



## Competing Theories of Binocular Rivalry: A Possible Resolution

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**Abstract.** The neural basis of binocular rivalry has been the subject of vigorous debate. Do discrepant monocular patterns rival for awareness because of neural competition among pattern representations or monocular channels? In this article, I briefly review psychophysical and neurophysiological evidence pertaining to both theories and discuss important new neuroimaging data which reveal that rivalry is fully resolved in monocular visual cortex. These new findings strongly suggest that interocular competition mediates binocular rivalry and that V1 plays an important role in the selection of conscious visual information. They further suggest that rivalry is not a unitary phenomenon. Interocular competition may fully account for binocular rivalry whereas a separate mechanism involving pattern competition likely accounts for monocular and stimulus rivalry.

**Key words:** binocular rivalry, human, magnetic resonance imaging, visual perception, visual cortex

A fundamental question in the fields of vision, psychology, and neuroscience is how the brain selects one of many competing visual signals for access to consciousness. When different monocular patterns are simultaneously presented to the two eyes, they rival for perceptual dominance such that only one monocular image is perceived at a time while the other is temporarily suppressed from awareness (Levelt, 1965; Wheatstone, 1838). This phenomenon of binocular rivalry has attracted the interest of psychologists and neuroscientists alike as a method of probing the mechanisms that determine our visual awareness.

Despite over two century's worth of investigation, however, the nature of the competitive interactions that mediate binocular rivalry has remained unresolved. Specifically, it is debated whether discrepant monocular patterns rival as a result of neural competition among monocular channels or pattern representations. Human psychophysical studies have been interpreted to suggest that binocular rivalry results from interocular competition among monocular neurons in either primary visual cortex (V1) (Blake, 1989) or the lateral geniculate nucleus (Lehky, 1988). In contrast, single-unit recordings in awake-behaving monkeys suggest that rivalry arises from competition among incompatible pattern representations at higher levels of the visual pathway, well after inputs from the two eyes have converged in V1 (Leopold and Logothetis, 1996; Logothetis and Schall, 1989; Sheinberg and Logothetis, 1997).

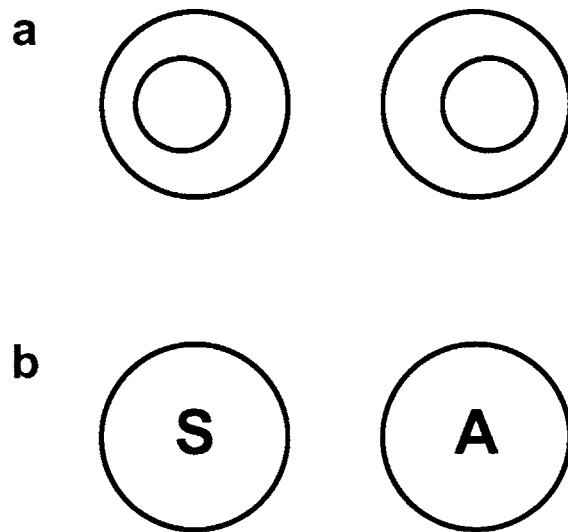
In this article, I briefly review the various theories of binocular rivalry from antiquity to present, then focus on the present-day debate regarding whether rivalry arises from interocular competition or pattern competition. The strengths and weaknesses of these two theories are discussed with respect to relevant psychophysical and neurophysiological findings. I then describe the contribution of human neuroimaging studies and present critical new data showing that rivalry is fully resolved at the earliest stage of cortical processing among monocular V1 neurons (Tong and Engel, 2001). These new findings strongly suggest that interocular competition mediates binocular rivalry. In contrast, a separate mechanism of pattern competition likely accounts for the perceptual alternations that can occur during monocular and stimulus rivalry.

### Early Theories of Binocular Rivalry

DuTour was among the first to describe the phenomenal alternations of binocular rivalry (1760, translated by O'Shea, 1999). When he viewed a piece of blue taffeta with one eye and a piece of yellow taffeta with the other eye, the two monocular colors did not yield a combined impression of green as one might predict based on their optical combination. Instead, perception alternated between each color. DuTour concluded that dichoptic viewing (i.e., the presentation of a different image to each of the two eyes) revealed the natural state of human vision: at any moment, the mind can apprehend only one of the two corresponding retinal points.

DuTour's theory, often called 'suppression theory', was brought into question by Wheatstone's (1838) discovery of stereopsis. Wheatstone found that stereo-image pairs with shifted local features can yield a stable, fused impression of stereoscopic depth (Figure 1a). Thus, in certain instances the mind can combine information from both eyes. However, Wheatstone also discovered the phenomenon of binocular contour rivalry in which very different monocular patterns fail to fuse and instead lead to perceptual alternation (Figure 1b). Voluntary attention did not seem to determine the appearance of each competing pattern but did seem to influence the duration of its appearance. Wheatstone concluded that: "*The mind is inattentive to impressions made on one retina when it cannot combine the impressions on the two retinae together so as to resemble the perception of some external objects.*" This insight predates current theories of interocular competition in which rivalry is considered the default outcome when binocular fusion fails (Blake and Boothroyd, 1985). However, Wheatstone's conclusion also foreshadows current theories of pattern competition which predict that rivalry should occur when two monocular images are too different to yield a singular perceptual interpretation (Logothetis, Leopold and Sheinberg, 1996).

Helmholtz (1866/1924) proposed a very different notion that rivalry arises from spontaneous fluctuations in visual attention. Unlike Wheatstone, Helmholtz believed that inputs from the two eyes are not organically (physiologically) combined. Although information from the two eyes could be combined to yield



*Figure 1.* **a**, Example of Wheatstone's (1838) stereoscopic display. When these two images are fused by crossing one's eyes, the shifted central circles yield an fused impression of stereoscopic depth, appearing in front of the larger background circles. **b**, Example of binocular contour rivalry. When cross-fused, these two images lead to alternating perception of the "S" versus the "A".

stereoscopic depth, this presumably reflected a psychological rather than an organic act. This conclusion arose in part from Helmholtz's finding that dichoptic colors cannot be combined to yield an intermediate impression but instead lead to rivalry. Helmholtz interpreted these findings to suggest that inputs from either eye remain potentially available to awareness until the very latest stages of attentional selection.

Consistent with this attentional view, Helmholtz found that he could increase the predominance of either rivaling pattern by attending to that pattern. Although rivalry still occurred when no attempt was made to shift attention, these spontaneous alternations were assumed to reflect that attention itself is always in flux and cannot remain fixed on a particular object for more than a few seconds.

Helmholtz discovered that a similar but weaker form of perceptual conflict can occur when two objects are optically superimposed and presented to the same eye, a phenomenon later termed 'monocular rivalry' by Breese (1899). Monocular rivalry could not be explained by DuTour's suppression theory but did appear consistent with Helmholtz's attentional theory, and also agreed with the later notion that rivalry involves a general form of pattern competition (Diaz-Caneja, 1928; Logothetis *et al.*, 1996).

## Modern Theories of Binocular Rivalry

### INTEROCULAR COMPETITION THEORY

In his highly influential monograph “On binocular rivalry”, Levelt (1965) described rivalry as a competitive mechanistic process involving reciprocal inhibition between the two eyes. This theory developed at a time when considerable advances were being made in neurophysiology, including Hubel and Wiesel’s (1962) discovery that inputs from the two eyes are combined by binocular neurons in cat striate cortex.

According to Levelt’s theory, inputs from the two eyes are relatively weighted such that they add to unity (cf. Hering, 1868/1977) and these weights depend upon the amount and strength of contour in each eye. When dichoptic contours differ greatly, as during binocular contour rivalry, they directly compete with one another via reciprocal interocular inhibition. Specifically, the signal strength of one monocular stimulus determines the extent of interocular suppression for the contralateral stimulus.

These ideas were later implemented in several interocular competition models of rivalry (Blake, 1989; Lehky, 1988; Matsuoka, 1984; Sugie, 1982). Although these models may differ in certain details or in the proposed neural implementation, they share a common structure and lead to similar predictions.

Figure 2 shows an example of an interocular competition model proposed by Lehky (1988). Rivalry arises from reciprocal inhibition between the left versus right monocular channel. When one monocular input is stronger than the other, it activates an inhibitory neuron that can entirely suppress input from the other eye. However, this inhibition adapts over time, eventually leading to the dominance of the previously suppressed eye. This simple model successfully captures the temporal dynamics of rivalry. It also predicts an important psychophysical finding that increasing the strength (e.g., contrast) of one monocular stimulus does not increase its own predominance but instead, decreases the predominance of the competing stimulus (Levelt, 1965).

