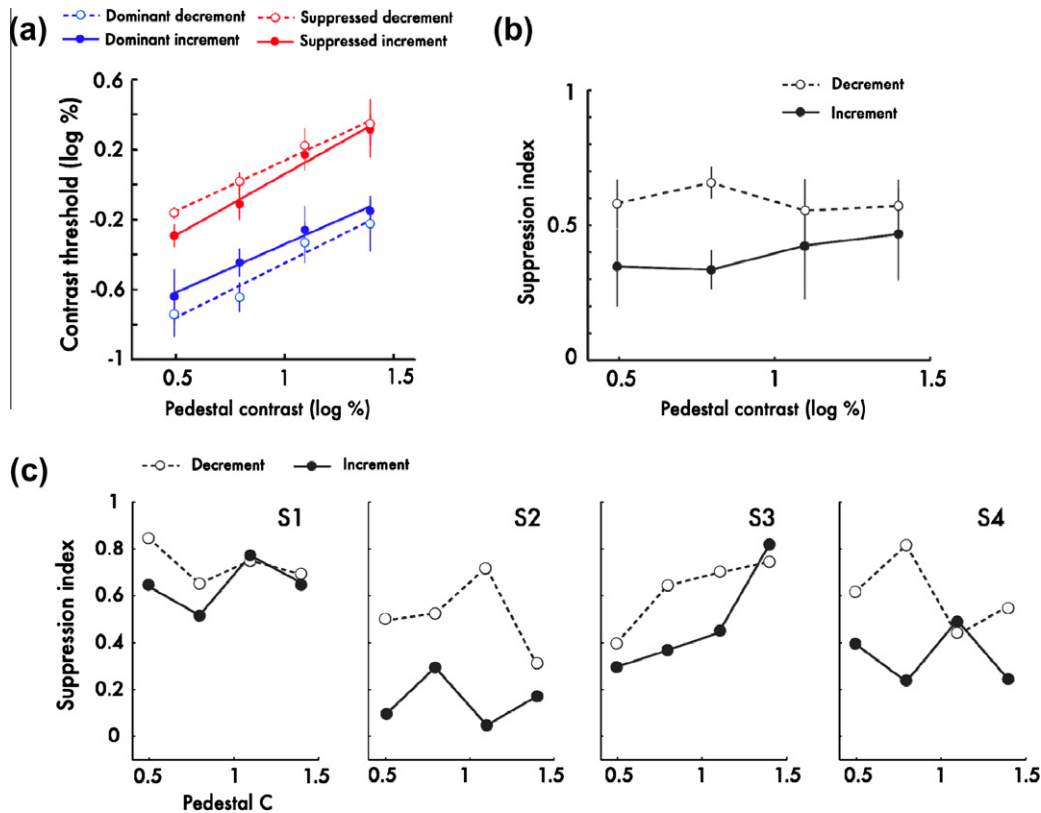


Fig. 6. Data from Experiment 2. (a) Contrast thresholds for detection of probes comprising either increments (filled symbols) or decrements (open symbols) as a function of the RMS contrast of the pedestal face against which the probes appeared. Probes were presented either when the pedestal grating was dominant in rivalry (blue) or was suppressed in rivalry (red). Data points are averages over four observers. Error bars correspond to ± 1.96 C.I. Lines correspond to best-fit linear regression. (b) Magnitude of suppression (dominance thresholds – suppression thresholds) as a function of pedestal contrasts, for increments and decrements, averaged across observers. (c) Magnitude of suppression plots for individual observers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

measured during suppression relative to those measured during dominance), for instance, has been found to be greater for rivalry between faces and houses compared to suppression depth measured during rivalry between gratings (Alais & Melcher, 2007). In our study, the difference in thresholds between dominance and suppression was hardly different for the faces (~ 0.49 log units) than for simple sinusoidal stimuli (~ 0.43 log units). However, because our measurements only capture the rising portion of the TvC curve, we only have a rough estimate as to where the contrast levels we chose lay on the CRF. Thus, without the ‘dipper’ portion of the TvC curve, it is difficult to draw direct quantitative comparisons of suppression depth between Experiments 1 and 2 – particularly due to the multiplicative nature of rivalry suppression.

While our data cannot confirm whether depth of suppression depended on stimulus complexity, the modulatory effects of suppression on the CRF did not appear to depend on stimulus complexity; rivalry suppression seems to modulate the CRF via a large reduction in the response gain of neurons responding to the stimuli, accompanied by a shift in the contrast gain. In other words, this multiplicative, response gain reduction of neural activity predicts that in binocular rivalry studies, the deepest rivalry suppression will tend to occur for high-contrast stimuli, with relatively weak suppression depth modulation for lower-contrast stimuli. Our results square with the only single-unit recording study that has measured the influence of interocular suppression on the CRF of anaesthetized cats (Sengpiel & Blakemore, 1994). While they did not quantify the contribution of the different gain modulations, they did find that interocular suppression evoked a large reduction in the response gain of both simple and complex cells in the primary visual cortex.

