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Binocular Rivalry: A Window into Cortical Competition and Suppression

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Abstract | When the two eyes view very dissimilar images, the visual system often fails to combine the images and one experiences stochastically alternating percepts. This phenomenon, called binocular rivalry, has fascinated researchers for centuries since it provides insights into two critical aspects of visual perception: visual consciousness and cortical suppression. Here, we review the mechanisms of binocular rivalry from a cognitive neuroscience perspective, focusing on empirical findings from two widely used methods—functional magnetic resonance imaging (fMRI) and electroencephalography (EEG). With these techniques, researchers have been able to identify the cortical sites of suppression in binocular rivalry, probe neural responses evoked by unconscious (invisible) visual stimuli, and examine the role of top-down attentional signals in rivalry. We conclude by proposing some future directions for the study of binocular rivalry.

1 Introduction

One fundamental challenge the visual system faces is to process immense amounts of input information and construct an accurate and coherent representation of the visual environment. This process is further complicated by intrinsic noise, ambiguities, and conflicts in visual inputs. Binocular rivalry, one of the most captivating perceptual phenomena, presents a unique situation where conflicts of visual inputs are so drastic that the brain fails to merge them into a single percept. In a typical binocular rivalry paradigm, an observer views two different static images in the two eyes. Unlike ordinary viewing conditions where there is a single, unitary percept, subjective visual experience will stochastically switch between the two images, with full dominance of one image followed by full dominance of the other (Fig. 1). This situation can be interpreted as if the inputs into the two eyes are competing (or rivaling) to gain access to an observer's perceptual awareness.

Binocular rivalry is of particular scientific interest because it provides insights into two fundamental aspects of human perception. On one hand, binocular rivalry can be viewed as a visual illusion in which dynamic changes in perception occur without a change in the physical stimulus. Thus, rivalry provides a powerful way to isolate and study the nature of mental states, a topic that has fascinated philosophers, thinkers, and scientists for thousands of years[1]. On the other hand, binocular rivalry also highlights the challenge faced by the human brain of resolving conflicting information. One effective strategy the brain might use is to suppress weaker, less informative signals and enhance stronger, more behaviorally relevant signals. Such cortical suppression is thought to occur in real-world visual situations, and moreover, abnormalities in suppression are implicated in many visual disorders, such as amblyopia and strabismus. Understanding the mechanisms of rivalry, and more generally, cortical suppression, could lead to development of

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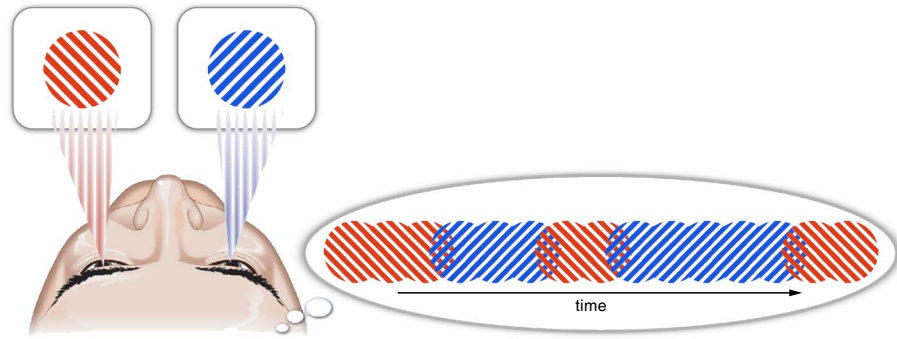*kendrick@post.harvard.edu

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Figure 1: Schematic of binocular rivalry, from Dieter and Tadin [88]. An observer is presented with two different images to the two eyes. During binocular rivalry, the observer experiences alternating percepts in a temporally stochastic fashion, rather than a constant mixture of the two images.

therapeutic interventions that might help resolve these disorders.

