



Binocular Rivalry: A Window into Cortical Competition and Suppression

Ruyuan Zhang¹, Stephen A. Engel² and Kendrick Kay^{1*}

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 years¹. 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

¹ Department of Radiology, Center for Magnetic Resonance Research, University of Minnesota, Minneapolis, MN 55455, USA.

² Department of Psychology, University of Minnesota, Minneapolis, MN 55455, USA.

*kendrick@post.harvard.edu

Functional magnetic resonance imaging (fMRI): Functional magnetic resonance imaging is a non-invasive brain imaging technique that measures brain activity by detecting changes in blood oxygenation level. It has excellent spatial resolution (e.g., ~1–2mm) but relatively poor temporal resolution (~1 s).

Electroencephalography (EEG): Electroencephalography is a non-invasive technique that measures electrical activity in the brain using small, flat metal discs (electrodes) placed on the scalp of the head. Compared to fMRI, EEG has complementary characteristics: poor spatial resolution but excellent temporal resolution (< 1 ms).

Fusiform face area (FFA): The fusiform face area is located on the ventral surface of the temporal lobe on the lateral side of the fusiform gyrus. It is thought to engage in specialized processing for faces.

Parahippocampal place area (PPA): The parahippocampal place area is a sub-region of the parahippocampal cortex that lies medially in ventral occipitotemporal cortex. It is thought to play an important role in processing visual scenes.

Blood oxygenation-level dependent (BOLD) signal: The BOLD signal is what is measured in functional magnetic resonance imaging. Neural activity results in increased energy usage and a subsequent hemodynamic response. The hemodynamic response alters the relative levels of oxyhemoglobin and deoxyhemoglobin in blood, and these levels are reflected in the strength of the MR signal

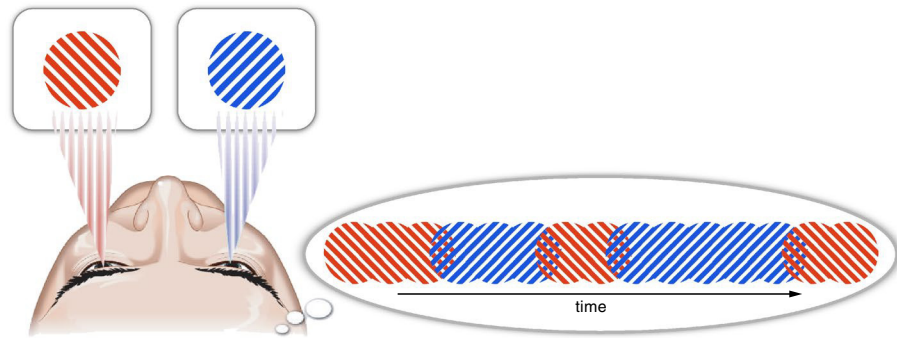


Figure 1: Schematic of binocular rivalry, from Dieter and Tadin⁶⁸. An observer is presented with two different images to the two eyes. During binocular rivalry, the observer experiences alternating percepts in a temporally stochastic fashion, rather than a constant mixture of the two images.

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 BOLD responses** during binocular rivalry in **fusiform face area (FFA)** and **parahippocampal 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**. 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}.

Although there is much evidence that responses follow perception in high-level visual areas,

