V1 activity is reduced during binocular rivalry

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During binocular rivalry, one of two incompatible monocular stimuli is erased from perceptual awareness for seconds at a time. To examine whether this “rivalry suppression” occurs in V1, we measured functional magnetic resonance imaging activity during binocular rivalry and compared it with those in the two reference conditions: one representing complete suppression and the other representing no suppression. We found that the amplitude of V1 activity during rivalry fell midway between those in the two reference conditions; the amount of V1 activity associated with the nondominant pattern was reduced by 48% to 77% during rivalry. The same pattern of results was obtained with meaningful rival targets (i.e., a human face and a house). In this work, using a different experimental protocol, we confirmed the findings of earlier imaging studies that neuronal events associated with binocular rivalry occur as early as V1. Furthermore, our findings extend those earlier findings by demonstrating robust neural suppression during binocular rivalry regardless of the stimulus complexity of the rivaling targets.

Keywords: binocular rivalry, functional imaging, visual awareness, visual suppression

Introduction

Dissimilar monocular patterns presented to corresponding regions of the two eyes compete for perceptual dominance, producing alternations in the visibility of one pattern and then the other over time; this is the well-known phenomenon called binocular rivalry (Fox, 1991; Blake & Logothetis, 2002). The striking feature of binocular rivalry is the complete erasure of one of the two competitors from visual awareness for several seconds at a time, even though the optical input associated with that stimulus remains unchanged. Because of this dramatic dissociation between physical stimulation and phenomenal appearance, binocular rivalry represents a potentially useful tool for studying the neural bases of consciousness (Crick & Koch, 1995; Logothetis, 1998; Blake, 1997).

Where within the visual pathways are the neural events normally associated with vision being disrupted? Evidence bearing on the answer to this question has come from several sources. Single-cell recording experiments in awake, behaving monkeys have revealed that neural responses within cells of the inferotemporal (IT) cortex are modulated in synchrony with the awake monkey’s perceptual reports of binocular rivalry (Sheinberg & Logothetis, 1997). In fact, essentially all IT cells behave in this fashion, with their activity being almost completely abolished coincident with phenomenal suppression of their preferred stimulus. Likewise, the involvement of extrastriate cortical areas in binocular rivalry has also been demonstrated in humans using functional magnetic resonance imaging (fMRI). Lumer, Friston, and Rees (1998) found a high correlation between fMRI activity in the right frontoparietal cortex and transitions in rivalry dominance; they also mentioned in a footnote that activity levels in some brain areas correlated with the observer’s perceptual state in rivalry. In a more systematic study of this latter effect, Tong, Nakayama, Vaughan, and Kanwisher (1998) showed that blood-oxygen-level-dependent (BOLD) signals originating from two extrastriate visual areas - the parahippocampal “place” area (PPA) and the fusiform “face” area (FFA) - fluctuated reciprocally in magnitude during binocular rivalry. Their study capitalized on the fact that the FFA and the PPA can be selectively activated by two different classes of stimuli (faces and houses, respectively). The modulations in BOLD signal in the FFA and the PPA during binocular rivalry were as pronounced as those produced by physically turning the visual stimuli on and off over time in a pattern mimicking the alternations of rivalry. This pattern of results led Tong et al. (1998) to conclude that binocular rivalry had been “resolved” by this stage of visual processing.

Given these results, it is natural to wonder at what stage of visual processing the neural concomitants of rivalry are first evidenced. Here there is an apparent discrepancy among studies. Single-cell recordings from awake monkeys indicate that about only 20% of neurons in areas V1 and V2 exhibit statistically significant modulations in firing rate during binocular rivalry (Leopold & Logothetis, 1996). In contrast, a recent human fMRI study found significant modulations in BOLD signals measured from V1 during binocular rivalry, with the magnitudes of those modulations being anywhere from 45% to 83% as large as those produced by alternately presenting two monocular images without...
rivalry (Polonsky, Blake, Braun, & Heeger, 2000). And even more recently, Tong and Engel (2001) found fluctuations in V1 BOLD signals during rivalry that were every bit as large as those produced by physical presentation and removal of the stimuli. Of course, interpretation of these fMRI results hinges on an understanding of the origins of the BOLD signal in V1. Logothetis, Pauls, Augath, Trinath, and Oeltermann (2001) present evidence implying that the V1 BOLD signals can arise both from spiking activity in V1 neurons and from fluctuations in local field potentials whose sources might include feedback from extrastriate areas. Logothetis et al. (2001) speculate that strong fluctuations in BOLD signal in V1 could be triggered, in part, by feedback from higher areas, which, by implication, could mean that the neural events instigating rivalry arise outside of V1. Still, this possibility does not detract from the critical involvement of V1 in binocular rivalry, for activity modulations in this structure will be conveyed to and perhaps amplified in higher visual areas.

