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# Neural bases of binocular rivalry

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**During binocular rivalry, conflicting monocular images compete for access to consciousness in a stochastic, dynamical fashion. Recent human neuroimaging and psychophysical studies suggest that rivalry entails competitive interactions at multiple neural sites, including sites that retain eye-selective information. Rivalry greatly suppresses activity in the ventral pathway and attenuates visual adaptation to form and motion; nonetheless, some information about the suppressed stimulus reaches higher brain areas. Although rivalry depends on low-level inhibitory interactions, high-level excitatory influences promoting perceptual grouping and selective attention can extend the local dominance of a stimulus over space and time. Inhibitory and excitatory circuits considered within a hybrid model might account for the paradoxical properties of binocular rivalry and provide insights into the neural bases of visual awareness itself.**

## Introduction

Something fascinating happens when conflicting monocular images are presented to each of the two eyes. Rather than forming a stable composite, the two images rival for exclusive dominance, with perceptual awareness spontaneously alternating every few seconds between one image and the other (Figure 1). Called binocular rivalry, this remarkable phenomenon provides an effective means for investigating neural circuits involved in visual competition, perceptual grouping and selective attention. Moreover, because the observer's conscious state is continually in flux while the visual stimulus remains invariant, binocular rivalry might ultimately shed light on the dynamical properties of visual awareness and its underlying neural bases [1–4].

Vigorous debate about binocular rivalry has centered on three main issues: the potential sites of neural competition, the types of visual representations that compete at these sites, and the integrative mechanisms that coordinate competitive interactions between large-scale neuronal populations. According to one view, binocular rivalry arises from low-level interocular competition between monocular neurons in the primary visual cortex (V1) [5,6] or in the lateral geniculate nucleus (LGN) of the thalamus [7]. According to another view, binocular rivalry transpires later in visual processing and reflects competition between incompatible patterns rather than competition between the eyes [8,9]. In recent years, a coherent picture incorporating elements of both views has emerged [1], built around the idea that rivalry involves neural competition at multiple levels of the visual pathway [10,11].

Here, we review recent human neuroimaging and psychophysical studies that reveal the paradoxical nature of rivalry. Results from some of these studies indicate that binocular rivalry involves neural competition at remarkably early sites of the visual pathway, and that the instigation of rivalry depends on local, low-level competition. Other results, however, indicate that information about a suppressed stimulus reaches higher brain areas, and that perceptual grouping and top-down influences of selective attention can promote the dominance of a stimulus during rivalry. To make sense of these seemingly paradoxical results, we first describe a plausible hybrid framework to account for both low- and high-level properties of binocular rivalry.

It should be emphasized that this review focuses on recent evidence obtained from human observers. Reviews of neurophysiological [12] and earlier psychophysical studies [5] of rivalry can be found elsewhere, as can discussions of pattern rivalry [1,9,13,14]. In this review, we favor the notion that binocular rivalry is unlikely to result from a single process but, rather, from an assembly of perceptual processes underlying instigation of rivalry, promotion of dominance and implementation of suppression.

## A hybrid model of binocular rivalry

To account for spontaneous rivalry alternations, most models have emphasized the importance of reciprocal inhibition between competing visual neurons, with inhibitory influences adapting over time [5,7,10,11,15–17]. Consequently, one set of neurons maintains dominance only temporarily, until they can no longer inhibit the activity of competing neurons, leading to a reversal in perceptual dominance.

According to hybrid views of binocular rivalry [10,11,15], inhibitory interactions could take place among both monocular neurons (interocular competition) and binocular pattern-selective neurons (pattern competition). Figure 2a provides a schematic illustration of these lateral inhibitory connections, which can mediate visual suppression at multiple levels of processing. (For simplicity, only two layers are depicted, although competitive interactions might occur at multiple levels. Here, we refer to monocular neurons as any neurons with some eye-of-origin preference; these neurons need not be strictly monocular or restricted solely to area V1 or the LGN.) It is worth noting that eye-based competition could involve pattern selectivity – inhibition could occur between monocular neurons tuned

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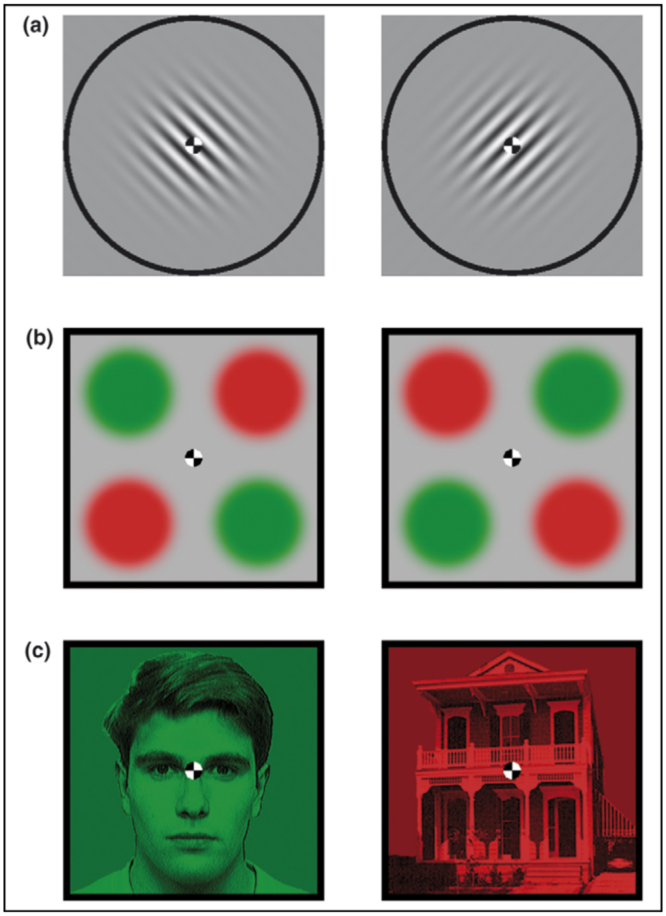


