

# Suppressed images selectively affect the dominant percept during binocular rivalry

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During binocular rivalry, perception alternates between dissimilar images that are presented dichoptically. It has been argued that perception during the dominance phase of rivalry is unaffected by the suppressed image. Recent evidence suggests, however, that the suppressed image *does* affect perception of the dominant image, yet the extent and nature of this interaction remain elusive. We hypothesize that this interaction depends on the difference in feature content between the rivaling images. Here, we investigate how sensitivity to probes presented in the image that is currently dominant in perception is affected by the suppressed image. Observers performed a 2AFC discrimination task on oriented probes ([Experiment 1](#)) or probes with different motion directions ([Experiment 2](#)). Our results show that performance on both orientation and motion direction discrimination was affected by the content of the suppressed image. The strength of interference depended specifically on the difference in feature content (e.g., the difference in orientation) between the probe and the suppressed image. Moreover, the pattern of interference by the suppressed image is qualitatively similar to the situation where this image and the probe are simultaneously visible. We conclude that perception during the dominance phase of rivalry is affected by a suppressed image as if it were visible.

Keywords: binocular vision, masking, detection/discrimination

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## Introduction

When incompatible images are presented to corresponding retinal locations of each eye, perception becomes unstable and alternates between the images. This phenomenon is known as binocular rivalry (Wheatstone, 1838; see Blake & Wilson, [in press](#) for a recent review). During rivalry, one of the images will be temporarily dominant in perception, while the other will be suppressed. Several studies on the nature of binocular rivalry suppression show that sensitivity to probes presented in the suppressed image is reduced by a factor of about 2 to 3 (Blake & Fox, 1974; Ooi & Loop, 1994; O’Shea & Crassini, 1981). Traditionally, this suppression of an image during binocular rivalry is considered to be non-selective: All inputs from the suppressed eye (i.e., the eye to which the suppressed image was presented) are thought to be uniformly affected (e.g., Blake, 1989; Blake & Fox, 1974; Blake & Logothetis, 2002; Blake, Westendorf, & Overton, 1980; Fox & Check,

1966, 1968; Freeman, Nguyen, & Alais, 2005; Nguyen, Freeman, & Wenderoth, 2001; Wales & Fox, 1970). However, evidence that challenges this view is accumulating (Alais & Parker, 2006; O’Shea & Crassini, 1981; Paffen, Alais, & Verstraten, 2005; Stuit, Cass, Paffen, & Alais, 2009; Vergeer & van Lier, 2010). These latter studies argue that the magnitude of suppression during rivalry depends on the similarity in feature content between the competing images. For example, sensitivity to oriented probes presented in a suppressed image depends on the orientation difference between the probe and the suppressed image (Stuit et al., 2009). A similar dependency was shown for spatial frequency content. In addition, these studies suggest that the above dependency is only apparent for the features that *drive the interocular conflict*. For instance, variations in the magnitude of suppression for different combinations of spatial frequencies can only be found when rivalry is based on conflicting spatial frequencies of the images, not when the images have conflicting orientations with the same spatial frequency (Stuit et al., 2009). These findings

show that suppression during binocular rivalry is indeed *(feature) selective*: Inputs originating from a suppressed image are not necessarily affected equally.

The magnitude of suppression is not only affected by the relative difference in feature content between the rivaling images; variations in feature content within one image can influence suppression as well. Local feature differences within a single image can also alter the magnitude of suppression during rivalry (Paffen, Naber, & Verstraten, 2008; Stuit, Verstraten, & Paffen, 2010). That is, when a suppressed image contains multiple homogeneously oriented items and one oddball, the deviating item will reach perceptual dominance first. This bias in the origin of a perceptual alternation suggests that suppression is attenuated for regions in the suppressed image that are perceptually salient. Again, these findings indicate that binocular rivalry suppression can be selective.

While a loss of awareness for suppressed images is accompanied by a loss in sensitivity as described above, sensitivity during the dominance phase is believed to be unaffected by the presence of a suppressed rival image. Correspondingly, sensitivity to probes presented in the dominant image appears to remain largely unaffected by suppressed images (Blake & Camisa, 1979; Westendorf, 1989). Based on these results, perception during dominance has often been referred to as equivalent to non-rivalrous monocular viewing conditions (Alais & Blake, 2005; Gilroy & Blake, 2004; Tsuchiya, Koch, Gilroy, & Blake, 2006). However, in 1962, Treisman already showed that stereo depth perception can coexist with binocular rivalry. This suggests that at least some of the suppressed signals can survive rivalry suppression to alter perception during dominance. Recent findings strengthen this idea (Andrews & Blakemore, 2002; Carlson & He, 2000; Pearson & Clifford, 2005). For instance, Andrews and Blakemore (2002) showed that dichoptically presented gratings with orthogonal orientations and motion directions could combine during rivalry. Specifically, when perception alternated, the two drifting gratings often combined into a plaid with a single motion direction. Temporal frequency information has also been shown to integrate during rivalry. Carlson and He (2000) have shown that temporal luminance modulations of two competing images, having different modulation frequencies, can integrate into binocular beats (a slow flicker amplitude modulation that corresponds to the difference between the two primary frequencies), during rivalry of the images. We believe that this integration can be explained by the lack of rivalry between dichoptically presented slow and fast motion signals (van de Grind, van Hof, van der Smagt, & Verstraten, 2001). These findings show that part of the visual information of a suppressed image can actually escape phenomenal suppression to be part of the percept during rivalry. However, perception of part of the suppressed image (i.e., the temporal frequency or the orientation and motion signals) means that the image is not completely suppressed during rivalry. Using an