Given this discrepancy between the monkey electrophysiology experiments and the human fMRI experiments, we felt it would be useful to employ a somewhat different experimental strategy to examine the extent to which BOLD signals arising from V1 and other early visual areas are correlated with perception during binocular rivalry. In one experiment, we attempted to estimate the amount of neural activity suppressed during rivalry by comparing fMRI responses evoked by rivalry stimuli (dichoptically viewed, orthogonal sinusoidal gratings) with those evoked by two types of physically alternating monocular stimuli: one type that putatively mimics the BOLD signal that would be generated if the neural activity associated with the nondominant pattern were completely suppressed, and the other type that mimics the BOLD signal that would be generated if a nondominant pattern continued to produce normal levels of activation. In a second experiment, we sought to discover whether modulations in V1 BOLD signal were limited to simple grating patterns, such as those used in previous studies of rivalry and V1 (Polonsky et al., 2000; Tong & Engel, 2001). One might argue that the degree to which V1 is involved during rivalry depends on the level of stimulus complexity. After all, the face image, which strongly activates PPA but not FFA, would both produce robust activation of V1. Perhaps, then, these kinds of complex, meaningful rival patterns would be less likely to produce rivalry-related fluctuations in V1 BOLD signals. Our second experiment examined this possibility.

### Methods

#### Observers

Data were collected from three adult observers, all with normal binocular vision and good acuity in each eye. Each participant gave informed consent, and the study was approved by the Vanderbilt University Institutional Review Board.

#### Stimuli

Observers viewed a pair of red/green gratings (Experiment 1) or a pair of red/green line drawings (Experiment 2) through red/green anaglyphic glasses (see Figures 1 and 3). Each observer completed two sessions of fMRI scans in each experiment. In the first session, the red image and green image were viewed with the left eye and the right eye, respectively. The eye assignment was reversed in the second session. The contrasts of paired images were calibrated at the beginning of each session so that the dominance periods of the two images during rivalry were sufficiently long (3-10 s) and roughly equal. Throughout each scanning period, the observer maintained his/her gaze on a continuously visible, high-contrast fixation mark located at the center of the display.

#### Gratings

Two orthogonally oriented sinusoidal gratings were displayed against a uniform background; the contours of the gratings were oriented diagonally (45 deg clockwise for one and 45 deg anticlockwise for the other) and their spatial frequency was 1.5 cycles/deg. The luminance of the gratings was varied between red and black or between green and black. The contrast of the gratings underwent continuous counterphase reversal at 2.5 Hz, to discourage formation of afterimages. The gratings appeared within an annular region whose inner and outer borders subtended 2.5 and 6 deg; each annular grating appeared centered around the fixation mark and both were surrounded by a thin, high-contrast peripheral ring (8 deg) to help maintain stable binocular alignment (which was easy to achieve with this anaglyphic display technique).

#### Line drawings

Starting with photographic images used by Tong et al. (1998), we created line drawings of a human face and of a house (Figure 3). The lines were flickered between red and black or between green and black against a uniform background at the rate of 2.5 Hz. The face stimulus and the house stimulus subtended approximately equivalent regions of the visual field (4 x 6 deg).

#### MRI Acquisition

For each observer, we conducted a series of MRI scanning sessions using a standard clinical 1.5 T General Electric Signa scanner with a birdcage head coil. High-resolution, whole-brain structural images (lasting 10 min, 124 T1-weighted images, .9375 x .9375 x 1.3 mm) were obtained before fMRI scanning sessions. These structural images were used for surface reconstruction of cortical hemispheres of each observer using BrainVoyager (Brain...
Innovation, Maastricht, The Netherlands) (Goebel, 2000). The resulting cortical surfaces were then used as the reference for projecting functional data on flattened representations.