According to Lehky, this competitive circuit may be implemented in the form of inhibitory feedback signals from V1 to monocular layers of the lateral geniculate nucleus. However, it could be applied equally well to competitive lateral interactions among monocular V1 neurons as has been proposed in an alternative model by Blake (1989).

To account for the absence of rivalry during stereopsis, Lehky proposed that a separate stereopsis mechanism detects the amount of correlation between inputs from the two eyes and appropriately modulates the strength of interocular inhibition. Fusion would occur when inhibition is low whereas rivalry would occur when inhibition is high.

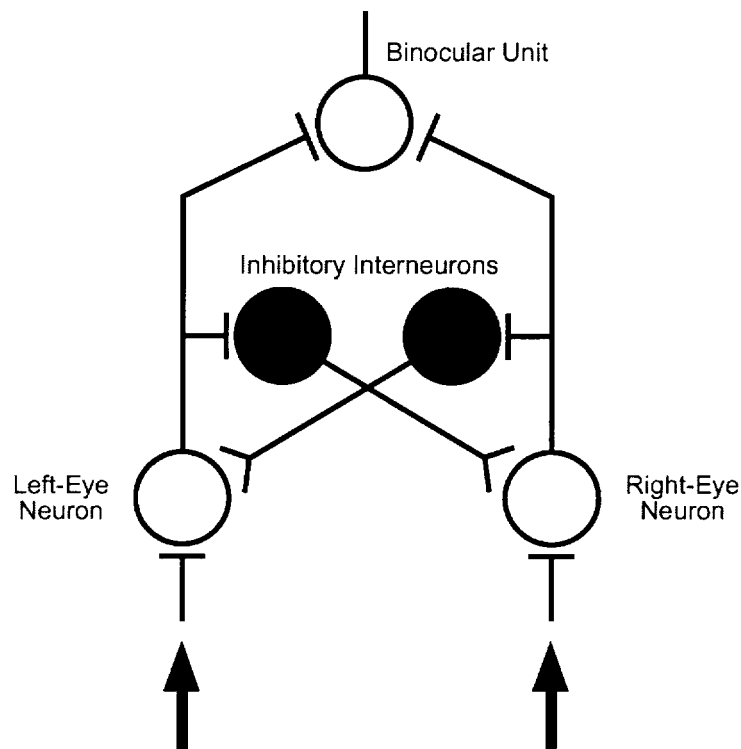


Figure 2. Example of a neural network model of binocular rivalry (adapted from Lehky, *Perception*, 1988). Reciprocal inhibition occurs between left-eye and right-eye neurons as a result of inhibitory interneuronal connections. As a consequence, left-eye versus right-eye inputs are alternately suppressed during binocular rivalry. These competitive interactions take place prior to binocular convergence.

#### PATTERN COMPETITION THEORY

In contrast to interocular competition theory, Logothetis and colleagues (Leopold and Logothetis, 1996; Logothetis, 1998; Logothetis *et al.*, 1996) have proposed that binocular rivalry arises from competition among incompatible pattern representations, well after inputs from the two eyes have converged in primary visual cortex (V1). For example, rivalry between a left-eye vertical grating and a right-eye horizontal grating is assumed to reflect competition between the perceptual representations for vertical and horizontal rather than competition between left-eye and right-eye channels (cf. Diaz-Caneja, 1928).

Such pattern competition can be realized using a simple competitive circuit like the model proposed by Lehky (1988) with the exception that reciprocal inhibition occurs between different pattern representations rather than between monocular channels. A more elaborate model involving multiple levels of pattern competition and feedback organizational effects has also been proposed (Dayan, 1998).

Although the structure of the competitive circuitry may not appear to differ greatly between interocular and pattern competition models, the latter theory holds that rivalry involves a much higher-level form of competition between equally valid perceptual interpretations of the external world. In this respect, binocular rivalry is presumed to reflect very similar or identical mechanisms as those that mediate the reversal of ambiguous figures such as the Necker Cube or Rubin's face/vase (Logothetis, 1998).

#### STRENGTHS AND WEAKNESSES OF INTEROCULAR COMPETITION THEORY

The strength of interocular competition theory lies in its simplicity, specificity, and testability. This theory provides a simple mechanistic account of binocular rivalry in sufficient detail to generate specific testable predictions. Several psychophysical findings support the notion that rivalry arises from interocular competition (for reviews see Blake, 1989; Blake, this issue). For example, if a left-eye vertical grating is currently dominant and a right-eye horizontal grating is suppressed, a sudden exchange of the two monocular patterns leads to the perception of the *left-eye* horizontal grating (Blake, Westendorf and Overton, 1980). These experiments suggest that it is the eye rather than the pattern that maintains perceptual dominance, consistent with the predictions of interocular competition. Similarly, if a brief monocular probe is presented during rivalry, detection performance is diminished by roughly 0.5 log units when the probed eye is undergoing perceptual suppression rather than dominance (Fox and Check, 1972; Wales and Fox, 1970).

Interocular competition is also supported by the finding that stimuli presented to the temporal hemifield tend to dominate over stimuli in the nasal hemifield (Fahle, 1987). This hemifield asymmetry is difficult to explain in terms of pattern competition. However, it can be easily understood when one considers that ocular dominance columns in V1 show a similar asymmetry with greater representation of the temporal hemifield (input from the contralateral eye) than of the nasal hemifield (input from the ipsilateral eye) (LeVay, Connolly, Houde and Van Essen, 1985).

Finally, it is known that rivalry interactions can extend over certain distances among non-overlapping stimuli and that the spatial range of binocular rivalry increases as a function of eccentricity (Levelt, 1965). Thus, a monocular point stimulus will frequently disappear when a surrounding but non-overlapping annulus is presented to the other eye. Such rivalry among non-overlapping stimuli seems difficult to explain in terms of pattern competition, especially given that monocular or dioptic viewing of such stimuli would lead to minimal perceptual fading. Instead, these findings are consistent with the notion that competitive lateral interactions between monocular V1 neurons have a limited spatial range corresponding to the cortical magnification properties of V1 (Blake, O'Shea and Mueller, 1992).

Certain psychophysical findings, however, remain difficult to explain in terms of interocular competition. Adaptation studies have suggested that a suppressed rivalry stimulus can still lead to the development of visual aftereffects that likely

involve cortical mechanisms. These studies have shown that contrast-threshold-elevation, motion, and tilt aftereffects are equally strong irrespective of whether the monocular adapting stimulus is continuously perceived or periodically suppressed by a rivaling stimulus (Blake and Fox, 1974; Lehmkuhle and Fox, 1975; Wade and Wenderoth, 1978). In comparison, much weaker aftereffects occur if the adapting stimulus is physically removed for a duration comparable to the suppression period. These findings suggest that the site of binocular rivalry occurs after the site of adaptation. More important, suppression does not reduce the amount of interocular transfer for the spatial frequency or motion aftereffect (Blake and Overton, 1979; O'Shea and Crassini, 1981). Given that the interocular transfer of aftereffects is likely mediated by binocular neurons, these results appear to suggest that rivalry suppression takes place after binocular convergence.

However, an alternative possibility is that monocular signals are greater during the dominance phase of rivalry than during dioptic (fused) or monocular viewing (Lehky, 1988). Thus an adapting stimulus that is perceived for only half the time during rivalry may still lead to equivalent adaptation effects because it is a more effective adapting stimulus. Consistent with this notion, a recent study replicated the finding of equal contrast adaptation for a continuously perceived adapting stimulus versus an adapting stimulus that was perceived for only half the time because of rivalry suppression. However, when the adapting stimulus was perceived for only 10% of the time (by boosting the contrast of the rivaling stimulus), much weaker adaptation was found to occur (Lehky and Blake, 1991). Contrary to previous studies, these findings suggest that rivalry suppression occurs *prior to* the site of adaptation but that much more extensive suppression is required to reveal these effects.

Further studies should be conducted to test if the same holds true for other aftereffects including those involving interocular transfer. Also, separate studies should assess whether monocular activity is enhanced during the dominance phase of rivalry as compared to monocular or dioptic viewing (Makous and Sanders, 1978).

