



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.

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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 & Grabowecy, 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 re-

ported 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 ($L = 14.12 \text{ cd m}^{-2}$) and a lighter grey grid ($L = 60.38 \text{ cd m}^{-2}$). On the grid, there were three squares ($0.51^\circ \times 0.51^\circ$) 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 ($\text{CIE}_{xy} = 0.4211, 0.3270, L = 15.59 \text{ cd m}^{-2}$) and grey ($L = 8.01$

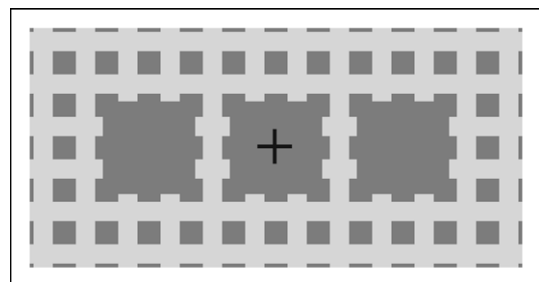


Fig. 1. The background frame, with dimensions $3.31^\circ \times 1.70^\circ$ was presented to each eye.

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