**Figure 1**. Examples of binocular rivalry stimuli. **(a)** Dichoptic orthogonal gratings. **(b)** Stimuli used to study interocular grouping, adapted from Ref. [52]. **(c)** Rivalry using complex objects, adapted from Ref. [23]. The reader can experience binocular rivalry by cross-fusing the left and right pairs of images. This involves crossing one's eyes until the two images appear aligned (with left eye focused on the right image and right eye focused on the left image). Alternatively, the reader can use a pair of red–green anaglyph glasses to view the rivalry images on the following website: http://www.psy.vanderbilt.edu/faculty/blake/Rivalry/BR.html.

to different orientations, whereas excitatory interactions between monocular neurons with matching orientation preferences could minimize rivalry and promote binocular fusion [5]. When rivaling patterns such as dichoptic orthogonal gratings are viewed, strong inhibition between eye-selective or pattern-selective neurons can alter the balance in the relative strengths of responses to the two stimuli, leading to the initiation of rivalry.

If rival stimulation leads to only partial suppression of the inputs from one eye at the monocular level, then persisting neural signals could be passed on to higher stages of processing, where visual competition can continue. According to this hybrid view, the neural correlates of binocular rivalry should be evident in monocular brain areas but rivalry-related modulations should be amplified in higher areas. This model can also account for perceptual alternations that can occur when observers view pattern rivalry displays that effectively bypass interocular competition [9,11,13].

In this model, lateral excitatory connections promote perceptual grouping by coordinating the activity of neurons representing separate regions of visual space. Figure 2b shows neurons representing two adjacent regions of visual space; each set of neurons receives inputs from *both* eyes. Among monocular neurons, reciprocal excitatory connections can promote grouping by eye or interocular grouping between neurons with similar orientation preferences. Excitatory connections between binocular neurons can also lead to pattern-based grouping across adjacent regions.

Feedback projections from higher areas can modulate the activity of neurons in earlier areas (Figure 2c). Excitatory feedback to pattern-selective neurons could account for modulatory effects of selective attention. Similarly, feedback to neurons representing adjacent parts of the visual field could lead to perceptual grouping. Finally, feedback projections could directly or indirectly activate inhibitory neurons and modulate the strength of neural inhibition.

In this model, we attempt to consider all types of neuronal connections that might account for the various properties of rivalry, including initiation of rivalry, monocular suppression, pattern suppression and the promotion of dominance resulting from perceptual grouping or voluntary attention. Even a fairly simple model with only two levels of representation and bidirectional connections might prove complex when trying to infer the causal source of a specific interaction, in particular because influences could result indirectly through combinations of excitatory and/or inhibitory connections. Nonetheless, recent studies reviewed below suggest that the diverse attributes of rivalry can be succinctly understood within such a framework. These and future studies will help to reveal which components of this model are essential to the various properties of rivalry.

## Neuroimaging studies of binocular rivalry

Neuroimaging studies have provided important evidence about the inhibitory components of binocular rivalry. EEG and fMRI studies have investigated the neural correlates of rivalry perception by 'tagging' the activity corresponding to each of the two rivaling stimuli.

EEG studies were the first to show that occipital potentials evoked by a flickering stimulus are greater during periods of dominance than suppression [18,19]. Subsequent EEG and MEG studies found that the amplitudes of these potentials are attenuated by as much as 50–85% when the evoking stimulus is suppressed during rivalry [20,21]. Because it is difficult to pinpoint the cortical sources of potentials measured from the scalp, it is unclear exactly where in the occipital lobe these competitive rivalry interactions are taking place.

fMRI provides better spatial precision for measuring changes in neural activity, as indexed by changes in local blood oxygenation levels. The first fMRI studies of rivalry focused on higher brain areas. One study found that regions in the parietal and prefrontal cortex were transiently activated during rivalry alternations [22]. Another study found that activity in face- and house-selective regions of the ventral temporal cortex closely reflected the observer's perceptual state during rivalry between a face and a house [23]. In that study, cortical responses during rivalry were as strong as those evoked by physical alternations between the face and house. Subsequent