Interocular competition theory provides a compelling account of binocular rivalry but provides no explanation for why rivalry can sometimes occur in the absence of interocular competition. For example, a weaker form of perceptual alternation can occur during monocular rivalry when two low-contrast patterns are viewed by a single eye or by both eyes (Andrews and Purves, 1997; Helmholtz, 1924; Wade, 1975). Such rivalry cannot be explained in terms of interocular competition and must instead reflect some form of pattern competition. Although monocular rivalry leads to weaker perceptual alternations than binocular rivalry, both phenomena share many similarities that could potentially reflect the operation of a common neural mechanism (Andrews and Purves, 1997).

To summarize, interocular competition theory provides a simple, powerful explanation of binocular rivalry and leads to clear, testable predictions. It is supported by several psychophysical studies showing eye-specific effects during

rivalry. However, this theory cannot generalize to related phenomena such as monocular rivalry and may have difficulty explaining the persistence of visual adaptation during binocular rivalry suppression.

### **Strengths and Weaknesses of Pattern Competition Theory**

Modern theories of pattern competition theory developed from an influential single-unit study that found negligible evidence of rivalry-related activity in primary visual cortex of awake-behaving monkeys (Leopold and Logothetis, 1996). Monkeys were trained to report their moment-to-moment perception during binocular rivalry by intermixing rivalry trials with catch trials in which the stimulus itself alternated between one of two monocular patterns. Only a small percentage of neurons in V1/V2 (9%), V4 (18%), and MT (12%) showed greater activity when monkeys reported perceiving the preferred stimulus during rivalry, and some neurons in V4 (9%) and MT (11%) actually fired more when the preferred stimulus became phenomenally suppressed (Leopold and Logothetis, 1996; Logothetis and Schall, 1989). These findings led to the novel suggestion that perhaps only a small sub-population of neurons in V4 and MT carry information about conscious perception and perhaps some neurons serve to represent the suppressed stimulus. Unlike the neurons in V4 and MT, most inferotemporal neurons (84%) showed significant changes in neural activity corresponding to the perceived stimulus during rivalry (Sheinberg and Logothetis, 1997).

These neurophysiological findings revealed no evidence of competition among monocular V1 neurons and thus fail to support the predictions of interocular competition. Instead, they support the notion that rivalry arises from competition among binocular pattern-selective neurons at much higher levels of the visual pathway.

A major strength of pattern competition theory lies in its ability to provide a parsimonious account of binocular rivalry and related forms of rivalry involving pattern competition. As already discussed, monocular rivalry can occur when two competing patterns are presented to the same eye or to both eyes (Andrews and Purves, 1997; Helmholtz, 1924). Pattern competition has also been demonstrated in a recently discovered phenomenon called stimulus rivalry. When dichoptic orthogonal gratings are rapidly flickered (18 Hz) to mask the frequent reversal of left-eye and right-eye patterns (every 333 ms), subjects often report that one pattern remains dominant for durations that far exceed the interval at which the stimuli are swapped from eye to eye (Logothetis *et al.*, 1996). These findings, like those of monocular rivalry (e.g., Helmholtz, 1924), indicate that rivalry alternations can sometimes occur between discrepant patterns independent of the eyes.

However, subsequent studies have shown that stimulus rivalry can occur only within a limited range of reversal rates and only for low contrast stimuli (Lee and Blake, 1999). In contrast, binocular rivalry occurs across a wide range of viewing conditions and stimulus contrasts (Blake, 1989). The discrepancy between these

two phenomena may indicate that the competitive interactions underlying stimulus rivalry differ from those that mediate binocular rivalry.

Pattern competition theory is consistent with the fact that perceptual grouping can sometimes occur across image elements in the two eyes during binocular rivalry. Kovács and colleagues (1996) created heterogeneous color displays consisting of many small equiluminant red and green patches presented to one eye and the opposite pattern of green and red patches presented to the other eye such that color rivalry occurred between dichoptic red/green patches at each visual location. If the perception of such displays involves grouping information by eye, then subjects should perceive only intermingled red/green patches. However, if monocular elements across the two eyes can be grouped together during rivalry, then subjects should sometimes report seeing all-red or all-green patches. Kovács and colleagues observed the latter finding indicating that perceptual grouping can occur across the eyes.

One interpretation of these findings is that rivalry is occurring between coherent pattern representations rather than between the eyes. However, an alternative interpretation is that binocular rivalry involves local interocular competition but that this local competition can be influenced by perceptual grouping factors that occur both *within* and *across* monocular channels. A counterexample against the notion of global pattern competition is the phenomenon of piecemeal rivalry. For example, large dichoptic gratings presented to the fovea rarely lead to the coherent perception of only one monocular pattern or the other and instead lead to piecemeal rivalry – observers perceive a dynamically changing mixture of fragments from each of the two monocular patterns. Interestingly, the incidence of piecemeal rivalry increases as a function of stimulus size and decreases as a function of eccentricity in agreement with the cortical magnification properties of V1 (Blake *et al.*, 1992). The phenomenon of piecemeal rivalry is very difficult to explain in terms of global pattern competition but can be understood in terms of local competition between monocular neurons that have a limited spatial range.

Pattern competition theory provides a more parsimonious account of why binocular rivalry, monocular rivalry, and stimulus rivalry should all lead to some degree of perceptual alternation. However, it provides little explanation for their differences. In binocular rivalry, subjects typically report experiencing powerful alternations and frequent periods of exclusive dominance across a wide range of viewing conditions. In contrast, monocular and stimulus rivalry require low contrast stimuli and often yield much weaker perceptual alternations (Lee and Blake, 1999; Wade, 1975). A complete theory should explain why binocular rivalry leads to eye-specific effects and more complete perceptual alternations than those during monocular and stimulus rivalry (Blake *et al.*, 1980; Fahle, 1987; Fox and Check, 1972; Wales and Fox, 1970).

Perhaps the most compelling evidence to support the role of pattern competition in binocular rivalry is the finding that single-unit recordings in awake-behaving monkeys have yielded inconsistent effects of rivalry-related activity in V1 and V4

but much stronger effects in higher visual areas (Leopold and Logothetis, 1996; Sheinberg and Logothetis, 1997). However, as we shall see, functional imaging studies in humans reveal a much more powerful correspondence between binocular rivalry and neural activity in early visual areas.

#### OTHER THEORIES OF RIVALRY: TOP-DOWN SELECTION AND INTERHEMISPHERIC SWITCHING

In addition to the theories of interocular competition and pattern competition, there are alternative proposals that rivalry may instead reflect some type of top-down selection or switching mechanism. These selection-based theories are still in development and the evidence to support them is still quite preliminary. These theories are briefly described below.

Top-down selection theories forward that executive frontal-parietal brain areas are responsible for initiating rivalry alternations by sending top-down signals to steer activity in visual cortex towards one representation or another (Leopold and Logothetis, 1999; Lumer, Friston and Rees, 1998). This theory resembles Helmholtz's (1866/1924) attentional theory and is consistent with the finding that observers can learn to develop some degree of voluntary control over the rate of rivalry alternations (Lack, 1970).

Preliminary support for top-down selection comes from a functional imaging study showing that frontal and parietal brain regions are more active when subjects report rivalry alternations than when they report steady-state periods in which one stimulus maintains dominance (Lumer, Friston and Rees, 1998). One interpretation is that these executive brain areas are directly mediating these rivalry alternations via top-down selection, but alternatively, these brain regions may simply be activated by the detection of these perceptual alternations. Further studies are needed to test whether these frontal-parietal areas play a necessary role for rivalry to occur.

Pettigrew and Miller have proposed a different theory forwarding that rivalry results from interhemispheric switching between two rivaling stimuli and that this switching arises because each stimulus is represented by a different hemisphere (see this issue for reviews). A major challenge for this theory will be to provide compelling evidence of how each hemisphere comes to adopt a different monocular image during rivalry given that corresponding regions in the two eyes are known to project to a single hemisphere in retinotopic cortex (Serenio *et al.*, 1995).

