When and where is binocular rivalry resolved in the visual cortex?

Michael A. Pitts

Department of Neurosciences,
University of California San Diego,
La Jolla, CA, USA

Antígona Martínez

Department of Neurosciences,
University of California San Diego,
La Jolla, CA, USA, &
Nathan Kline Institute for Psychiatric Research,
Orangeburg, NY, USA

Steven A. Hillyard

Department of Neurosciences,
University of California San Diego,
La Jolla, CA, USA

Anatomically "early" visual areas including striate cortex (V1) are known to play a role in the resolution of binocular rivalry. However, the time course of such activity and its relationship with subjective perception are unclear. The present study used an intermittent stimulation design to measure event-related potentials (ERPs) associated with perception during binocular rivalry and during physical alternations of the same stimuli. When gratings of high or low spatial frequencies were presented in physical alternation, the amplitude of the earliest cortical ERP component (the C1, at 60–100 ms) was larger for high spatial frequencies. When the same two stimuli competed during rivalry, however, C1 amplitudes were equivalent for perceptions of high versus low spatial frequency. These findings suggest that rivalry is not resolved before or during the initial cortical response at 60–100 ms. At longer latencies (~130–160 ms), however, occipital ERPs with similar topographies and estimated sources as the C1 differed according to perception in both the rivalry and physical alternation conditions. These results suggest that during rivalry, neural activity coupled with the dominant percept first emerges in anatomically early visual cortex, but at delayed latencies.

Keywords: bistable perception, C1, ERP, perceptual rivalry, spatial frequency

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Introduction

Binocular rivalry occurs when two incompatible images are presented simultaneously, one to each eye. Observers typically perceive only one image at a time, and their perception alternates between the two images every few seconds. Because sensory input does not change while subjective perception does, binocular rivalry can be used to investigate the stages of sensory processing that give rise to perceptual experience.

Studies using brain imaging in humans and electrophysiology in non-human primates have suggested a link between neural activity in primary visual cortex (V1) and subjective perception during rivalry. Human fMRI studies (Haynes, Deichmann, & Rees, 2005; Lee, Blake, & Heeger, 2005, 2007; Meng, Remus, & Tong, 2005; Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001) have consistently found a close correspondence between V1 activity and perception. Single- and multi-unit studies in monkeys (Leopold & Logothetis, 1996; Logothetis, 1998; Logothetis & Schall, 1989; Sheinberg & Logothetis, 1997) have also shown correlations between neuronal firing rates in V1 and animals' perceptual reports. A recent study (Maier et al., 2008) that combined these techniques in monkeys reported that fMRI signals and low-frequency local field potentials (LFPs), but not neuronal spiking or high-frequency LFPs in V1, correlated with perception during rivalry.

While both fMRI and single-unit studies clearly indicate a role for V1 in the resolution of rivalry, the timing of neural activity in V1 during rivalry remains unclear. To explore this issue further, we measured event-related potentials (ERPs) while human subjects reported their

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perceptions during rivalry. The main question was whether rivalry is resolved during the earliest stages of cortical visual processing (i.e., from 60 to 100 ms after stimulus onset in visual areas V1, V2, and V3). Previous ERP studies of rivalry (Khoe, Mitchell, Reynolds, & Hillyard, 2008; Mishra & Hillyard, 2009; Roeber & Schroger, 2004; Roeber et al., 2008; Valle-Inclan, Hackley, de Labra, & Alvarez, 1999) reported differences related to perception in the time frame of the P1 and N1 components (~100–200 ms), but none of these studies specifically targeted the earliest visual evoked component, the C1 (~60–100 ms). We hypothesized that the initial visual cortical response reflects low-level sensory processing and would thus correlate with sensory input but not necessarily with perception, whereas delayed processing in these same "anatomically early" areas might be more closely linked with perception during rivalry. This hypothesis was tested here in an intermittent stimulus presentation paradigm that exploited several well-known properties of the visual ERP.

Traditionally, rivalry-inducing stimuli are presented continuously while observers report perceptual transitions. In order to elicit a visual ERP however, a stimulus transient is required. The present study used an intermittent stimulus presentation approach to allow time locking of visual ERPs to stimulus onset. Stimuli were presented for 600-ms durations, followed by blank screen intervals (500–700 ms) during which observers reported their perceptions. Previous studies using bistable stimuli such as the Necker cube (Brascamp, Pearson, Blake, & van den Berg, 2009; Kornmeier & Bach, 2004; Pitts, Martinez, Stalmaster, Nerger, & Hillyard, 2009) have shown that with appropriate stimulus parameters only one percept is typically experienced during each presentation, and perceptual transition rates across successive presentations are equivalent to those found using continuous displays. In the current study, this method was applied to binocular rivalry.