While binocular rivalry has a long history, scientific research using modern neuroscience techniques has only recently been conducted. The aim of this review was to summarize recent work on binocular rivalry involving different neuroimaging approaches, in particular, functional magnetic resonance imaging (fMRI) and electroencephalography (EEG). Neuroimaging methods have been particularly informative for three key aspects of rivalry research: the cortical loci of binocular rivalry, the processing of unconscious (invisible) information, and the role of attention in binocular rivalry. We will also discuss several future directions for the next stage of study on binocular rivalry, or more broadly, suppression mechanisms and consciousness in the human brain.

2 Imaging Rivalry Signals in the Human Brain

The most prominent feature of binocular rivalry is the dynamic competition between two monocular signals for perceptual awareness. This astonishing perceptual phenomenon triggers great interest in neuroscientists with respect to its underlying neural causes. One fundamental question is, in what part of the brain does visual competition occur? Neuroimaging techniques are well-suited to answer this question, as they can be used to localize the brain regions involved in a particular psychological process. Determining the cortical site of binocular rivalry has critical theoretical implications. For instance, it is known that the human visual system can be segregated into an array of regions dedicated to distinct aspects of visual processing. Such functional specialization has been vigorously studied[2, 3]. Linking rivalry signals to a specific visual region would allow us to infer the scope and limitations of binocular vision and understand the specific stage of visual processing at which the visual system discards certain information and permits other information to enter awareness. In a sense, the cortical site of rivalry could be interpreted as the "gate" for visual consciousness.

A large body of neuroimaging studies has identified rivalry signals at multiple levels of visual processing in the human brain. Despite differences in experimental details, a common finding is that cortical activity in many higher-level visual areas is tightly coupled to the subjective perceptual alternations in rivalry. A prototypical example comes from Tong et al. [4]. This study measured blood-oxygenation-level dependent (BOLD) responses during binocular rivalry in fusiform face area (FFA) and parahippocampal place area (PPA), two brain regions that exhibit selectivity to face and house stimuli, respectively. Responses within the two areas exhibited a clear trend of rising and falling that was temporally coincident with the participant's dominant percept (Fig. 2). Similar patterns of results have been observed in several other fMRI studies[5–7]. Brain responses following the temporal pattern of perceptual alternation were discovered using the technique of EEG even earlier than with fMRI. For instance, in a rivalry paradigm, visual evoked potentials were reduced during periods of visual suppression[8, 9]. As another example, using frequency-tagging (a technique in which different stimulus inputs are placed in different EEG frequency bands), clear evidence for counter-phase binocular rivalry signals has been found[10–12].
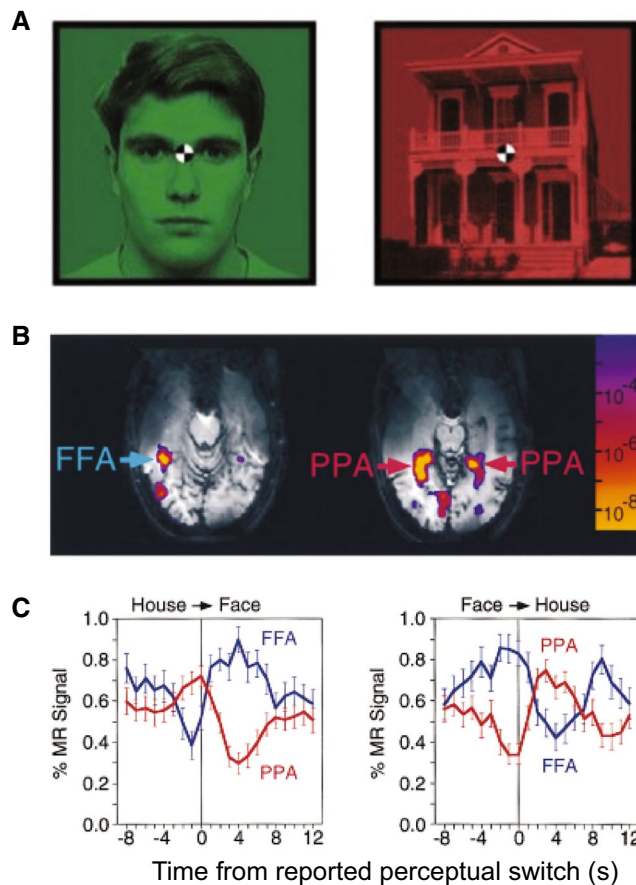
478

