Orientation-tuned suppression in binocular rivalry reveals general and specific components of rivalry suppression

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During binocular rivalry (BR), conflicting monocular images are alternately suppressed from awareness. During suppression of an image, contrast sensitivity for probes is reduced by ~0.3–0.5 log units relative to when the image is in perceptual dominance. Previous studies on rivalry suppression have led to controversies concerning the nature and extent of suppression during BR. We tested for feature-specific suppression using orthogonal rivaling gratings and measuring contrast sensitivity to small grating probes at a range of orientations in a 2AFC orientation discrimination task. Results indicate that suppression is not uniform across orientations: suppression was much greater for orientations close to that of the suppressed grating. The higher suppression was specific to a narrow range around the suppressed rival grating, with a tuning similar to V1 orientation bandwidths. A similar experiment tested for spatial frequency tuning and found that suppression was stronger for frequencies close to that of the suppressed grating. Interestingly, no tuned suppression was observed when a flicker-and-swap paradigm was used, suggesting that tuned suppression occurs only for lower-level, interocular rivalry. Together, the results suggest there are two components to rivalry suppression: a general feature-invariant component and an additional component specifically tuned to the rivaling features.

Keywords: vision, binocular rivalry, suppression, orientation, spatial frequency


Introduction

Presenting conflicting visual information to each eye results in perceptual alternations between the two monocular images such that each undergoes suppression in a stochastic alternation. This phenomenon of fluctuating perception with constant visual input is referred to as binocular rivalry (BR) and has been a popular topic with visual scientists for nearly two hundred years (Wheatstone, 1838). Many different kinds of images will induce BR provided their features differ sufficiently. BR has been demonstrated in many primary stimulus domains, for instance, motion (Moutoussis, Keliris, Kourtzi, & Logothetis, 2005), orientation (Polonsky, Blake, Braun, & Heeger, 2000), spatial frequency (Julesz & Miller, 1975), and color (Breese, 1909), as well as between global motion and complex visual objects such as houses and faces (Alais & Melcher, 2007; Alais & Parker, 2006; Tong, Nakayama, Vaughan, & Kanwisher, 1998). Even though the kinds of stimuli used can differ greatly between experiments, the dynamics of BR and the basic phenomenology of perceptual suppression are highly similar. The lack of awareness during suppression and the diversity of stimuli that engage in rivalry have led to two major questions within BR research: Where in the brain is rivalry initiated, and what is the fate of the suppressed stimulus?

In an attempt to answer the first question and identify the level at which rivalry occurs, two conflicting theoretical viewpoints on the nature of rivalry suppression have been developed. One theory proposes that BR is a low-level process where there is competition at an early stage between monocular visual channels to determine which eye will dictate perception (Blake, 1989). This view is often referred to as “eye-rivalry” and has been supported by functional imaging studies (Polonsky et al., 2000; Tong & Engel, 2001) as well as psychophysical experiments (Blake & Fox, 1974; Blake, Westendorf, & Overton, 1980). The second theory holds that rivalry is a higher-level process that occurs between representations of visual
stimuli that compete for conscious expression at a late stage of visual processing. The prime example of this comes from a study employing rapid switches of stimuli between the eyes, where observers reported slow rivalry-like alternations that could not have been due to rivalry between the eyes (Logothetis, Leopold, & Sheinberg, 1996; Silver & Logothetis, 2007). This theory of “stimulus-rivalry” also has considerable empirical support (Alais, O’Shea, Mesana-Alais, & Wilson, 2000; Logothetis et al., 1996) and a general consensus that both theories can coexist (Blake et al., 2002; Silver & Logothetis, 2007), with some suggesting that BR suppression may occur at multiple stages along the visual processing pathway (Freeman, 2005; Lee, 2004; Nguyen, Freeman, & Alais, 2003; Wilson, 2003).

To investigate the second question—the fate of the suppressed stimulus—a measure is needed that can quantify the extent of rivalry suppression. Suppression strength is usually calculated by measuring a threshold for a brief probe stimulus presented to one eye while it is suppressed and comparing that with the probe’s threshold for the same eye when it is dominant (Fox & Check, 1968). The ratio of dominance to suppression thresholds, when subtracted from unity, gives an index that ranges from zero (no suppression) to 1.0 (complete suppression). Visual sensitivity for detecting probes during suppression is reduced by about ~0.3–0.5 log units relative to when the image is dominant (Blake & Fox, 1974; Ooi & Loop, 1994; O’Shea & Crassini, 1981), although suppression is generally greater for more complex images (Alais & Melcher, 2007; Alais & Parker, 2006; Nguyen et al., 2003). This typical reduction in sensitivity during suppression corresponds to a suppression strength of ~0.4–0.52. Suppression strength studies such as these show that signals associated with the suppressed image are not entirely lost even though perception of the suppressed image can be completely absent (Blake, 1989).