Previous reports (Clark, Fan, & Hillyard, 1995; Di Russo, Martinez, & Hillyard, 2003; Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2001; Di Russo et al., 2005; Martinez et al., 1999, 2001) have suggested that the earliest component (~60–100 ms) of the visual ERP, the "C1", is generated primarily in area V1 (but see Ales, Yates, & Norcia, 2010). The amplitude of the C1 has been shown to be substantially larger for stimuli of higher spatial frequencies (Butler et al., 2007; Kenemans, Baas, Mangun, Lijffijt, & Verbaten, 2000; Proverbio, Zani, & Avella, 1996). Based on these findings, the present design pitted a high spatial frequency (SF) stimulus against a low SF stimulus during rivalry in order to find out whether early visually evoked cortical activity correlates with perception of one or the other of these stimuli when presented simultaneously to the separate eyes. To verify that the particular stimuli used would produce C1 amplitude differences under normal viewing conditions, ERPs were also obtained during physical alternations of these same stimuli.

Methods

Participants

A group of twenty healthy adults (11 females; mean age: 20, ranging from 18 to 23) participated in the experiment. The binocular rivalry and physical alternation conditions were run during separate sessions (order was counterbalanced across subjects). All participants were recruited as volunteers and gave informed consent prior to the beginning of each experiment. The experimental procedures were approved by the University of California San Diego Institutional Review Board in compliance with the Declaration of Helsinki.

Design and procedure

Stimuli were presented on a dark background (0.07 cd/m^2) and were centered horizontally within the left and right halves of the computer screen (60-Hz refresh rate). Participants viewed the stimuli through a mirror stereoscope allowing separate stimulation of the left and right eyes with spatially superimposed images. At the beginning of each session, participants adjusted the angle of the mirrors to achieve stereo-fusion. To help maintain fusion, participants fixated 1° crosses centered in 0.75° gray/white circles (see Figure 1). All stimuli were presented at fixation.

The stimuli were square-shaped sinusoidal gratings (6° in diameter) presented as pairs, one to each eye. The stimuli presented to the left and right eyes differed along each of three orthogonal dimensions: color (red/green), orientation (45°/135°), and spatial frequency (1 cpd/5 cpd). With the additional dimension of eye (left/right), this resulted in 8 different pairs of stimuli. Each pair was equated in luminance at ~10 cd/m^2 (by chromatic photometry) and was presented during 6 non-consecutive blocks of trials (counterbalanced across blocks), resulting in 48 total blocks. Each block consisted of 50 stimulus presentations after which participants took self-paced breaks. In the rivalry condition (48 blocks), stimuli were presented to the two eyes simultaneously. In the physical alternation condition (48 blocks), one stimulus (from a pair) was presented to one eye while input to the other eye was kept blank, and the two stimuli of each pair were interchanged between eyes at rates that mimicked perceptual switching rates during rivalry (random alternations every ~1.2–6.0 s).