Each fMRI scanning session began by acquiring a set of whole-brain, low-resolution images used for slice selection. We chose 14 oblique slices roughly perpendicular to the calcarine sulcus of the occipital lobe. A set of anatomical images was then acquired in the same slices as the functional images. These anatomical images were later aligned to the high-resolution, whole-brain scan so that all functional images acquired across different scans could be co-registered. Functional images were acquired using a T2*-sensitive, gradient-recalled echo, single-shot sequence. Three types of functional scans were conducted for each observer: (1) retinotopic mapping scans to functionally define retinotopically organized visual areas; (2) localizing scans to localize subregions of each visual area that responded to experimental stimuli; and (3) experimental scans to measure fMRI responses in the different viewing conditions.

The stimuli were generated using Matlab in conjunction with routines from the Psychophysics Toolbox (http://psychtoolbox.org) (Brainard, 1997) and were displayed on an LCD panel (640 x 480 pixels, 60 Hz; Psychology Software Tools, Inc., Pittsburgh, PA, USA) mounted on the birdcage head coil. Observers viewed the display through a pair of mirrors attached to the head coil.

**Retinotopic Mapping of Visual Areas**

In a separate fMRI scanning session, two retinotopic mapping scans were administered for each observer. Following conventional procedures (Engel et al., 1994; Engel, Glover, & Wandell, 1997; Schneider, Noll, & Cohen, 1993; Sereno et al., 1995), fMRI images were acquired while observers viewed a slowly rotating, contrast-reversing checkerboard wedge subtending 22.5 deg in polar angle. From these functional images, the boundaries of retinotopically organized visual areas (V1, V2, V3, and V4v) were estimated on the flattened cortical surface based on whether a given area contained a mirror-image or nonmirror image representation of the visual field.

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**Figure 1.** Experimental design and stimuli used in Experiment 1. Stimuli were sinusoidal gratings and were viewed through anaglyphic glasses. Each scan consisted of nine alternating blocks of rest and stimulus periods. a. Rivalry scan. Observers viewed a pair of orthogonal gratings dichoptically presented to the two eyes and tracked their percepts by pressing one of two buttons. Green and red bars indicate, respectively, periods of dominance by the green and red images. b. Monocular single-alternation scan. The stimuli physically alternated between the two monocular gratings, mimicking what observers perceived in the preceding rivalry scan. c. Monocular double-alternation scan. The stimuli were identical to the monocular single-alternation scan except that the stimuli were red and green plaid patterns. The bottom panel shows actual displays that are associated with patches used to describe various viewing conditions in the stimulus bands above.
Localizing Regions of Interest

Two localizing scans were run during each functional scan session, at the beginning and then at the end of the session. During the localizing scan, fMRI responses were measured while observers viewed alternating 18-s phases of a uniform gray field and a high-contrast, contrast-reversing checkerboard pattern. The position and size of the checkerboard pattern were identical to those of the experimental stimuli. We followed two steps to define a region of interest (ROI) in each visual area. First, we identified a cluster of neighboring voxels that were highly correlated ($r > .3$ and $6 \pm 2$ s time lag) with the checkerboard phases. From these voxels, we then discarded voxels that represented the visual field within 20 deg on either side of the boundaries between visual areas.

Experimental Scans

Each experimental scan began with an initial 18-s period during which observers passively viewed a fixation mark on a uniform gray field. After the initial rest period, the display alternated between a stimulus period and a rest period. The stimulus and rest periods lasted for 18 s and were repeated alternately four times. During the stimulus period, observers tracked their percepts by pressing one of two buttons depending on what they perceived. Observers were instructed not to press any button during transitions between the two percepts or during piecemeal dominance.