approach that bypasses this problem, Pearson and Clifford (2005) showed a different example of suppressed visual features altering perception during the dominance phase of binocular rivalry. In their experiment, Pearson and Clifford used rivaling gratings to show that the perceived orientation of a *dominant* grating is systematically biased by the orientation of a suppressed grating. The magnitude of the difference between the perceived and the physical orientation, as well as the direction of this effect (a clockwise or counterclockwise shift in perceived orientation), depended on the orientation difference between the two competing images. These results suggest that a suppressed image affects the percept of a dominant image in a way that depends on the relative difference in feature content between the two images. Note that this dependence on feature content is similar to the dependence observed between feature content and the magnitude of suppression (see above).

In the current study, we aim to unravel the mechanisms underlying the interaction between a suppressed image and perception of a dominant one. The suggested dependence on relative differences in feature content between two images is of particular interest. Moreover, if such a dependency is present, how does this relate to a non-rivalrous situation where suppression is not a factor and both images are simultaneously perceived?

## Experiment 1

In **Experiment 1**, we investigated how suppressed images affect perception of dominant images during binocular rivalry. We measured sensitivity to orientated probes added to a dominant retinal image to assess the influence of suppressed visual information, referred to as the mask, on perception during rivalry dominance. This constituted our dichoptic condition. We used a baseline condition without a suppressed image to test if performance during the dominance phase of binocular rivalry differs from non-rivalrous monocular viewing. Furthermore, to test the role of the visibility of the masks, we also measured performance during a monocular condition where the test probes were directly presented onto the masks, while a flat gray image of background luminance was presented to the other eye.

## Methods

### Observers

Six observers, including one of the authors (SS) participated in the experiment. All had normal or corrected-to-normal vision, and all but SS were naive as to the purpose of the study. All observers were experienced psychophysical observers.

## Apparatus

Stimuli were created on an Apple Mac Pro computer running system OS X and Matlab 7.4 with the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). The stimuli were presented on a linearized LaCie III 22" display at 75 Hz. Observers viewed the stimuli through a mirror stereoscope. The length of the optical path, from the eyes via the mirrors to the monitor, was 57 cm.

## Stimulus and procedure

In [Experiment 1](#), observers performed a 2AFC orientation discrimination task on the oriented test probes presented in three different viewing conditions ([Figure 1](#)). The test probes (1.5° of visual angle, 6.25 cpd) consisted of sine-wave gratings whose edges were smoothed with a cosine ramp of 0.32° of visual angle. The orientation of the test probes was either 5° clockwise (cw) or counter-clockwise (ccw) from vertical. The presentation of the probes was self-initiated via a press of the space bar. The timing of this initiation by the observer depended on the viewing condition (see below). After presentation of the probe, observers used the arrow keys to indicate whether the probe was oriented cw or ccw from vertical. The contrast of the probes was varied using two independent, randomly interleaved, staircases (QUEST; Watson & Pelli, 1983), both estimating the 75% correct threshold for orientation discrimination.

Using a block design, the probes were presented in different viewing conditions: a dichoptic viewing condition, a monocular viewing condition, and a baseline condition. In the dichoptic viewing condition ([Figure 1A](#)), a sine-wave grating, which we will refer to as the “mask,” was presented to one eye, while a spatial-frequency-filtered pixel noise image was presented to the other. The masks (6.25 cpd, 98% Michelson contrast) could have one of five orientations (5, 15, 20, 45, or 90° cw relative to the probe orientation). The noise image (98% Michelson contrast) was used to initiate binocular rivalry but also served as a pedestal for the probe. The pixel noise was band-pass filtered such that the frequency power spectrum matched that of the gratings. Both the mask and the noise image were presented within a circular aperture with a diameter of 2° of visual angle. Observers were explicitly instructed to only initiate the presentation of the probe during the dominance phase of the noise image. The observers repeated the trial if an alternation occurred during the presentation of the probe. After initiation by the observer, the probe was superimposed on the noise image. The contrast of the probe first increased and subsequently decreased along a Gaussian profile to avoid abrupt temporal onsets. The sigma of the Gaussian was 7 ms and its amplitude was chosen to match the contrast of the probe. Note that the amplitude of the Gaussian thus varied on a trial-by-trial basis based on the current QUEST estimate. To keep the mean luminance of the image

constant, the increase in contrast of the probe was mirrored by an equal decrease in the (local) contrast of the noise image on which it was presented. The total presentation duration of the probe, from 0% contrast to the desired probe contrast and back again, was 400 ms. This viewing condition resulted in binocular rivalry between the grating and the noise image.

In the monocular viewing condition ([Figure 1B](#)), the masks from the dichoptic viewing condition were presented to one eye while a uniform gray field of average luminance was presented to the other eye. In this condition, the probes were superimposed on the masks. Observers initiated the probes, via a press of the space bar, when the masks were clearly visible. This viewing condition resulted in continuous perceptual dominance of the masks and the probes.