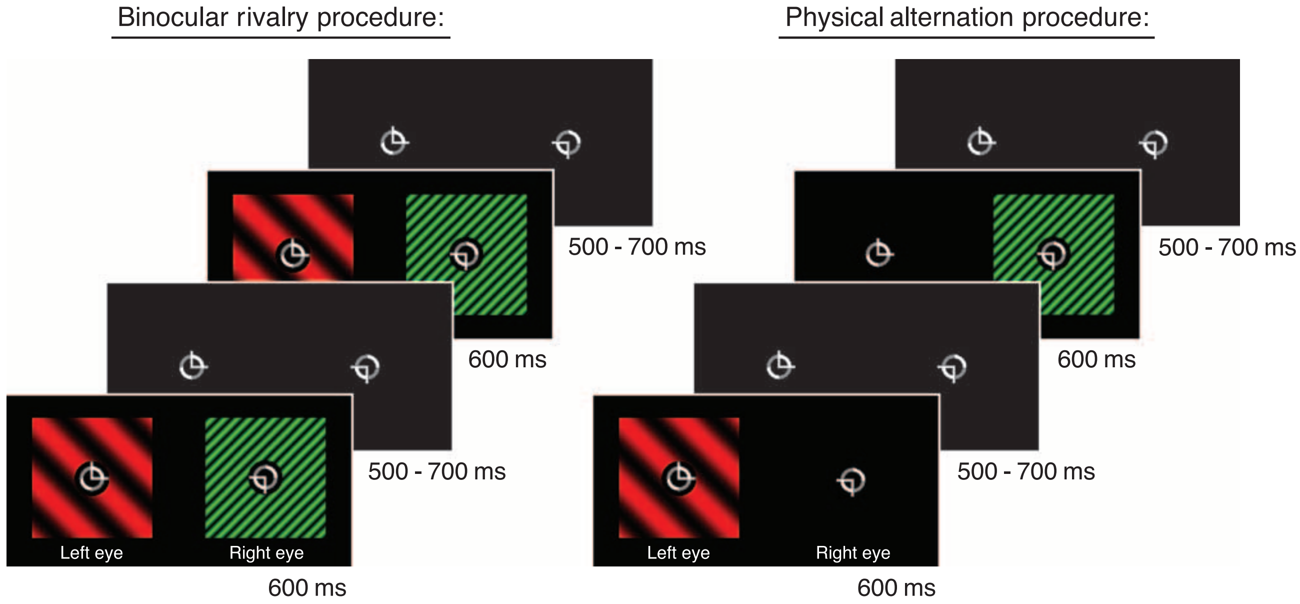


Figure 1. Stimulus presentation procedure for the (left) rivalry and (right) physical alternation conditions. Observers viewed the stimuli through a mirror stereoscope that allowed isolated stimulation of the left and right eyes. Binocular pairs (rivalry) or single monocular stimuli (physical alternation) were presented for 600 ms followed by a variable 500–700 ms blank screen (fixation only) interval. On each trial, observers reported the color they perceived (red or green) by pressing one of two keys.

All stimuli were presented for 600-ms durations separated by variable 500–700 ms blank screen (fixation cross only) intervals. Participants were instructed to report their red/green perceptions after each stimulus presentation by pressing one of two keys. In the rivalry condition, participants were also given the option of withholding their response if they perceived a piecemeal mixture of the red and green stimuli or an apparent superimposition of the two gratings (a plaid). Because the goal of the study was to measure the initial visual cortical response, the C1, which has been shown to be differentially sensitive to high versus low SF, ERPs were collapsed across the dimensions of eye, color, and orientation.

EEG/ERP methods

Brain electrical activity was recorded non-invasively from the scalp using commercially available electrode caps (Electro-Cap International) with 64 electrode placements. Electrode impedances were kept below 5 kΩ. Scalp signals were amplified by a battery powered amplifier (SA Instrumentation) with a gain of 10,000 and band-pass filtered from 0.1 to 80 Hz. Signals were digitized to disk at 250 Hz. During task performance, eye position and eye movements were monitored by means of vertical and horizontal electrooculogram (EOG) recordings. A right mastoid electrode served as the reference for all scalp channels and the vertical EOG. Left and right horizontal EOG channels were recorded as a bipolar pair. Each recording session lasted 120–180 min including setup and cap/electrode preparation.

ERPs were time-locked to stimulus onset, baseline corrected from -100 to 0 ms, and low-pass filtered at 30 Hz. Trials were discarded if they contained an eye blink or eye movement artifact or if any electrode channel exceeded signal amplitudes of 50 μV. On average, 15% of trials per individual were rejected due to a combination of these artifacts. Prior to analysis, ERPs were re-referenced to averaged mastoids by calculating the difference between each scalp channel and an average of the left and right mastoid channels.

Comparisons of interest were between ERPs associated with perceptions (or physical presence) of high SF versus low SF. ANOVA with the factors spatial frequency (high, low) and electrode site (SIZ, IZ, OZ, POZ, O1, O2) was used to test mean amplitude differences within subjects during the C1 time window (68–108 ms) and during a delayed time window (132–160 ms) separately. Additional running *t*-tests were conducted at each time point (every 4 ms) for each electrode (64 sites) to assess the latencies at which the ERP waveforms first diverged. Differences were deemed significant if at least 4 adjacent electrode sites across at least 4 consecutive time points differed significantly at $p < 0.05$.

Source analyses

The locations of neural generators of the C1, the P1, and subsequent modulations in the grand-averaged ERPs were estimated via a Laplacian weighted minimum norm inverse solution (LORETA) and through dipole modeling (BESA, 2000; version 5).

A LORETA inverse solution (Michel et al., 2004; Pascual-Marqui, Michel, & Lehmann, 1994) was first used to estimate intracranial current distributions across three time intervals: 72–92 ms, 100–120 ms, 132–160 ms. The current distributions were computed in a grid of 3005 solution points that were regularly distributed within the gray matter of the cerebral cortex and limbic structures of the average brain provided by the Montreal Neurological Institute (MNI 152). No a priori assumptions were made regarding the number or location of active sources. LORETA solutions were computed using Cartool software (http://brainmapping.unige.ch/Cartool.php).