Functional MRI Data Analysis

Each experimental fMRI scan lasted 162 s. The first nine images (18 s data) were discarded from any further analysis to allow for stabilization of the MR signal. The remaining 72 images (4 cycles) were recorded as a time-series for each slice and were corrected for any residual head movements during each scan. For each voxel ($3.75 \times 3.75 \times 4$ mm), the time-series data were low-pass filtered to remove any slow signal drift and were then divided by their mean intensity. For each visual area, the time-series data were averaged over the set of voxels belonging to the ROI, which was previously identified through the localizing scan. Four-cycle time-series data were averaged resulting in a 36-s time-series (18 data points) for each ROI within each visual area.

We calculated the amplitude of each ROI as follows. First, we defined a hemodynamic impulse function for each ROI because the hemodynamic impulse function can vary both across subjects and across visual areas (Aguirre, Zarahn, & D’Esposito, 1998). The hemodynamic impulse functions were estimated by fitting the time-series data from the localizing scan using a hemodynamic impulse response model developed by Ress, Backus, and Heeger (2000). Second, we estimated the amplitude of underlying neural activity by finding an fMRI response model function that best fits a given time-series data. It was assumed that the fMRI response function can be derived by convolving the underlying neural activity over time with the hemodynamic impulse response function.

Results

Three Viewing Conditions

In our first experiment, we measured the levels of fMRI signal under three viewing conditions: (1) rivalry condition, in which observers viewed a pair of orthogonal gratings dichoptically presented to the two eyes (rivalry occurs under this condition); (2) monocular single-alternation condition, in which the two gratings were alternately presented to one of the two eyes; and (3) monocular double-alternation condition, in which a monocular plaid was alternately presented to one of the two eyes (see Figure 1). By comparing the amplitudes of fMRI signals in these three viewing conditions, we sought to measure the amount by which neural activity (as inferred from the BOLD signal) was attenuated during binocular rivalry.

It is well established that most, if not all, neurons in visual area V1 are selective for orientation; moreover, neurons in at least some layers of V1 also vary systematically in terms of the ocular dominance, meaning that a given neuron is more strongly activated by stimulation through one eye versus the other eye. Based on these known response properties of V1, we reasonably assumed that the monocular double-alternation condition (two superimposed, orthogonally oriented gratings presented to one eye and then the other, and so on) would activate a larger ensemble of neurons than would the monocular single-alternation condition (one grating presented to one eye and then another grating presented to the other eye, and so on). These differences in activation strength, in turn, should lead to a stronger BOLD signal in the monocular double-alternation condition compared to the monocular single-alternation condition, because the strength of a BOLD signal in a given voxel depends on neural activities summed across active neurons within a region of cortical surface representing that voxel. This assumption, which was confirmed by results in the experiments, allowed us to estimate the extent to which neural responses to a nondominant stimulus are suppressed in V1 during binocular rivalry (in the rivalry condition). Depending on the level of neural suppression, the level of BOLD signal in the rivalry condition is predicted as follows. If neural activity associated with a suppressed (nondominant) grating is completely abolished, the level of BOLD signal would be close to that in the monocular single-alternation condition. In contrast, the level of BOLD signal would be close to that in the monocular double-alternation condition.
condition if neural activity in V1 remains high in response to a stimulus that is intermittently suppressed during rivalry.

Each observer participated in two experimental sessions. An experimental session consisted of four sets of functional scans. Each set began with a rivalry scan, which was followed by a monocular single-alternation scan and then a monocular double-alternation scan. In all of these scans, four 18-s stimulus periods were preceded and followed by rest periods, resulting in nine alternating blocks of rest and stimulus periods. During the stimulus periods in the rivalry scan, observers viewed a red, left-tilted grating with one eye and a green, right-tilted grating with the other eye (Figure 1a). During these stimulus periods, observers experienced binocular rivalry and tracked the fluctuations in dominance by pressing one button when they perceived a red grating and the other button when they perceived a green grating. Observers were instructed to press neither button during piecemeal rivalry; in fact, we selected the size, luminance, and contrast of the rival targets to minimize the incidence of piecemeal rivalry (which accounted for 11.5% of the total viewing period in Experiment 1 and 9.9% of the viewing period in Experiment 2). We recorded the time courses of the observers’ reported percepts during the stimulus periods. During stimulus periods in the following monocular single-alternation scan, the stimuli physically alternated between the two monocular gratings (Figure 1b), mimicking what observers perceived in the preceding rivalry scan. Thus the durations of stimulus displays were determined by the durations reported during the rivalry scan. To mimic what observers experienced during transitions between two percepts, the contrast of one pattern (e.g., red, left-tilted grating presented to the left eye) was gradually decreased following a 750-ms sigmoidal function, whereas the contrast of the other pattern (e.g., green, right-tilted grating presented to the right eye) was increased following an identical sigmoidal function – transitions from one grating to the other exactly mimicked the durations of the actual transitions measured with rivalry. Observers again reported fluctuations in dominance by pressing buttons; this task was included to maintain attention and motor response engagement at the same level as in the rivalry scan. The monocular double-alternation scan was identical to the monocular single-alternation scan except that the stimuli were red and green plaid patterns (made by adding two orthogonal gratings) instead of single gratings (Figure 1c).

