

Neural bases of binocular rivalry

Frank Tong¹, Ming Meng² and Randolph Blake¹

¹ Psychology Department, 301 Wilson Hall, Vanderbilt University, Nashville, TN 37203, USA

² Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology, 77 Massachusetts Avenue, Cambridge, MA 02139, USA

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

Corresponding author: Tong, F. (frank.tong@vanderbilt.edu).
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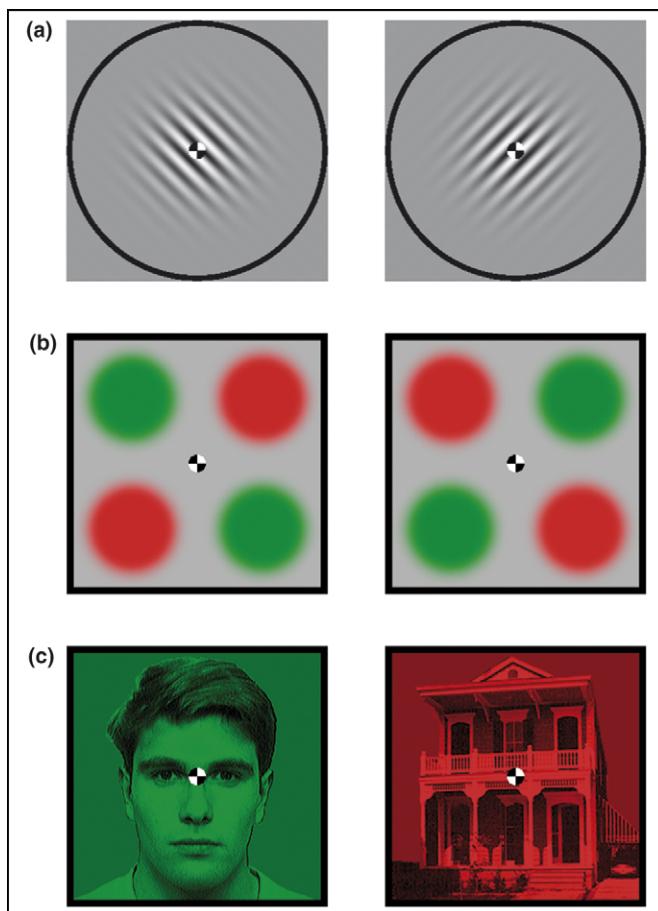


Figure 1. Examples of binocular rivalry stimuli. **(a)** Dichoptic orthogonal gratings. **(b)** Stimuli used to study interocular grouping, adapted from Ref. [52]. **(c)** Rivalry using complex objects, adapted from Ref. [23]. The reader can experience binocular rivalry by cross-fusing the left and right 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