Dipole modeling was then carried out using the number and locations of sources inferred from the LORETA solutions. The BESA algorithm calculates the scalp distribution that would be obtained for a given model (forward solution) and compares it to the actual ERP scalp distributions (Scherg & Picton, 1991). The algorithm interactively adjusted (fit) the orientation of the dipole sources in order to minimize the residual variance (RV) between the model and the observed spatiotemporal ERP distribution. To model the C1, we first fit a single dipole during the leading edge of the C1 (72–92 ms; Talairach coordinates for both conditions: −3, −82, 7) and then fit a mirror symmetric pair of dipoles during the leading edge of the P1 (100–120 ms; Talairach coordinates for physical alternation: ±49, −67, 6; for rivalry: ±43, −62, 6). Because the RV of the 3-dipole model was relatively low (<12%, across 0–200 ms) for the rivalry condition, we did not model any subsequent components. For the physical alternation condition, we added an additional pair of dipoles across 160–200 ms (Talairach coordinates: ±48, −67, 1) to account for a vertex positivity that began around 160 ms.

Results

In the rivalry condition, participants on average perceived the high SF stimulus as dominant 44% of the time, the low SF stimulus as dominant 49% of the time, and piecemeal/superimpositions 7% of the time. In the physical alternation condition, stimuli were balanced at 50% and were interchanged between eyes at rates that mimicked perceptual transitions during rivalry.

Figure 2 shows ERP results from the physical alternation and binocular rivalry conditions. When stimuli were presented in physical alternation (Figure 2a), the C1 component was larger for high SF versus low SF, replicating previous results. During rivalry however (Figure 2b), C1 amplitudes did not differ based on observers' perceptions. Importantly, when the high SF stimulus was perceptually invisible (blue waveform in Figure 2b) a substantial C1 was still produced, indicating that this stimulus was being processed at this early stage in spite of being perceptually suppressed. Difference topographies formed by subtracting ERPs associated with low SF stimuli/percepts from those associated with high SF stimuli/percepts are shown in Figure 2c.

Mean C1 amplitudes (from 68 to 108 ms) were compared by ANOVA with the factors spatial frequency (high, low) and electrode channel (6 occipital sites—see Methods section). As expected, significant C1 amplitude differences were found between high and low SFs in the physical alternation condition, $F(1,19) = 37.33$, $p = 0.00007$. In contrast, in the rivalry condition C1 amplitude differences between high and low SF percepts were not evident, $F(1,19) = 0.18$, $p = 0.68$. While Figures 2a and 2b show ERPs averaged across the 6 occipital electrode sites tested, ERPs recorded from a broader range of occipital, parietal, central, and frontal sites are shown in Supplementary Figures S1 and S2. C1 amplitudes during rivalry appeared roughly equivalent to an average of the C1 amplitudes during physical alternation. While caution must be taken in comparing results across the two conditions, given that the stimuli and method of presentation differed, ANOVA revealed that overall C1 amplitude (averaged across high and low SF stimuli and percepts) was marginally reduced during rivalry, $F(1,19) = 3.96$, $p = 0.06$.

During subsequent time windows (∼130–160 ms), ERP differences associated with rivaling perceptions of high versus low SF were evident. These differences can be seen in the ERPs (Figure 2b), as well as in the difference wave topographies formed by subtracting the ERPs associated with low SF percepts from those associated with high SF percepts (Figure 2d). ERPs from 130 to 160 ms were more positive for high versus low SF stimuli in the physical alternation condition and for high versus low SF percepts in the binocular rivalry condition.

ANOVA confirmed that these differences across 132–160 ms were significant: for physical alternation, $F(1,19) = 20.01$, $p = 0.0003$; and for rivalry, $F(1,19) = 8.23$, $p = 0.009$. To better assess the timing of these modulations, *t*-tests were conducted at each electrode, at each time point from −100 to 200 ms. In the physical alternation condition, differences were significant ($p < 0.05$) across at least 4 time points (20 ms) for at least 4 adjacent electrode sites from 68 to 108 ms and 124 to 184 ms. In contrast, in the rivalry condition the perception-related differences were only significant over the later interval, 120–172 ms.

To evaluate the neuroanatomical sources of these ERP differences, the locations of the neural generators were estimated with a Laplacian weighted minimum norm inverse solution (LORETA) and with dipole modeling (BESA). First, the regional sources for the grand-averaged ERPs were estimated using LORETA, across three time windows (72–92 ms; 100–120 ms; 132–160 ms) that covered the C1, P1, and delayed difference intervals, respectively. Figure 3a shows the LORETA estimates for ERPs to high and low SFs, as well as the differences between the two. In the physical alternation condition,