The levels of pattern contrast were chosen separately for each observer based on several criteria designed to (1) minimize the percentage of time that portions of the two images are perceived simultaneously; (2) obtain roughly equal periods of dominance for two rival patterns; and (3) maintain the levels of contrast as low as possible while satisfying 1 and 2 to avoid fMRI signal saturation. The mean duration of dominance varied across observers: 3.8 s for S.L., 3.4 s for E.G., 5.8 s for R.B. (meaning that within the 18-s viewing period observers experienced anywhere from 2 to 4 rivalry alternations, on average). Contrast values for these three observers were, respectively, 5.2%, 7.1%, and 10.0%.

**BOLD Responses to Grating Patterns**

To quantitatively compare neural activity across these three viewing conditions, we estimated the amplitude of fMRI response for each viewing condition in the following way. First, the data from each scan were divided into four cycles, where one cycle consisted of one stimulus period and one rest period. This resulted in 32 individual time series of fMRI data (8 scans x 4 cycles). Second, these individual time series were averaged to obtain a mean time series consisting of 18 data points. For each data point, SE was computed based on variation across the individual time series. Third, the amplitude of neural activity (the difference in neural activity between a stimulus period and a rest period) was estimated by fitting the mean time series with a hemodynamic response model (see “Methods”). The model accounted for 85% to 99% of the variance in the data. Fourth, for statistical tests, the SEM amplitude was estimated using a bootstrap technique (Efron & Tibshirani, 1993).

Figure 2 summarizes results from three observers. The amplitudes of V1 activity evoked by the monocular double-alternation stimuli were significantly greater than those evoked by the monocular single-alternation stimuli (S.L., p < .008; R.B., p < .004; E.G., p < .01). This merely confirms the validity of the a priori reasonable assumption upon which our strategy rests, namely that two superimposed gratings activate more V1 neurons than does a single grating.

The amplitudes of V1 activity evoked by the rivalry stimuli fell midway between those evoked by the monocular single-alternation stimuli and those evoked by the monocular double-alternation stimuli. There was a general tendency for the amplitudes in the rivalry condition to be greater than those in the monocular single-alternation condition. For all three observers, the amplitudes in the rivalry condition were smaller than those in the monocular double-alternation condition (S.L., p < .04; R.B., p < .09; E.G., p < .02). This implies that V1 activity associated with a nondominant grating was reduced significantly during rivalry, albeit not completely. A suppression index was derived to quantify the extent to which V1 activity associated with a nondominant grating was suppressed during rivalry. The suppression index was computed as the ratio of < the amplitude during rivalry - the amplitude during monocular single alternation> to <the amplitude during monocular double alternation - the amplitude during monocular single alternation>. This ratio normalizes the amplitude in the rivalry condition by those in the two nonrivalry conditions for each observer and each cortical area; an index value of 0.00 would denote complete
suppression, and an index of 1.00 would indicate no effect of suppression. The suppression indices in V1 S.L., R.B., and E.G. were .35, .52, and .23, respectively (Figure 2b).

Results from V2, V3, and V4 were very similar to those from V1. Again, the amplitudes during rivalry were greater than those during monocular single alternation and smaller than those during monocular double alternation. The ranges of suppression index were roughly equal across all of the visual areas, and there was no significant, systematic increase or decrease in amplitude from V1, to V2, to V3, and to V4v (the slope of linear trend from averaged data across observers was not significantly different from 0 [slope = -.051, p > .23]).