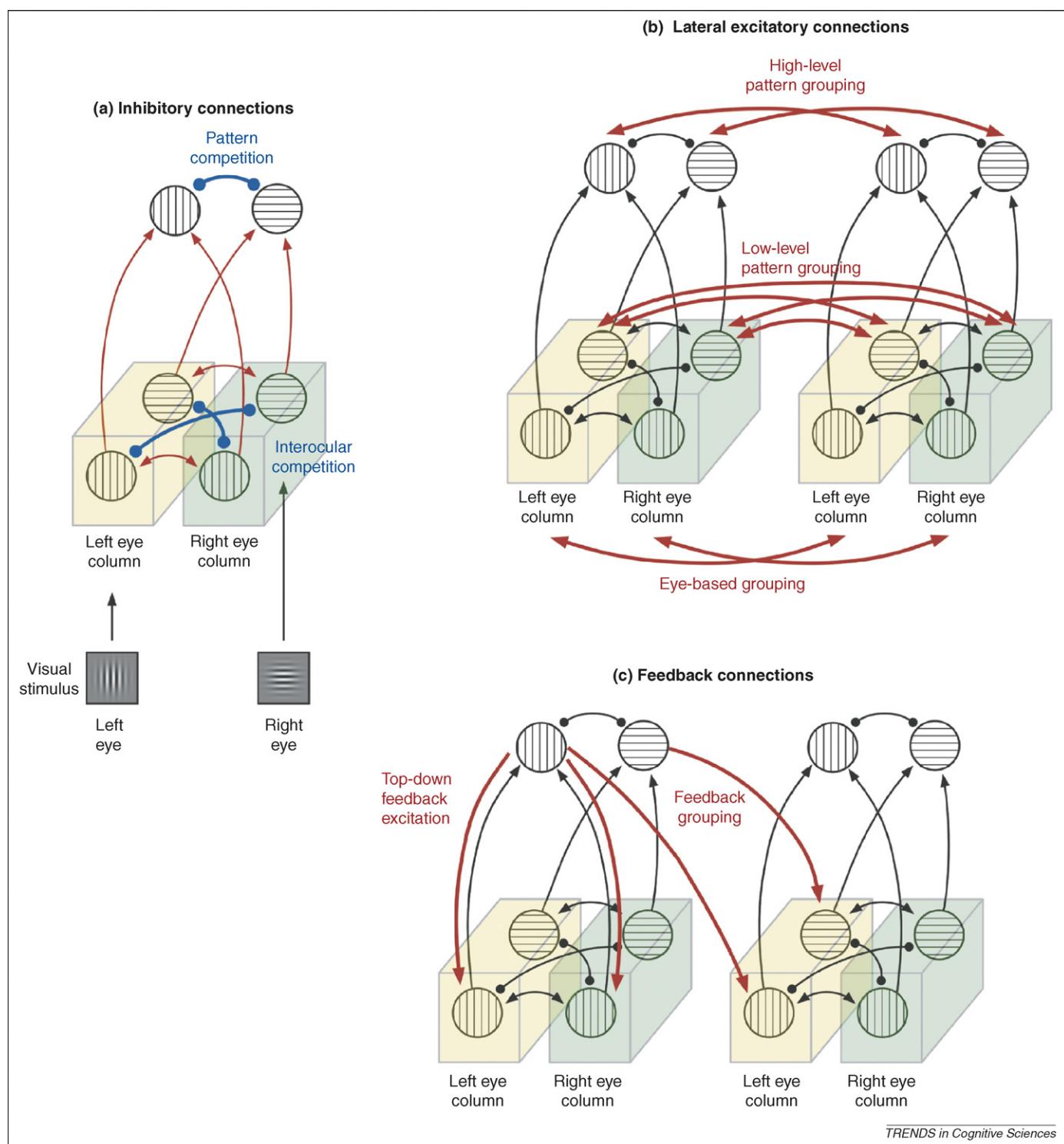


Figure 2. Schematic diagram of inhibitory connections and excitatory connections in a hybrid rivalry model. Inhibitory, lines with filled circles; excitatory, lines with arrows. (a) Reciprocal inhibitory connections between monocular neurons and binocular neurons (blue lines with circles); these connections might account for eye-based and pattern-based visual suppression, respectively. (b) Reciprocal excitatory connections (red lines with arrows). These lateral interactions might account for eye-based grouping, low-level grouping between monocular neurons with similar pattern preferences including interocular grouping, and high-level pattern-based grouping between binocular neurons. (c) Excitatory feedback projections (red lines with arrows), to minimize clutter, only a subset of possible projections is shown. These projections might account for top-down influences of visual attention and also feedback effects of perceptual grouping.

studies revealed that activity changes in several other visual areas are correlated with the observer's perception during rivalry, including the primary visual cortex [24–28], extrastriate areas [24,27–29] and the LGN [30,31]. Moreover, activity in human V1 mirrors the spatiotemporal

dynamics of rivalry perception [26] and can reliably predict which of two rivaling stimuli is currently dominant [27]. When rivalry suppresses the visibility of an illusory visual pattern, neural filling-in responses in V1 are also severely suppressed [28].

