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Feature-based activation and suppression during binocular rivalry

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ABSTRACT

In the past decade, effects of pattern coherence have indicated that perception during binocular rivalry does not result solely from reciprocal inhibitory competition between monocular channels. In this study we were interested in feature selectivity both during dominance and during suppression. The first experiment shows that a suppressed stimulus perceptually appears earlier when it shares features with a visible stimulus than when it does not. Subsequently, our second experiment suggests a reversal of this effect when similarity is exhibited with a suppressed stimulus. These findings hint at a role for both selective enhancing (Experiment 1) and selective inhibitory cortical mechanisms (Experiment 2) in causing image rivalry. From a phenomenological perspective these results suggest that we are not only selectively aware but also selectively unaware of specific features in the visual scene.

1. Introduction

When incompatible information is presented at the same retinal location to the left and the right eye, the input of both eyes compete for awareness. As a result, parts of the information presented on the retina are perceptually suppressed. Traditionally, this so-called binocular suppression has been argued to result from reciprocal inhibitory competition between monocular channels (Blake, 1989; Lehky, 1988). This low-level eye rivalry account is supported by neuropsychological data showing percept-correlated activity in early visual areas like the LGN (Haynes, Deichmann, & Rees, 2005; Wunderlich, Schneider, & Kastner, 2005). Although the important role of low-level monocular inhibitory mechanisms in binocular rivalry is widely acknowledged in the literature, there is accumulating evidence showing that, at least to a certain extent, competition can also occur between (binocular) image representations (e.g., Alais & Blake, 1999; Diaz-Caneja, 1928; Kovács, Papathomas, Yang, & Feher, 1996; Logothetis, Leopold, & Sheinberg, 1996). Such effects in binocular rivalry are commonly being referred to as image rivalry, as opposed to eye rivalry.

Support for the role of image rivalry can broadly be divided into two categories. First of all, there is a convincing line of research showing that as a result of interocular pattern coherence, perceptual dominance can be distributed between the input of both eyes. In a classical study on the role of pattern coherence in binocular rivalry, Diaz-Caneja (1928, translated by Alais, O'Shea, Mesana-Alais, & Wilson, 2000) presented two in itself irregular images to the eyes. Observers indicated that they were not only capable of seeing the monocular images presented to each eye, but also of seeing the more regular patterns which could be formed by combining parts of the images presented to each eye. Evidence for the role of (interocular) pattern coherence in determining perceptual dominance has not only been found at a featural level (see also e.g., Alais & Blake, 1999; Kovács et al., 1996; Ooi & He, 2003; van Lier & de Weert, 2003). Structural, more Gestalt-like grouping cues have also been shown to be effective in causing interocular pattern dominance (De Weert, Snoeren, & Koning, 2005; Suzuki & Grabowecky, 2002). All these demonstrations of perceptual grouping during binocular rivalry seem to support an image competition view on rivalry in which incompatible pattern representations compete for awareness at a higher level of visual processing. But, as argued by Lee and Blake (2004), local eye-based rivalry cannot be ruled out. Possibly, local competition between monocular channels dominates the rivalry process with top-down grouping factors modulating spatial interactions in perceptual dominance. Papathomas, Kovács, and Conway (2005) showed that the eye of origin and pattern coherence both play a role in binocular rivalry and from their results they argue in line with Lee and Blake that their result point to a theory somewhere between the extreme eye-based and image-based theories of binocular rivalry.

The influence of image interpretations on binocular rivalry processes has also been shown by using the so-called flicker and swap technique (Logothetis et al., 1996), in which rivaling stimuli are rapidly and repetitively swapped between the eyes. The basic effect is that a stimulus can maintain its dominance for a longer period than would be expected from an account purely based on eye competition (Bonneh, Sagi, & Karni, 2001; Kang & Blake, 2008; Lee & Blake, 1999; Logothetis et al., 1996; Pearson & Clifford, 2004). Although this effect is in itself convincing evidence for com-

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petitive interaction between pattern representations during binocular rivalry, the effect has been shown to be restricted to a rather narrow range of stimulus characteristics, like a rapid reversal rate and low-contrast stimuli (Lee & Blake, 1999). Furthermore, an investigation of the temporal characteristics of stimulus rivalry (Bartels & Logothetis, 2008) revealed an initial larger influence of eye-dependent processes on perceptual dominance. Over time, however, the effect reverses, with eye independent (stimulus-related) processes increasingly influencing perceptual switches.