**BOLD Responses to Complex Patterns**

The viewing conditions for this experiment were identical to those in the first experiment except that the rivalry patterns were line drawings of a human face and a house (Figure 3), not sinusoidal gratings. Figure 4 shows results from two observers (the third observer experienced difficulty seeing the low luminance, edge-defined images and, therefore, was not tested). The patterns of data from these two observers were very similar to those from the first experiment. Again, the amplitudes of V1 activity evoked by the monocular double-alternation stimuli were significantly greater than both those evoked by the monocular single-alternation stimuli (S.L., p < .0001; E.G., p < .02) and those evoked by the rivalry stimuli (S.L., p < .001; E.G., p < .05). The amplitudes in the rivalry condition were greater than those in the monocular single-alternation condition and smaller than those in the monocular double-alternation condition for all visual areas (suppression index: S.L., .25; E.G., .37). Again, we did not observe a systematic increase or decrease in the suppression index in the later visual areas (the slope of linear trend from averaged data across observers was not significantly different from 0).
The suppression indices were very similar to those in the first experiment, where gratings were used as the stimuli.

![Figure 4. Cortical activity in Experiment 2 (same format as Figure 2).](image)

### Discussion

During binocular rivalry, one of two rival patterns is erased from visual awareness. It is natural to assume, therefore, that the neural activity normally evoked by that pattern has been attenuated at some stage of visual information processing during suppression phases. To examine whether this rivalry suppression occurs in V1, we measured V1 activity during binocular rivalry and compared it with those in the two reference conditions: one representing complete suppression (monocular single alternation) and the other representing no suppression (monocular double alternation). We found that the amplitude of V1 activity during rivalry fell midway between those in the two reference conditions; the suppression index analysis indicated that the amount of V1 activity associated with the nondominant pattern was reduced by 48% to 77% during rivalry. The amount of suppression during rivalry did not systematically vary within extrastriate visual areas. Significantly, the same pattern of results was obtained with meaningful rival targets (i.e., a human face and a house), demonstrating that earlier fMRI findings on rivalry and V1 (Polonsky et al., 2000; Tong & Engel, 2001) were not specific for one-dimensional grating patterns.

If anything, our data may underestimate the magnitude of neural suppression during rivalry in these early visual areas. For one thing, one might argue that heightened visual attention was required during actual rivalry, possibly amplifying neural signals during dominance and during suppression and, thus, shrinking the numerator in the suppression index. On the other hand, the fluctuations during the single-grating condition embodied the same degree of unpredictability and, hence, should engage nearly comparable levels of attention. For another, the actual contrast ramps in the grating alternation condition might lead to stronger transient neural responses than those associated with phenomenal shifts in perceptual state, again reducing the suppression index by elevating the denominator. Finally, it is conceivable that inhibitory events triggered by actual rivalry produce enhanced BOLD signals, which, of course, would dilute differences between actual rivalry and the other comparison conditions. For these reasons, we must be cautious in drawing conclusions about the actual magnitude of reduction in neural activity during binocular rivalry.

One could argue that neural activity (and hence BOLD signal) associated with a dominant stimulus during rivalry is simply weaker than the neural activity associated with that same stimulus viewed monocularly without rivalry, thereby contributing the differences observed in our data. In other words, it is a reduction in BOLD response during dominance, not during suppression, that contributes to the overall weaker BOLD signal during rivalry. This argument seems highly unlikely, however, because psychophysical evidence overwhelmingly shows that the dominance state of rivalry is equivalent to ordinary monocular vision. Thus visual sensitivity assessed by probe detection is the same under both conditions (Fox & Check, 1972; Blake & Camisa, 1979), reaction times to test stimuli presented to a dominant eye in rivalry are equivalent to those measured to monocular stimuli presented under nonrival conditions (O'Shea, 1987), and the magnitude of several visual adaptation aftereffects is the same for rivalry stimulation as it is for nonrival, monocular stimulation (Lehmkuhle & Fox, 1975; Wade & Wenderoth, 1978). These findings all point to the equivalence of nonrival, monocular vision and the dominance state during rivalry. There is no reason, in other words, to expect BOLD signals to be weakened during dominance phases of rivalry.