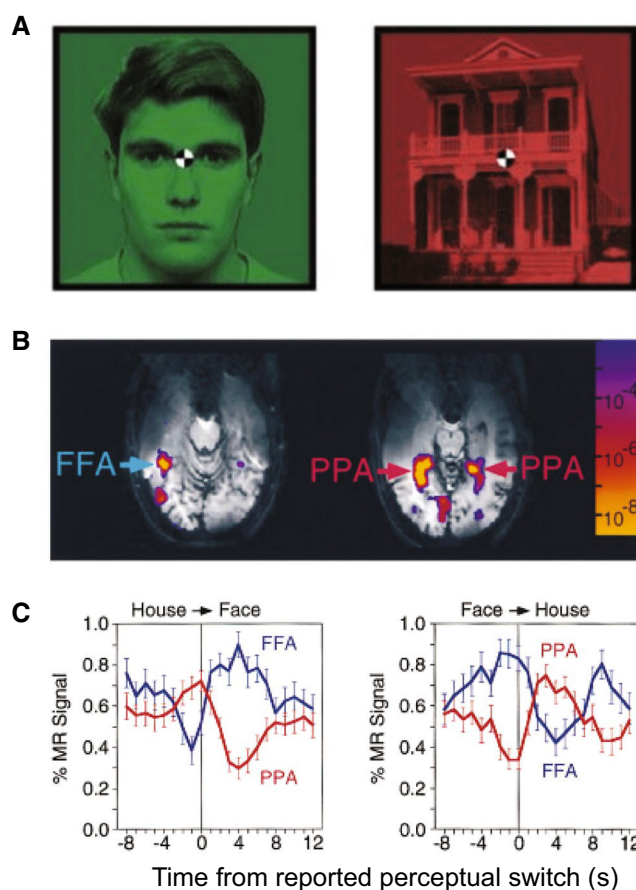


Figure 2: Cortical correlates of binocular rivalry in face- and house-selective regions, from Tong et al.⁴. **a** Stimuli. A face and a house stimulus are dichoptically presented to participants. **b** The cortical loci of fusiform face area (FFA) and parahippocampal place area (PPA). **c** BOLD signal 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.

opinion is divided as whether low-level visual areas, especially the **primary visual cortex (V1)**, is involved in resolving binocular rivalry¹³. 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 be 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 diminished²¹.

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 perceptual interpretations (pattern-based)²⁴. At

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'

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 rabbit-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. 2a), 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 matter²⁶. 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-scales²⁸.

3 Cortical Responses to Invisible Stimuli

Many philosophers and scientists have emphasized the significance of unconscious perception¹. 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 orientation³², spatial frequency^{33, 34}, and color³⁵, can produce substantial visual aftereffects though rendered invisible (but see³⁶), whereas more complex visual features, such as contour³⁷, shape³⁸, or objects (e.g., faces^{39, 40}; see review in⁴¹), 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 Rees⁴² 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.

pathway remained active. This study suggests a clear functional disassociation of ventral and dorsal visual pathways to invisible information⁴⁸.

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, i.e., higher contrast or luminance, generate stronger responses in the brain and thus tend to maintain longer dominance during rivalry⁴⁹. Other factors also mediate binocular rivalry, such as visual context⁵⁰, center-surround organization^{51, 52}, perceptual grouping^{53, 54}, and even some high-level features⁵⁵. Lee et al.⁵⁶ present a compelling demo of spatially dependent binocular rivalry (Fig. 2b). 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 brain⁶¹. Furthermore, training not only enhances stimulus-driven visual processing but also strengthens the efficiency of top-down feature selection⁶².

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 V1⁶⁵. 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 task⁶⁶. However, one recent study using optical imaging in primates found that rivalry-like neural signals in visual cortex are still robust even under anesthesia⁶⁷.

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 fluctuation⁶⁸ and is consistent with the hybrid model in which rivalry can occur as a result of both eye-based and pattern-based processing²⁸. 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 subtraction⁶⁸, 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 conditions⁶⁹. The existence of these neurons receives empirical support using EEG on humans⁷⁶.

Besides neural network models, other theoretical approaches, such as probabilistic sampling^{77, 78} and predictive coding⁷⁹, 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 (Fig. 3).

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 V1⁸⁰. Moreover, one study examined neurons in LGN during binocular rivalry and found no substantial presence of rivalry modulations⁸¹. 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 crowding⁸² and masking⁸³, 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