Past studies dealing with the nature of rivalry suppression have predominantly argued that it is a nonselective process, with evidence indicating that an eye is insensitive to all stimuli during suppression, not just the suppressed stimulus (Blake et al., 1980). The idea of nonselective suppression has been based on results showing that probes very dissimilar to the rival stimuli were consistently harder to detect in suppression than in dominance (Fox & Check, 1966, 1968; Wales & Fox, 1970). Although this does show that all visual input to the suppressed eye is subject to suppression, it does not necessarily mean that all these inputs are suppressed to the same extent. Previous research has shown that the dominant percept during rivalry can be influenced by the suppressed stimulus in a rather specific manner (Andrews & Blakemore, 2002; Carlson & He, 2000; Pearson & Clifford, 2005; Treisman, 1962). For example, Treisman (1962) showed that different stimulus attributes may combine between the eyes into a percept that is based on a combination of the two competing stimuli. Moreover, Pearson and Clifford (2005) found that, during rivalry of competing orientations, a suppressed orientation systematically biases the perception of the dominant orientation. However, research examining the degree to which suppressed probes are suppressed has led to contradicting results. Several studies have looked at specificity in suppression and while some did show selective suppression effects for high- as well as low-level features (Alais & Parker, 2006; Apthorp, Wenderoth, & Alais, 2009; O’Shea & Crassini, 1981), others did not (Nguyen, Freeman, & Wenderoth, 2001). For example, although O’Shea and Crassini (1981) found that, during rivalry of differently oriented gratings, small orientation changes in the suppressed image are more suppressed than larger changes, Nguyen et al. (2001), also measuring during orientation-based rivalry, found no such effect. An example of high-level feature specificity in rivalry suppression comes from a study by Alais and Parker (2006). They found that, when face stimuli are in rivalry, a face probe is much more suppressed than a motion probe, whereas the motion probe is more suppressed when motion stimuli are in rivalry. Even though some of these studies show strong evidence for feature specific suppression during BR, suppression is still argued to “operate non-selectively to weaken all inputs to the suppressed eye” (Blake & Logothetis, 2002). With evidence in favor of both selective and non-selective suppression, it’s important to examine the nature of suppression more closely. First of all, can we find selectivity in suppression? If so, what is suppression specific to? Moreover, when is suppression specific? If suppression is only selective under certain conditions, this might explain the conflicting results of previous studies examining these questions.

In this study we tested whether suppression during binocular rivalry between orthogonal gratings is uniform across a range of orientations and spatial frequencies, or whether it is specific to the particular features engaged in rivalry. If suppression is uniform, all orientations and spatial frequencies within the rivalry region should be suppressed to a similar extent since it is the eye that is being suppressed. However, if rivalry is specific to the neurons representing the conflicting stimulus inputs, we would expect that probes with features dissimilar to the rivaling stimuli should be easier to detect than probes similar to the rival stimuli. This hypothesis was tested using orthogonal rivaling gratings and by measuring contrast sensitivity to grating probes at a range of orientations and spatial frequencies in a forced-choice probe-orientation task (see Figure 1).

### Methods

#### Observers

A total of four observers (three males and one female, mean age = 33 years), including three of the authors,
participated in Experiment 1, all having normal or corrected-to-normal vision. All observers were trained in BR and provided informed consent at the start of the study. For all observers, the behaviorally dominant eye was the right.

Apparatus

All stimuli were computed using an Apple G5 computer running system OS X and Matlab software with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). The stimuli were presented on a LaCie Electron Blue 22-in. (series 3) monitor with a resolution of 1024 × 768 pixels × 75 Hz. All stimuli were presented using a 9-bit color look-up table that afforded 512 gray levels. This allowed for a more precise measure of probe thresholds at low contrasts compared to the standard 8-bit color look-up table that affords only half the gray levels. All stimuli were viewed through a mirror stereoscope.

Stimuli

The rival stimuli were two orthogonally oriented sine-wave gratings. The gratings were presented at maximum contrast (98% Michelson Contrast, space-average luminance: 37.55 cd/m²) except for when a probe was presented in it (see below). The rivaling gratings appeared in circular apertures whose edges were softened by a cosine ramp of 0.16° of visual angle on a gray screen (37.55 cd/m²). The stimuli subtended a diameter of 2° when viewed from the viewing distance of 57 cm. The gratings were oriented ±45° from vertical, with the +45 degree grating (clockwise from vertical) always presented to the observers’ right eyes. Both gratings had a spatial frequency of 3 cpd.

The probe stimuli for Experiment 1 consisted of a small circular sine-wave grating (0.65°) that was monocularly presented in the center of the +45 degree grating and thus always presented to an observers’ right eye. The edge of the probe was spatially smoothed by a cosine ramp (0.32°). The probe was presented in either the dominant or the suppressed image (depending on the condition, see Procedure section) and was smoothly presented over time using a Gaussian cross-fade. Over time, the contrast of the probe first increased and subsequently decreased along a Gaussian profile. The amplitude of the Gaussian corresponded to the probe’s contrast and thus varied between trials. The increase in contrast of the probe was mirrored by an equal decrease in the (local) contrast of the rival grating in which it was presented, such that mean luminance and RMS contrast remained constant throughout the transition. This procedure avoided transient increases in contrast which can disrupt rivalry suppression (Walker, 1978). The Gaussian had a standard deviation of 57 ms and was truncated at ±3.5 standard deviations (±200 ms). The full width of the Gaussian at half-maximum was 133 ms, and we used this period to define the effective probe duration (the period in which probe contrast was above half-maximum). The probe’s orientation ranged from ±10° (close to the probed eye’s orientation) to ±45° as follows: ±10°, ±20°, ±30°, and ±45°.