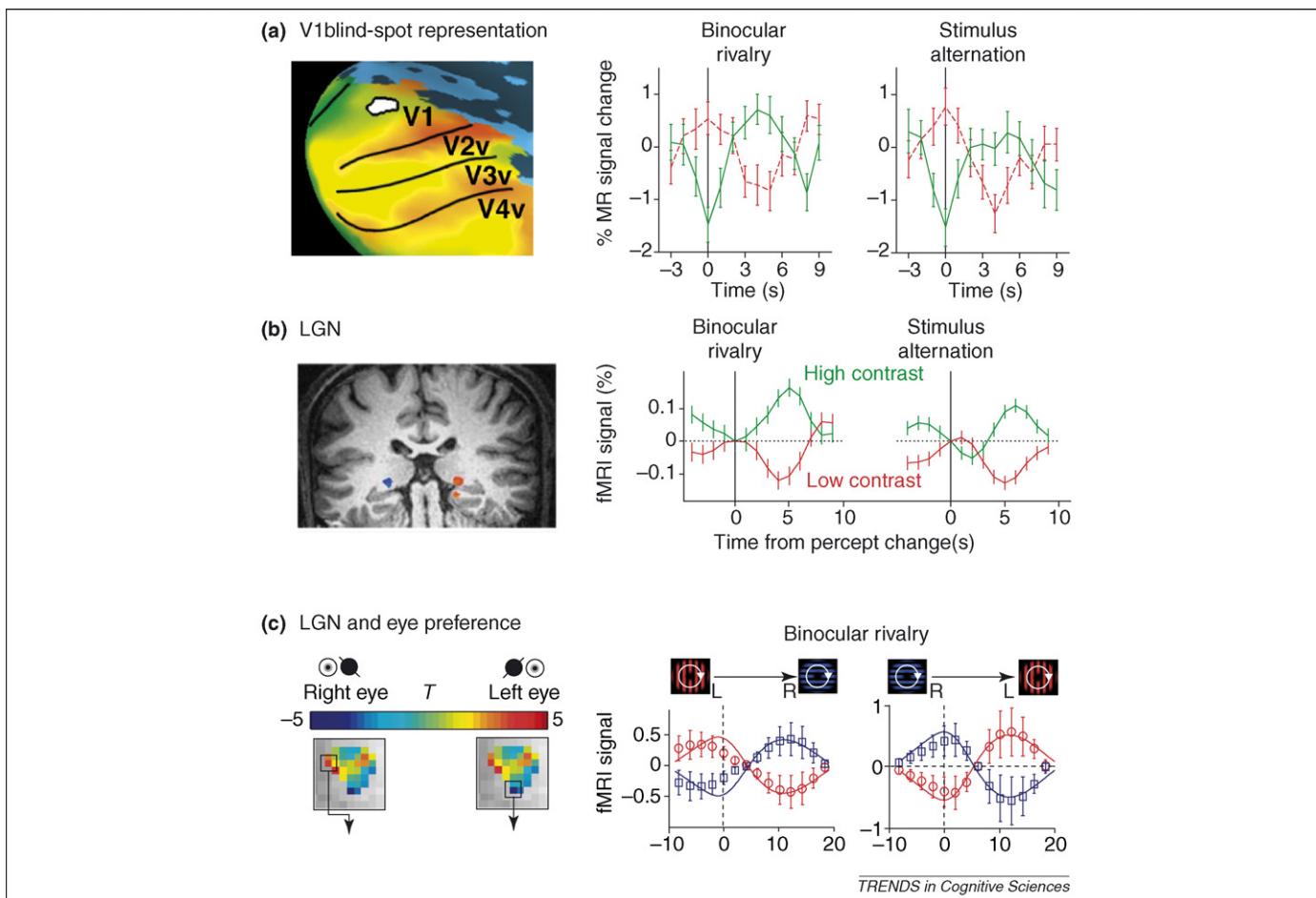


Figure 3. Neuroimaging evidence of binocular rivalry in monocular brain areas. **(a)** fMRI responses in the monocular V1 representation of the blind spot during binocular rivalry and stimulus alternation [25]. Green curve, preferred ipsilateral grating; red curve, non-preferred blind-spot grating. **(b)** fMRI responses in the human LGN during rivalry between high-contrast and low-contrast gratings and during stimulus alternation [30]. **(c)** Eye-specific preferences of voxels in the LGN (left), measured with pattern analysis, and modulations in left-eye and right-eye selective activity patterns during rivalry [31]. Reproduced from Refs. [25,30,31], with permission from Macmillan Publishers Ltd.

Evidence of interocular competition

According to hybrid theories of rivalry, neural events underlying suppression are initiated early in visual processing and might include inhibitory interactions between monocular neurons (Figure 2a). An fMRI study of the cortical representation of the blind spot, an exclusively monocular region in V1, provided the first physiological evidence of eye-specific suppression of activity during rivalry fluctuations in awareness [25]. Unlike the eye-specific columns in human V1, which are extremely narrow (~ 1 mm width), the blind spot representation is sufficiently large for reliable functional imaging. Activity in this monocular region was strongly modulated during rivalry (Figure 3a). Awareness-related responses during rivalry were just as strong as those evoked by physical alternations between one monocular stimulus and the other, which led to the conclusion that rivalry can fully suppress monocular responses to an unperceived stimulus under these conditions.

How might interocular competition be realized in the human visual system? One possibility is that inhibitory interactions result from lateral competition among monocular neurons in V1 [5,6]. Another possibility is that inhibitory feedback occurs between monocular V1 regions and monocular layers of the LGN [7].

Two recent studies have found reliable rivalry modulations in the human LGN, a structure whose distinct

layers receive segregated inputs from each of the two eyes. In one study, fMRI activity measured during binocular rivalry between high-contrast and low-contrast gratings revealed much higher levels of activity when observers perceived the high-contrast grating, in both LGN (Figure 3b) and V1 [30]. For both areas, rivalry modulations were almost as strong as stimulus-driven responses evoked by physical alternations between high- and low-contrast gratings. The other study looked for modulations in eye-specific activity during rivalry [31] using a pattern analysis technique that can recover neural preferences inherent at fine spatial scales by pooling information from many coarse-scale fMRI signals [32,33]. Applying this technique to rivalry, ensemble measures of eye-specific activity were obtained by pooling the weighted response of weakly biased monocular signals from voxels in the LGN and V1 (Figure 3c). In both brain areas, activity patterns corresponding to a particular eye were stronger when the image viewed by that eye became perceptually dominant.