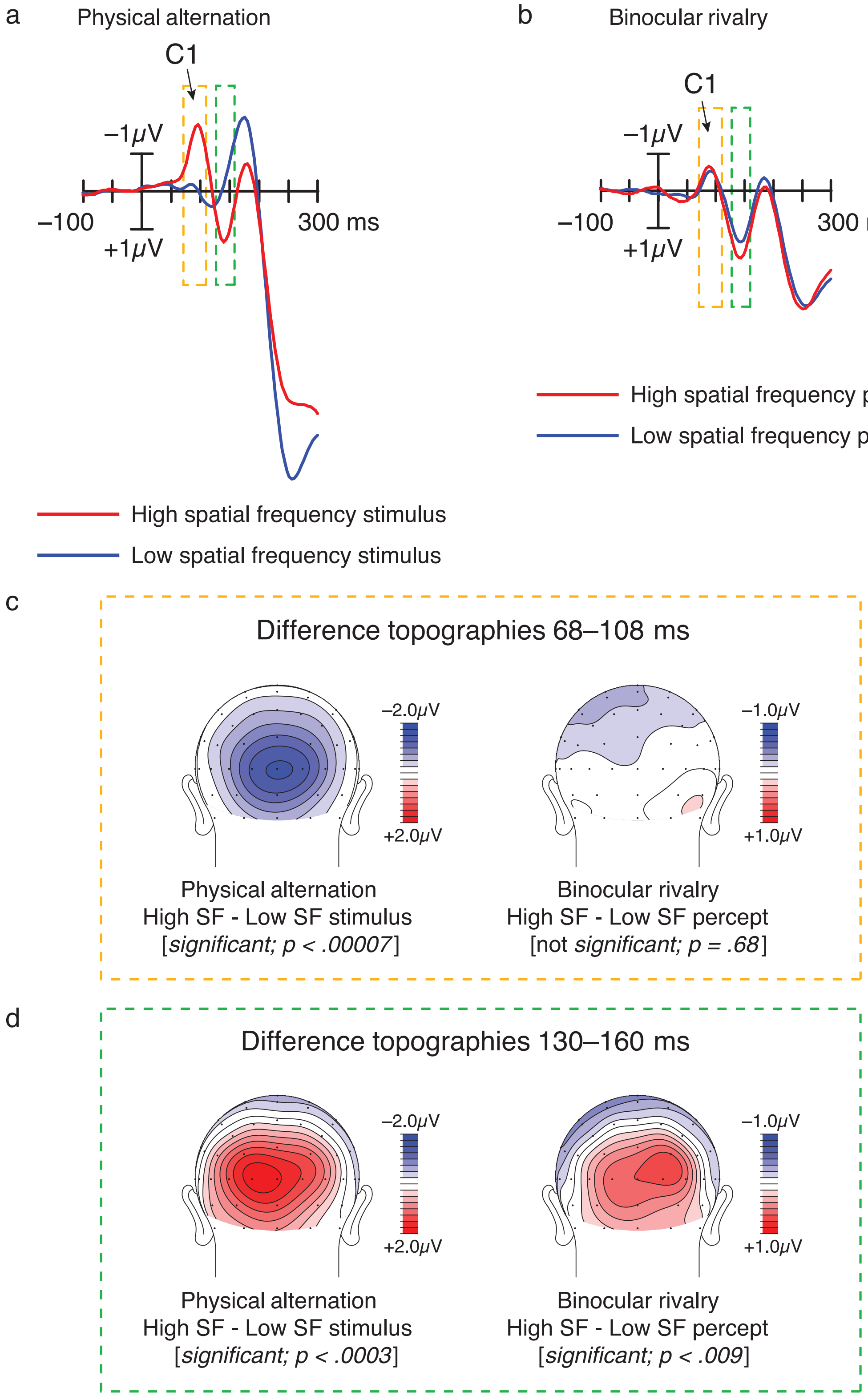
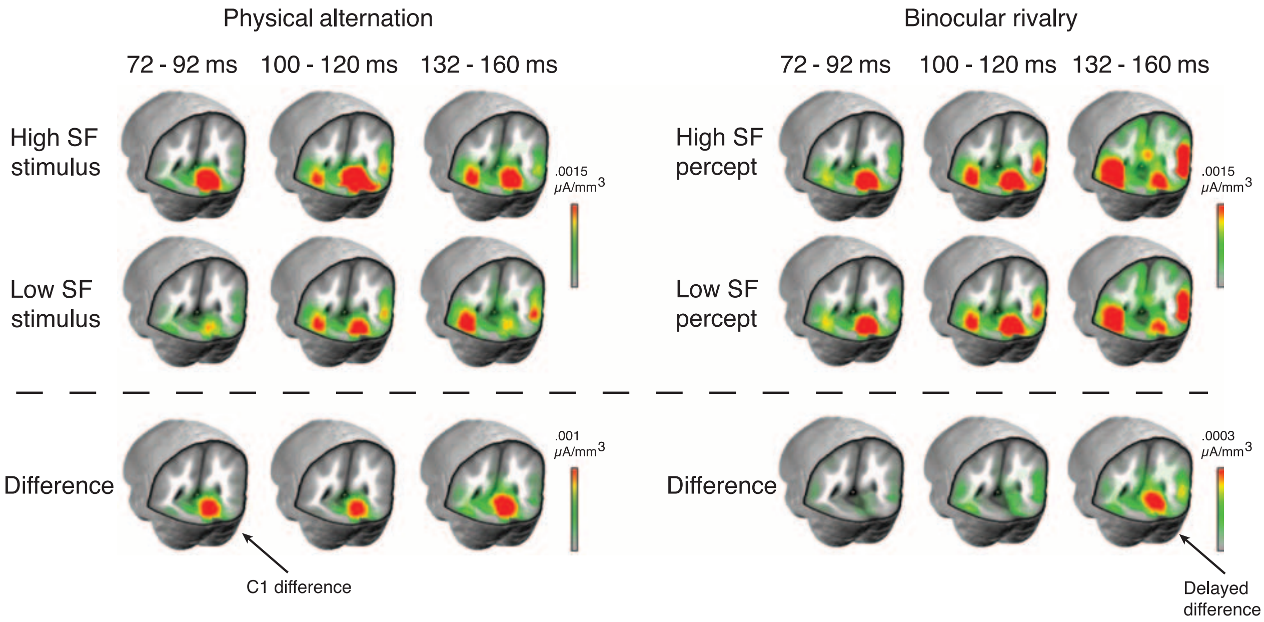


