

# Strength and coherence of binocular rivalry depends on shared stimulus complexity

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## Abstract

Presenting incompatible images to the eyes results in alternations of conscious perception, a phenomenon known as binocular rivalry. We examined rivalry using either simple stimuli (oriented gratings) or coherent visual objects (faces, houses etc). Two rivalry characteristics were measured: Depth of rivalry suppression and coherence of alternations. Rivalry between coherent visual objects exhibits deep suppression and coherent rivalry, whereas rivalry between gratings exhibits shallow suppression and piecemeal rivalry. Interestingly, rivalry between a simple and a complex stimulus displays the same characteristics (shallow and piecemeal) as rivalry between two simple stimuli. Thus, complex stimuli fail to rival globally unless the fellow stimulus is also global. We also conducted a face adaptation experiment. Adaptation to rivaling faces improved subsequent face discrimination (as expected), but adaptation to a rivaling face/grating pair did not. To explain this, we suggest rivalry must be an early and local process (at least initially), instigated by the failure of binocular fusion, which can then become globally organized by feedback from higher-level areas when both rivalry stimuli are global, so that rivalry tends to oscillate coherently. These globally assembled images then flow through object processing areas, with the dominant image gaining in relative strength in a form of ‘biased competition’, therefore accounting for the deeper suppression of global images. In contrast, when only one eye receives a global image, local piecemeal suppression from the fellow eye overrides the organizing effects of global feedback to prevent coherent image formation. This indicates the primacy of local over global processes in rivalry.

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## 1. Introduction

The major debate in the recent binocular rivalry literature has concerned whether rivalry is a low-level ‘eye-based’ process or a high-level ‘stimulus-based’ process (Blake & Logothetis, 2002). There is evidence supporting both points of view and this debate is not entirely resolved (Alais & Blake, 2005; Kovacs, Papathomas, Yang, & Feher, 1996; Logothetis, Leopold, & Sheinberg, 1996; Tong & Engel, 2001; Wilson, 2003). In light of this conflicting evidence, however, there has been a growing acceptance that rivalry

must involve activity at various levels of cortical processing. Consequently, the more pertinent question currently concerns how these different levels interact to produce the perceptual switches from one eye’s view to the other that characterize binocular rivalry.

A number of papers provided evidence suggesting that rivalry could not be simply a low-level alternation between monocular processes. In one psychophysical study, two stimuli divided into a patchwork and intermingled between the eyes still produced periods of alternation between coherent images (Kovacs et al., 1996), indicating grouping between the eyes based on image coherence. In neurophysiological studies it was found that few single units in V1 exhibited activity alternations that correlated with perceptual alternations, whereas units in ascending areas were

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found increasingly to exhibit alternations correlated with perception (Leopold & Logothetis, 1996; Logothetis, 1998). Some neuroimaging studies also supported this finding, showing perceptually correlated signal changes occurring in extrastriate areas (Tong, Nakayama, Vaughan, & Kanwisher, 1998). Together, this evidence was interpreted as the conflicting binocular inputs not being resolved until extrastriate cortical areas (although strictly, the Tong et al. study indicated a resolution at *or before* extrastriate object processing areas). Other imaging papers, however, showed that activity in V1 did indeed correlate with perceptual oscillations (Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001), and that interocular grouping is possible within an interocular competition framework (Lee & Blake, 2004; Wilson, Blake, & Lee, 2001). The most recent neuroimaging evidence shows that even in LGN neural activity correlates with perceptual oscillations (Haynes, Deichmann, & Rees, 2005; Wunderlich, Schneider, & Kastner, 2005).

Recent psychophysical findings shed interesting new light on this conflicting literature, suggesting that it may not be a question of a low-level process or a high-level process, but a distributed process. These recent results suggest that low-level processes retain a central role in initiating rivalry (since rivalry is triggered by the failure of binocular fusion) and possibly also in regulating rivalry alternations since monocular neurons are only found in early visual cortex, but that they are modulated by higher-level processes through feedback (Carlson & He, 2004; Watson, Pearson, & Clifford, 2004). This arrangement allows global factors to influence rivalry, which is useful given the small extent and narrow tuning of V1 neurons, without needing to posit that the rivalry process actually occurs at those higher levels. This can be seen in a couple of examples. Kovacs et al. (1996) demonstration of interocular grouping seemed to be evidence against a low-level model of rivalry because such grouping would have to have occurred after the monocular ‘eye-based’ conflict posed in the traditional rivalry model (Blake, 1989). However, Lee and Blake (2004) showed that eye-based processes could explain interocular grouping, perhaps by invoking lateral cooperativity among local rivalry processes (Alais & Blake, 1999) and feedback from higher cortical areas responsive to global stimulus properties (Alais & Blake, 1998), both very reasonable assumptions given the wealth of psychophysically and neurophysiologically evidence for lateral and feedback interactions (Felleman & Van Essen, 1991; Gilbert, Das, Ito, Kapadia, & Westheimer, 1996). On their view, interocular grouping is simply a low-level rivalry process that becomes globally organized.

The role of global feedback onto local rivalry processes has been shown previously (Alais & Blake, 1998), although two recent demonstrations are particularly relevant. Carlson and He (2004) placed a fine-scale grid over two dichoptic drifting gratings. Without the grid, the gratings engaged in robust rivalry (as expected), however they failed to rival when the grid was added. They reasoned that fine-scale bin-

ocular fusion of the images was made possible by the grid, and that therefore rivalry failed to initiate. In the absence of rivalry, the component motions in each eye were simply integrated into a dichoptic plaid by a global motion mechanism downstream of V1. Plaid motion is known to be detected in area MT but not in V1, although MT does feedback strongly to V1. Their findings therefore support the idea that rivalry is initiated early (if fusion is not possible) but that global conflicts alone are not sufficient to provoke rivalry.

Watson et al. (2004) drew a similar conclusion. They induced binocular rivalry between global, point-light-walker stimuli. However, intermixing the stimulus elements between the eyes dramatically reduced rivalry. Clearly, at the binocular extrastriate levels thought to underlie detection of biological motion stimuli (Oram & Perrett, 1994), there are still two opposed walkers globally represented despite interocular mixing, but this was not sufficient to provoke rivalry. The point to be taken from both studies is that global processes appear to be unable to initiate rivalry themselves, and are instead only able to modulate rivalry once it is initiated, providing a global frame of reference for organization of local rivalry processes.

There are several aspects of the feedback model of rivalry that remain to be specified. It is known that feedback from extrastriate areas to primary visual cortex is widespread and it probably occurs regardless of whether viewing conditions give rise to normal fused vision or to rivalrous vision. One of the functions of feedback is to provide large-scale organization for the fine-scale topography of V1. Because feedback from global processes endows spatial organization on V1, we predict that there should be greater coherence in rivalry alternations when two global stimuli rival. We also predict that this spatial organization should lead to widespread coordination of rivalry activity at early levels, causing suppression depth to deepen for rivalry between global stimuli. The rationale for this is that coordination of many local rivalry processes into a coherent ensemble would make them all either dominant or suppressed at the same time, something that would rarely occur if they were not coordinated and were tending to operate independently. As independent processes, the average level of suppression over the whole stimulus area (encompassing several local rivalry processes at various phases of the rivalry cycle) would have to be shallower than when all are suppressed at the same moment. Experiment 1 will address the prediction regarding suppression depth, while Experiment 2 will examine the coherence of rivalry alternations.

## 2. Methods

### 2.1. Subjects

In total, nine subjects participated in these experiments, two of whom were the authors (DA & DM). The other seven observers were naïve with respect to the aims of the

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