These neuroimaging studies provide compelling new evidence for the involvement of interocular competition in binocular rivalry. It remains to be learned why neurophysiological studies have failed to observe equally strong effects of rivalry in the early visual areas of awake-behaving monkeys (Box 1). A goal for future research will be to bridge

Box 1. Neurophysiological studies of binocular rivalry

Neurophysiological studies have looked for neural correlates of binocular rivalry by recording action potentials from single neurons in alert monkeys trained to report the perceptually dominant stimulus during rivalry [12]. In these studies, the vast majority of neurons in the inferior temporal cortex showed changes in firing rate that closely tracked the monkey's perceptual report [48]. In comparison, about 40% of neurons recorded in extrastriate areas MT and V4 showed reliable activity fluctuations during rivalry, and some neurons exhibited paradoxical increases in activity when their preferred stimulus was suppressed from awareness [8,74]. Perception-related activity changes were found in only about 20% of neurons sampled from areas V1/V2, and across the entire sample, rivalry modulations were about one-third the strength of responses evoked by stimulus alternation. One study targeting the LGN of alert monkeys found no evidence of rivalry modulations, although these animals were not trained to report their perceptions [75].

Thus, single-unit results, especially those from V1/V2 and LGN, point to much weaker perception-related modulations than the more robust effects obtained in human neuroimaging studies of V1 and LGN [24,25,30,31]. What is responsible for these seemingly incompatible findings? Possible reasons include genuine species differences, differences in visual displays, subject sampling bias in human studies favoring those who report strong rivalry alternations, or neuronal sampling biases in recording studies. Of course, single-unit recordings and fMRI BOLD responses reflect very different measures of neural activity at different spatial scales. Studies of visual cortex in anesthetized monkeys show that BOLD activity is more closely associated with local field potentials (LFPs), which reflect slow

synaptic potentials, than with neuronal spiking activity [76]. Studies in alert humans have found high correlations between single-unit activity, LFPs and BOLD responses in auditory cortex [77]; although these results cannot distinguish whether BOLD activity is caused by spiking or synaptic activity, they do suggest that BOLD provides a reliable proxy for neuronal spiking activity. It will be helpful to learn whether BOLD activity can be strongly dissociated from spiking activity in alert subjects, and if so, under what situations.

If BOLD activity is indeed driven primarily by non-spiking, synaptic activity [78], then might the rivalry-related BOLD responses found in the LGN be attributed to modulatory feedback from higher visual areas? In theory, feedback to the LGN could induce slow synaptic potentials – and, hence, modulations in BOLD signals – yet fail to alter spiking activity. Nevertheless, feedback modulation of LGN activity can only arise from spiking activity from another source. What might be the spiking source of such feedback signals? V1 represents a reasonable candidate, as this region has the most extensive feedback projections to the LGN of any cortical area and includes projections to specific monocular layers of the LGN [79], so the ocular dominance columns in V1 provide a plausible, eye-based architecture for producing the layer-specific modulations implied by fMRI results from the LGN [31]. If V1 is indeed a source of rivalry-related modulation in the LGN, it is all the more puzzling why neurophysiological studies have failed to uncover strong variations in spiking activity during rivalry. Regardless of how this puzzle is eventually resolved, it is fair to surmise that the neural bases of rivalry will not be found in a single brain structure but, instead, must be sought within a complex, hierarchical network comprising excitatory and inhibitory mechanisms.

the potential differences between studies, perhaps by using fMRI to investigate rivalry in monkeys or, if opportunity warrants, by measuring single-unit activity in early visual areas of humans.

Responses to suppressed visual stimuli

Despite the strong suppressive effects of rivalry found in the human LGN and V1, some visual information about the unperceived image can still reach brain areas outside of the early visual system. The amygdala, a structure in the anterior medial temporal lobe involved in processing emotional stimuli, responds more strongly to fearful faces than to neutral stimuli, even when those stimuli are suppressed from awareness by rivalry [34,35] (Figure 4a). By contrast, activity in face-selective regions of the ventral temporal cortex is almost entirely suppressed under such conditions [23,34]. Subliminal responses can also be found in dorsal regions of the visual cortex, including regions of the intraparietal sulcus (Figure 4b). Dorsal regions that respond more strongly to tools than to faces maintain this response preference even when the images are rendered invisible by interocular masking [36]. Thus, despite the pronounced effects of rivalry suppression seen at early stages of the visual pathway, some information about object form still activates other brain areas, including higher parietal areas. Evidently, however, this neural activity in higher brain areas is insufficient to support visual awareness.