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J. Indian Inst. Sci.|VOL 97:4|477–485 December 2017|journal.iisc.ernet.in

Figure 2: Cortical correlates of binocular rivalry in face- and house-selective regions, from Tong et al. [4]. **a** Stimuli. A face and a house stimulus are dichoptically presented to participants. **b** The cortical loci of fusiform face area (FFA) and parahippocampal place area (PPA). **c** BOLD signal changes following perceptual switches. Once a participant reports a perceptual switch, activity in the brain area corresponding to the dominant percept rises and activity in the other area falls.

Although there is much evidence that responses follow perception in high-level visual areas, opinion is divided as whether low-level visual areas, especially the primary visual cortex (V1), are involved in resolving binocular rivalry[13]. Results from different studies[5–7] seem to depend critically on the particular task and stimulus design used. There is even some evidence that rivalry-related neural signals can been found in the subcortical lateral geniculate nucleus (LGN)[14, 15].

A limitation of these various neuroimaging studies is that although they can serve as the evidence of correlation between neural signals and perception, they cannot establish their causal relationship. In other words, it is unclear whether rivalry signals that dynamically rise and fall within a given brain region produce perceptual fluctuations, or whether perceptual fluctuations arise first and then prompt certain brain regions to exhibit oscillations in activity. The former possibility suggests a feed-forward scheme in which some intrinsic stochasticity (e.g. neural noise) arises within sensory cortex and then generates perceptual consequences. In contrast, the latter possibility suggests a feed-back scheme in which a percept is decided by a high-level cognitive region and then decision signals project back to sensory cortex, thereby giving rise to fluctuations of responses. Earlier fMRI work followed the former view, but several recent studies support the latter view that rivalry-related activity in high-level brain areas is due to cognitive processes such as attention and self-monitoring[16–20]. For instance, neural activity in frontal and parietal cortex is largely abolished when the conspicuousness of perceptual switches is diminished[21].

Identifying the cortical locus of binocular rivalry also impinges on the critical question of whether binocular rivalry takes place between two monocular channels (eye-based)[22, 23] or two

Primary visual cortex (V1): The first cortical area to receive inputs from the eye via the geniculostriate pathway, also referred to as Area 17 and 'striate cortex'

479

J. Indian Inst. Sci. |VOL 97:4|477–485 December 2017|journal.iisc.ernet.in

perceptual interpretations (pattern-based)[24]. At first glance, the term "binocular rivalry" implies the former case. However, some studies have contended that what actually compete are the two visual representations that can be derived from sensory inputs, and these representations may not necessarily correspond to monocular channels. On this view, binocular rivalry is similar to other forms of bistable perception, e.g., the Necker cube and rabbi–duck illusions. Striking evidence supporting the theory of pattern-based rivalry comes from Kovacs et al.[25]. In this study, when participants viewed mosaic images composed of small patches of a monkey and a background scene (Fig. 3a), participants perceived a fully coherent image (either a full monkey or a full background scene) at each given point in time. However, one subsequent study controlled local image differences and reached the seemingly opposite conclusion that local image differences matter[26]. These conflicting findings suggest that various bottom-up and top-down factors contribute to binocular rivalry, which complicates our attempts to understand its neural mechanisms.

Most cortical neurons respond binocularly, that is, respond to inputs from both eyes. There are only two sites in the visual system—the LGN and blind spots in V1—that process purely monocular signals, which provides an opportunity to adjudicate the eye-based and pattern-based theories of rivalry. Two studies measured neural activity in the LGN and V1 blind spots and found that fluctuating responses strongly correlate with the eye-preference of individual voxels, thereby providing support for eye-specific competition[15, 27]. Given that both eye-based and pattern-based rivalry receive considerable empirical support, researchers have proposed a hybrid model in which rivalry can occur between two monocular channels as well as between two representations, but various top-down and bottom-up factors can resolve or promote rivalry at multiple levels of visual processing and at multiple time-scales[28].