Figure 2. Grand-averaged ERPs for the two conditions averaged across occipital electrodes (a, b) and voltage distributions of the differences between high and low spatial frequency stimuli/percepts (c, d) across the two time windows of interest (yellow, green outlines). (a) In the physical alternation condition, the amplitude of the C1 component was larger for high versus low spatial frequency stimuli. (b) In the rivalry condition, C1 amplitudes did not differ based on observers' dominant percept (high versus low spatial frequency). Voltage distributions show differences during the C1 interval (c) only in the physical alternation condition. These differences were absent in the rivalry condition. Delayed modulations (d) were evident in both conditions (note that amplitudes are scaled differently between the conditions).

a LORETA regional sources



b BESA dipole models

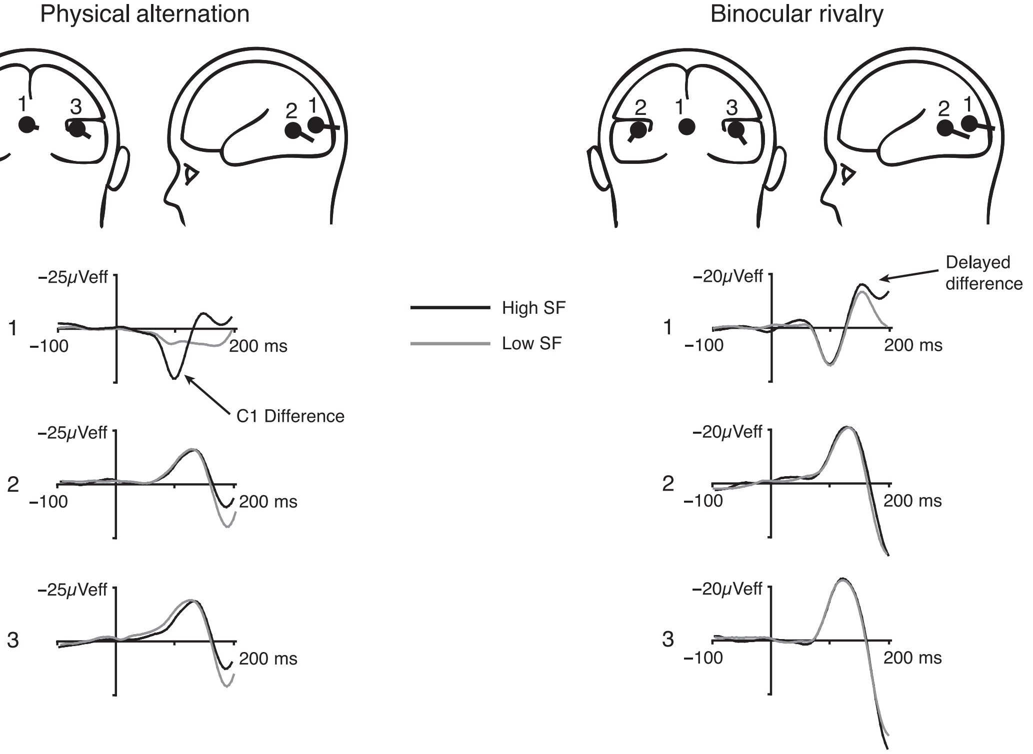


Figure 3. (a) LORETA source estimations and (b) dipole models for the two conditions. The top row shows LORETA estimates for high spatial frequency stimuli/percepts, the second row for low spatial frequency stimuli/percepts, and the bottom row shows differences between the two. Each column represents different time intervals. In both conditions, C1 sources were located in early visual areas. However, significant differences in C1 source strength were found only in the physical alternation condition. During delayed intervals (132–160 ms), sources in these same early visual areas were stronger for high spatial frequencies compared to low spatial frequencies in both conditions (note that the difference results are plotted on different scales). Dipole orientations and source waveforms (b) confirmed a C1 generator with two distinct phases as well as intervening P1 generators. In accordance with the ERP results, differences in source waveform amplitudes were evident during the C1 and delayed intervals for physical alternation but only during delayed intervals for rivalry.