A major limitation of both top-down selection and interhemispheric switching theories is that they provide no explanation for the many stimulus determinants of rivalry. For example, why does binocular rivalry cease to occur for very low-contrast stimuli (Liu, Tyler and Schor, 1992) or why does increasing the strength of one monocular stimulus decrease the predominance of the competing stimulus (Levelt, 1965)? Why should piecemeal rivalry occur for large stimuli? It seems unlikely that top-down selection or interhemispheric switching can account for the many stimulus determinants of rivalry. Although selection mechanisms may

bias the time course of perceptual alternations to some extent, the stimulus-driven nature of binocular rivalry indicates that this phenomenon is largely determined by competitive interactions at an early stage of visual processing.

### **Review of Human Neuroimaging Studies**

As described above, it remains unclear whether binocular rivalry stems from interocular competition or pattern competition in visual cortex. Whereas human psychophysical studies tend to support the former theory, neurophysiological studies in the monkey support the latter. Ultimately, this debate must be addressed to understand the neural basis of binocular rivalry and how the human brain selects visual signals for awareness.

Here, I consider a separate line of physiological evidence from human neuroimaging studies. In early electroencephalogram (EEG) studies, researchers monitored electrical signals from the human scalp to investigate whether neural activity is correlated with conscious perception during binocular rivalry. Since then, functional magnetic resonance imaging (fMRI) studies have attempted to address two critical questions regarding the neural basis of binocular rivalry: At what stages of the human visual pathway is rivalry fully resolved and at what stage does this neural competition for awareness first emerge?

#### EEG STUDIES OF BINOCULAR RIVALRY

Early EEG studies in humans provided the first evidence that neural activity correlates with conscious perception during binocular rivalry. Lansing (1964) monitored electrical activity from the occipital scalp and found that EEG responses to a monocular flickering light were significantly reduced when a rivaling static pattern was presented to the other eye. The extent of physiological suppression corresponded well to the subject's report of rivalry suppression. Cobb *et al.* (1967) investigated binocular rivalry between two oscillating gratings that evoked EEG modulations that were 180° out of phase. The phase of the EEG response tightly corresponded to the subject's report regarding which grating pattern appeared to be dominant. Remarkably, the magnitude of these rivalry-related responses were as large as those observed when either grating pattern was presented alone, suggesting that the physiological suppression during rivalry was essentially complete. These powerful EEG modulations found in humans differ from the weak rivalry effects subsequently found in early visual areas of the monkey (Leopold and Logothetis, 1996; Logothetis and Schall, 1989).

More recent EEG studies have demonstrated that two rivaling stimuli can be uniquely tagged using different flickering frequencies to reveal real-time response modulations that correspond to the subject's perception (Brown and Norcia, 1997). Magnetoencephalography (MEG) has also been used to investigate the neural correlates of binocular rivalry. Compared to the poor spatial resolution of EEG,

MEG provides somewhat better source localization by measuring neurally induced changes in local magnetic-field potentials from multiple sites on the human scalp (in this study, 148 sites). Tononi and colleagues (1998) compared MEG responses during rivalry alternations to those evoked by *actual* stimulus alternations between the two frequency-tagged stimuli. They found strong rivalry-related responses throughout occipital cortex and also from some anterior temporal and frontal sites. These MEG responses during rivalry were about 50–85% of the magnitude of those observed during stimulus alternation. Although the origin of these rivalry-related responses could not be localized, their widespread nature may indicate that rivalry interactions occur quite early in the processing stream and that the result of this competition is propagated throughout the rest of the brain.

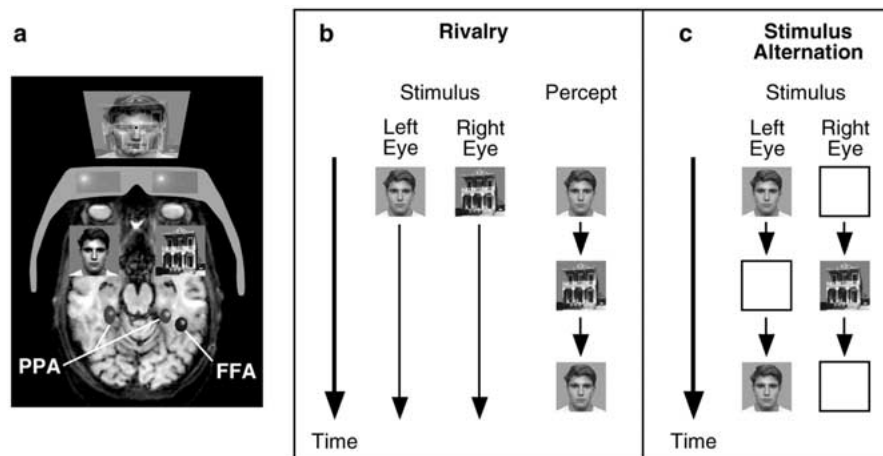
#### BACKGROUND ON FUNCTIONAL MAGNETIC RESONANCE IMAGING (fMRI) OF VISUAL CORTEX

The advent of functional MRI began with the discovery that visual stimulation leads to enhanced MRI signals in occipital cortex (Kwong *et al.*, 1992; Ogawa *et al.*, 1992). It is now understood that there is a tight coupling between local changes in neural activity and local changes in blood flow, blood volume, and blood oxygenation level – what is commonly called the blood oxygenation level-dependent (BOLD) response – and it is the BOLD response that is measured by fMRI. Thus, fMRI estimates changes in neural activity within a local brain region on the basis of changes in the BOLD response. Given that fMRI provides an indirect measure of neural activity, how confident can we be of its reliability?

First, it is known that fMRI can localize functional activity with high spatial resolution on the order of about 1–2 millimeters to produce reliable maps of retinotopically organized visual areas (V1–V4) (Engel *et al.*, 1994; Sereno *et al.*, 1995). Sub-millimeter resolution is even possible; however, under such situations subject motion becomes an increasingly difficult problem (Menon and Goodyear, 1999).

Second, there is a strong agreement between single-unit estimates of neuronal firing rate and fMRI estimates of neural activity in studies measuring V1 responses to different stimulus contrasts (Heeger, Huk, Geisler and Albrecht, 2000) and MT responses to different motion velocities (Rees, Friston and Koch, 2000). For example, fMRI signals in V1 increase in an approximately linear fashion as a function of log stimulus contrast (Boynton, Demb, Glover and Heeger, 1999).

Third, fMRI responses increase systematically as a function of visual stimulus duration, and these responses summate in a roughly linear fashion, especially for stimulus durations greater than 3 seconds (Liu and Gao, 2000). Typically, BOLD responses lag behind the initial neural response, peaking 2–6 seconds after stimulus onset depending upon the strength and duration of the stimulus. However, the lag in the BOLD response is highly consistent such that one can detect small temporal differences (less than 50 ms) in visual or motor responses by averaging across multiple fMRI trials (Menon, Luknowsky and Gati, 1998). Taken together, the



*Figure 3.* a, Schematic illustration of the binocular rivalry display and extrastriate areas of interest superimposed on a transverse MRI slice. The Fusiform Face Area (FFA, right hemisphere) and Parahippocampal Place Area (PPA, bilateral) are shown. During rivalry scans, a face and house were continuously presented to different eyes (using red/green filter glasses). Observers reported alternately perceiving only the face or house for a few seconds at a time as illustrated in b. c, On stimulus alternation scans, the physical stimulus alternated between the face image and house image using the same temporal sequence of alternations reported in a previous rivalry scan (adapted from Tong *et al.*, *Neuron*, 1998).

above findings indicate that the fMRI BOLD response provides a reliable estimate of the both the magnitude and duration of neural activity in local brain areas.

#### RIVALRY IN HIGH-LEVEL EXTRASTRIATE AREAS

In one of the first fMRI studies of binocular rivalry, my colleagues and I found that rivalry is fully resolved in high-level regions of human extrastriate cortex (Tong, Nakayama, Vaughan and Kanwisher, 1998). We monitored fMRI activity in two stimulus-selective extrastriate areas during rivalry, the fusiform face area (FFA) which responds preferentially to face stimuli, and the parahippocampal place area (PPA) which responds preferentially to house stimuli (Figure 3a). These regions lie anteriorly to retinotopic areas such as V4V and are situated at roughly equivalent levels of the visual pathway as the inferotemporal cortex of monkeys (Halgren *et al.*, 1999).