In addition to the dichoptic and monocular viewing conditions, we used a baseline condition ([Figure 1C](#)) in which the probe was presented in the pixel noise image, as was the case for the dichoptic condition. However, a uniform gray field of average luminance was presented to the other eye. Observers initiated presentation of the probes when the noise image was perceived. This viewing condition also resulted in continuous perceptual dominance of the noise image and the probes.

## Results and discussion

Results for [Experiment 1](#) are shown in [Figure 2](#). For each observer’s monocular as well as dichoptic viewing condition, the threshold estimates from the two QUEST staircases for each mask orientation were averaged to obtain a single 75% correct threshold for probe orientation discrimination. To test whether thresholds for the monocular and dichoptic viewing conditions were different from the baseline condition, performance was first pooled across the 5 different orientations of the mask for both the monocular and dichoptic viewing conditions separately. This resulted in two scores reflecting performance across all mask orientations, one for dichoptic viewing and for monocular viewing. The average threshold for the dichoptic viewing condition was significantly higher than the average of the baseline condition ( $t(5) = 2.87, p = 0.035$ ). Similarly, the average threshold for the monocular viewing condition was also higher than that of the baseline condition ( $t(5) = 13.18, p < 0.001$ ). This indicates that the mask significantly interfered with discriminating the orientation of the probe, both when the mask was perceived (monocular viewing condition) and when it was suppressed from awareness (dichoptic viewing condition). These results show that perception during binocular rivalry dominance (dichoptic viewing condition) is *not* the same as non-rivalrous monocular viewing (baseline condition).

Next, we compared performance in the monocular and dichoptic viewing conditions using a  $2 \times 5$  (viewing condition by relative orientation) repeated measures