Studies on image rivalry have primarily focused on dominance patterns. This has been the case both for studies on effects of pattern coherence (e.g., Diaz-Caneja, 1928; Kovács et al., 1996) and for studies showing effects of image rivalry using the flicker and swap technique (e.g., Logothetis et al., 1996; Pearson & Clifford, 2004). All these studies consistently show that (coherent) images can remain perceptually dominant for a longer period of time than what would be expected from an account of binocular rivalry purely based on eye competition. On the suppression side of binocular rivalry, so far, only a few studies have hinted at similar effects of image selectivity. Instead, binocular suppression has commonly been assumed to be the result of a non-selective attenuation of the visual input to the suppressed eye (Blake & Logothetis, 2002).

The common method to study binocular suppression is to measure suppression depths (e.g., Blake & Fox, 1974; Fox & Check, 1968; Nguyen, Freeman, & Wenderoth, 2001; O'Shea & Crassini, 1981; Ooi & Loop, 1994; Smith, Levi, Harwerth, & White, 1982; Wales & Fox, 1970). A typical finding is that sensitivity is reduced for probes presented to the suppressed eye compared to when they are presented to the dominant eye, which in itself can be seen as evidence for suppression within monocular channels. It has also been shown that the relative sensitivity to a test probe is largely independent of the similarity between a test probe and a suppressed stimulus on which the test probe was presented (Nguyen et al., 2001), which is again support for the dominant role of eye suppression in the process of resolving binocular rivalry. Furthermore, suppression depth is larger during conventional rivalry than during eye swapping (Bhardwaj, O'Shea, Alais, & Parker, 2008), which led to the conclusion that eye rivalry is reduced during eye swapping. It has been demonstrated that the chromatic sensitivity curve as a function of stimulus wavelength are different during dominance and during suppression (Smith et al., 1982). Where during the dominance phase the sensitivity curve clearly shows three peaks, corresponding with the chromaticity channels, the curve shows one single broad peak at 555 nm during suppression. These results are interpreted as indicating differential attenuation of chromatic and achromatic information during suppression. At this point it might be sensible to distinguish between two different definitions of stimulus selectivity during suppression. The selectivity shown in the study by Smith et al. and also by some other studies (e.g., Ooi & Loop, 1994) indicates that suppression depth is not similar for all stimulus features. In this study we want to investigate whether suppression of one or more specific features leads to a reduction of sensitivity to those features. Previous studies on suppression depth, like the one by Nguyen et al. (2001), suggest that this is not the case. The methods to investigate underlying mechanisms of binocular suppression in the past, however, have all been quite similar, focusing on the sensitivity to probes presented on the suppressed stimulus. There are a few studies that are indicative of the possible involvement of selective mechanisms during suppression. Alais and Parker (2006), for example, showed that, where sensitivity to face probes is reduced during suppression in face rivalry, a similar reduction of sensitivity for face probes does not occur when, instead of faces, motion pattern are engaged in rivalry. This shows that sensitivity to a test probe depends on its featural similarity with a suppressed stimulus, supporting the idea of selectivity during suppression. Furthermore, it has been reported that sensitivity to an orientation change during suppression is reduced depending on the magnitude of this change (O'Shea & Crassini, 1981) and that suppression of center motion was contingent on the direction of surround motion (Paffen, Alais, & Verstraten, 2005). A recent study of Stuit, Cass, Paffen, and Alais (2009) showed lower contrast sensitivity to a probe with orientations close to the orientation of a suppressed stimulus on which the probe is presented. All these findings point towards the involvement of feature selective mechanisms during suppression. In this study we take a rather different approach investigating feature selectivity during binocular rivalry. Two experiments are presented that provide support for the claim that feature selective processes do play a role not only during dominance (Experiment 1) but, to certain extent, also during suppression (Experiment 2).