Psychophysical studies of binocular rivalry

Visual adaptation and rivalry

Psychophysical studies provide a complementary method for inferring where in the processing stream rivalry takes place, relative to other types of visual processing.

There is long-standing evidence suggesting that rivalry cannot suppress the build-up of low-level aftereffects resulting from visual adaptation to orientation [37,38] or translational motion [39]. This led to the conclusion that rivalry suppression takes place at a *later* stage of processing than orientation and direction-selective adaptation, which is thought to originate in primary visual cortex. How can these results be reconciled with recent evidence of eye-specific suppression in neuroimaging studies, as well as psychophysical evidence of eye-specific impairments in visual sensitivity during rivalry suppression [40]?

A recent re-examination of the effect of suppression on orientation and motion adaptation might resolve the conflict: orientation and motion aftereffects are *weakened* by rivalry suppression [41]. However, this suppression is revealed only when observers are presented with adapting stimuli at relatively low contrasts, because high levels of stimulus contrast can saturate the response of the visual system (Figure 5). Note that some adaptation continues to occur during rivalry, even for weak stimuli, implying that suppression weakens but does not abolish neural activity at the site of adaptation.

Rivalry suppression or prolonged dichoptic masking can also weaken the formation of visual afterimages [42,43], providing further evidence that rivalry can attenuate low-level adaptation. This outcome, incidentally, is surprising because afterimage formation is usually attributed to the adaptation of retinal neurons, and implies that adaptation at some site beyond the retina also contributes to the perception of afterimages.

These adaptation studies imply that rivalry suppression attenuates, but does not abolish, neural activity emanating from early cortical stages. Consistent