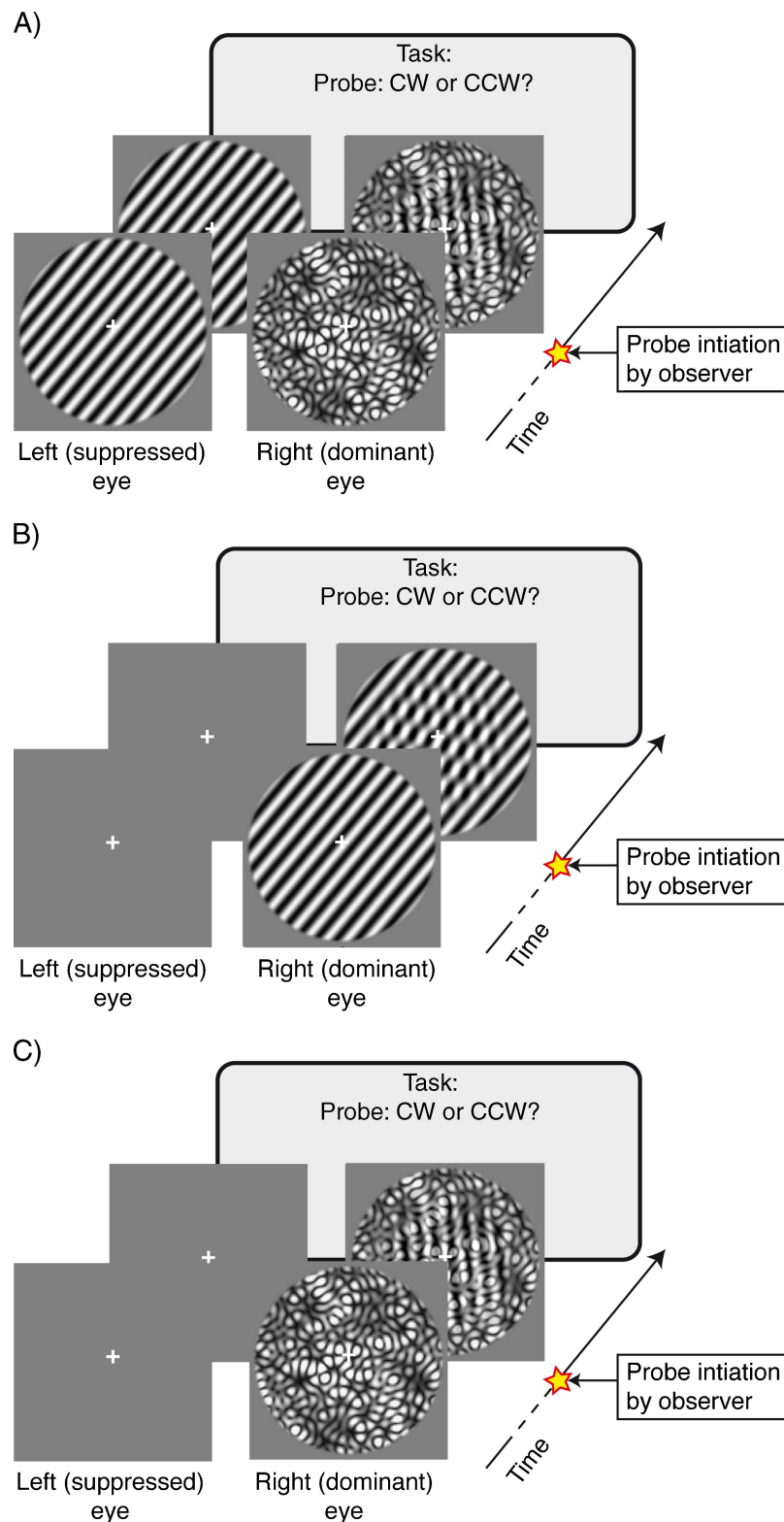


Figure 1. Schematic representation of the stimulus and task for each condition of [Experiment 1](#). (A) In the dichoptic viewing condition, a pedestal consisting of band-pass-filtered pixel noise was presented to the right eye. A grating (mask) was presented to the left eye. After the observer indicated that the pedestal was perceptually dominant, a test grating (probe) was presented in the center of the image. This grating was oriented either  $5^\circ$  cw or ccw from vertical. The observer's task was to indicate the orientation of the grating. (B) In the monocular viewing condition, the mask was replaced with an image of background luminance. However, the pedestal was replaced with the mask. The probe was now presented in this image. (C) The baseline condition also used background luminance as the left eye's image. The task and the right eye's image were identical to the dichoptic viewing condition.

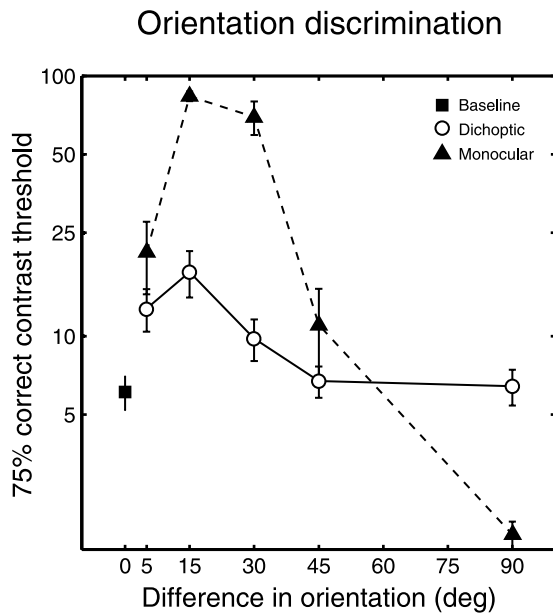


Figure 2. Results of Experiment 1. The solid line with open circles indicates the 75% correct orientation discrimination thresholds for the dichoptic viewing condition. The dashed line with black triangles indicates the thresholds for the monocular viewing condition. Thresholds are presented in Michelson contrast. The black square indicates average baseline performance. Error bars represent  $\pm 1$  SEM. Note that, although the amplitudes differ, both conditions show similar effects of relative orientation. In both conditions, interference peaks at a mask orientation of  $\sim 15$  degrees relative to the probe.

ANOVA. The results show main effects for viewing condition (dichoptic compared to monocular;  $F(1,5) = 68.54$ ,  $p < 0.001$ ) and for the relative orientation of the mask ( $F(4,20) = 47.15$ ,  $p < 0.001$ ) as well as an interaction between viewing condition and relative mask orientation ( $F(4,20) = 29.07$ ,  $p < 0.001$ ). Further comparisons based on the main effect of orientation show that both the dichoptic ( $F(4,20) = 6.831$ ,  $p < 0.01$ ) and monocular viewing conditions ( $F(4,20) = 40.885$ ,  $p < 0.001$ ) contain significant effects of relative orientation. This shows that under both monocular and dichoptic viewing conditions, the effect of the mask depends on the difference between the orientation of the mask and that of the probe. For both viewing conditions, the highest discrimination thresholds for the probes are at the  $15^\circ$  masks. However, based on previous results showing suppressive interactions during rivalry, one can expect the peak in our distribution to be at  $5^\circ$  relative to the probe (Stuit et al., 2009; also see Ling, Pearson, & Blake, 2009). We suggest that this is due to the spatial phase of our probes relative to that of the masks. It is known from masking studies that iso-oriented masks that are in-phase can facilitate probe detection (Georgeson & Georgeson, 1987). Indeed, our masks and probes were in-phase. The correspondence to these lower thresholds in our results and effects found in masking

studies strengthens previous suggestions that binocular rivalry and masking involve a common suppressive process (Baker & Graf, 2009).

The pattern of dependency on relative orientation difference between the probes and masks was similar for both conditions. However, all thresholds, except for the  $90^\circ$  masks, were larger in the monocular viewing condition (see Figure 2). The interaction between viewing condition and the relative orientation of the mask reflects the lower threshold for the  $90^\circ$  mask in the monocular viewing condition in combination with all other thresholds being higher. We suggest that the lower threshold for  $90^\circ$  mask is due to center-surround interactions. For orthogonal orientations, center-surround interaction can result in facilitation to the center (Cass & Spehar, 2005; Gilbert & Wiesel, 1990). However, this effect is not observed in the dichoptic condition. We suggest that this is because the surrounds were suppressed during the presentation of the probes and weaker surrounds result in weaker center-surround interactions (Snowden & Hammett, 1998). In conclusion, our results indicate that perception during binocular rivalry dominance (dichoptic viewing condition) depends on the content of the suppressed image. The suppressed image therefore has a selective influence on sensitivity to the dominant image.