In both experiments we will use a dichoptic suppression paradigm (van Lier & de Weert, 2003), which is pre-eminently efficient in exposing effects of image rivalry. In Experiment 1, we show that the visibility of a central grating speeds up the perceptual appearance of a similar, though suppressed peripheral grating, as compared to the perceptual appearance of a dissimilar suppressed peripheral grating. In Experiment 2, we subsequently show that the similarity effect from Experiment 1 tend to reverse when the central grating is perceptually suppressed during each trial. The results of the latter experiment show that a suppressed peripheral grating identical to a suppressed central grating tends to become visible later than a dissimilar suppressed peripheral grating. We interpret these results as support for the idea of feature selectivity during binocular suppression.

2. Experiment 1

2.1. Method

2.1.1. Observers

Fourteen undergraduate students (mean age 21.9 years) participated in this experiment. All observers had normal or corrected-to-normal vision and were naive with respect to the experimental questions. Observers received course credits for their participation.

2.1.2. Stimuli and material

In each trial, the same frame (Fig. 1) was presented to each eye at the same retinal location. This frame consisted of a dark grey background surface ($L = 14.12$ cd m^{-2}) and a lighter grey grid ($L = 60.38$ cd m^{-2}). On the grid, there were three squares (0.51° × 0.51°) with the same homogeneous grey color as the background frame. These three squares (the stimulus locations) were presented next to each other with a visual angle of 0.64° between the centers of each two neighboring squares. Stimuli were gratings with a diameter of 0.32°. These gratings were square-waved with a spatial frequency of 7.85 cycles/deg. The color of the gratings was either red ($CIE_{xy} = 0.4211$, 0.3270, $L = 15.59$ cd m^{-2}) and grey ($L = 8.01$

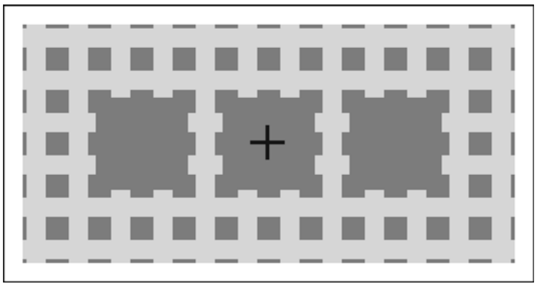

Fig. 1. The background frame, with dimensions 3.31° × 1.70° was presented to each eye.

cd m^{-2}), or green (CIE$_{xy}$ = 0.2665, 0.4160; L = 20.18 cd m^{-2}) and grey (L = 8.01 cd m^{-2}) with luminance contrast of 0.32 and 0.43 for the red–grey and the green–grey gratings, respectively. The orientation of the gratings was either horizontal or vertical.

The experiment was run on a PC-Pentium-III configuration, and stimuli were presented on a 19 in. CRT monitor. Stereoscopic vision was established by using a double mirror arrangement. The viewing distance (i.e., the length of the optical path) was 135 cm. Colorshop 2.6/monitor optimizer, X-Rite Inc., was used for monitor calibration and color measurements.

2.1.3. Procedure

During each trial, colored gratings were presented at all three stimulus locations, but each grating was presented to one eye only. The left flanking grating was always presented to the same eye as the right flanking grating, with both being presented either to the same eye as the central grating or to the other eye. In the first stage of each trial, the two flanking gratings were suppressed by two high contrast circular stimuli (suppressors) presented to the contralateral eye (Fig. 2). In most trials, suppression was complete during the whole first stage of 600 ms. This suppression was the result of the suppressors' high contrast compared to that of the gratings. The central grating remained visible for the participants during the whole trial.

In the second stage, the two suppressors were removed from the screen. As a result, the background frame was visible at the flanking gratings locations. Next, the suppressed gratings perceptually appeared at these locations. The moment of perceptual appearance of the two flanking gratings, however, was not necessarily the same. The task for the participants was to indicate after each trial with a key press which of the two flanking gratings became visible first in that trial. We chose not to measure reaction times, because we argued that instructing the participant to give a fast response could interfere with passively viewing the stimulus sequence during a trial. A third response button could be used by the participant to mark a trial as invalid if one of the flanking gratings became visible before removal of the suppressors or when for any other reason they were not able to judge which of the two flanking gratings became visible first.