On rivalry scans, subjects viewed a face stimulus with one eye and a house with the other eye (Figure 3b). Although retinal stimulation remained constant, subjects perceived changes from house to face that were accompanied by increasing FFA activity and decreasing PPA activity; perceived changes from face to house led to the opposite pattern of responses (Figure 4a). Remarkably, these awareness-related responses during rivalry were equal in magnitude to those evoked by actual alternations between the face stimulus alone and house stimulus alone (Figure

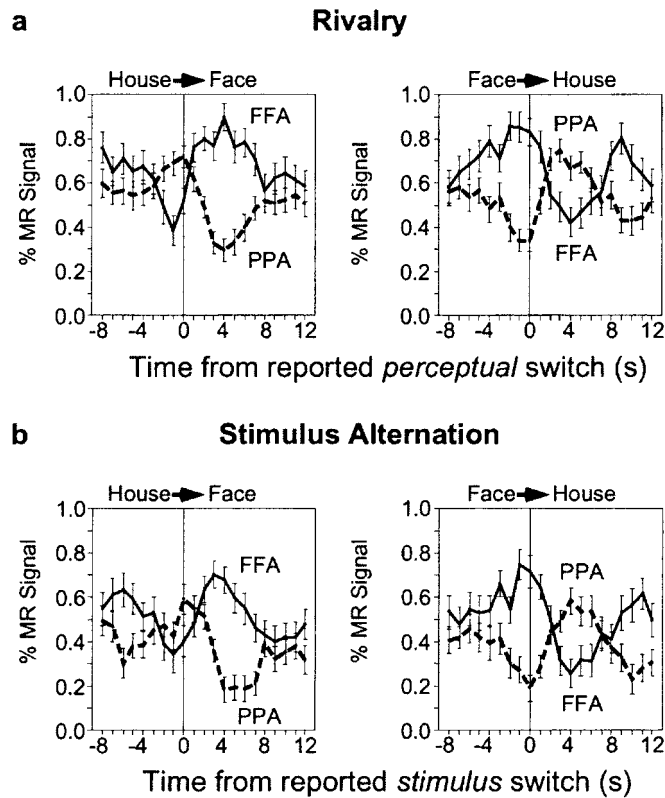


Figure 4. Average FFA (solid line) and PPA (dashed line) activity during reported house-to-face switches (left) or face-to-house switches (right) for rivalry (a) and stimulus alternation (b) scans for one representative subject. Note that fMRI responses are virtually identical for rivalry versus stimulus alternation. All participants showed very similar patterns of fMRI responses and equivalent responses in the two conditions. Vertical line indicates the time of the observer's perceptual report (rounded to the nearest second). Vertical bars represent  $\pm 1$  SEM (from Tong *et al.*, *Neuron*, 1998).

4b). The equivalence of rivalry and stimulus alternation strongly suggests that by the time visual information reaches the FFA and PPA, binocular rivalry has been fully resolved such that the neural activity in these regions reflects the subject's perceptual state rather than the retinal stimulus.

These findings differ somewhat from the weaker effects found in single-unit recordings in the inferotemporal cortex of the monkey. Although most inferotemporal neurons (84%) showed significant activity changes corresponding to perception during rivalry, the magnitude of these responses were only about half the magnitude of those evoked by actual stimulus alternations between the two monocular patterns (Sheinberg and Logothetis, 1997). If binocular rivalry

were fully resolved, one would expect to find equivalent neural modulations for perceived changes during rivalry and actual stimulus changes.

Our findings strongly suggest that rivalry is fully resolved at high levels of the human visual pathway. These findings raise the following question: At what stage of the human visual pathway do these rivalry interactions first begin to emerge?

#### RIVALRY IN PRIMARY VISUAL CORTEX

In a recent fMRI study, Polonsky, Blake, Braun and Heeger (2000) investigated whether rivalry-related activity occurs in human primary visual cortex by measuring V1 activity during binocular rivalry between high- versus low-contrast (moving or counterphasing) gratings. Previous fMRI studies have shown that V1 responses increase as a monotonic function of stimulus contrast (Boynton *et al.*, 1999; Tootell *et al.*, 1998). Thus, if V1 activity reflects conscious perception during rivalry, then one would predict greater activity during the perception of high- versus low-contrast gratings.

Consistent with these predictions, Polonsky *et al.* found highly reliable V1 responses during rivalry (Figure 5a). These responses were roughly half the magnitude of those observed during actual stimulus alternations between the high-versus low-contrast grating (Figure 5b). They also found that the relative magnitude of fMRI responses for rivalry versus stimulus alternation remained roughly equal across V1 (56%), V2 (42%), V3 (46%), V3a (28%), and V4v (51%). These findings fail to support the notion that rivalry is gradually resolved among pattern-selective neurons across multiple levels of the visual pathway (Logothetis, 1998). Furthermore, they differ from the much weaker rivalry effects found in V1 neurons of the monkey (Leopold and Logothetis, 1996) although they do not reveal a complete resolution of rivalry as was found in anterior human extrastriate cortex (Tong *et al.*, 1998).

Polonsky *et al.* were careful to conclude that their findings were consistent with interocular competition theory but were also amenable to pattern competition theory. From single-unit studies in the cat and monkey, it is known that most V1 neurons are binocularly driven and only a subset of neurons are strongly monocular (Hubel and Wiesel, 1962, 1968). Because this fMRI study could not isolate the response of monocular V1 cells, it could not directly address whether binocular rivalry arises from competition between monocular neurons or binocular pattern neurons.

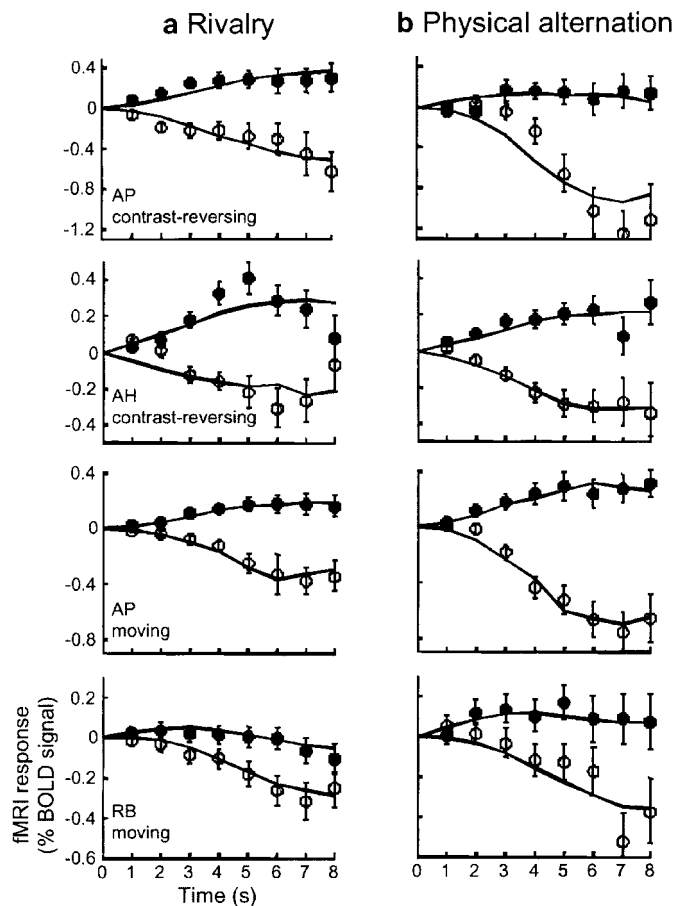
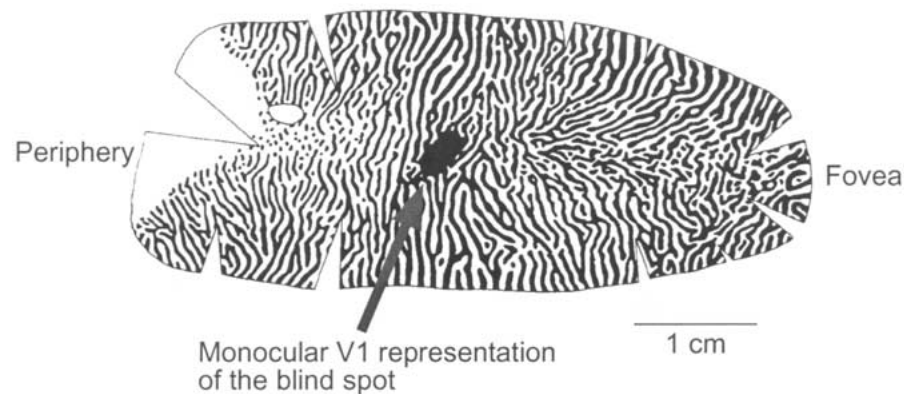


Figure 5. Average V1 activity for four subjects during reported switches to the low-contrast grating (open circles) or high-contrast grating (filled circles) for rivalry (a) versus physical alternation (b). Solid curves represent model fits (from Polonsky *et al.*, *Nature Neuroscience*, 2000).