3 Cortical Responses to Invisible Stimuli
Many philosophers and scientists have emphasized the significance of unconscious perception[1]. In contrast to conscious perception in which the participant can report his or her percept, unconscious perception is unreportable. Nevertheless, unconscious perception can still exert powerful influences on behavior. Researchers often use interocular suppression (IS)[29], a paradigm closely related to binocular rivalry, to render visual stimuli invisible. In IS, the experimenter intentionally designs the input for one eye to be very strong so that it completely and persistently overrides the input from the other eye.

One might suspect that unconscious information is eliminated early in visual processing and thus does not contribute to any explicit perceptual outcome. In contrast, a large body of evidence indicates that unperceived visual information is still received and analyzed by the visual system, but the extent of unconscious processing gradually diminishes as the complexity of the visual features rises[30, 31]. For instance, some simple visual features, such as orientation[32], spatial frequency[33, 34], and color[35], can produce substantial visual aftereffects though rendered invisible (but see [36]), whereas more complex visual features, such as contour[37], shape[38], or objects (e.g., faces[39,40]; see review in [41]), do not produce large effects.

Studying unconscious perception is technically challenging since suppressed information is unreportable by the participant and, therefore, unavailable to the experimenter. Using neuroimaging, a common approach is to examine whether invisible stimuli elicit cortical activity patterns that are similar to the situation in which stimuli are clearly perceivable. The fundamental question here is what aspect of visual information under unconsciousness is still processed in the brain. With regard to low-level visual features, Haynes and Rees[42] used multivariate pattern analysis (MVPA)[43] to successfully decode the orientation of invisible gratings in V1, indicating that V1 maintains orientation information even when the stimulus is removed from visual awareness. For high-level features, invisibility extinguishes cortical responses to most perceptually related properties, such as face identity, but processing of affective or semantic information seems still preserved[40, 44]. For instance, robust fMRI responses to invisible fearful faces have been found in the amygdala, likely due to subcortical pathways for processing emotional information[44, 45]. Similarly, behavioral studies suggest that residual neural processing of semantic information still persists under IS[46, 47]. Moreover, most investigations on unconscious perception have largely focused on visual features that are processed along the ventral visual pathway. There is also evidence showing that cortical responses in the dorsal visual pathway exhibit different patterns from in the ventral pathway. One study contrasted face- and tool- evoked responses towards invisible stimuli in the ventral and the dorsal pathway and demonstrated that responses in ventral FFA were very minimal but tool-selective region in dorsal

Multivariate pattern analysis (MVPA): Multivariate pattern analysis exploits the diversity of multiple units, extracting information from distributed activation patterns. This contrasts with univariate analysis in which responses of all units in a region are pooled (averaged) to create a summary region-level response.

480

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J. Indian Inst. Sci.| VOL 97:4| 477–485 December 2017| journal.iisc.ernet.in

pathway remained active. This study suggests a clear functional disassociation of ventral and dorsal visual pathways to invisible information[48].

4 Bottom-Up and Top-Down Influences on Binocular Rivalry

It is well established that visual perception reflects both bottom-up and top-down factors. Bottom-up processing refers to feed-forward analysis of sensory input, while top-down processing involves one's goals or beliefs, such as attention and experience. Characterizing the distinct roles of bottom-up and top-down interactions during binocular rivalry has been intensely studied in the past few decades.

Bottom-up factors certainly play a critical role in binocular rivalry since, by definition, it is the inconsistency between two input images that produces binocular rivalry. In general, "stronger" stimuli, e.g., higher contrast or luminance, generate stronger responses in the brain and thus tend to maintain longer dominance during rivalry[49]. Other factors also mediate binocular rivalry, such as visual context[50], center-surround organization[51, 52], perceptual grouping[53, 54], and even some high-level features[55]. Lee et al.[56] present a compelling demo of spatially dependent binocular rivalry (Fig. 3b). When contrast of a local patch in a suppressed visual pattern is boosted, the previously suppressed pattern emerges and expands gradually from this region to others in the visual field. The suppressed pattern eventually overrides the dominant one, resulting in a vivid perception of traveling waves. More importantly, spatiotemporal characteristics of BOLD responses tightly follow the perceptual waves. This intriguing visual phenomenon highlights the significance of image-level properties for controlling binocular rivalry.