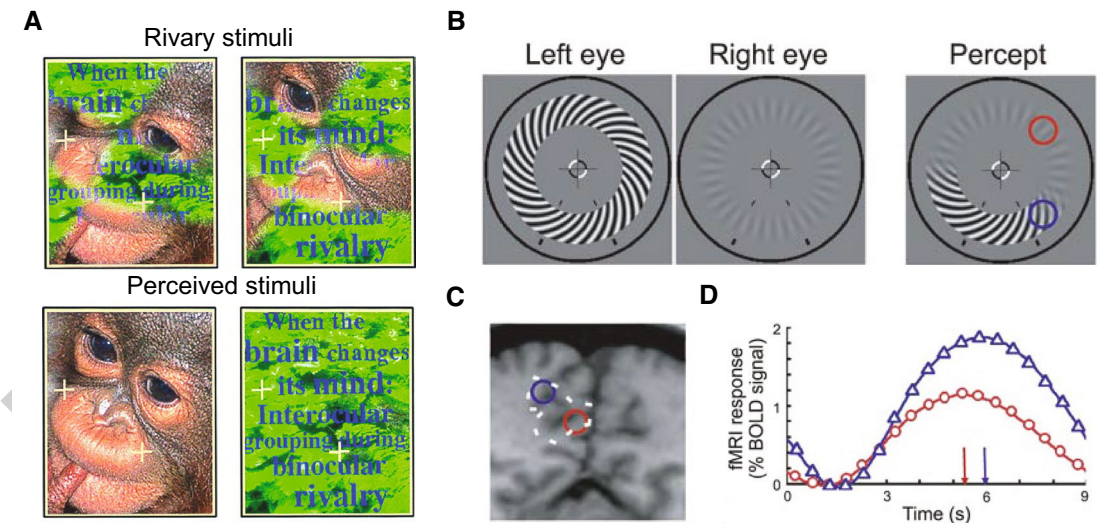


Figure 3: Perceptual grouping and spatiotemporal neural signals during binocular rivalry. **a** Stimuli used in Kovacs et al. ²⁵. Participants view two images that are mixed in a patch-wise fashion from a monkey face and a background (rivalry stimuli). Subjective percepts alternate between the full monkey 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 stimulation than the location distant from the top part of annulus (blue spot) and thus exhibits lower magnitude and earlier latency in the BOLD response.

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 autism⁸⁵, ADHD⁸⁶, and bipolar disorder⁸⁷.