Procedure

The two gratings were presented in separate halves of the monitor and viewed through a mirror stereoscope. Observers first aligned the stimuli by adjusting the
orientation of the mirrors. Depending on whether the block of trials was a dominance or suppression condition, observers waited for the target stimulus (in which the probe would be presented) to become either completely visible (dominant) or completely invisible (suppressed), after which they triggered the presentation of the probe with a key-press which was then presented instantly. The orientation of the probe was randomly assigned to be either clockwise or counterclockwise relative to the orientation of the grating in which it was presented. A range of probe orientations was tested in separate blocks to test for orientation tuning. After presentation of the probe the rival stimuli remained present for an additional 300 ms before observers were presented with two adjacent circular gratings showing the two possible responses. Observers indicated which of the two probe orientations had been presented. A schematic diagram of one trial for Experiment 1 is depicted in Figure 1.

In all conditions, the dependent variable was the probe contrast required to perform the probe discrimination task at 75% correct. Contrast was varied using the adaptive Quest procedure (Watson & Pelli, 1983), which effectively varied the amplitude of the Gaussian cross-fade (see Figure 1). Observers first performed in the condition with the probe presented to the dominant eye to become familiar with the task and performed in at least four Quest staircases for dominance and suppression in an alternating order. The Quest data were then pooled (as were clockwise and counterclockwise probe trials for a given orientation) and fitted with a psychometric function (cumulative Gaussian) using a maximum likelihood fitting procedure. The strength of suppression was calculated by dividing the 75% correct threshold for dominance by its suppression counterpart and subtracting that value from 1.

Two-factor rivalry suppression model

To test for specificity in orientation suppression we fitted the following Gaussian model to our results:

\[ S_{\text{total}} = S_{\text{spec}} \times \exp\left(-\frac{x^2}{(2\sigma^2)}\right) + S_{\text{gen}}. \]

The model is simply a Gaussian function with a baseline offset, where \( S_{\text{spec}} \) = suppression strength of the specific (tuned) component; \( S_{\text{gen}} \) = suppression strength of the general (untuned) component; \( \sigma \) = standard deviation of the tuned Gaussian portion; and \( x \) = the dimension over which the probe varies. In Experiments 1, 3, and 5, the dimension was orientation; in Experiments 2 and 4, the dimension was spatial frequency. At \( x = 0 \), the probe has the same value as the suppressed grating.

Results

**Experiment 1: Orientation discrimination during orientation rivalry**

The aim of Experiment 1 was to determine whether there is an orientation tuning for rivalry suppression by measuring contrast discrimination thresholds for probes presented at a range of orientations. The rival stimuli were orthogonal gratings and the probe stimuli were small centrally presented gratings oriented either clockwise or counterclockwise with respect to the probed eye’s grating as described in the Methods section.

**Results and discussion**

Data from Experiment 1 are shown in Figure 2, with panel A showing the contrast thresholds for orientation discrimination separately for dominance and suppression conditions. Thresholds for discriminating the probe during suppression show a strong trend to increase as the angular difference between the rival stimulus and the probe grating decreases, with suppression thresholds at 10° being about six times the value of suppression thresholds at 45°. There is also a similar but weaker trend in the dominance thresholds, although this can be attributed mainly to masking at 10°. With such a small orientation difference, the probe’s orientation is hard to discriminate when presented in a similarly oriented dominant grating as both would activate the same orientation channel and inevitably lead to an increase in dominance threshold.

More important are the suppression strength indices plotted for each observer in Figures 2B–2E. Suppression strength takes into account variations in dominance threshold by normalizing suppression thresholds relative to dominance thresholds. Effectively, it takes the dominance threshold at each level of orientation difference as a baseline and expresses suppression as a proportionate change from that baseline. Therefore, all suppression strength indices are directly comparable even though probe visibility in dominance changes over orientation. This index clearly shows that suppression is greater for probes oriented close to the orientation of the suppressed grating and reduces in strength as the probe orientation moves away from the suppressed grating. That is, for probes close to the suppressed grating’s orientation, there is a far greater proportionate increase in suppression thresholds. Correspondingly, the data show a significant effect of orientation difference (\( F(3,9) = 11.49, p < 0.01 \)), indicating that suppression strength varies depending on the orientation difference between the test probe and the pedestal.

To further investigate the nature of this orientation effect, we fitted our Gaussian model to the data. The \( r^2 \) for each observer are indicated in Figures 2B–2E. Our model fits the data well, with \( r^2 \) averaging 0.93 across the four
observers shown. To remove individual differences in the absolute suppression strengths, we normalized the data to their maximum by dividing each score by the greatest suppression strength index (10\(^{0}\), for each observer). When the normalized data are averaged across observers the fit is improved to \(r^2 = 0.99\) (see Figure 2F for model parameters). These results indicate an orientation tuning function for rivalry suppression that is centered on the suppressed grating’s orientation and has a half-width of approximately 26\(^\circ\). For large orientation differences (beyond about 40\(^\circ\)), the strength of suppression flattens out to an approximately constant level. Suppression strength, however, does not reach zero even for a 45\(^\circ\) orientation difference (\(t(3) = 4.86, p < 0.01\)). Together, these results suggest that while there is significant rivalry suppression at all orientations, there is an additional specific component to rivalry suppression that is tuned to the suppressed grating’s orientation.