2.1.4. Design

There were three similarity conditions: (1) Color & Orientation Similarity; the central grating had the same color and orientation as one of the flanking gratings but was different on both features compared to the other flanking grating, (2) Color Similarity; the central grating had the same orientation and color as one of the flanking gratings, but was different on color compared to the other flanking grating, and (3) Orientation Similarity; the central grating had the same color and orientation as one of the flanking gratings, but was different on orientation compared to the other flanking grating. Varying feature similarity (color vs orientation) and the degree of similarity (one feature vs two features) provides more insight in the generalizability of the similarity effects. As mentioned earlier, the two flanking gratings were always presented to the same eye, both either ipsilateral (intraocular feature similarity) or contralateral (interocular feature similarity) to the central grating. The distinction between intra- and interocular feature similarity is similar to the study by van Lier and de Weert (2003). Here we further explore whether effects of similarity to occur for both intra- and ocular conditions. The experiment was counterbalanced on each of the factors. For the Color Similarity conditions this means that in half of the trials the similar gratings were green and in the other half they were red. A similar balancing was applied to the other similarity conditions. Furthermore, the experiment was counterbalanced with respect to the side of the visual field on which the grating similar to the central grating was presented, and also with respect to the eye in which the central grating and the flanking gratings were presented, respectively. In total, there were 192 trials, which were presented in a randomized fashion.

2.2. Results

Analyses were performed on trials in which the flanking gratings were indeed suppressed during the suppression phase and in which participants were able to judge which of the two flanking gratings became visible first. Of all valid trials (82.0%; SD = 14.1), percentages were calculated in which the grating identical to the central grating perceptually appeared before the dissimilar grating. The Shapiro Wilk test revealed that for none of the conditions the distribution of percentages differed significantly from normality. Fig. 3 shows the results on the three similarity conditions. For all reported effects, mean percentages are given. Two-tailed student's t-tests reveal significant effects for each condition. In a majority of trials in the Color & Orientation Similarity condition (62.2%) participants saw the grating identical to the visible central grating appear before the dissimilar grating ($t_{13} = 4.14$, $p < 0.005$). This was also the case in the Color Similarity condition (58.6%; $t_{13} = 3.469$, $p < 0.005$), and in the Orientation Similarity condition (58.0%; $t_{13} = 4.648$, $p < 0.001$).

We will now focus on the trials in which the flanking gratings were presented ipsilaterally to the central grating (i.e., the intraocular feature similarity condition). In a majority of trials in the Color

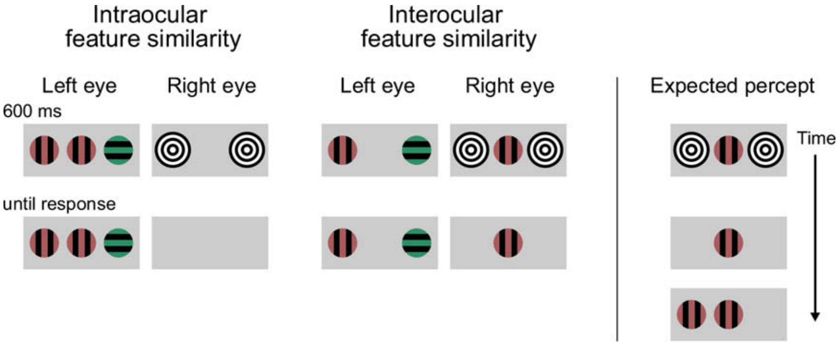

Fig. 2. A schematic representation of a trial in Experiment 1. In the first stage, two gratings were perceptually suppressed by presenting two high contrast elements at the same retinal locations to the other eye. Two feature similarity conditions were defined, in which two flanking gratings were presented either to the same eye as a central grating (intraocular feature similarity) or to the other eye (interocular feature similarity). Next, the suppressors were removed from the screen, which led to the visibility of the background grid at the flanking locations, followed by the perceptual appearance of the two suppressed flanking gratings. We expected that the grating similar to the suppressed central grating would become visible earlier than the dissimilar grating.