## Experiment 2

In Experiment 1, we observed interactions in both the dichoptic and monocular viewing conditions, based on the orientation of the mask relative to the probe. Although this is in accordance with our hypothesis, stating that the difference in feature content modulates the degree to which suppressed and dominant images interact during binocular rivalry, this interaction may be limited to *orientation* information. To test the possibility that other features show similar interactions during rivalry, we set out to extend the findings of Experiment 1 using a different feature: *global motion direction*. The main reason for this choice is the assumed dependency on visual areas more upstream in the visual system compared to orientation processing (Albright, 1984; Schiller, Finlay, & Volman, 1976). In Experiment 2, we measured the influence of masks containing a range of different motion directions on motion direction discrimination of the probe. As in Experiment 1, the masks and probes could be presented either monocularly or dichoptically.

## Methods

### Observers

Six observers, including one of the authors (SS) and 2 observers from Experiment 1, participated in the experi-

ment. All had normal or corrected-to-normal vision and, except for SS, were naive to the purpose of the study.

### Apparatus

The experimental setup was the same as for [Experiment 1](#), except that the refresh rate of the monitor was increased to 85 Hz to facilitate the percept of smooth motion.

### Stimulus and procedure

In [Experiment 2](#), observers performed a 2AFC motion direction discrimination task under three different viewing conditions ([Figure 3](#)). The probes in this experiment consisted of pixel noise images in which the noise was moving either left- or rightward at a velocity of 1.13 deg/s. To obtain the 75% correct threshold for motion direction discrimination, the contrast of the probes was varied using adaptive staircases for each mask direction (QUEST; Watson & Pelli, 1983). Each threshold was estimated twice using independent, randomly interleaved, staircases. As in [Experiment 1](#), presentation of the probes was self-initiated via a press of the space bar after which observers indicated (in a 2AFC design) whether the motion in the probe was to the left or to the right using the arrow keys.

As in [Experiment 1](#), we had three viewing conditions: dichoptic, monocular, and baseline conditions. In the dichoptic viewing condition, a mask was presented to one eye, while the pedestal for the probe was presented to the other eye ([Figure 3A](#)). The masks consisted of white noise images in which the noise moved linearly in one of several possible directions. The speed in the masks was identical to that in the probes. The difference in motion direction between mask and probe was varied from 15° to 165°, in 15° steps. The mask was always presented at 7.2% RMS contrast. The relatively low contrast for the masks, compared to [Experiment 1](#), was chosen to counter the strong tendency for linear motion signals to be dominant during rivalry (as seen in a pilot version of the experiment). We did not expect any difference in using low-contrast compared to high-contrast masks since performance on global motion performance saturates at relatively low contrasts (Edwards, Badcock, & Nishida, 1996; Müller & Greenlee, 1994). For the pedestal, which was used for the superimposition of the probes as well as to instigate binocular rivalry, we again used a white noise image (29% RMS contrast). The noise in the pedestal, however, rotated at .24 revolutions/s. The rotation direction was randomized and could be either cw or ccw. To avoid abrupt onsets, the probes were superimposed on the pedestal using a temporal Gaussian profile. This means that the probe contrast first increased and subsequently decreased over time. The sigma of the Gaussian was 8 ms and the amplitude corresponded to the contrast of the probe. Note that the amplitude thus varied per trial based

on the current QUEST threshold estimate. To keep the average luminance of the image constant, the increase in contrast of the probe was mirrored by an equal decrease in the (local) contrast of the image on which it was presented. The total presentation duration of the probe, from 0% contrast to the desired probe contrast and back to zero, was 258 ms. During the dichoptic viewing condition, observers waited for the dominance phase of the pedestal before they initiated the presentation of the probe. Observers were instructed to repeat the trial in case an alternation occurred during presentation of the probe. This viewing condition resulted in binocular rivalry of the competing noise images.

In the monocular viewing condition ([Figure 3B](#)), the probes were superimposed on a combination of the pedestal and masks used in the dichoptic viewing condition. This combination was created using the alpha blending functions of the Psychophysics Toolbox, which kept the contrast ratio of the images the same as in the dichoptic viewing condition. This combined image was presented to one eye while a uniform gray field of average luminance was presented to the other. We chose to combine the mask and pedestal into a single image since the contrast of the mask was only 7.2% RMS in this experiment. Superimposing the probes onto the masks as in [Experiment 1](#) would result in different contrast-based signal-to-noise ratios of the probe and pedestal between the two viewing conditions. More specifically, the signal-to-noise ratio of the probe would be almost four times greater in the monocular viewing condition compared to the dichoptic viewing condition. This would make the comparison between the two viewing conditions very difficult. Note that this viewing condition resulted in continuous perceptual dominance of the mask–pedestal combination onto which the probes were presented.

As in [Experiment 1](#), we also used a baseline condition in which no mask was presented ([Figure 3C](#)). The probe was presented on the rotating white noise only, just as in the dichoptic condition. However, here a uniform gray field of average luminance was presented to the other eye. This viewing condition resulted in continuous perceptual dominance of the white noise image onto which the probes were presented.