Experiment 2: Discriminating probe orientation across spatial frequency

The implication of Experiment 1 is that there is a feature-specific component to rivalry suppression. The goal of Experiment 2 was to extend this result by determining whether suppression during orientation rivalry is tuned to all the features in the rivaling stimuli or only the conflicting features. Although the rival gratings in Experiment 1 were orthogonally oriented, and therefore conflicted in orientation, they both shared the same spatial frequency (3 cpd) and therefore there was no conflict in the spatial frequency dimension. The question therefore arises: Will all features of the suppressed grating undergo a tuned suppression, or only those features that are in interocular conflict? Experiment 2 addresses this question by using the same rival gratings as in Experiment 1 (both 3 cpd) but presenting probes with a range of spatial frequencies (five values spanning 2...
octaves). The orientation difference was fixed at ±25°, the phase of the small (0.65°) probe was determined randomly for each trial, and again we measured contrast thresholds for discriminating clockwise from anticlockwise probes. The rest of the methods were the same as for Experiment 1, which are describe in detail in the Methods section. If the evidence for tuned suppression found in Experiment 1 is limited to the conflicting stimulus dimension, then we would expect to find no tuning for probe spatial frequency. If, however, there is tuned suppression for all features of the suppressed stimulus, then probes should become more suppressed as spatial frequency approaches that of the rivaling gratings.

**Results and discussion**

Figure 3 plots the results from Experiment 2, with the contrast thresholds for dominance and suppression on the orientation discrimination task shown in Figure 3A, and the suppression strength indices shown in Figures 3B–3F. Looking at the mean dominance thresholds (Figure 3A), it is clear that there is little variation in probe visibility across spatial frequency. There is a tendency for thresholds at lower spatial frequencies to be slightly higher, although this effect is probably due to fewer cycles of the probe grating being visible within the aperture, which tends to make orientation judgments more difficult. For the most part, however, this trend is echoed by equivalent proportionate changes in the suppression thresholds over probe spatial frequency, so that the suppression indices do not vary much over spatial frequency. The mean normalized suppression strength data (Figure 3F) shows a significant spatial frequency effect ($F(4,12) = 3.56, p < 0.05$), although this does not appear to be due to tuning. Neither the individual data (Figures 3B–3E) nor the average data fitted our Gaussian model well ($r^2$ (average data) = 0.02). The data fitted better to a standard linear regression model ($r^2 = 0.69$) although the fit was still only modest.

Figure 3. (A) Thresholds, averaged across observers, for discriminating the probe’s orientation during dominance (solid line) and during suppression (dotted line) as a function of probe spatial frequency. The rival gratings both had a spatial frequency of 3 cpd. (B–E) Strength of probe suppression across a range of probe spatial frequencies for each observer. The dotted lines indicate the tuned suppression model’s fit to each subject’s data. Solid lines represent each observer’s data’s fit to a standard regression line. The $r^2$ values of both the suppression model and regression line are shown in the lower left corners. Note that our tuning model does not fit the data. Linear regression provides better fits for most observers although the $r^2$ values are still only modest. (F) Average suppression strength across observers’ normalized data. The data were normalized to the 3-cpd probe score. Error bars represent the standard error of the mean. Again note that our suppression-model does not fit the data well. The regression line, however, does show a modest fit. The data show significant suppression at all spatial frequencies but no clear tuning function over a 2-octave range of spatial frequency.
modest. Note that the plus and minus 1 octave range of spatial frequencies differences tested should be more than sufficient to reveal evidence of spatial tuning as estimates of the width of spatial frequency channels in humans and primates indicate that they have a full bandwidth of between 1 and 1.5 octaves (Blakemore & Campbell, 1969; De Valois, Albrecht, & Thorell, 1982; Wilson & Gelb, 1984). Notably, even the probe showing the least suppression (1 cpd) still had a suppression strength index that was significantly greater than zero ($t(3) = 4.71, p < 0.01$), confirming the existence of a general component in rivalry suppression.

Overall, in the absence of a tuning function centered on the frequency of the rival gratings, we conclude that there is no evidence of rivalry suppression being specifically tuned to the spatial frequency of the rival gratings. We therefore suggest that tuned suppression during binocular rivalry may be limited to features that are driving the interocular conflict. However, an alternative interpretation for the lack of tuning is that the orientation difference between probe and target ($±25$ degrees) was too large for any tuning in spatial frequency to occur: tuned suppression is at an intermediate level for this orientation difference in Experiment 1. It therefore remains possible that the amount of spatial frequency tuning is dependent on the orientation difference between the rival gratings. Still, at least for the settings used here, spatial frequency tuning is absent when an orientation difference is driving the interocular conflict. In Experiment 4, we return to the issue of feature selectivity in suppression.

**Experiment 3: Controlling for center-surround effects**

Experiment 3 tests an alternative interpretation of the results presented so far, specifically, that the results might be explicable in terms of center-surround inhibition. In Experiment 2, where the probe was fixed in orientation at $±25^\circ$, there was no tuning, yet there was a clear tuning observed in Experiment 1 where the probe varied in orientation. Indeed, the tuning in Experiment 1 peaked when the central probe was nearly collinear with the surrounding rival grating. This suggests an alternative interpretation of the data based on center-surround interactions. It is well established neurophysiologically that orientation-selective cells driven by their preferred stimulus become suppressed when an iso-oriented surround is added (Jones, Grieve, Wang, & Sillito, 2001). This is similar to the stimulus configuration that produced the strongest suppression in Experiment 1, and suppression due to center-surround interactions such as these have been shown to combine with rivalry suppression to alter visibility of targets during rivalry (Paffen, Alais, & Verstraten, 2005; Paffen, Tadin, Te Pas, Blake, & Verstraten, 2006). Potentially, the “tuning” of rivalry suppression found in Experiment 1 could be due to rivalry suppression combining with a strengthening iso-orientation inhibition as the probe stimulus moves closer in orientation to the surround stimulus. In Experiment 3, we test this possibility by using a larger probe ($2^\circ$) that is the same size as the rival stimuli. This allows us to present the probe without it being embedded in a surround grating and therefore removes any effect of separate center and surround regions with different orientations. Probe orientations used were $±10^\circ$, $±25^\circ$, and $±45^\circ$. Stimuli were presented using a 9-bit color look-up table. Remaining methods are as described in the Methods section.