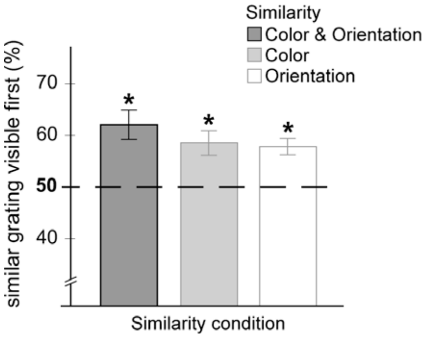

Fig. 3. Results of Experiment 1. Bars represent the percentage of trials (mean ± 1 SEM) in which the flanking grating similar to the visible central grating became visible first. For each bar, the maximum value (100%) corresponds with the total number of valid trials for that specific condition. Each percentage was tested against chance level ($^*p < .005$).

& Orientation Similarity condition (63.8%) participants saw the grating similar to the visible central grating appear before the dissimilar grating ($t_{13} = 4.276$, $p < 0.001$). This was also the case in the Color Similarity condition (60.0%; $t_{13} = 3.304$, $p < 0.01$), and in the Orientation Similarity condition (56.6%; $t_{13} = 3.848$, $p < 0.005$). Similar results were found when the flanking gratings were presented contralaterally to the central grating (i.e., the interocular feature similarity condition). In a majority of trials in the Color & Orientation Similarity condition (60.7%), participants saw the grating similar to the visible central grating appear before the dissimilar grating ($t_{13} = 2.756$, $p < 0.05$). Again, this was also the case in the Color Similarity condition (57.6%; $t_{13} = 2.493$, $p < 0.05$) and in the Orientation Similarity condition (59.1%; $t_{13} = 3.258$, $p < 0.01$).

2.2.1. Control experiment

To test whether the effects we found could be the result of a response bias, we have performed a control experiment. More specifically, we tested whether observers tended to respond that a flanking grating which was similar to the central grating was seen first. The stimuli used for this experiment were similar to the ones used in the original experiment. Each trial started with the presentation of the central colored grating to one of the eyes. After a short period (random between 500 ms and 1500 ms) the two flanking gratings were presented. This time, no suppressors were presented. Like in the original experiment, one of these flanking gratings was similar on color and orientation to the central grating. The other flanking grating was dissimilar to the central grating on both features. The flanking gratings were either presented at the same time or there was a 22 ms time interval between the presentation of the left and the right flanking grating. Observers ($n = 5$, 192 trials each) had to judge which of the two flanking gratings appeared first. When observers were not able to decide which grating appeared first they could indicate so, just like in the original experiment. For the trials in which both flanking gratings were presented simultaneously, observers were not able to make a judgment in 68.4% of the trials, i.e., they correctly indicated simultaneity. In 15.9% of the trials, they reported that they first saw the grating similar to the central grating and in 15.6% of the trials they first saw the dissimilar grating. All in all, there was no effect of similarity on the responses that were given. From these results we conclude that the effects found in Experiment 1 are not the result of a response bias and that the effects in Experiment 1 are caused by differential activation of suppressed gratings.

2.3. Discussion

In a majority of trials, observers saw the grating similar to the central grating appear before the dissimilar grating. The effects are similar for the intraocular and interocular similarity conditions and hold for both color and Orientation Similarity, but appear to be largest when feature similarity is defined by both features (color and orientation). These results add to the converging evidence for competition between image representations in binocular rivalry, in which similar stimuli have the tendency to be visible at the same time (e.g., Alais & Blake, 1999; de Weert et al., 2005; Diaz-Caneja, 1928; Kovács et al., 1996; Suzuki & Grabowecky, 2002; van Lier & de Weert, 2003). It should be noted that when the suppressors are taken away it takes some time before the flanking gratings become visible anyway (see also van Lier & de Weert). To get an indication of the duration of the interval between removal of the suppressors and perceptual appearance of the suppressed flanking gratings, we have additionally measured response times (five observers, 128 trials each) using an experimental setup in which both flanking gratings were either the same or different as compared to the central grating (having all other parameters similar to Experiment 1). The results revealed response times for the same and different conditions of 1191 ms and 1387 ms, respectively. In case of immediate visibility, one would expect mean reaction times no longer than 500 ms. So, when the suppressors are removed, all gratings tend to remain suppressed for some time as a result of rivalry between the gratings and the background grid in the contralateral eye. In fact, this stage in which gratings remain temporarily suppressed is crucial in our method, as it can reveal small differences in suppression strength between the two flanking gratings. Note that the method as used in Experiment 1 is rather different from the paradigms used in most previous studies on this topic. In most studies, dominance durations in ongoing perceptual alternations are used to measure effects of stimulus coherence. It has recently been shown that initial dominance characteristics during binocular rivalry are fundamentally different compared to dominance patterns during continuous viewing (Carter & Cavanagh, 2007), which could explain the discrepancy between previous findings and our current findings. Sobel and Blake (2002) used a paradigm where they suppressed one of four gratings by presenting a rotating checkerboard to the other eye. They found that global motion did not influence the perceptual appearance of the suppressed grating. The diverging results suggest that effects of perceptual grouping between visible and suppressed elements are rather feature dependent and that one has to be cautious in generalizing effects obtained with different paradigms and different stimulus characteristics.