Despite sensitivity to image-level properties, binocular rivalry is also subject to top-down influence. For instance, visual perception strongly relies on prior experience, either explicitly or implicitly[57, 58]. One way to impose visual experience is through perceptual learning, in which a particular visual skill is extensively reinforced by behavioral training[59, 60]. Surprisingly, perceptual training has been shown to profoundly alter eye-dominance, a low-level visual property that is typically considered to be highly stable in the adult brain[61]. Furthermore, training not only enhances stimulus-driven visual processing but also strengthens the efficiency of top-down feature selection[62].

Another critical question that remains elusive is whether binocular rivalry requires visual attention, an information-processing operation that underlies many visual and cognitive processes[63, 64]. If visual attention is diverted away from competing stimuli, does binocular rivalry persist or cease? Using the aforementioned traveling-wave paradigm, researchers have found that abolishing attention eliminates rivalry-related BOLD dynamics in V2 and V3, but these dynamics are still preserved in V1[65]. This suggests that the absence of attention hampers the transformation of rivalry signals from V1 to higher-level visual areas such as V2 and V3. A separate study further substantiates this argument by showing that the typical counter-phase frequency-tagged EEG signals found during binocular rivalry became irregular when participants perform a demanding fixation task[66]. However, one recent study using optical imaging in primates found that rivalry-like neural signals in visual cortex are still robust even under anesthesia[67].

4.1 Box. Computational Models of Binocular Rivalry

Moving beyond theories that merely characterize the mechanisms of binocular rivalry at a conceptual level, several quantitative models have been proposed[68–73]. Most of these models are developed within the framework of recurrent neural networks, which have demonstrated promising power to explain various forms of time-dependent neural oscillations[74, 75]. One common feature of these models is to set active neurons in at least two neural layers that correspond to low-level monocular representation and high-level pattern-based representation. This two-layer design is necessary to generate rivalry-like fluctuation[68] and is consistent with the hybrid model in which rivalry can occur as a result of both eye-based and pattern-based processing[28]. Another prominent feature of these models is the feedback and inhibitory effects implemented by recurrent connections. Inhibitory connections are carried out either linearly, such as subtraction[68], or nonlinearly, such as divisive normalization[69, 73]. Finally, neurons that detect interocular differences, which very likely also contribute to stereo vision, have been shown to be critical, as their feedback connections onto monocular representations can account for several seemingly conflicting behavioral findings, such as binocular integration and rivalry under different stimulus conditions[69]. The existence of these neurons receives empirical support using EEG on humans[76].

J. Indian Inst. Sci. |VOL 97:4|477–485 December 2017|journal.iisc.ernet.in

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481

Besides neural network models, other theoretical approaches, such as probabilistic sampling[77, 78] and predictive coding[79], have also been suggested. These approaches have the attraction of offering normative explanations for the processes that underlie binocular rivalry. They cast rivalry within the context of various computational theories of the brain, such as probabilistic inference or/and free energy minimization, and thereby could show the relationship between binocular rivalry and other visual phenomena. However, these frameworks have seldom been directly vetted against empirical data, so their veracity is still questionable.

5 Future Directions for Binocular Rivalry Research

The application of modern neuroimaging techniques greatly expands our understanding of the neural mechanisms underlying binocular rivalry. Despite the exciting findings described in this review, there remain several important unanswered questions.

First, results from primate neurophysiology seem to be inconsistent with results from human fMRI. In primate neurophysiology, perceptually locked modulations of neuronal spiking in low-level visual areas are considerably weaker than what is found in neuroimaging. Only 20% of sampled neurons exhibit rivalry-like activity in V1[80]. Moreover, one study examined neurons in LGN during binocular rivalry and found no substantial presence of rivalry modulations[81]. One potential explanation is that the two techniques measure fundamentally different aspects of neural signals. The BOLD signal is believed to closely relate to local field potentials, which is not identical to the spiking activity of individual neurons. It would be informative to directly compare the two types of signals within the same experiment..