**Results and discussion**

The data from Experiment 3 using the large full-field probes are plotted in Figure 4. Similar to our first experiment, we find a main effect for orientation difference ($F(2,6) = 14.19, p < 0.01$) and significant suppression for even the least suppressed orientation difference of $45^\circ$ ($t(3) = 19.53, p < 0.01$). The suppression strength data (Figure 4F) replicate the orientation-tuned rivalry suppression observed in Experiment 1 and the data showed a good fit to the same model as used for Experiment 1 ($r^2 = 1$). These results confirm that the orientation tuning seen in Experiment 1 is not due to the addition of iso-orientation surround suppression when the central probe and surround grating are nearly collinear.

**Experiment 4: Probe discrimination during “spatial frequency” rivalry**

Having shown that the orientation tuning found for rivalry suppression in Experiment 1 cannot be due to any center-surround effect interacting with rivalry suppression, we now focus on the lack of spatial frequency tuning for Experiment 2. This lack of tuning can be explained by several possible accounts. One is that there is simply no selectivity in the inhibition between monocular spatial frequency channels. Also, the lack of tuning in Experiment 2 could have been due to a floor effect in suppression. Since we used a probe orientation that showed relatively little specific suppression in Experiment 1, suppression may have been too weak to show any signs of specificity. Another possibility, however, is that rivalry suppression is only specifically tuned to spatial frequency when spatial frequency is the main source of the interocular conflict. The failure to find spatial tuning in Experiment 2 might simply be a consequence of the fact that the two rival stimuli shared the same spatial frequency. Experiment 4 was designed to dissociate between these possible interpretations. The experiment measured probe orientation discrimination at a range of probe spatial frequencies during rivalry between gratings that differ in spatial frequency. The aim was to test whether rivalry suppression exhibits a...
specific spatial frequency tuning around the spatial frequency of the suppressed image. This experiment used a pair of gratings that were both oriented +45° from vertical in order to remove interocular orientation conflict. Rivalry between these gratings was induced by adding an interocular spatial frequency difference. In one version, we used 0.75 and 1.5 cpd for the rival gratings, with the probe presented to the eye receiving the high spatial frequency grating. This was referred to as Experiment 4A, and all probes were higher than the 1.5 cpd of the probed eye to provide an upper half-tuning for spatial frequency. In a second version, we used rival gratings of 1.5 and 3 cpd with the probe presented to the low spatial frequency grating. This was referred to as Experiment 4B, and all probes were lower than the 1.5 cpd of the probed eye to provide the lower half-tuning around the suppressed grating. Probe size was increased to 1.4° to make sure that the lowest spatial frequency probes contained enough orientation information to do the task, which was to judge whether the probe (randomly either ±25° from the probed grating’s orientation) was clockwise or counterclockwise with respect to the suppressed grating. Both versions were presented using a 10-bit color lookup table. All other aspects of this experiment were similar to Experiment 2.

**Results and discussion**

In Figure 5, results from our two half-tuning experiments (Experiments 4A and 4B) are combined and expressed as suppression strength indices plotted across the seven probe spatial frequencies. Although there were four observers, observer JC could not do the task at the very low spatial frequencies (Experiment 4B) due to a recurring lack of rivalry. For this reason, those data points were not included in the group mean analysis and only the four points visible in Figure 5D were included in the group means. Despite this, the pattern of data is clear and shows strong evidence of spatial tuning (Figure 5F). The effect of probe spatial frequency was significant in both versions of Experiment 4: $F(3,9) = 4.24, p < 0.05$ for Experiment 4A; $F(3,6) = 22.05, p < 0.05$ for Experiment 4B. As in the previous experiments, suppression strength was always significantly greater than zero even beyond the tuned portion (see Figure 5F).
These results show that when a low and a high spatial frequency are engaged in rivalry, adding a probe to the low frequency grating shows a clear suppression tuning for probes of lower spatial frequency. Conversely, adding a probe to the high frequency grating and testing for suppression at even higher spatial frequencies shows a corresponding tuning to higher spatial frequencies. In each case, suppression strength decreases as the probe frequency moves away from the frequency of the probed grating. Together with the results from Experiment 2, the implication is that there are specific inhibitory connections between monocular spatial frequency channels, and that binocular rivalry will not specifically suppress a particular spatial frequency channel unless there is spatial frequency conflict between the rival images. In such a case, it appears that rivalry suppression involves targeted suppression of a particular spatial frequency, which acts in combination with an untuned general suppression. In contrast, if there is no spatial frequency conflict (as in Experiment 2), there is only a general component to rivalry suppression that is weaker but applies to all spatial frequencies approximately equally. When spatial frequency conflict exists, a tuned suppression component centered near the suppressed spatial frequency is added to the general suppression.