## Results and discussion

Results for [Experiment 2](#) are displayed in [Figure 4](#). For each observer, the two threshold estimates for each mask direction from the monocular and dichoptic viewing conditions were averaged to obtain a single threshold for motion discrimination. We first tested whether performance during the monocular and dichoptic viewing conditions was different from the baseline condition. For this, the threshold estimates for all mask directions of both viewing conditions were first pooled separately. The

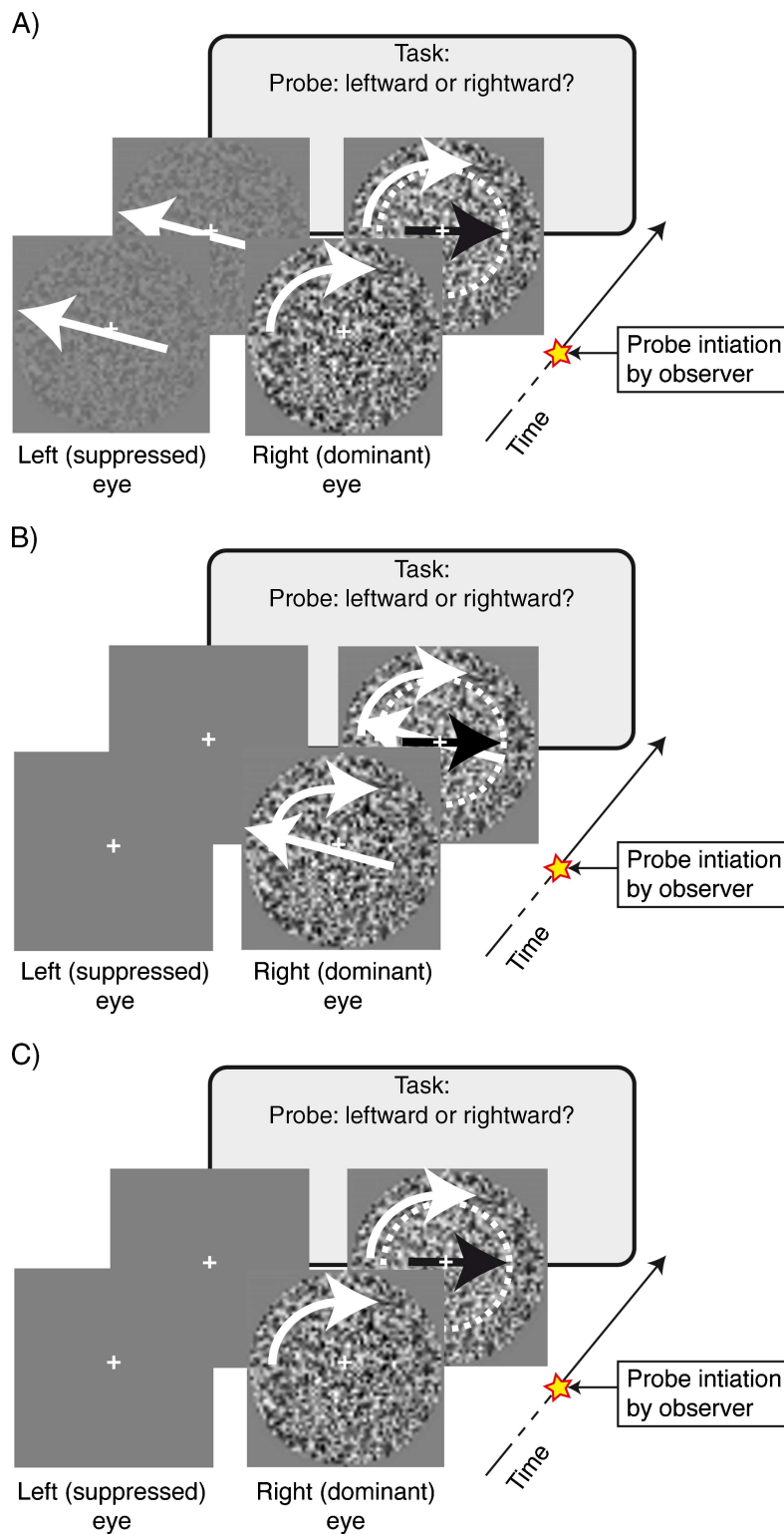


Figure 3. Schematic representation of the stimulus and task for each condition of [Experiment 2](#). The arrows indicate one of the possible directions of motion. (A) In the dichoptic viewing condition, the pedestal consisted of an image of rotating pixel noise and was presented to the right eye. The rotation direction could be either cw or ccw. A pixel noise image (mask) was presented to the left eye. After the observer indicated that the rotating noise image was perceptually dominant, a probe was presented in the center of the image, as indicated by the dotted white circle. The probe contained either leftward or rightward moving noise. The observer's task was to indicate the direction of motion in the probe. (B) In the monocular viewing condition, the left eye's image was background luminance only. The right eye's image consisted of a combination of the mask and the rotating noise image. (C) In the baseline condition, the right eye's image was the same as in the dichoptic viewing condition. An image of background luminance was presented to the left eye.