sources were clearly stronger in early visual areas from 72 to 92 ms for stimuli of high compared to low SF. Consistent with the ERP amplitude analyses, differences in source strength for the rivalry condition emerged only around 132–160 ms (after the C1 and P1 phases) but were located in anatomically early visual areas (V1, V2, V3).

The sources of these same ERPs were also modeled with dipoles. The number of dipoles and their locations were determined from the LORETA results. For the rivalry condition, a 3-dipole model, with a single C1 dipole (72–92 ms) and a pair of P1 dipoles (100–120 ms), accounted for 90.20% of the variance for high SF percepts and 88.92% of the variance for low SF percepts (from 0 to 200 ms). The source waveforms for the C1 dipoles showed two phases, one from ~70 to 100 ms and another from ~120 to 170 ms, with a difference in source strength only during the second phase (stronger for high SF percepts). For the physical alternation condition, a 5-dipole model, with the same C1 and P1 dipoles as in rivalry and an additional pair of dipoles fitted across a 160–200 ms interval, accounted for 91.33% of the variance for high SF stimuli and 94.12% of the variance for low SF stimuli (from 0 to 200 ms). Figure 3b shows the orientations and source waveforms for the C1 and P1 dipoles of these models.

Discussion

Recordings of event-related potentials (ERPs) to dichoptic stimuli of high and low spatial frequencies showed that the initial visual cortical response (reflected by the C1 component at ~60–100 ms) did not vary in amplitude according to the perception of high versus low spatial frequencies. This finding suggests that interocular competition during rivalry is not resolved during the initial stage of processing in early visual cortex. Instead, the observed ERP modulations suggest that neural activity underlying the dominant percept emerges at longer latencies (~130–160 ms), and source analyses suggest that this delayed modulation originated in anatomically early levels of the visual cortex.

An important distinction between this study and previous studies is the stimulus presentation approach used to measure the time course of perceptual processing during rivalry. In previous studies (Haynes et al., 2005; Khoe et al., 2008; Lee et al., 2005; Mishra & Hillyard, 2009; Polonsky et al., 2000; Valle-Inclan et al., 1999; Wunderlich, Schneider, & Kastner, 2005), the competing stimuli were presented continuously, while in the current study, stimuli were presented intermittently with blank screen intervals, and observers reported their percepts after each stimulus. With this intermittent presentation design, it was possible to measure the time course of sensory and perceptual processing and to dissociate early stages of low-level sensory processing from later stages of perceptual processing. The stimulus duration (600 ms) and interstimulus intervals (500–700 ms) were tested in pilot studies to ensure that perceptual rivalry (not fusion; see Wolfe, 1983) occurred and that perceptual reversal rates approximated those found with continuous rivalry. While it is difficult to extrapolate results from intermittent to continuous rivalry, previous fMRI studies reporting percept-related differences in early visual cortex or LGN (Haynes et al., 2005; Lee et al., 2005; Polonsky et al., 2000; Wunderlich et al., 2005) may have been measuring delayed activity similar to that found in the current study. It is particularly interesting to note the similarities between Haynes et al.'s (2005) results and those of the current study. Haynes et al. found that percept-based V1 modulations during rivalry were 28% as strong as stimulus-based V1 modulations during physical alternation of the same stimuli. In the current study, while the C1 was not modulated by perception during rivalry, percept-based modulations during later time intervals (130–160 ms) were 29% as large as stimulus-based modulations during physical alternation.

If rivalry is resolved in early visual cortex but only at delayed latencies, feedback from higher to lower level areas may play an important role (Tong, Meng, & Blake, 2006). The potential role of feedback (or "recurrent") processing in perceptual awareness has gained considerable support over recent years. Lamme et al. (Fahrenfort, Scholte, & Lamme, 2007; Heinen, Jolij, & Lamme, 2005; Lamme, 1995; Lamme, Zipser, & Spekreijse, 1998, 2002; Scholte, Jolij, Fahrenfort, & Lamme, 2008; Scholte, Witteveen, Spekreijse, & Lamme, 2006; Super & Lamme, 2007; Super, Spekreijse, & Lamme, 2001) have provided converging evidence from experiments using single-cell neurophysiology in monkeys, human fMRI, and human ERPs, which suggest the existence of at least two functionally distinct phases of V1 activity. When observers are made perceptually unaware of stimuli, either by backward masking (Fahrenfort et al., 2007; Lamme et al., 2002), TMS (Heinen et al., 2005), attentional distraction (Scholte et al., 2006), or even anesthesia (Lamme et al., 1998), the initial response of V1 remains unaffected, while delayed responses in V1 mediated by feedback are modified or eliminated. During binocular rivalry, stimuli are made perceptually invisible by the suppressive interaction between the two eyes. Similar to the findings of Lamme et al., the present data showed that the initial cortical response—indexed by the C1 component—was unaffected by perceptual suppression, but that delayed activity (possibly generated in V1) was modified.