#### RIVALRY IN MONOCULAR VISUAL CORTEX: EVIDENCE OF INTEROCULAR COMPETITION

To test whether binocular rivalry arises from interocular competition, Stephen Engel and I devised a method of measuring fMRI responses in monocular visual cortex (Tong and Engel, 2001). In primary visual cortex, inputs from the left and right eye form roughly parallel bands of ocular dominance columns (see Figure 6). These ocular dominance columns are very narrow (0.5–1.0 mm in human V1, Horton *et al.*, 1990) and difficult to isolate at the resolution of conventional fMRI methods (Menon and Goodyear, 1999; Menon, Ogawa, Strupp and Ugurbil, 1997).



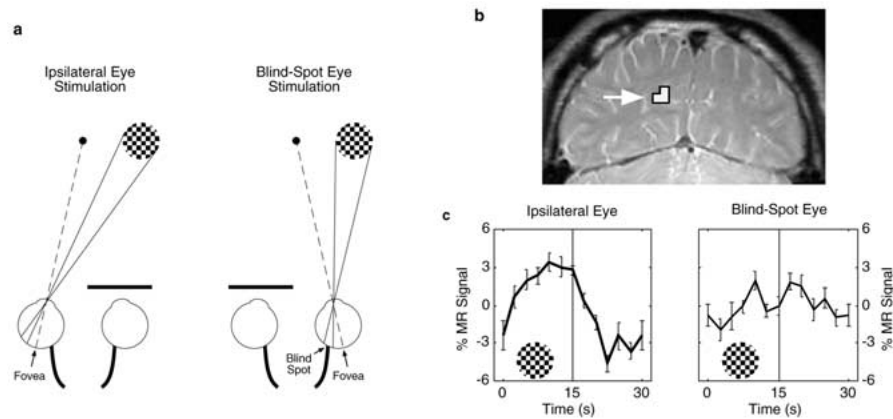
*Figure 6.* Pattern of ocular dominance columns revealed in a flattened representation of monkey primary visual cortex. Light regions were stained by injection of proline into the left eye and a flattened representation of the right hemisphere was constructed using computer algorithms. Note the large unstained monocular region corresponding to the V1 representation of the blind spot (from LeVay *et al.*, *Journal of Neuroscience*, 1985).

Furthermore, even the slightest subject motion can confound the reliability of such monocular responses.

However, Figure 6 reveals a large monocular region corresponding to the cortical representation of the blind spot. The blind spot is a retinal region that has no photoreceptors (size  $\sim 4^\circ \times 6^\circ$ , position  $\sim 15^\circ$  medial to fovea, see Figure 7a right). In human primary visual cortex, the blind spot is represented as a relatively large monocular region ( $\sim 10 \times 5$  mm; J.C. Horton, personal communication) that receives direct input solely from the ipsilateral eye and not from the (contralateral) blind-spot eye. The V1 blind-spot representation is large enough for functional imaging (Tootell *et al.*, 1998).

To localize the V1 blind-spot representation, we first had subjects map the visual field location of the right eye's blind spot. During fMRI localization scans, a flickering checkerboard pattern was presented to the subject's left ipsilateral eye or right blind-spot eye (see Figure 7a) in the region of visual space corresponding to the blind spot and its immediate surround ( $8^\circ$  diameter,  $\sim 2\times$  size of blind spot). Although the blind spot could not register the central portion of the checkerboard, the stimulus nonetheless appeared to be perceptually filled in due to stimulation of the region surrounding the blind spot (Walls, 1954).

Figure 7b shows the V1 blind-spot representation of one representative subject. This region was highly monocular, responding vigorously to ipsilateral eye stimulation (Figure 7c left) and negligibly to blind-spot-eye stimulation (Figure 7c right). Having isolated the monocular V1 blind-spot representation, we could now assess the effects of binocular rivalry in monocular visual cortex.



**Figure 7.** **a**, Localization of the V1 blind-spot representation. Subjects maintained fixation on a reference point while viewing a flickering checkerboard pattern (stimulus size  $8^\circ$ , check size  $1^\circ$ , temporal frequency 7.5 Hz, contrast 100%) with either their left ipsilateral eye or right blind-spot eye. Note how the central portion of the checkerboard falls on the blind spot (optic nerve head, size  $\sim 4^\circ \times 6^\circ$ ) of the right eye but not of the left eye. **b**, V1 representation of the right eye's blind spot appears in the left calcarine sulcus (3 voxels highlighted in white, slice plane perpendicular to calcarine). **c**, Average fMRI responses in the V1 blind-spot representation during ipsilateral eye stimulation (left) vs. blind-spot eye stimulation (right). Note how this region is activated by ipsilateral stimulation only (from Tong and Engel, *Nature*, 2001).

During rivalry scans, subjects viewed dichoptic orthogonal gratings that oscillated within a stationary circular aperture in the visual location corresponding to the blind spot and its surround (size  $8^\circ$ , spatial frequency 0.67 cycles/ $^\circ$ , speed 2 Hz, direction reversal every 500 ms, mean luminance 3.4 cd/m $^2$ , contrast 75%). The grating presented to the blind-spot eye was approximately twice the diameter of the blind spot; thus the blind-spot grating appeared to be perceptually filled in. On subsequent stimulus alternation scans, the physical stimulus alternated between monocular presentations of either the ipsilateral grating alone or blind-spot grating alone using the same sequence of alternations reported by the subject in a previous rivalry scan.

Subjects reported normal rivalry alternations between the ipsilateral grating versus blind-spot grating with extensive periods of exclusive dominance and minimal perceptual blending (Table I). The ability of the blind-spot surrounding grating to suppress the entire ipsilateral grating, including its central “unpaired” region, is consistent with the spatial spread of rivalry interactions (Levelt, 1965). Furthermore, in separate psychophysical studies we have confirmed the competitive nature of these interactions encompassing the blind spot – increasing the contrast of either grating decreased the dominance duration of the opposing grating as is found in foveal vision (Levelt, 1965).

Interestingly, three out of four subjects showed significantly longer dominance durations for the ipsilateral grating than for the blind-spot grating (S1, S2, S4,  $t >$

Table 1. Perceptual dominance durations.

Subject	Mean dominance duration (seconds)			Relative predominance (percent)		
	Ipsilateral	Blind-spot	Blend	Ipsilateral	Blind-spot	Blend
S1	4.8	3.6	0.0	58	42	0
S2	2.9	2.3	0.7	55	41	4
S3	4.4	4.1	2.2	45	42	13
S4	6.1	2.8	1.4	65	29	6
Mean	4.6	3.2	1.1	56	38	6

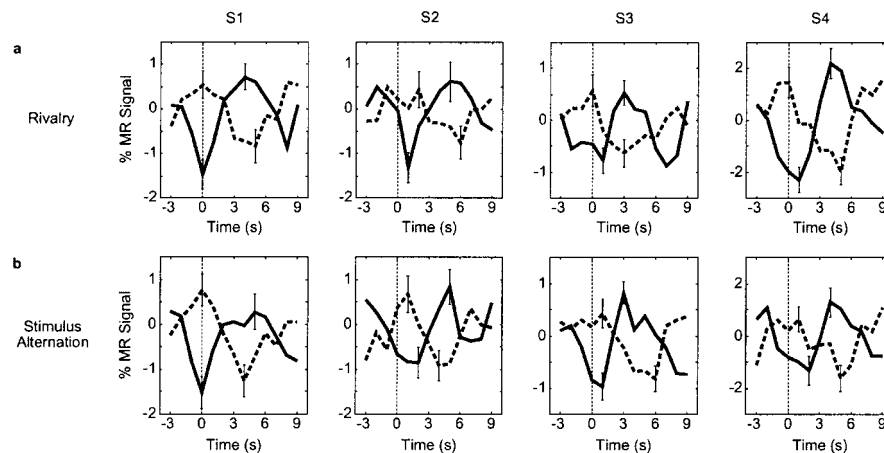
Dominance durations for each grating followed a gamma-shaped distribution characteristic of binocular rivalry (Levelt, 1965); mean dominance durations are shown. Relative predominance is the percentage of total viewing time that the subject reported perceiving the ipsilateral grating only, the blind-spot grating only, or a perceptual blend of both gratings (from Tong and Engel, *Nature*, 2001).