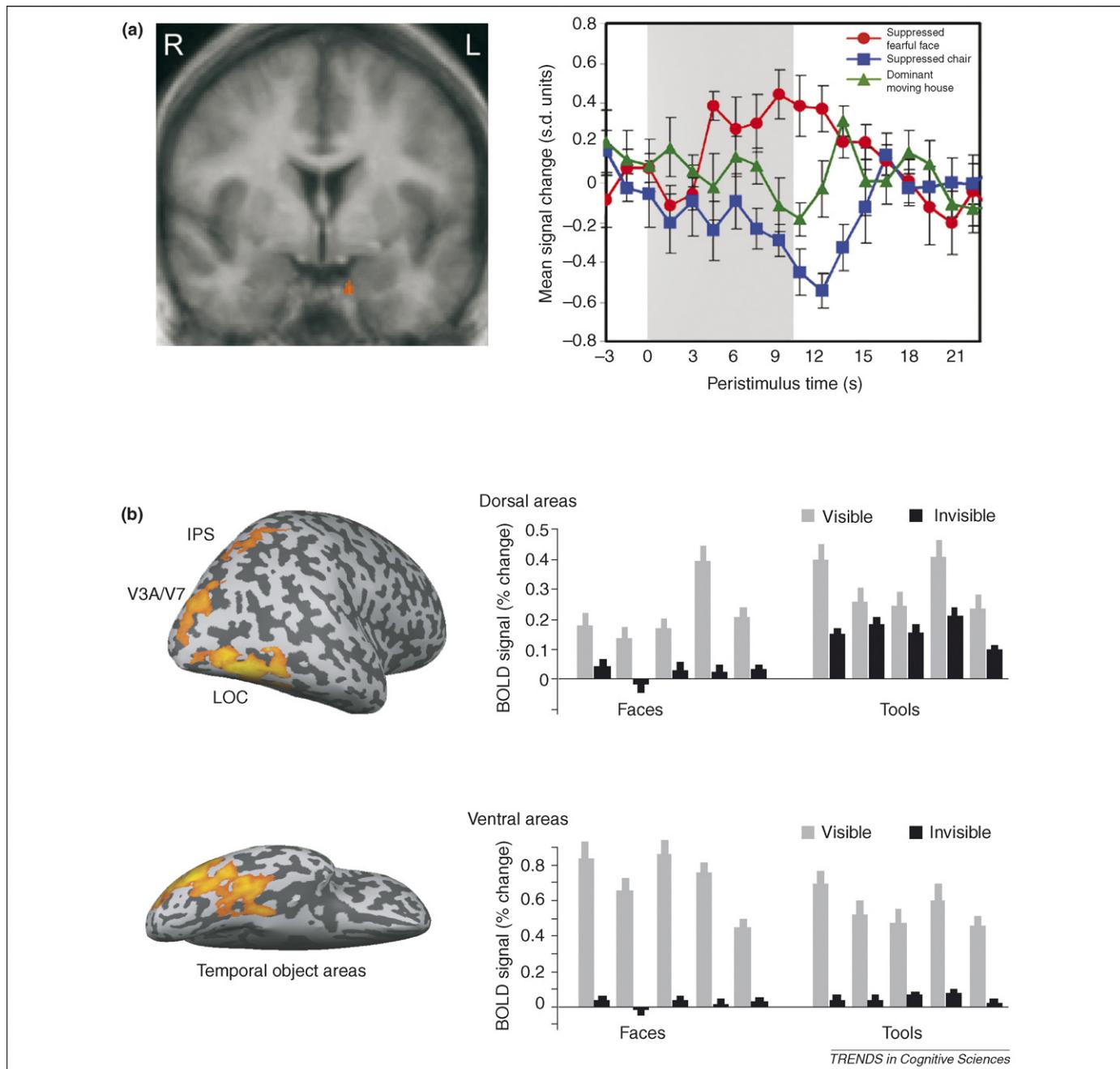


Figure 4. fMRI responses to unperceived stimuli during rivalry suppression. **(a)** Activity in the amygdala while a flashing house was presented to the dominant eye and either the same house, an unperceived face or an unperceived chair was presented to the suppressed eye. According to one hypothesis, the amygdala retains sensitivity to suppressed visual information because it receives subcortical inputs bypassing the geniculostriate pathway, although evidence of direct anatomical connections remains to be demonstrated. Alternatively, this structure might be more sensitive to low contrast or low spatial frequency content than visual cortical areas of the ventral temporal lobe. Reproduced from Ref. [34], with permission from Elsevier. **(b)** fMRI responses in dorsal and ventral visual areas to visible faces and tools, and responses to the same stimuli rendered invisible by rivalry suppression. Note how unperceived tools continue to activate dorsal regions. IPS, intraparietal sulcus; LOC, lateral occipital complex. Reproduced from Ref. [36], with permission from Macmillan Publishers Ltd.

with this notion, many studies have found that a suppressed stimulus retains some effectiveness despite its invisibility. During rivalry, characteristics of the phenomenally suppressed stimulus can affect the appearance of the dominant stimulus, including its perceived motion direction [44], flicker rate [45] and orientation [46].

Although the consequences of rivalry are evident at early stages of processing, suppression could grow in potency at subsequent cortical stages [47], culminating

in near complete suppression of neural activity within object-selective areas of the ventral visual pathway [23,48]. This could result from the cumulative effects of lateral competition across multiple levels of the visual pathway (Figure 2a). Indeed, aftereffects of perceptual adaptation to faces [49] and semantic priming to objects [50] are eliminated when those stimuli are subjected to interocular suppression. However, other recent studies suggest that highly familiar visual forms, such as words, faces or human bodies, can emerge from rivalry