Second, the relationship between binocular rivalry and other forms of cortical suppression is not clear. Interocular suppression, as a particular type of binocular rivalry, renders certain stimulus inputs invisible. Other forms of visual suppression, such as crowding[82] and masking[83], can achieve similar behavioral consequences. Are all of these phenomena different aspects of a common suppression mechanism, or do they reflect different neural processes? Both views so far have
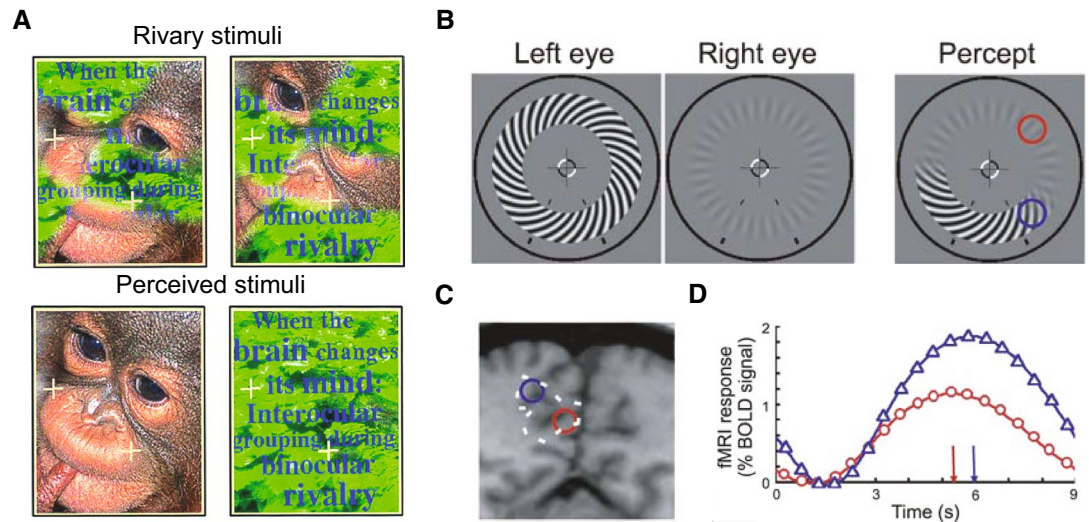

Figure 3: Perceptual grouping and spatiotemporal neural signals during binocular rivalry. **a** Stimuli used in Kovacs et al. [25]. Participants view two images that are mixed in a patch-wise fashion from a monkey face and a background (rivalry stimuli). Subjective percepts alternate between the full monkey image and the full background image (perceived stimuli). **b** Stimuli used in Lee et al. [56]. The experimenter abruptly enhances contrast of the top part of the low-contrast suppressed stimulus (the radial grating). Emergence of the radial grating expands and progressively overrides the high-contrast spiral grating from top to bottom. **c** Retinotopic cortical loci of the two spots (red and blue) in (**b**). **d** BOLD dynamics of the two cortical loci in (**c**). Due to the traveling wave from top to bottom of the stimulus annulus, the location closer to the origin of the traveling wave (red spot) receives shorter high-contrast simulation than the location distant from the top part of annulus (blue spot) and thus exhibits lower magnitude and earlier latency in the BOLD response.

482

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received some empirical support[44, 84], so further investigation is necessary.

Finally, future research could link our understanding of the neural mechanisms underlying binocular rivalry to the diagnosis and treatment of mental disorders involving abnormal neural inhibition. For example, studies have demonstrated an intriguing relationship between individual variability in rivalry (i.e., switching rate) and several known mental dysfunctions, such as autism[85], ADHD[86], and bipolar disorder[87].

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483

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484

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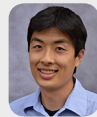
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485

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