2.0,  $p < 0.05$ ). These behavioral findings, though preliminary, are consistent with the hypothesis that rivalry dominance depends upon the ratio of monocular neurons activated by each eye (Blake, 1989).

Figure 8a reveals that activity in the V1 blind-spot representation was tightly linked to visual awareness during binocular rivalry for all four tested subjects. This monocular region, which receives direct input from only the ipsilateral eye, showed a sharp increase in fMRI activity soon after subjects reported that the ipsilateral grating had become perceptually dominant (Figure 8a, solid line). Conversely, fMRI activity sharply decreased when the blind-spot grating became dominant (Figure 8a, dotted line). Thus, the signals from the ipsilateral eye to the V1 blind-spot representation were suppressed when the stimulus entering the competing eye became perceptually dominant. These findings confirm the predictions of interocular competition theory.

fMRI responses during rivalry (Figure 8a) and stimulus alternation (Figure 8b) were remarkably similar and did not reliably differ in magnitude ( $F < 1$ ). The fact that fMRI responses for rivalry and stimulus alternation were indistinguishable strongly suggests that rivalry has been fully resolved among monocular neurons in the V1 blind-spot representation such that neural activity entirely reflects the subject's perceptual state. Thus, functionally equivalent neural responses are observed when the subject's conscious state alternates between the ipsilateral grating and blind-spot grating during constant rivalry stimulation and when physical stimulus itself alternates between the ipsilateral grating alone and the blind-spot grating alone.

Our results provide the first demonstration that binocular rivalry is resolved in monocular visual cortex and thus the first physiological evidence to support interocular competition theory. Whereas previous human studies using fMRI or electroencephalography have found strong correlations between neural activity



*Figure 8.* Average fMRI activity in the V1 blind-spot representation during perceptual switches to the ipsilateral grating (solid line) or blind-spot grating (dotted line) for rivalry (**a**) versus stimulus alternation (**b**). Data of all four subjects are plotted on individually scaled y-axes. Vertical dotted lines at time zero indicate the time of the subject's response. **a**, During rivalry, fMRI activity sharply increased soon after the ipsilateral grating became dominant in awareness and decreased when the blind-spot grating became dominant, consistent with the predictions of interocular competition. **b**, Very similar fMRI responses occurred during stimulus alternations between the two monocular gratings. Hemodynamic lag in the BOLD signal typically leads to a temporal delay of 2–6 s from initial to peak fMRI response. All fMRI responses were significant ( $F > 4.0$ ,  $p < 0.05$ ) and did not reliably differ in magnitude for rivalry versus stimulus alternation ( $F < 1$ ) (from Tong and Engel, *Nature*, 2001).

and perception during rivalry, none has been able to establish the involvement of monocular neurons (Brown and Norcia, 1997; Cobb, Morton and Ettliger, 1967; Lansing, 1964; Lumer *et al.*, 1998; Polonsky, Blake, Braun and Heeger, 2000; Tong *et al.*, 1998; Tononi, Srinivasan, Russell and Edelman, 1998). In contrast, our findings suggest the origin and underlying neural mechanism for these rivalry-related responses. Namely, interocular competition leads to the early selection of only one monocular stimulus for conscious perception and further processing by subsequent visual areas.

### General Discussion

The nature of the competitive interactions that underlie binocular rivalry has been the subject of debate for over two centuries. In recent years, this debate has greatly intensified, focusing on two competing views of binocular rivalry as arising from interocular competition versus pattern competition.

To address this debate, researchers have used human neuroimaging techniques to probe the neural correlates of awareness during rivalry. These studies have consistently shown a tight correspondence between neural activity and subjective

perception. This relationship was first revealed in pioneering EEG studies (Cobb *et al.*, 1967; Lansing, 1964). More recent MEG studies have shown that rivalry leads to widespread neural modulations in occipital cortex and also in some temporal and frontal areas (Tononi *et al.*, 1998). Functional MRI studies have attempted to pinpoint the origin of these rivalry-related responses and have shown successively that: i) binocular rivalry is already fully resolved by the time visual information reaches anterior extrastriate areas (Tong *et al.*, 1998), ii) rivalry is evident in primary visual cortex (Polonsky *et al.*, 2000), and iii) rivalry is resolved in monocular visual cortex (Tong and Engel, 2001). These studies reveal the progress of our understanding of the neural basis of binocular rivalry and how we have come to discover that rivalry interactions occur among monocular V1 neurons.

In particular, Tong and Engel's fMRI study of rivalry in the monocular V1 blind-spot representation provides a critical test of the two competing theories of binocular rivalry. Our finding that rivalry is resolved in monocular visual cortex confirms the predictions of interocular competition theory and fails to support the notion that rivalry occurs only among binocular pattern neurons at higher levels of the visual pathway (Leopold and Logothetis, 1996). These findings therefore help resolve the debate regarding the neural basis of binocular rivalry.

Although these studies provide an answer regarding the neural mechanisms underlying binocular rivalry, they also raise a number of questions for further discussion. How can one explain the discrepancies between the human neuroimaging results and the single-unit monkey data? Might mechanisms other than interocular competition be responsible for the modulation of monocular neurons during binocular rivalry? What is the relationship between binocular rivalry, monocular and stimulus rivalry, and ambiguous figure reversal? And finally, what do the above findings imply about the role of V1 in conscious vision? These issues are discussed below.

#### DISCREPANCIES BETWEEN FMRI HUMAN STUDIES AND SINGLE-UNIT MONKEY STUDIES

How can one account for the much weaker rivalry effects found in monkeys than in humans? In single-unit studies, the percentage of neurons that show significant activity changes corresponding to the monkey's perceptual report is very small in V1 (9%), small to moderate in V4 (18%), and substantial in IT (84%) (Leopold and Logothetis, 1996; Sheinberg and Logothetis, 1997). These findings were interpreted to suggest that rivalry is gradually resolved across a hierarchy of successive visual areas.

However, a reanalysis of these data reveals much more comparable effects across these visual areas. Specifically, one can evaluate the strength of rivalry modulations relative to stimulus alternation responses by constructing a ratio of these two response magnitudes. I will refer to this ratio (rivalry response/stimulus

alternation response) as the Rivalry Modulation Index. A value equal to 0% indicates no rivalry modulation. In contrast, a value of 100% indicates that rivalry is fully resolved such that neural responses are indistinguishable for perceptual alternations and stimulus-driven alternations.

A reanalysis of all recorded single-units, irrespective of whether they showed statistically significant rivalry modulations or not, reveals quite comparable Rivalry Modulation Indices across V1 (33%), V4 (27%), and IT (~50%) (data from Leopold, 1997; Sheinberg and Logothetis, 1997; reanalyses by Polonsky *et al.*, 2000; Tong *et al.*, 1998). According to Polonsky *et al.*, the differences between the single-unit monkey data and the somewhat stronger fMRI effects that they observed in human visual cortex (V1 modulations = 56%, V4v = 51%) may reflect any of several factors. These include genuine interspecies differences, the indirect nature of fMRI in estimating neural activity, smaller neuronal sample sizes in single-unit studies than in fMRI studies, the effect of eye movements on the response of single units with small receptive fields, and possible confounding effects of transient responses at the time of perceptual switches.

However, the above explanations do not account the fact that Polonsky *et al.* observe much weaker modulations in human V1 (56%) than we do in monocular visual cortex (99%) (Tong and Engel, 2001). Clearly, such variations can also occur among studies that rely on the same measuring techniques and the same species of subjects.

In our view, the observation of equally robust rivalry and stimulus alternation responses is very likely to indicate that rivalry is fully resolved. We have observed such complete rivalry modulations in two independent studies and in three visual areas: the Fusiform Face Area, the Parahippocampal Place Area (91% rivalry modulation index for FFA/PPA), and the monocular V1 blind-spot representation (Tong and Engel, 2001; Tong *et al.*, 1998). Such powerful rivalry responses would be very difficult to obtain by chance – few studies have successfully demonstrated such equivalence between perceptually-driven versus stimulus-driven neural activity.