**Experiment 5: No orientation-tuned suppression for “flicker-and-swap” rivalry**

Rapid interocular switching of rival stimuli has been used to demonstrate that a form of binocular rivalry can occur that must entail processes beyond the early interactions between monocular channels thought to underlie conventional binocular rivalry (Blake, 1989). Often known as flicker-and-swap rivalry, this demonstrates that perceptual alternations can arise independently

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Figure 5. (A) Combined data from Experiments 4A and 4B showing average probe discrimination thresholds as a function of spatial frequency. The solid line indicates the dominance thresholds and the dotted line the suppression thresholds. (B–E) Suppression strength data from both versions of Experiment 4 combined per observer. Stars refer to data from Experiment 4A and diamonds to Experiment 4B. The $r^2$ values indicating model fit are presented in the graphs. (F) Averaged normalized suppression strength data across observers. Error bars indicate standard errors. The data have been fitted with the same model as Equation 1 with the modification of leaving $x$ as a free parameter. The fit value is depicted in the upper left corner of the graph. Panel F shows a decrease in suppression strength for probes decreasing in spatial frequency when they are presented within a low spatial frequency grating (compared to a grating with a higher spatial frequency; black diamonds). When the probes are imposed on a high spatial frequency grating (relative to its rivaling counterpart; black stars), increasing the spatial frequency of the probes will also lead to a decrease in suppression strength indicating that, when spatial frequency is in conflict, suppression is tuned around a spatial frequency approximating that of the suppressed grating.
of the eye of origin (Logothetis et al., 1996). In Experiment 5, we test whether flicker-and-swap rivalry produces a similar orientation tuning for rivalry suppression to that observed in Experiment 1 for conventional rivalry stimuli. Since flicker-and-swap rivalry must involve binocular levels of processing that operate without regard to eye of origin (Logothetis et al., 1996) and is not tied to early interocular interactions as in conventional rivalry (Pearson, Tadin, & Blake, 2007; Tong & Engel, 2001), we expect that tuning to the suppressed orientation will be weaker than observed for conventional rivalry. The reasoning behind this prediction is that orientation tuning-functions become progressively broader after V1 (Desimone, Albrecht, Gross, & Bruce, 1984; Desimone, Schein, Moran, & Ungerleider, 1985), resulting in progressively weaker tuning in suppression when rivalry is instigated at relatively late levels of visual processing.

Experiment 5 used interocular “flicker-and-swap” rivalry (Logothetis et al., 1996). To optimize the strength of perceptual alternations the stimulus parameters chosen closely matched those used by Logothetis et al. (1996), confirmed by Lee and Blake (1999) to be optimal for producing flicker-and-swap rivalry. The stimuli were orthogonally oriented gratings with the same orientation and spatial frequency as described in the general Methods section; however, the size of the apertures was increased slightly (2.4° in diameter). The probe orientations used in this experiment were the same as in Experiment 1 with the addition of probes oriented ±60, ±70, and ±80 degrees away from the suppressed grating. Probe diameter and spatial frequency remained similar to Experiment 1 (0.65°, 3 cpd). The effective probe duration, defined as the full-width at half-maximum of the temporal Gaussian used to presented the probe, was 125 ms. However, because the stimuli underwent on–off flicker, probe duration times were doubled leading to a total presentation time of 250 ms (of which the total “on” time was 125 ms). The gratings were colored (one red (x = 470, y = 287, 8.97 cd/m²) the other green (x = 273, y = 506, 27.06 cd/m²), as in Logothetis et al., 1996) and flickered continuously at a rate of 18.75 Hz while also swapped between their screen positions (and thus between eyes) every 210 ms. Both gratings were presented at 28% contrast using a standard 8-bit color lookup table. Unlike the other experiments, the probe could not be exclusively combined with the observer’s dominant eye. Instead, the color-matched probe followed the stimulus with which it was being combined (always the +45° grating) and thus swapped eye every 210 ms in synchrony with the probed grating. Also, because a probe would not be presented in isolation, the presentation of the probe was delayed if an observer made a response during the “off-phase” of the flickering gratings. The delay had a maximum duration of 53 ms. Because of this potential delay and increased duration of probe presentation, observers were given the opportunity, via key press, to abort trials if perception alternated before, or during, the presentation of the probe. Observer DMA did not take part in this experiment on account of not displaying any stimulus rivalry.

Results and discussion

The data from Experiment 5, plotted in Figure 6, do not show a main effect for orientation difference, in contrast to what was found in Experiment 1 (F(6,12) = 1.68, p = 0.209). This shows there is no significant difference between suppression strengths exerted on test probes at any of the tested orientations, indicating that suppression in the case of flicker-and-swap rivalry is not tuned to the orientation of the suppressed stimulus. This can be seen in the values of suppression strength being roughly constant across all probe orientations within 45° of the suppressed orientation. If suppression in flicker-and-swap rivalry were orientation tuned, there would be clear evidence of increasing suppression strength as the probe orientation difference decreased, particular at values of 10° and 20°, yet this did not occur. Similarly, for probe orientations more than 45° from the suppressed orientation, suppression strength shows no orientation tuning.

Overall, there are two key differences that emerge between suppression in conventional rivalry and in flicker-and-swap rivalry. The first is that suppression is not feature tuned (at least for orientation) in the case of flicker-and-swap rivalry, and the second is that suppression is relatively weak in flicker-and-swap. The point regarding weak suppression in flicker-and-swap rivalry (evident when comparing suppression strength for the two types of rivalry in Figures 2 and 6) confirms the same finding in a recent report on suppression in flicker-and-swap rivalry (Bhardwaj, O’Shea, Alais, & Parker, 2008). The lack of specificity for rivalry suppression in the flicker-and-swap paradigm suggests that it does not occur at the stage of early cortical processing where neurons exhibit tight tunings for orientation. In V4, for example, orientation tunings are broader (Desimone et al., 1985), and in IT such tuning is present in only a minority of cells (Desimone et al., 1984). This, together with the fact that it must involve a binocular substrate, suggests that flicker-and-swap rivalry occurs at a later stage of processing than conventional binocular rivalry. This ties in with other recent evidence for a late site for flicker-and-swap rivalry showing that TMS pulses over occipital cortex tend to induce dominance switches for conventional rivalry but not for flicker-and-swap rivalry (Pearson et al., 2007).