After having shown that the suppression paradigm we used is a successful tool for exposing feature selective facilitative effects during binocular rivalry, we will use a modification of the paradigm to investigate possible effects of stimulus selectivity during binocular suppression. Where the central oriented grating was visible during the whole trial in Experiment 1, this central grating will be perceptually suppressed during the whole trial in Experiment 2.

3. Experiment 2

3.1. Method

3.1.1. Observers

Twenty-four undergraduate students (mean age 20.8 years) participated in this experiment. All observers had normal or corrected-to-normal vision and were naive with respect to the experimental questions. Observers received course credits for their participation.

3.1.2. Stimuli and material

In Experiment 2, the same stimuli and material were used as in Experiment 1.

3.1.3. Procedure and design

During each trial, colored gratings were presented at all three locations, as in Experiment 1. Again, the left flanking grating was always presented to the same eye as the right flanking grating, with both flanking gratings presented either ipsilaterally or contralaterally to the central grating. The main difference with Experiment 1 was that in this second experiment the central grating was suppressed during the whole trial (Fig. 4). Thus, in the first stage of each trial (600 ms), all three gratings were perceptually suppressed by presenting high contrast suppressors at each location to the eye contralateral to the grating. In the second stage, the two flanking gratings were removed from the screen. As mentioned earlier, the central grating remained suppressed during this stage. As in Experiment 1, the task for participants was to indicate with a button press which of the flanking gratings became visible first. The design of Experiment 2 was the same as the design of Experiment 1, with the same (counterbalanced) similarity conditions (Color & Orientation Similarity, Color Similarity, and Orientation Similarity). Again, participants had a third response option to indicate a trial as invalid, either when suppression was incomplete or when for any reason he or she was not able to judge which of the flanking gratings was visible first.

3.2. Results

Again, we have analyzed all valid trials (69.1%, SD = 16.0) in which the flanking gratings were indeed suppressed during the suppression phase. Of the valid trials, percentages were calculated in which the grating similar to the central grating perceptually appeared before the dissimilar grating. The Shapiro Wilk test revealed that for none of the conditions the distribution of percentages differed significantly from normality. Fig. 5 shows the results on the three similarity conditions. For all reported effects, mean percentages are given. Two-tailed student's *t*-tests reveal significant effects for the Color & Orientation Similarity condition. In a minority of trials in this condition (44.8%) participants saw the grating identical to the visible central grating appear before the dissimilar grating ($t_{13} = 2.589$, $p < 0.05$). There were no significant effects in the Color Similarity condition (46.7%; $t_{13} = 1.716$, $p = 0.10$) and in the Orientation Similarity condition (50.5%; $t_{13} = .524$, $p = 0.61$).

We will now focus on the trials in which the flanking gratings were presented ipsilateral to the suppressed central grating (intraocular feature similarity). The effect of the Color & Orientation Similarity condition was marginally significant ($t_{23} = 1.947$, $p = 0.064$), revealing that in a minority of trials (44.5%) participants saw the grating similar to the suppressed central grating before they saw the dissimilar grating. For Color Similarity this was the case in 44.2% of the trials ($t_{23} = 2.947$, $p < 0.01$). There was no significant effect of Orientation Similarity. For the trials in which the flanking gratings were presented contralateral to the suppressed central grating (interocular feature similarity) the results were as follows. For the Color & Orientation Similarity condition, in a minority of trials (44.7%) participants saw the grating similar to the suppressed central grating before they saw the dissimilar grating ($t_{23} = 2.345$, $p < 0.05$). For interocular feature similarity, there were no significant effects for the interocular Color Similarity and Orientation Similarity conditions.