averages of the pooled estimates were subsequently compared to the baseline performance. Unlike the results of [Experiment 1](#), the dichoptic and monocular viewing conditions did not differ from the baseline condition (dichoptic:  $t(5) = 0.133$ ,  $p = 0.899$ ; monocular:  $t(5) = 0.908$ ,  $p = 0.405$ ). However, inspection of [Figure 4](#) suggests that the effect of the masks might be limited to the probe–mask combinations with the greatest difference in direction. To test whether direction discrimination performance of the probes is differentially affected by the direction of the mask, we used a  $2 \times 11$  (viewing condition by relative motion direction) repeated measures ANOVA to test for a dependency on (relative) motion direction of the mask. The analysis revealed a significant main effect of direction ( $F(10,50) = 6.78$ ,  $p < 0.001$ ). Interestingly, we found no difference between the viewing conditions (dichoptic vs. monocular;  $F(1,5) = 1.573$ ,  $p = 0.265$ ) and no interaction between mask direction and viewing condition ( $F(10,50) = 0.84$ ,  $p = 0.590$ ). These results show that the masks affected probe discrimination similarly across viewing conditions, irrespective of whether the mask was dominant in perception or not.

Interestingly, the pattern of results differs from that of [Experiment 1](#). In that experiment, the magnitude of the orientation effect differed between viewing conditions. The discrepancy in effect sizes for orientation (dichoptic mask effect differs from the monocular mask effect) and motion direction (no difference in masking effects between the dichoptic and monocular viewing conditions) may be explained by a difference in methods between the monocular viewing conditions of the experiments. In [Experiment 1](#), we used the masks from the dichoptic viewing condition as the pedestal for the monocular viewing condition. This means that the interfering orientation signals were stronger in the monocular viewing condition, compared to the dichoptic, since they were not suppressed from awareness. However, in the monocular viewing condition of [Experiment 2](#), we used a combination of the mask and the noise image as the pedestal. Here, the strengths of the interfering motion signals were the same for both the monocular and dichoptic viewing conditions. The relatively greater strength of the orientation masks (for monocular compared to dichoptic, in [Experiment 1](#)) may explain why the probe discrimination thresholds were higher in the monocular compared to the dichoptic viewing condition. To test this possibility, we ran a control experiment in which we combined the oriented mask and noise image in the same manner as [Experiment 2](#). Three observers from the original experiment completed the 15°, 30°, and 45° (relative to the probe) mask conditions. We found no difference between the control and the original monocular condition (mean thresholds for original 15°, 30°, and 45° conditions: 84.96, 62.64, and 7.96, respectively; mean thresholds for control 15°, 30°, and 45° conditions: 92.32, 66.18, and 13.10, respectively;  $F(1,2) = 0.461$ ,  $p = 0.567$ ) nor did we find any interaction between the version of the experiment (original or control) and

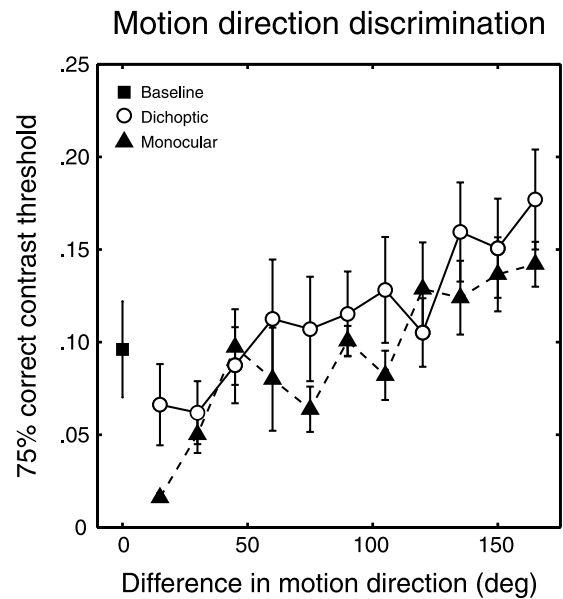


Figure 4. Results of [Experiment 2](#). The solid line with open circles indicates the average 75% correct motion direction discrimination thresholds for the dichoptic condition; the dashed line with the black triangles shows the average thresholds for the monocular condition. The black square indicates the average threshold of the baseline condition. Thresholds are represented in RMS contrast. Error bars represent  $\pm 1$  standard error of the mean. These results show the dependency on the difference in motion direction between mask and probe for both the monocular and dichoptic conditions. Note also that the thresholds are similar for the different conditions.

relative orientation (15°, 30°, or 45°;  $F(2,4) = 0.064$ ,  $p = 0.939$ ). This shows that the composition of the pedestal cannot explain the larger orientation effects in the monocular compared to the dichoptic viewing condition.

## General discussion

In this study, we investigated the interactions between suppressed and dominant images when engaged in binocular rivalry. We measured sensitivity to both orientation probes and motion direction probes added to a dominant retinal image to assert the influence of suppressed visual information on perception during rivalry dominance. The results show that, in contrast with a long-standing belief, perception during the dominance phase of binocular rivalry is affected by the suppressed image. Moreover, we show that, for features like orientation and motion direction, the effect exerted by suppressed images on perception during dominance depends on the difference in feature content (e.g., orientation difference) between the rivaling images. The nature of the interaction was the same during non-rival viewing conditions. This suggests that an image, which is



suppressed from awareness, affects a perceptually dominant image *as if* it were actually visible.