General discussion

In this paper, we have tested whether binocular rivalry suppression is specific to the stimulus features engaged in rivalry or whether it entails a wholesale suppression
operating over the rivalry region in a non-selective manner. Our results clearly support the claim that rivalry suppression is selective because plots of suppression strength for orientation and spatial frequency rivalry (Figures 2 and 5) exhibit clear tunings that peak at the value of the suppressed features. Probes similar to the feature driving the interocular conflict (e.g., orientation or spatial frequency) required much more contrast to become visible than did gratings that were further away along these feature dimensions. Importantly, however, there is no value of orientation or spatial frequency in the tunings in Figures 2 and 5 that failed to produce significant rivalry suppression. Therefore, our results do not entirely rule out the alternative position of non-selective suppression. That is, although the strong evidence of tuned suppression rules out the wholesale suppression proposal in its strongest form, there clearly is a component of untuned rivalry suppression. This is evident by the fact that rivalry suppression remains significant at all points beyond the tuned portion of the suppression strength plots. The clear implication of these results is that rivalry suppression involves two components. According to this two-component theory of rivalry suppression, there is a general component that acts non-selectively to uniformly suppress the rivalrous region of the suppressed image, and a specific component that is selectively tuned to the features driving the interocular conflict within that rivalrous region. We suggest that the increasing strength of suppression within the tuned portion of the suppression strength curves is due to the specific suppression component combining with the general suppression component.

An alternative explanation of our results that does not involve the tuning of suppression is that any tuning effect found is due to an apparent motion signal associated with the probes used in the experiments. Even though the probes had a smooth temporal onset, one might perceive apparent motion signals. As the orientation or spatial frequency changes increase, the apparent motion becomes greater and thresholds might decrease, producing a tuning curve in the results. The lack of tuning found in Experiment 5 may be based on the lack of, or degraded, apparent motion effects due to the transient nature of the
flicker-and-swap stimulus. However, apparent motion does not appear to be a causal factor in the results presented in this paper. Any apparent motion effects should affect performance during dominance as well as suppression. Using suppression depth as our index should control for the apparent motion effects since it expresses performance during suppression relative to that during dominance. However, apparent motion itself may be affected by suppression in such away that would lead to a tuning function in our experiments. Results from Experiments 2 and 4 suggest this is not the case. Since any apparent motion would have been the same for each condition of Experiment 2, the lack of tuning does indeed correspond to an explanation of our tuning results by apparent motion. Yet, in Experiment 4, using the exact same probe, we did find tuning. This argues against the idea that apparent motion is responsible for tuning in suppression.

It has previously been asserted in several influential rivalry reviews that rivalry suppression acts non-selectively (Blake, 1989; Blake, 2001; Blake & Logothetis, 2002). By this it is meant that suppression is not limited to the features of the suppressed image, which obviously disappear from awareness, but may also include many other kinds of stimuli unrelated to the rivaling images. The evidence in support of this has a long history and goes back to Fox's original probe studies (Blake & Fox, 1974; Fox & Check, 1968; Fox & Check, 1972; Wales & Fox, 1970) where it was shown that a probe stimulus superimposed on a rival target was harder to detect in suppression than in dominance, even when the probe was quite unrelated to the suppressed image. In some of these studies (Blake & Fox, 1974; Fox & Check, 1968), the dependent measure was the reaction time to detect the probe (and was found to increase in suppression), whereas in others it was detection thresholds for probes such as spots of light (Blake & Camisa, 1977; Smith, Levi, Harwerth, & White, 1982). These studies concluded that rivalry suppression is not limited to the features of the suppressed image. Although Blake and Fox (1974) did find a spatial frequency effect on suppression, no evidence for feature-specific tuning of suppression to the conflicting spatial frequencies was found.

The experiments we report in this paper were designed to systematically test the tuned suppression hypothesis with respect to orientation and spatial frequency. Our results provide clear support for feature-specific suppression, and our study stands out as a rare attempt to explicitly test this hypothesis. Two other studies have attempted a similar investigation of rivalry suppression. The first was conducted by O'Shea and Crassini (1981) and used a rather different approach from ours. Their study included two tasks. In the first, orthogonal gratings were presented dichoptically and observers responded as soon as possible to a change in orientation in either the suppressed or the dominant grating. An 80° range of test orientations was used. An overall increase in reaction times was found when the test grating was suppressed relative to when it was dominant with a greater increase found for larger orientation changes. The second experiment O'Shea and Crassini presented used a 2AFC paradigm where observers had to detect a change in orientation. Surprisingly, performance for orientation changes between 20° and 70° were identical for both suppression and dominance. However, for orientation changes outside this range, performance during suppression declined relative to dominance. O'Shea and Crassini argued that binocular rivalry suppression is sensitive to orientation, reaching a similar conclusion to ours. Important differences with our study are that (i) we used a depth of suppression paradigm, which gives the suppression performance relative to dominance performance, and (ii) the extension of our results to a tuned suppression effect for spatial frequency.