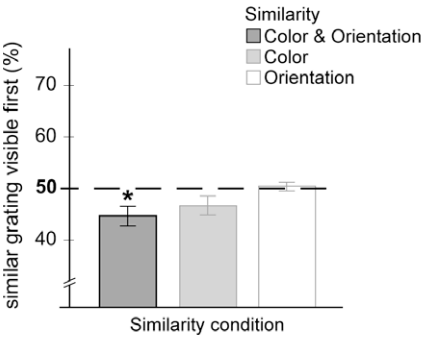

Fig. 5. Results of Experiment 2. Bars represent the percentage of trials (mean ± 1 SEM) in which the flanking grating similar to the suppressed central grating became visible first. For each bar, the maximum value (100%) corresponds with the total number of valid trials for that specific condition. Each percentage was tested against chance level ($^{*}p < .05$).

3.3. Discussion

When feature similarity between the suppressed central grating and one of the flanking gratings was defined by both color and orientation, similar results were obtained for the intraocular and interocular similarity conditions. That is, gratings identical to the suppressed grating tended to remain invisible for a longer duration than gratings which were different on both features, although this effect is marginally significant for the intraocular similarity condition. The relative delay in visibility as a result of similarity with a suppressed stimulus suggests feature selectivity during suppression. Such feature selectivity would counter the assumption that suppression is non-selective with respect to the features of the suppressed stimulus. For the conditions with a weaker similarity, defined by just one feature, the results are less clear-cut. Only for the intraocular Color Similarity condition we found a significant

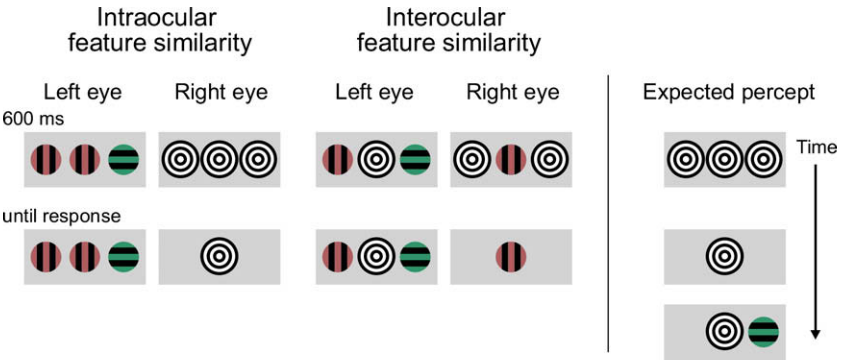

Fig. 4. A schematic representation of a trial in Experiment 2. In the first stage, all three gratings were perceptually suppressed. As in Experiment 1, feature similarity could be either intraocular or interocular. Next, the two flanking suppressors were removed from the screen, which led to the visibility of the background grid at the flanking locations, followed by the perceptual appearance of the two suppressed flanking gratings. We expected that the grating similar to the suppressed central grating would appear later than the dissimilar grating, as a result of feature suppression.

suppressive effect of feature similarity, which seems to suggest that also for suppressed stimuli the strength of perceptual grouping depends on the degree of similarity.

The effects of feature selectivity presented here seem to reveal two important characteristics of binocular suppression. First of all, they suggest that effects of perceptual grouping do not only occur during perceptual dominance, but also during suppression, outside visual awareness. In addition, these grouping effects during suppression reveal that the cortical representations of suppressed stimuli are, at least to a certain extent, selectively inhibited while suppressed. This goes against the idea that during suppression all input to the suppressed eye is attenuated in a non-selective fashion. Our findings converge with results of a few other studies which, using different methods, have already indicated that there might be a (feature) selective component to binocular suppression (Alais & Parker, 2006; O'Shea & Crassini, 1981; Paffen et al., 2005; Stuit et al., 2009). We must note that the selective effects found during binocular suppression in our study and in previous studies tend to be relatively subtle compared to similar selective effects during perceptual dominance, which leaves the question to which extent the mechanisms underlying this selective suppression influence the perceptual outcome during binocular rivalry.