In contrast, the failure to observe equally large responses for rivalry and stimulus alternation need not imply that rivalry has been only partially resolved. Many factors could dilute the strength of rivalry responses including sub-optimal viewing conditions that lead to frequent rivalry-blend percepts, inadequate reliability in either the accuracy or timing of the subject's perceptual report, and individual differences in the strength of binocular rivalry (Halpern, Patterson and Blake, 1987). For example, subjects reported perceiving blends more often in the study by Polonsky *et al.* (20% of the total viewing time) than in our study of the V1 blind-spot representation (6%). These or other factors might explain the weaker V1 rivalry effects found in their fMRI study and in previous single-unit monkey studies (Leopold and Logothetis, 1996).

## MIGHT INTEROCULAR RIVALRY ARISE FROM FEEDBACK SELECTION?

Although competition among binocular pattern neurons alone cannot account for the effects of rivalry in monocular visual cortex (Tong and Engel, 2001), it remains possible that feedback signals from binocular neurons to monocular neurons could account for alternating monocular suppression. Such a theory could be described as a “pattern competition/monocular selection” model of binocular rivalry.

However, such a theory provides no explanation for why pattern competition should lead to selection at the monocular level. Furthermore, it remains unclear how feedback projections from binocular pattern neurons might target a specific monocular channel. Given these difficulties, it seems that interocular competition provides the most compelling and parsimonious explanation for rivalry in monocular visual cortex.

It is important to note that while a completely top-down account of monocular suppression seems unlikely, it remains possible that top-down influences such as visual attention could potentially bias the activity of monocular neurons. Observers can learn to develop some degree of voluntary control over the rate of rivalry alternations with training (Lack, 1970, 1978). It remains an open question, however, whether such control reflects the attentional modulation of monocular neurons, the modulation of higher visual areas, or an eye-movement based strategy of influencing the rate of rivalry alternations.

## BINOCULAR RIVALRY VERSUS PATTERN RIVALRY: SEPARATE OR COMMON MECHANISMS?

A much-debated issue is whether binocular rivalry and pattern rivalry reflect common or separate neural mechanisms (Andrews and Purves, 1997; Lee and Blake, 1999; Logothetis *et al.*, 1996; Wade, 1975). Examples of pattern rivalry include the phenomena of monocular and stimulus rivalry in which perceptual alternations occur between two different patterns despite the absence of consistent interocular competition.

Although pattern rivalry typically involves weaker perceptual alternations than binocular rivalry and occurs under a more limited set of viewing conditions (e.g., low contrast), it has been proposed that both types of phenomena may reflect a common neural mechanism (Andrews and Purves, 1997; Helmholtz, 1924; Logothetis *et al.*, 1996). However, the complete rivalry modulations found in monocular visual cortex suggest otherwise (Tong and Engel, 2001). Interocular competition appears to account entirely for phenomenon of binocular rivalry. In contrast, monocular and stimulus rivalry likely reflect a higher level form of perceptual competition.

Thus, it appears that binocular rivalry and pattern rivalry reflect similar but separate neural mechanisms, the former arising from competition among monocular V1 (and perhaps also LGN) neurons and the latter occurring among

binocular pattern neurons at an unknown level of the visual pathway. Investigating the neural mechanism that underlies pattern competition in monocular and stimulus rivalry will be important for future research.

Sengpiel and colleagues (1998, see also this issue) have conducted related single-unit studies in cat striate cortex. They find evidence of independent mechanisms that mediate interocular suppression and cross-orientation suppression using briefly presented stimuli. These two mechanisms may provide a plausible basis for binocular rivalry and pattern rivalry. However, further research is required to link these mechanisms directly to the slow phenomenal alternations that characterize these forms of rivalry.

#### RIVALRY AND AMBIGUOUS FIGURES

According to pattern competition theory, rivalry and the perceptual reversal of ambiguous figures (e.g., Necker Cube, Rubin's Face/Vase) are presumed to reflect very similar or identical neural mechanisms of competition among equally valid perceptual interpretations (Logothetis, 1998). Interestingly, the phenomena of binocular rivalry, pattern rivalry, and ambiguous figure reversal all share similar temporal dynamics. Perceptual dominance durations are distributed according to a gamma-shaped distribution and each sequence of dominance durations typically exhibits stochastic independence (Borsellino, De Marco and Allazetta, 1972; Fox and Herrmann, 1967; Logothetis *et al.*, 1996). These similarities raise the possibility that a common neural mechanism may underlie these alterations. However, our findings in monocular visual cortex (Tong and Engel, 2001) suggest that binocular rivalry arises from a distinct mechanism of interocular competition and that binocular rivalry differs from pattern rivalry.

Regarding the possible similarities between rivalry and figure reversal, the perceptual characteristics of these diverse phenomena suggest that the underlying mechanisms are quite distinct. During both binocular rivalry and pattern rivalry, the features of one stimulus fade from view. In contrast, the feature elements in ambiguous figures remain continuously intact – instead, it is the global organization of those features that can change. Another important difference is that rivalry can occur in a fragmented piecemeal manner suggestive of local feature interactions whereas ambiguous figure reversal typically involves coherent global changes in phenomenological perspective. These differences likely indicate that both binocular rivalry and pattern rivalry occur at an earlier stage of visual processing involving local feature representation. In contrast, figure reversal likely occurs at a higher stage in which different global organizations of stable feature elements are represented.

Consistent with this distinction, low-level manipulations of contrast, size, eccentricity, and so forth can have profound effects on monocular rivalry and binocular rivalry but generally have very weak influences on figure reversal

(Atkinson, Campbell, Fiorentini and Maffei, 1973; Levelt, 1965). Although binocular rivalry, pattern rivalry, and figure reversal may arise from similar neural interactions such as competitive reciprocal inhibition (e.g., Lehky, 1988), the actual neural sites or stages of visual representation appear to differ for these phenomena.

#### THE ROLE OF V1 IN CONSCIOUS VISION

The findings that binocular rivalry occurs in V1 (Polonsky *et al.*, 2000) and is fully resolved in monocular visual cortex (Tong and Engel, in press) demonstrate that neurons can reflect conscious perception at a much earlier level of the visual pathway than previously thought (Crick and Koch, 1995; Leopold and Logothetis, 1996). These results have one of two implications. One possibility is that certain aspects of conscious vision begin to emerge at the very earliest stage of cortical processing among monocular V1 neurons. Alternatively, these findings may suggest a new role for V1 as the “gatekeeper” of consciousness, a primary cortical region that can select which visual signals gain access to awareness. In either case, these studies suggest that primary visual cortex plays an important role in binocular rivalry and conscious vision.

The importance of V1 for visual awareness is supported by studies of brain-damaged patients. Patients with V1 lesions typically report having no conscious visual experience in their damaged field of vision. Interestingly however, some of these patients can perform surprisingly well on forced-choice visual discrimination tasks, a paradoxical phenomenon called “blindsight” (Stoerig and Cowey, 1997). This residual visual performance does not seem attributable to response bias as blindsight subjects show much better sensitivity ( $d'$ ) on forced-choice than yes-no tasks whereas normal subjects do not (Azzopardi and Cowey, 1997).

Functional MRI studies of blindsight patients have revealed preserved visual activations in extrastriate regions such as MT and no evidence of V1 activity (Barbur, Watson, Frackowiak and Zeki, 1993; Stoerig, Kleinschmidt and Frahm, 1998). Preserved MT responses also have been found in single-unit studies of monkeys with V1 lesions (Rodman *et al.*, 1989). It seems likely that these preserved extrastriate responses are responsible for mediating intact performance on forced-choice visual tasks but apparently the activity in these regions is insufficient for mediating perceptual awareness.

Taken together, these V1 lesion studies and studies showing V1's role in binocular rivalry raise the intriguing possibility that primary visual cortex plays an important and perhaps necessary (though not sufficient) role for conscious visual experience. Further research along these lines may lead scientists to reconsider the current view that V1 is a passive visual area that analyzes and transmits information but does not directly contribute to awareness (Crick and Koch, 1995). It will also be important to tease apart how different visual areas contribute uniquely to perception by probing when these regions agree or fail to agree with the conscious experience

of the observer. Ultimately, studies such as these may help us understand how the brain gives rise to subjective visual experience.

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