Previous ERP studies of binocular rivalry (Roeber & Schroger, 2004, 2008; Valle-Inclan et al., 1999) did not specifically target early visual cortex by presenting rivalrous stimuli of different spatial frequencies, but nevertheless they reported perception-based modulations at latencies similar to those found in the current study (~100–300 ms). Interestingly, when selective attention was manipulated during rivalry (Khoe et al., 2008;

Mishra & Hillyard, 2009), ERP modulations of the P1 component at latencies of ~100–144 ms were found. The timing of these effects overlap with the timing of the delayed modulations found in the current study, although the scalp distributions of the previously reported P1 modulations showed bilateral occipital–parietal foci, while the delayed effects in the current study had a central–occipital focus. Future studies that combine these approaches may help clarify the role of top-down (attention-based) modulation in binocular rivalry.

Although comparisons between ERPs elicited in the rivalry condition and those elicited in the physical alternation condition are not readily interpretable because the method of presentation differed markedly, the amplitude of the C1 during binocular stimulation was less than the sum of the amplitudes during monocular stimulation. This pattern of results indicates a physiological interaction between the left and right eye inputs at the latency of the C1 (60–100 ms). At subsequent latencies (130–160 ms), the ERPs elicited during rivalry began to diverge according to the *perceived* stimulus, and this difference had the same polarity, scalp distribution, and latency as in the physical alternation condition. Thus, while competition between the stimuli was evident during the initial cortical response, neural activity coupled with the dominant percept during rivalry did not emerge until subsequent time intervals.

Whether competition during rivalry occurs only at specific levels of visual processing or in more widespread cortical areas remains unclear. A large body of work has reported evidence suggesting that rivalry-related activity occurs across multiple cortical regions, including temporal, parietal, and frontal areas (Cosmelli et al., 2004; Doesburg, Kitajo, & Ward, 2005; Fang & He, 2005; Lumer, Friston, & Rees, 1998; Lumer & Rees, 1999; Miller et al., 2000; Pasley, Mayes, & Schultz, 2004; Srinivasan, Russell, Edelman, & Tononi, 1999; Sterzer & Rees, 2008). However, recent work (Brouwer & van Ee, 2007; Kamphuisen, Bauer, & van Ee, 2008; Raemaekers, van der Schaaf, van Ee, & van Wezel, 2009) has challenged this idea, demonstrating that the frontally detected EEG signals in some of these studies could actually be explained by occipital neuronal activity. In order to compare data across different studies, it is important to consider how variations in stimuli (e.g., gratings, objects, moving dots), experimental paradigms (e.g., static, intermittent, probe-based), comparisons (percept A versus B, reversal versus stability, rivalry versus physical alternation, etc.), and physiological measurements (e.g., EEG/MEG, fMRI, single units) might lead to incongruent results. The present study utilized stimuli, measurements, and an experimental design particularly sensitive to revealing activity in early visual cortex. The results support the view that temporally early visual cortical activity is not associated with perceptual awareness during binocular rivalry, whereas subsequent activity, most likely generated in anatomically early visual cortex, does correlate with perception. While these data alone do not exclude the possibility that other cortical regions are also involved in rivalry, they do support the view that the initial visual conflict created during rivalry is resolved within anatomically early occipital cortex.

Conclusions

An intermittent stimulus presentation design was used to measure event-related potentials during binocular rivalry with gratings of high and low spatial frequencies presented to the separate eyes. Results suggested that rivalry is not resolved during the earliest stages of cortical visual processing, as reflected by equivalent amplitudes of the initial C1 component (~60–100 ms) for perceptions of high versus low spatial frequencies. At longer latencies (~130–160 ms) however, occipital ERPs differed according to perception during rivalry, and source estimation of this difference pointed toward generators in anatomically early visual areas.

Acknowledgments

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Corresponding author: Michael A. Pitts.
Email: michaelapitts@ucsd.edu.
Address: School of Medicine, Department of Neurosciences, University of California San Diego, 9500 Gilman Drive MC 0608, La Jolla, CA 92093-0608, USA.

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