Our results provide converging evidence that neural activity within visual area V1 plays a substantial role in the intermittent suppression of vision characteristic of rivalry, consistent with results from previous fMRI studies (Polonsky et al., 2000; Tong & Engel, 2001) and magnetoencephalography (MEG) studies (Tononi, Srinivasan, Russell, & Edelman, 1998). In these studies, the ratio of the amplitude of modulations during rivalry to the amplitude during physical stimulus alternation ranged from 45% to 83% in V1 (Polonsky et al., 2000) and 50% to 85% in the occipital lobe (Tononi et al., 1998). Thus the magnitude of BOLD signal suppression in our study is comparable to that of suppression index.
values estimated in previous studies, even though those values were derived based on different measurements and experimental protocols. And to reiterate, the current results imply that V1 plays an important role in attenuating neural events during binocular rivalry regardless of the feature complexity of the competing stimuli.

It is noteworthy that the range of suppression index values is still less than 100%. This may be interpreted to mean that the suppression during rivalry is not complete in V1. As Polonsky et al. (2000) suggested, however, suppression index values less than 100% might be attributed to phenomenological differences between suppression of a pattern during rivalry and physical removal of that pattern. The neural manifestation of rivalry suppression may be just to attenuate or disrupt neural events associated with a given rival image in the normal viewing condition. An alternative interpretation is that there exists a subset of neurons in V1 that are not involved in rivalry, for example, binocular neurons responsive to visual inputs from both eyes. This interpretation is consistent with the results from a recent fMRI study (Tong & Engel, 2001), which showed that rivalry alternation and stimulus alternation did not differ in the amplitude of BOLD signal fluctuation when the analysis was confined to a monocular region in V1 representing the blind spot. We do note, however, that single-unit studies in monkeys did observe suppression effects in binocular neurons within visual area V1 (Leopold & Logothetis, 1996).

The involvement in rivalry of V1 is also supported by psychophysical findings. Blake, O’Shea, and Mueller (1992) demonstrated that the angular substense of rivalry zones where one of rival images is exclusively visible at a time is scaled with the eccentricity of the rival images. This observation coincides well with the magnification factor in V1. Recently, Wilson, Blake, and Lee (2001) found that the visibility of a rival pattern propagates spatially and its speed was influenced systematically by the pattern and eccentricity of rival stimuli in a manner implying that the cortical site associated with rivalry propagation has characteristics (retinotopic organization, cortical magnification and collinear facilitation) matching those of V1. In line with these previous imaging and psychophysical studies, our results support a view that the neuronal events underlying phenomenal suppression during rivalry are likely to involve the reduced activity of the neurons in V1. The involvement in rivalry of V1, however, does not conflict with the involvement in rivalry of other higher-level areas (Tong et al., 1998; Lumer et al., 1998; Scheinberg & Logothetis, 1997), because rivalry may be fully resolved by feedforward or feedback interactions among several cortical areas along the visual stream.

Perceptual alternations also can occur between two different patterns, spatially superimposed and presented to the same eye (Breese, 1999; Campbell, Gilinsky, Howell, Riggs, & Atkinson, 1973), a perceptual outcome termed monocular rivalry. Physiological studies (Sengpiel, Freeman, & Blademeore, 1995; Bonds, 1989; DeAngelis, Robson, Ohzawa, & Freeman, 1992) have also shown that in the cat striate cortex, neural responses to optimal stimuli are suppressed when another stimulus is superimposed in the same eye. This monocular pattern-suppression component was factored into the suppression index used in our study, by comparing BOLD signals to rivalry stimuli with those to single stimulus alternations (monocular single alternation) as well as to BOLD signals in response to superimposed stimulus alternations (monocular double alternation). Therefore, the suppression index values (.23 - .52) observed in our study represent the amount of suppression that cannot be accounted for by pattern rivalry.

Conclusions

This work, using a different experimental protocol, confirmed the findings of earlier imaging studies that neuronal events associated with binocular rivalry occur as early as V1. Furthermore, our findings extend those earlier findings by demonstrating robust neural suppression during binocular rivalry, regardless of the stimulus complexity of the rivaling targets.

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