Do the gain changes we estimated under suppression generalize to all stimuli, regardless of their complexity? Not necessarily. It is important to note that Alais and Melcher (2007) used a face-identification task to assess suppression depth associated with face/house rivalry. In our second experiment, we measured increment thresholds and decrement thresholds, because we were explicitly interested in comparing those thresholds to those measured with gratings. We suspect that the effects of suppression depend importantly on the nature of the task being used to measure suppression depth, an idea also voiced by Li et al. (2005). Using a form discrimination task to tap into higher-level neural populations, Li et al. (2005) found weak rivalry suppression when measuring contrast thresholds, yet strong suppression when measuring motion and form thresholds. These results were interpreted as the product of steeper CRFs along the visual hierarchy, which yield smaller contrast threshold elevation with higher-level neural populations. Our results support this general framework. While the stimuli in our study varied in complexity, the task remained a simple contrast discrimination that presumably tapped into early visual areas with shallower CRFs, regardless of stimulus complexity. This would explain why we observed such robust suppressive effects for both gratings and faces; despite the stimulus’ visual complexity, the task used in our experiments – contrast discrimination – relies importantly on neural events transpiring relatively early within the visual pathways. It is the task, in other words, and not just the stimuli, that likely governs the nature of suppression measured during rivalry.

What process could drive populations of contrast-sensitive neurons to decrease both their responsivity and sensitivity? Although the mechanisms subserving response gain and contrast gain modulation are still the focus of much study (e.g., Chance,

Abbott, & Reyes, 2002; Reynolds & Heeger, 2009), one recent theory, the normalization model, may provide some insight (Reynolds & Heeger, 2009). While the normalization model sought to explain attention's effect on the CRF, its general principles may hold for rivalry. Their model suggests that different response modulation signatures of the CRF arise due to the relative difference between the size of the stimulus being suppressed, and the size of the 'suppressive field.' Specifically, when the window of suppression is much larger than the stimulus' neural representation, a contrast gain signature would dominate. But as the window of suppression shrinks, and becomes smaller than the neural representation of the stimulus, the contrast gain modulation diminishes, and a response gain signature arises. Under this framework, our results imply that with binocular rivalry, the window of suppression is roughly proportional to the size of the stimulus' neural representation – thereby yielding a hybrid of both gain signatures. Although the hybrid model best matched our data for simple and complex stimuli, it is entirely possible that altering an observer's task to encourage the recruitment of 'higher-level' neural representations (for instance, a face-identification task) would shift this balance between the window of suppression and the size of the neural representation, causing qualitative changes in the modulation of the CRF under rivalry.

Our results confirm that observers can indeed detect contrast probes that decreased the visibility of already invisible rivalry targets. This outcome reminds us that rivalry suppression is not to be construed as equivalent to the physical removal of a monocular stimulus. While a suppressed stimulus may be perceptually indistinguishable from genuine physical absence of that stimulus, we know that some neural representation of that stimulus still lingers within portions of the visual pathways. Otherwise, observers would find it impossible to detect reductions in contrast of an invisible stimulus, something our data clearly does not show. It seems, therefore, that a suppressed stimulus may be genuinely out of sight, but it does not appear to be completely out of mind.

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Appendix A

Contrast response functions were modeled with the Naka-Rushton function (e.g., Albrecht & Hamilton, 1982; Boynton et al., 1999; Legge & Foley, 1980; Morrone et al., 2004)

$$response = \frac{R_{max} \cdot C^n}{C^n + C50^n} + M \quad (1)$$

where *response* represents the simulated neural response, *C* is the contrast intensity, *C50* is the contrast at half the saturating response (threshold), *n* is the exponent determining the steepness of the function (slope), *R_{max}* is the level at which the response saturates (asymptote), and *M* is the response at the lowest contrast level. For the purposes of our simulations, the exact parameters used are less relevant. We used this model to simulate the population contrast response function for a stimulus under the dominance condition, and kept all these parameters fixed in our simulations of the response gain, contrast gain, and hybrid models.

The response gain model is expressed as a modified Naka-Rushton of form

$$response = N_{RG} \cdot \frac{R_{max} \cdot C^n}{C^n + C50^n} + M \quad (2)$$

where the only additional parameter added was *N_{RG}*, which represents a multiplicative effect on the overall response (Fig. 4a, top panel), causing a change in the asymptote of the CRF.

The contrast gain model is expressed as a modified Naka-Rushton of form

$$response = \frac{R_{max} \cdot (C^n \cdot N_{CG})}{(C^n \cdot N_{CG}) + C50^n} + M \quad (3)$$

where the only additional parameter added was *N_{CG}*, which causes a lateral shift in the contrasts response function (Fig. 4b, top panel).

The hybrid model is simply a combination of the response gain and contrast gain models (Fig. 4c, top panel), of form

$$response = N_{RG} \cdot \frac{R_{max} \cdot (C^n \cdot N_{CG})}{(C^n \cdot N_{CG}) + C50^n} + M \quad (4)$$

where there are two modulatory parameters: one for response gain modulation (*N_{RG}*), and one for contrast gain modulation (*N_{CG}*).

The standard model for relating TvC curves to underlying contrast response functions assumes that the ability to detect a change in contrast relies on a change in neural response that exceeds a particular criterion (e.g., Boynton et al., 1999; Legge & Foley, 1980; Morrone et al., 2004). In other words, there is a direct relationship between the shape of the TvC curve, and the shape its underlying contrast response function, expressed as,

$$\Delta C \approx \Delta R \frac{1}{dR/dC} \quad (5)$$

where the TvC curve is considered proportional to the inverse of the slope (derivative) of the CRF. ΔC is the contrast change threshold, and ΔR is the criterion change in neural response. The bottom row in Fig. 4 depicts TvC curves derived from different CRF gain modulations.

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