4. General discussion

In this study we were interested in feature selectivity both during the dominance phase and during the suppression phase of binocular rivalry. There seems to be consensus in the literature that rivalry is resolved at multiple levels of visual processing. Both the literature on the neural correlates and recent hybrid models of binocular rivalry support this idea. Rivalry-related neural activity has been reported in lower-level visual areas LGN (Haynes et al., 2005; Wunderlich et al., 2005) and V1 (Lee, Blake, & Heeger, 2007; Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001), but also further up the visual stream in areas like V4 (Leopold & Logothetis, 1996) and MT (Logothetis & Schall, 1989). Hybrid models of binocular rivalry (Dayan, 1998; Freeman, 2005; Wilson, 2003) also suggest that reciprocal inhibitory interaction does not only occur between monocular neurons, but also between binocular pattern representations. The effects of pattern coherence (Alais & Blake, 1999; Diaz-Caneja, 1928; Kovács et al., 1996; Lee & Blake, 2004; van Lier & de Weert, 2003) and effects of image rivalry obtained from using the flicker and swap technique (Lee & Blake, 1999; Logothetis et al., 1996) emphasize the involvement of binocular image representations in binocular rivalry. In our Experiment 1, we also found effects of pattern coherence. More in particular, the similarity of a flanking grating with the central grating led to an earlier perceptual appearance compared to a dissimilar grating. One could speculate here about possible mechanisms by means of which stimuli with similar features facilitates removing of suppression. The results of Experiment 1 in fact resemble the results of previous studies (e.g., Kovács et al., 1996; van Lier & de Weert, 2003), showing that activation is facilitated by feature similarity. In addition, the results of Experiment 2 show that a relatively high similarity between a suppressed grating and a flanking grating may lead to a delayed visibility of the flanking grating. Note, however, that this inhibitory effect is weaker than the excitatory effect in Experiment 1. Nevertheless, the differential influence of the suppressed central grating on the visibility of the flanking gratings points at a selective feature-dependent mechanism during suppression.

Lateral connections that underlie perceptual groupings (e.g., Kovács et al., 1996) may have a role in the current feature selective effect. Both inhibitory and excitatory circuits as proposed in a hybrid account of binocular rivalry (Tong, Meng, & Blake, 2006) may further model the current effects. Tong et al., for instance, note that reciprocal excitatory connections among monocular neurons could account for grouping across adjacent areas of neurons with similar orientation preferences. Such mechanism could explain the feature selective facilitative effects we have reported in Experiment 1. It seems more difficult to account for the feature selective suppressive effects we have reported in Experiment 2 by means of similar mechanisms, purely relying on monocular excitatory–inhibitory circuits. Feedback projections from higher visual areas may also be involved in these effects of feature suppression. As Tong et al. argue, feedback projections could (in)directly activate inhibitory neurons at lower areas. That is, feature selective suppressive effects could possibly result from inhibitory feedback projections from binocular pattern representations to monocular inhibitory neurons. Note that, in a similar way, the facilitatory effects of feature similarity found in Experiment 1 could also be the result of (excitatory) feedback projections from binocular pattern representations.

All in all, our results show that, depending on the visibility of the central grating, the central grating may either lead to an earlier or to a later visibility of a the same flanking grating. Stating it in a different way, one could say that the current results suggest that identical stimuli have the tendency to be synchronized, not only in visibility, but also in invisibility. Notably, these results seem to challenge a non-selective view on binocular suppression. Further research should focus on the generalizabilty of these findings, e.g., when using other paradigms and different featural characteristics. Altogether, the results presented here suggest that the effects of image rivalry as reported in the binocular rivalry literature should not solely be explained in terms of selective enhancement, but also by selective inhibition of visual patterns. From a phenomenological perspective this would lead us to conclude that we are not just selectively aware, but also selectively unaware of specific parts of the visual scene.

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