References

1. James W (1890) The consciousness of self. *Princ Psychol*
2. Wandell BA (1999) Computational neuroimaging of human visual cortex. *Annu Rev Neurosci* 22:145–173
3. Grill-Spector K, Malach R (2004) The human visual cortex. *Annu Rev Neurosci* 27:649–677
4. Tong F, Nakayama K, Vaughan JT, Kanwisher N (1998) Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron* 21:753–759
5. Lumer ED, Friston KJ, Rees G (1998) Neural correlates of perceptual rivalry in the human brain. *Science* 280:1930–1934
6. Lumer ED, Rees G (1999) Covariation of activity in visual and prefrontal cortex associated with subjective visual perception. *Proc Natl Acad Sci USA* 96:1669–1673
7. Polonsky A, Blake R, Braun J, Heeger DJ (2000) Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. *Nat Neurosci* 3:1153–1159
8. Cobb WA, Morton HB, Ettliger G (1967) Cerebral Potentials evoked by pattern reversal and their suppression in visual rivalry. *Nature* 216:1123–1125
9. Lansing RW (1964) Electroencephalographic correlates of binocular rivalry in man. *Science* 146:1325–1327
10. Brown RJ, Norcia AM (1997) A method for investigating binocular rivalry in real-time with the steady-state VEP. *Vision Res* 37:2401–2408
11. Cosmelli D et al (2004) Waves of consciousness: ongoing cortical patterns during binocular rivalry. *Neuroimage* 23:128–140
12. Tononi G, Srinivasan R, Russell DP, Edelman GM (1998) Investigating neural correlates of conscious perception by frequency-tagged neuromagnetic responses. *Proc Natl Acad Sci USA* 95:3198–3203
13. Tong F (2003) Primary visual cortex and visual awareness. *Nat Rev Neurosci* 4:219–229
14. Wunderlich K, Schneider KA, Kastner S (2005) Neural correlates of binocular rivalry in the human lateral geniculate nucleus. *Nat Neurosci* 8:1595–1602
15. Haynes JD, Deichmann R, Rees G (2005) Eye-specific effects of binocular rivalry in the human lateral geniculate nucleus. *Nature* 438:496–499
16. Frassle S, Sommer J, Jansen A, Naber M, Einhauser W (2014) Binocular rivalry: frontal activity relates to introspection and action but not to perception. *J Neurosci* 34:1738–1747
17. Knapen T, Brascamp J, Pearson J, van Ee R, Blake R (2011) The role of frontal and parietal brain areas in bistable perception. *J Neurosci* 31:10293–10301
18. Safavi S, Kapoor V, Logothetis NK, Panagiotaropoulos TI (2014) Is the frontal lobe involved in conscious perception? *Front Psychol* 5:1063
19. Weilhhammer VA, Ludwig K, Hesselmann G, Sterzer P (2013) Frontoparietal cortex mediates perceptual transitions in bistable perception. *J Neurosci* 33:16009–16015
20. Zaretskaya N, Narinyan M (2014) Introspection, attention or awareness? The role of the frontal lobe in binocular rivalry. *Front Hum Neurosci* 8:527
21. Brascamp J, Blake R, Knapen T (2015) Negligible fronto-parietal BOLD activity accompanying unreportable switches in bistable perception. *Nat Neurosci* 18:1672–1678
22. Lee SH, Blake R (1999) Rival ideas about binocular rivalry. *Vision Res* 39:1447–1454
23. Tong F (2001) Competing theories of binocular rivalry: a possible resolution. *Brain Mind* 2(1):55–83
24. Blake R (2001) A primer on binocular rivalry, including current controversies. *Brain Mind* 2(1):5–38
25. Kovacs I, Papathomas TV, Yang M, Feher A (1996) When the brain changes its mind: interocular grouping during binocular rivalry. *Proc Natl Acad Sci USA* 93:15508–15511
26. Carlson TA, He S (2004) Competing global representations fail to initiate binocular rivalry. *Neuron* 43:907–914
27. Tong F, Engel SA (2001) Interocular rivalry revealed in the human cortical blind-spot representation. *Nature* 411:195–199
28. Tong F, Meng M, Blake R (2006) Neural bases of binocular rivalry. *Trends Cogn Sci* 10:502–511
29. Tsuchiya N, Koch C (2005) Continuous flash suppression reduces negative afterimages. *Nat Neurosci* 8:1096–1101
30. Pasley BN, Mayes LC, Schultz RT (2004) Subcortical discrimination of unperceived objects during binocular rivalry. *Neuron* 42:163–172
31. Pearson J, Clifford CW (2005) Suppressed patterns alter vision during binocular rivalry. *Curr Biol* 15:2142–2148
32. He S, Cavanagh P, Intriligator J (1996) Attentional resolution and the locus of visual awareness. *Nature* 383:334–337
33. He S, MacLeod DI (2001) Orientation-selective adaptation and tilt after-effect from invisible patterns. *Nature* 411:473–476
34. Blake R, Fox R (1974) Adaptation to invisible gratings and the site of binocular rivalry suppression. *Nature* 249:488–490