For rivaling orientations and motion directions, the amount by which a suppressed image affects perception during dominance depends on the relative differences between the two images. The dependency on these relative differences suggests a general role for feature interactions in binocular rivalry. This suggestion is in line with previous suggestions based on exclusivity during rivalry (Knapen, Kanai, Brascamp, van Boxtel, & van Ee, 2007) as well as the strength of rivalry suppression (Stuit et al., 2009). For instance, orientation discrimination performed on test probes during the suppression phase shows a similar dependency on the relative orientation difference between the probe and the suppressed image as found in the current study (Stuit et al., 2009). Thus, an image that is suppressed during rivalry affects probes presented during dominance similarly as those presented during suppression.

At first sight, a possible explanation for the results of [Experiment 1](#) is adaptation to the mask's orientation. Some adaptation effects have been shown to persist even when an image is suppressed from awareness (see Blake & He, 2005 for a review). Although some adaptation is likely to have occurred, our methods exclude adaptation as a causal factor. More specifically, adaptation to the mask orientation would affect both the clockwise and counterclockwise probes in the same manner within each mask condition with either attraction or repulsion (e.g., leading to a tilt aftereffect). This is because the masks were always presented cw relative to the probes. Adaptation to the masks would then result in one of the probes being perceived more tilted *toward* vertical (e.g., more difficult to discriminate from vertical), while the other probe is perceived as tilted more *away* from vertical (e.g., less difficult to discriminate from vertical). Since the orientation of the probe was counterbalanced, any adaptation effects would be averaged out of the discrimination thresholds. Although this does not mean that there was no adaptation to the different mask orientations in the experiment, it does imply that the pattern in our results is not caused by adaptation. Note that adaptation cannot be considered as a causal factor in [Experiment 2](#) since the pattern of direction dependency is opposite to what is expected for adaptation: Masks with similar directions to the probe do not interfere with probe direction discrimination.

Previous looks at interactions between images competing for awareness during rivalry have shown only modest effects. Pearson and Clifford (2005) showed that the effect of a suppressed grating on the percept of a dominant grating during rivalry is reduced approximately by a factor of 6, in comparison to the condition in which the suppressed grating was simultaneously perceived. We found a similar reduction in [Experiment 1](#). However, in [Experiment 2](#), the effect of the masks on motion discrimination was similar in terms of magnitude for both dichoptic and monocular viewing conditions. This shows that the reduction in effect size due to suppression does

not hold for all features. Instead, the different effect sizes demonstrate that orientation signals exert less influence on perception during dominance than motion signals.

The above is likely to be due to the difference in the loci of processing of orientation and motion direction stimuli. Compared to other areas, V1 has the greatest percentage of orientation-selective cells (Schiller et al., 1976), whereas area MT has the largest percentage of direction-selective cells (e.g., Albright, 1984; Snowden, 1994). While the majority of orientation-selective cells in V1 exhibit at least some eye preference (e.g., Hubel & Wiesel, 1962), the direction-selective cells in MT receive exclusive binocular inputs (e.g., Rodman, Gross, & Albright, 1989). If we take these different properties of areas V1 and MT into account, the neurons responsive to our stimuli in [Experiment 1](#) were only partly overlapping between the monocular and dichoptic viewing conditions, resulting in different effect sizes for the two conditions. However, the same neurons might have been involved in both the monocular and dichoptic viewing conditions of [Experiment 2](#). Hence, the similar results observed there. It is generally acknowledged that rivalry competition can occur at multiple stages of the visual processing hierarchy (Blake & Logothetis, 2002; Freeman, 2005; Lee, 2004; Nguyen, Freeman, & Alais, 2003; Silver & Logothetis, 2007). The occurrence of rivalry competition at different stages for motion direction and orientation stimuli is then relevant when one tries to explain the differences in the magnitude of interference between the monocular and dichoptic viewing conditions.

The assumption of different loci also concurs with the difference in interference patterns of the two experiments. In area V1, neighboring cells with *similar* orientation tuning inhibit each other (De Valois, Yund, & Helper, 1982). This property is reflected in the results of [Experiment 1](#) where we found greater interference of *similar* orientations compared to orthogonal orientations ([Figure 2](#)). Although V1 shows direction selectivity, this area does not seem to exhibit directional opponency (Snowden, Treue, Erickson, & Anderson, 1991). In addition, V1 is less sensitive to global motion compared to MT (Braddick, O'Brien, Wattum-Bell, Atkinson, & Turner, 2000), limiting its involvement in the direction-dependent effects seen in the results of [Experiment 2](#). In contrast to V1, area MT does exhibit directional suppression: Cells with *opposite* preferred directions inhibit each other (Braddick et al., 2001; Snowden et al., 1991). Correspondingly, in [Experiment 2](#), we find the greatest interference by the masks containing a motion direction that is near *opposite* to that of the probe ([Figure 4](#)). The difference of the patterns of interference between the orientation and motion direction masks thus appears to result from their difference in processing loci.

In conclusion, in contrast to long-standing beliefs, our results show that perception during binocular rivalry dominance is affected by the nature of, and the difference between, the features present in the competing images.

This influence of the suppressed image is bidirectional: Sensitivity during dominance is similarly affected by the suppressed image as sensitivity during suppression. Moreover, our results show that the suppressed image affects perception during dominance as if it were actually visible.

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