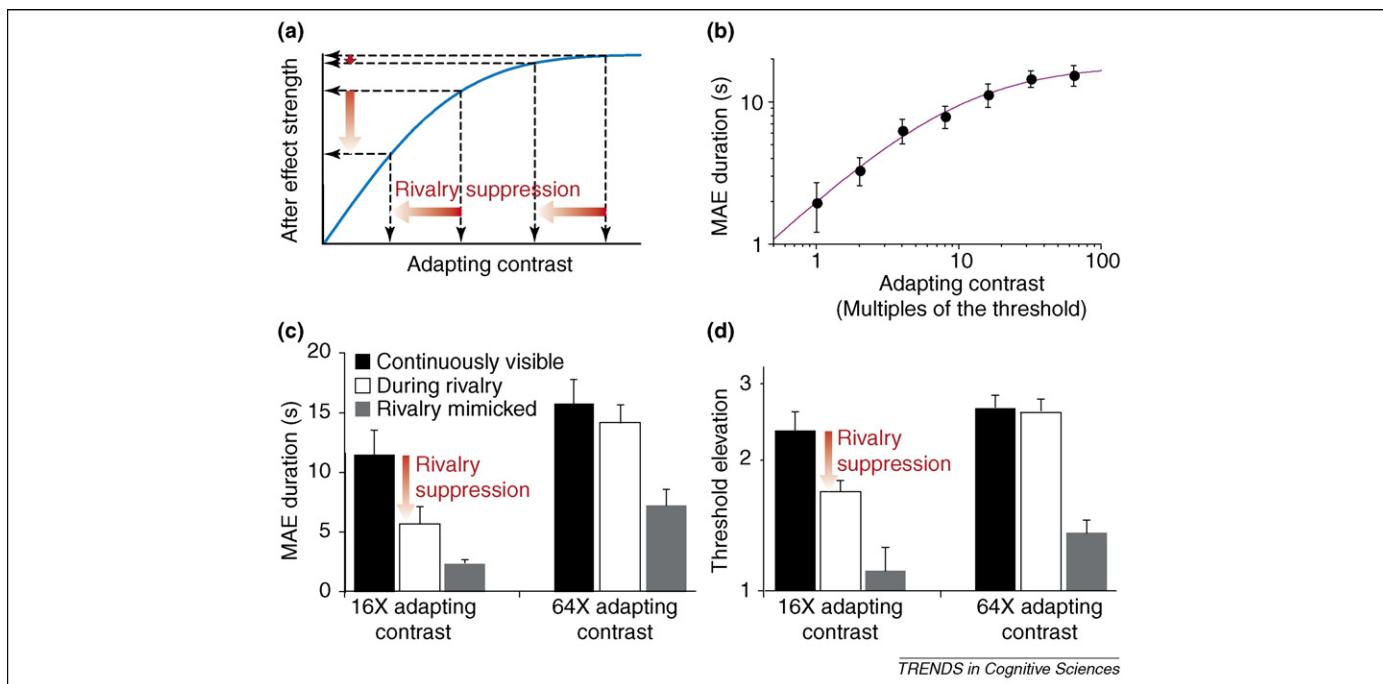


Figure 5. Binocular rivalry reduces visual adaptation to orientation and motion. **(a)** Hypothesized contrast-response curve illustrating the predicted strength of adaptation as a function of stimulus contrast. If rivalry reduces the effective contrast of a stimulus (leftward pointing arrows), then rivalry should reduce adaptation to stimuli of low contrast but not high contrast, as indicated by the downward pointing arrows. **(b)** Duration of the motion aftereffect (MAE) as a function of the contrast of the adapting motion stimulus. Note strong similarity to a. **(c)** Static MAE duration in different viewing conditions at two adapting contrasts. For low-contrast adapting stimuli (16 times threshold), rivalry suppression leads to weaker adaptation than when the adapting stimulus remains continuously visible, as indicated by the downward arrow. **(d)** Threshold-elevation aftereffect (TEAE) for oriented gratings in different viewing conditions at two adapting contrasts. Adapted from Ref. [41], with permission from National Academy of Sciences, U.S.A....

suppression more rapidly [51], and might even attract spatial attention despite the observer's lack of awareness of those forms.

Rivalry: local competition and global integration

The spatial-temporal dynamics of binocular rivalry can be strongly influenced by perceptual grouping mechanisms, which could be realized by excitatory connections between neurons that represent adjacent regions of visual space (Figure 2b). Spatially distributed rival targets matching in color or orientation tend to alternate in unison during rivalry [52,53], even when the components of those rival targets are distributed between the two eyes [52,54]. Evidence of eye-specific spatial grouping has also been shown [52,55]. More complex visual forms, including recognizable objects, can also serve as a perceptual grouping cue to enhance the predominance of a set of visual elements [56,57], either because these stimuli are represented more strongly in the visual system or because they attract greater visual attention. Perceptual alternations during binocular rivalry might also promote synchronization with other forms of pattern rivalry, thereby enhancing the perception of a common global pattern [14,58]. The above results can be understood in terms of lateral excitatory connections between neurons tuned to common visual features, such as orientation, color or eye of origin (Figure 2b). Pattern-grouping effects could occur at multiple levels, involving both monocular and binocular pattern-sensitive neurons. Such grouping interactions might explain the spreading, wave-like appearance of a stimulus emerging into dominance during rivalry [59], which is

accompanied by spreading waves of activity in V1 [26]. Excitatory feedback projections from higher areas to low-level areas might also be important for perceptual grouping (Figure 2c), especially when the perception of coherent objects is involved.

The above studies reveal how grouping interactions during rivalry can lead to organized competition between large-scale neuronal populations. Other evidence, however, indicates that the source of this competition depends importantly on local, eye-specific inhibition. When an array of intermixed red and green patches is presented to one eye and patches of the opposite color are presented to corresponding locations of the other eye (Figure 1b), observers perceive all elements of a single color for durations longer than expected based on chance alone [52]. However, if a subset of left-eye and right-eye elements are swapped during periods of coherent perception, it is the eye and not the dominant color that determines subsequent perceptual dominance at a given visual-field location. In other words, within local regions it is the information from one eye that is suppressed [55]. Also underscoring the importance of local interocular inhibition is the failure of binocular rivalry between different globally defined forms presented to the two eyes, unless local interocular differences are introduced into the displays [60]. These results suggest that local interocular competition is necessary for the instigation of binocular rivalry. Finally, perceptual grouping might fragment into piecemeal rivalry when global excitatory interactions are weak. Taken together, these results imply that binocular rivalry entails local interocular inhibition, with activity in these local inhibitory circuits

coordinated to modulate in unison because of global excitatory interactions between neurons tuned to common visual features. This combination of local inhibition and global integration can lead to coordinated competition between large-scale neuronal populations at the network level.