35. White KD, Petry HM, Riggs LA, Miller J (1978) Binocular interactions during establishment of McCollough effects. *Vis Res* 18:1201–1215
36. Blake R, Tadin D, Sobel KV, Raissian TA, Chong SC (2006) Strength of early visual adaptation depends on visual awareness. *Proc Natl Acad Sci U S A* 103:4783–4788
37. Harris JJ, Schwarzkopf DS, Song C, Bahrami B, Rees G (2011) Contextual illusions reveal the limit of unconscious visual processing. *Psychol Sci* 22:399–405
38. Sweeny TD, Grabowecky M, Suzuki S (2011) Awareness becomes necessary between adaptive pattern coding of open and closed curvatures. *Psychol Sci* 22:943–950
39. Stein T, Sterzer P (2011) High-level face shape adaptation depends on visual awareness: evidence from continuous flash suppression. *J Vis* 11:5
40. Moradi F, Koch C, Shimojo S (2005) Face adaptation depends on seeing the face. *Neuron* 45:169–175
41. Axelrod V, Bar M, Rees G (2015) Exploring the unconscious using faces. *Trends Cogn Sci* 19:35–45
42. Haynes JD, Rees G (2005) Predicting the orientation of invisible stimuli from activity in human primary visual cortex. *Nat Neurosci* 8:686–691
43. Kamitani Y, Tong F (2005) Decoding the visual and subjective contents of the human brain. *Nat Neurosci* 8:679–685
44. Jiang Y, He S (2006) Cortical responses to invisible faces: dissociating subsystems for facial-information processing. *Curr Biol* 16:2023–2029
45. Williams MA, Morris AP, McGlone F, Abbott DF, Mattingley JB (2004) Amygdala responses to fearful and happy facial expressions under conditions of binocular suppression. *J Neurosci* 24:2898–2904
46. Yang E, Zald DH, Blake R (2007) Fearful expressions gain preferential access to awareness during continuous flash suppression. *Emotion* 7:882–886
47. Costello P, Jiang Y, Baartman B, McGlennen K, He S (2009) Semantic and subword priming during binocular suppression. *Conscious Cogn* 18:375–382
48. Fang F, He S (2005) Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nat Neurosci* 8:1380–1385
49. Mueller TJ, Blake R (1989) A fresh look at the temporal dynamics of binocular-rivalry. *Biol Cybern* 61:223–232
50. Fukuda H, Blake R (1992) Spatial interactions in binocular rivalry. *J Exp Psychol Hum Percept Perform* 18:362–370
51. Paffen CL, Alais D, Verstraten FA (2005) Center-surround inhibition deepens binocular rivalry suppression. *Vision Res* 45:2642–2649
52. Paffen CL, Tadin D, te Pas SF, Blake R, Verstraten FA (2006) Adaptive center-surround interactions in human vision revealed during binocular rivalry. *Vision Res* 46:599–604
53. Alais D, Blake R (1999) Grouping visual features during binocular rivalry. *Vision Res* 39:4341–4353
54. Sobel KV, Blake R (2002) How context influences predominance during binocular rivalry. *Perception* 31:813–824
55. Yu K, Blake R (1992) Do recognizable figures enjoy an advantage in binocular rivalry? *J Exp Psychol* 18(4):1158
56. Lee SH, Blake R, Heeger DJ (2005) Traveling waves of activity in primary visual cortex during binocular rivalry. *Nat Neurosci* 8:22–23
57. Kersten D, Mamassian P, Yuille A (2004) Object perception as Bayesian inference. *Annu Rev Psychol* 55:271–304
58. Yuille A, Kersten D (2006) Vision as Bayesian inference: analysis by synthesis? *Trends Cogn Sci* 10(7):301–308
59. Sasaki Y, Nanez JE, Watanabe T (2010) Advances in visual perceptual learning and plasticity. *Nat Rev Neurosci* 11:53–60
60. Watanabe T, Sasaki Y (2015) Perceptual learning: toward a comprehensive theory. *Annu Rev Psychol* 66:197–221
61. Xu JP, He ZJ, Ooi TL (2010) Effectively reducing sensory eye dominance with a push-pull perceptual learning protocol. *Curr Biol* 20:1864–1868
62. Dieter KC, Melnick MD, Tadin D (2016) Perceptual training profoundly alters binocular rivalry through both sensory and attentional enhancements. *Proc Natl Acad Sci USA* 113(45):12874–12879
63. Chun MM, Golomb JD, Turk-Browne NB (2011) A taxonomy of external and internal attention. *Annu Rev Psychol* 62:73–101
64. Kastner S, Ungerleider LG (2000) Mechanisms of visual attention in the human cortex. *Annu Rev Neurosci* 23:315–341
65. Lee SH, Blake R, Heeger DJ (2007) Hierarchy of cortical responses underlying binocular rivalry. *Nat Neurosci* 10:1048–1054
66. Zhang P, Jamison K, Engel S, He B, He S (2011) Binocular rivalry requires visual attention. *Neuron* 71:362–369
67. Xu H et al (2016) Rivalry-like neural activity in primary visual cortex in anesthetized monkeys. *J Neurosci* 36:3231–3242
68. Wilson HR (2003) Computational evidence for a rivalry hierarchy in vision. *Proc Natl Acad Sci USA* 100:14499–14503
69. Said CP, Heeger DJ (2013) A model of binocular rivalry and cross-orientation suppression. *PLoS Comput Biol* 9:e1002991
70. Dayan P (1998) A hierarchical model of binocular rivalry. *Neural Comput* 10:1119–1135
71. Laing CR, Chow CC (2002) A spiking neuron model for binocular rivalry. *J Comput Neurosci* 12:39–53
72. Stollenwerk L, Bode M (2003) Lateral neural model of binocular rivalry. *Neural Comput* 15:2863–2882
73. Li HH, Carrasco M, Heeger DJ (2015) Deconstructing interocular suppression: attention and divisive normalization. *PLoS Comput Biol* 11:e1004510