The second study that attempted a similar investigation was conducted by Nguyen et al. (2001), who included among a series of rivalry studies an experiment designed to test for orientation tuning of rivalry suppression and another testing for spatial frequency tuning. Their spatial frequency study was similar to our Experiment 2 in which the two rival gratings had the same spatial frequency and, as in our experiment, no tuning was found for spatial frequency. They did not, however, include an experiment like our Experiment 4, in which there was spatial frequency conflict between the rival gratings and which did produce tuned suppression. Their study of orientation tuning for suppression was similar to our Experiment 1 but their results were equivocal. Of the three observers tested, one appeared to show some orientation tuning. Overall, however, the group effect was not statistically significant and the authors concluded that rivalry suppression was not tuned to orientation.

There are some important differences between our study and Nguyen et al. (2001) that might explain the differences in results with their orientation experiment. In their study, the task for the observers was to detect the probe's location while in our experiments observers had to discriminate between probe orientations. Although this alone should not lead to different results, combined with their probe presentation technique it could have. Nguyen and colleagues added their probes to the rival stimulus using a step function that did not maintain a constant level of mean luminance. This means that detection of the probe could have been done on local luminance variations alone and thus may not have sufficed to find any specific effects of orientation on suppression. Correspondingly, their conclusions agree with previous studies using luminance probes (Blake & Camisa, 1977). In our study, mean luminance was kept constant. Moreover, our task could not be performed on luminance information alone since observers had to discriminate the probe's orientation. These differences in methods could explain why no orientation tuning was found in the Nguyen et al. study.

The tunings implied in our suppression data are similar in bandwidth to the feature tunings observed in early
visual cortex. For example, neurophysiologic estimates of orientation bandwidth in V1 from single-unit studies indicate a median half-width at half-maximum of about 21° (De Valois, Yund, & Hepler, 1982). Psychophysical estimates from human observers using a variety of methods suggest very similar values (Blake & Holopigian, 1985; Govenlock, Taylor, Sekuler, & Bennett, 2009). These accord well with the measurements we obtained in Experiment 1, which correspond to a half bandwidth of 26°. Similarly, estimates from neurophysiology and psychophysics indicate a full bandwidth for spatial frequency channels of between 1 and 1.5 octaves. The average bandwidth of the spatial frequency tunings plotted in Figure 5 matches this closely with a value of approximately 1 octave. Since a tight tuning to a particular feature value is a hallmark of neurons in early visual cortex, the tuned pattern of suppression we report is consistent with the specific component of rivalry suppression having an early source. Moreover, as Experiments 2 and 4 reveal, the specific, tuned component of rivalry suppression only arises when the suppressed feature is in conflict with the dominant image. In other words, there has to be “spatial frequency rivalry” between the images for spatially-frequency tuned suppression to emerge or “orientation rivalry” for orientation tuning to emerge. Since visual neurons lose their feature specificity at successive stages beyond V1, this also squares with an early source for the specific component of rivalry suppression. Indeed, this component may stem from specifically targeted mutual inhibition between early feature detectors at the stage where the interocular mismatch is first detected and the rivalry process is initiated.

The specific feature tuning of suppression for conventional rivalry can be contrasted with the untuned suppression observed with flicker-and-swap rivalry in Experiment 5. Figure 6 plots suppression as a function of orientation for flicker-and-swap rivalry and compares that with the corresponding data for conventional rivalry from Experiment 1. Two major differences are evident: First, that there is no orientation tuning for flicker-and-swap rivalry, and second, that rivalry suppression overall is weaker for flicker-and-swap rivalry. The lack of feature tuning indicates that suppression in flicker-and-swap rivalry arises at a later stage than for conventional rivalry, supporting a similar conclusion from a TMS study showing that pulses over occipital cortex induced dominance switches for conventional rivalry but did not affect flicker-and-swap rivalry (Pearson et al., 2007). Together, these findings provide converging evidence that flicker-and-swap rivalry engages processes that are subsequent to those underlying conventional rivalry processes. The fact that it is unaffected by neurodisruptions in the occipital cortex and shows no orientation tuning is good evidence that it occurs after V1.

It may be tempting to conclude that the general component of rivalry suppression (the untuned baselines in Figures 2 and 5) may be the same as suppression in flicker-and-swap rivalry since both are untuned and both are weaker than the tuned portion in the conventional rivalry suppression curves. However, an important difference between these two forms of rivalry suppression is that they differ markedly in strength. This is evident when suppression strength in Figure 6E is compared to the results of Experiments 1, 3, and 4. For all probe orientations, suppression strength for conventional rivalry is far greater than for flicker-and-swap rivalry, even in the untuned baseline portion for conventional rivalry. This lack of suppression strength has been reported recently by Bhardwaj et al. (2008) and it also agrees with the phenomenal experience of flicker-and-swap rivalry which often appears to produce a less convincing perceptual alternation than is experienced during conventional rivalry. Therefore, on the grounds that their respective suppression strengths differ so markedly, we do not conclude that the untuned general component of conventional rivalry can be regarded as one and the same as flicker-and-swap suppression.

In summary, our results indicate that binocular rivalry suppression is feature dependent, with suppression strength peaking when probes are similar to the features currently suppressed in rivalry. Suppression, however, is not absent for dissimilar conflicting features but instead appears to drop off to a baseline level of suppression. Taking these findings together, we suggest that binocular rivalry suppression consists of two components, one general suppression component which is feature invariant, affecting the suppressed image as a whole and one specific component which is tuned to features in conflict and increases in strength when these conflicting features become more similar.

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