The predominance of a rivalry stimulus can also persist over time, even across successive presentations of a rivalry display, suggesting the formation of a perceptual trace [61]. Many of the same visual features that influence spatial grouping, such as eye of origin, color and orientation, also influence this form of perceptual grouping over time [62,63]. A goal for future models will be to account for grouping effects over space and time within a single framework.

Rivalry and visual attention

The idea that rivalry might exemplify a form of visual attention dates back to Helmholtz, and in recent years this idea has been revitalized [64–68]. Within the context of the hybrid model of rivalry, top-down effects of attention could be realized by excitatory feedback projections to early visual areas (Figure 2c).

Upon the initial presentation of rival targets, exogenous attention is very effective at determining which of the two stimuli will first achieve dominance [64,66]. But can observers control subsequent alternations of rivalry following initial dominance? Observers can indeed exert some selective attentional control over what they perceive during steady rivalry viewing [65,69], and this control can be further amplified if observers are given a challenging visual task requiring focused attention on one of two rivaling stimuli [67]. However, observers cannot hold one stimulus dominant indefinitely, and selective attentional control over binocular rivalry is considerably weaker than control over other forms of bistable perception, such as Necker cube reversal [65,68]. Attentional influences on rivalry might involve an increase in the effective contrast of the attended rival stimulus [70], although current evidence is mixed [65]. Eye movements might also play a role in the control of rivalry alternations, as evidenced by the high incidence of small eye movements just before a transition in rivalry state [71]. Eye movements produce transient stimulation at the retina, and transients are known to trigger reversals in rivalry state [72]. Other non-visual perturbations, including transcranial magnetic stimulation and caloric stimulation [73], can also alter the rate of rivalry alternations, perhaps by influencing eye movements or activity levels in the attention networks of the brain.

Concluding remarks

Recent discoveries indicate that rivalry is both low level and high level, much more so than proponents of either viewpoint once imagined. To account for these seemingly paradoxical findings, we considered neuroimaging and psychophysical evidence within the framework of a hybrid model of binocular rivalry. Current evidence suggests that local, low-level competition is essential for the instigation of binocular rivalry, that suppression is evident at early sites and continues to occur at higher cortical sites, and

Box 2. Outstanding questions

- What are the specific contributions of different inhibitory and excitatory circuits to binocular rivalry? How might different visual conditions alter the sites at which rivalry competition is most prevalent?
- Are the neural mechanisms that underlie perceptual grouping in binocular rivalry also responsible for perceptual grouping in normal vision?
- How does voluntary attention affect the neural representation of an item during rivalry? Does attention simply enhance the strength of the neuronal signal, similar to an increase by contrast gain, or does attention alter other components of the neural circuit, perhaps by modulating the strength of recurrent signals, the strength of inhibitory connections, or by promoting perceptual grouping and greater coherence among neurons?
- There exist several techniques for producing interocular suppression, including binocular rivalry, continuous flash suppression and dichoptic masking. To what extent do these different techniques tap into common neural mechanisms?
- What is the relationship between binocular rivalry and other forms of perceptual multistability, such as motion-induced blindness and ambiguous pictorial figures?
- Why do individuals differ substantially in their rate of alternations during rivalry, and why does this correlate with their alternation rates for other forms of bistable perception? Is this related to individual differences in cellular properties governing adaptation and inhibition within local neuronal circuits in a person's brain or, instead, to the operation of a central neural oscillator that exerts widespread control over a host of rhythmic activities [80]?
- Why is binocular rivalry so effective at suppressing the visibility (detectability) of almost any suprathreshold stimulus for long periods of viewing, when most other forms of visual suppression are much less robust, less enduring, or less adaptable to changes in stimulus conditions [4]?

that perceptual grouping and top-down influences of visual attention can enhance the dominance of specific visual representations during rivalry. These diverse components of rivalry can be understood in terms of causal neural interactions involving specific inhibitory or excitatory connections within a fairly simple, schematized network. Future empirical studies will facilitate the development of more formalized models and help to reveal which components and connections are essential to rivalry and which might be more modulatory or peripheral (Box 2). Binocular rivalry is remarkably effective at suppressing the visibility of almost any stimulus for prolonged periods, unlike many other forms of visual suppression. The efficacy of these inhibitory interactions might provide a model system for investigating the neural circuits involved in visual competition, perceptual grouping and selective attention, and might ultimately shed light on the dynamical properties of visual awareness itself.

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