74. Bartos M, Vida I, Jonas P (2007) Synaptic mechanisms of synchronized gamma oscillations in inhibitory interneuron networks. *Nat Rev Neurosci* 8:45–56
75. Vogels TP, Rajan K, Abbott LF (2005) Neural network dynamics. *Annu Rev Neurosci* 28:357–376
76. Katyal S, Engel SA, He B, He S (2016) Neurons that detect interocular conflict during binocular rivalry revealed with EEG. *J Vis* 16:18
77. Gershman SJ, Vul E, Tenenbaum JB (2012) Multistability and perceptual inference. *Neural Comput* 24:1–24
78. Haefner RM, Berkes P, Fiser J (2016) Perceptual decision-making as probabilistic inference by neural sampling. *Neuron* 90:649–660
79. Hohwy J, Roepstorff A, Friston K (2008) Predictive coding explains binocular rivalry: an epistemological review. *Cognition* 108:687–701
80. Leopold DA, Logothetis NK (1996) Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature* 379:549–553
81. Lehky SR, Maunsell JHR (1996) No binocular rivalry in the LGN of alert macaque monkeys. *Vision Res* 36:1225–1234
82. Whitney D, Levi DM (2011) Visual crowding: a fundamental limit on conscious perception and object recognition. *Trends Cogn Sci* 15:160–168
83. Breitmeyer BG, Ogmen H (2000) Recent models and findings in visual backward masking: a comparison, review, and update. *Percept Psychophys* 62:1572–1595
84. Baker DH, Graf EW (2009) On the relation between dichoptic masking and binocular rivalry. *Vis Res* 49:451–459
85. Robertson CE, Kravitz DJ, Freyberg J, Baron-Cohen S, Baker CI (2013) Slower rate of binocular rivalry in autism. *J Neurosci* 33:16983–16991
86. Casanova JAA, Campos JAA, Sanchez MM, Super H (2013) Onset time of binocular rivalry and duration of inter-dominance periods as psychophysical markers of ADHD. *Perception* 42:16–27
87. Miller SM et al (2003) Slow binocular rivalry in bipolar disorder. *Psychol Med* 33:683–692
88. Dieter KC, Tadin D (2011) Understanding attentional modulation of binocular rivalry: a framework based on biased competition. *Front Hum Neurosci* 5:155



Ruyuan Zhang is a postdoctoral research associate in the Center of Magnetic Resonance Research at University of Minnesota. Ruyuan received his B.A. in Psychology and minor in Computer Science from Peking University in Beijing, China. After that, he obtained Ph.D in Experimental Psychology from the Department of Brain & Cognitive Sciences at University of Rochester. Ruyuan Zhang's research interests lie broadly in human perception, learning, and decision making. The primary goal of his research is to elucidate the central mechanisms of visual processing and plasticity by combining various research techniques including fMRI, psychophysics, and computational modeling.

measurements made using functional MRI and electroencephalography. Main topics currently under investigation include visual plasticity, perceptual awareness, and perceptual learning.



Kendrick Kay Ph.D., is an Assistant Professor at the Center for Magnetic Resonance Research at the University of Minnesota. He uses experimental and modeling techniques to investigate how the visual system represents stimuli and makes perceptual judgments about these stimuli. He is an expert in functional magnetic resonance imaging methods, computational modeling, and data analysis methods.



Stephen Engel is a Professor in the Psychology Department at The University of Minnesota. His laboratory seeks to understand vision and cognition by combining measurements of behavior with neural