Binocular Rivalry Requires Visual Attention

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SUMMARY

An interocular conflict arises when different images are presented to each eye at the same spatial location. The visual system resolves this conflict through binocular rivalry: observers consciously perceive spontaneous alternations between the two images. Visual attention is generally important for resolving competition between neural representations. However, given the seemingly spontaneous and automatic nature of binocular rivalry, the role of attention in resolving interocular competition remains unclear. Here we test whether visual attention is necessary to produce rivalry. Using an EEG frequency-tagging method to track cortical representations of the conflicting images, we show that when attention was diverted away, rivalry stopped. The EEG data further suggested that the neural representations of the dichoptic images combined without attention. Thus, attention is necessary for dichoptic images to be engaged in sustained rivalry and may be generally required for resolving conflicting, potentially ambiguous input and giving a single interpretation access to consciousness.

INTRODUCTION

A striking feature of sustained binocular rivalry is the apparently spontaneous nature of perceptual switching. Effortful attempts to control rivalry, for example paying more attention to one percept in order to prevent its alternating with the rival percept, fail during sustained rivalry (Meng and Tong, 2004). Thus, it seems possible that the process controlling rivalry is automatic, independent of attention. However, the most basic question has remained unanswered: If observers do not attend to the rivalrous stimuli, do rivalry alternations still occur? This issue is not simply a variant of the philosophical chestnut "When a tree falls in a forest without a listener, is there a sound?" Rather, the open question is how the visual system processes conflicting information presented at an unattended spatial location. If binocular rivalry is an automatic process that does not require attention, even unattended stimuli should rival. On the other hand, attentional feedback might be necessary to resolve interocular competition, and thus rivalry might not occur for unattended stimuli.

This question is challenging to address because when subjects direct attention away from a rivalrous stimulus, they are unable to directly report its perceptual status. To overcome this difficulty, we adopted methods that infer the state of the visual system from brain signals driven by each of two dichoptically presented competing stimuli (Brown and Norcia, 1997; Cobb et al., 1967). We used an electroencephalogram (EEG) frequency-tagging technique (also called "method of multiple stimuli") to track the cortical signal driven by each eye's stimulus. The two stimuli were modulated (tagged) at different temporal frequencies, which allowed us to track each eye's contribution to the steady-state visual evoked potentials (SSVEPs). Using this method, binocular rivalry has been shown to produce a characteristic counterphase pattern in the signal from the two eyes: as the image in one eye becomes dominant, its cortical signal gains strength and the signal corresponding to the other eye weakens (Brown and Norcia, 1997). We tested whether this marker of rivalry remains present even when attention is diverted away from the rivaling images.

RESULTS AND DISCUSSION

Figure 1 shows our methods. In the two rivalry conditions (Figure 1A), a pair of incompatible checkerboard patterns was presented one to each eye through a mirror stereoscope. The two patterns reversed their contrast at different temporal frequencies (red stimulus at 7.5 Hz, green stimulus at 6.6 Hz; see Figure S1 available online). Subjects fixated a central mark and actively monitored the parafoveal rivalrous stimuli, reporting their perception by button presses (mean dominance duration = 2.45 s, standard deviation = 1.30 s). In the unattended rivalry condition, subjects ignored the rivalrous stimuli and performed a demanding color-shape conjunction task at fixation (see Supplemental Experimental Procedures for details). In two replay conditions (Figure 1B), monocular checkerboards physically alternated, creating the perceptual alternations that mimicked those recorded in the attended rivalry condition, and the same two tasks directed attention either toward or away from the checkerboards. EEG signals were recorded while subjects viewed the stimuli under these four conditions, and an adaptive recursive least-square (RLS) filter was used to extract the amplitude of the two frequency-tagged signals over time (Brown and Norcia, 1997; Tang and Norcia, 1995).

Our results indicate that sustained rivalry requires attention and is either greatly reduced or does not occur at all in the absence of attention. Figures 1C–1F illustrate the time courses of EEG amplitudes at the contrast-reversal frequencies
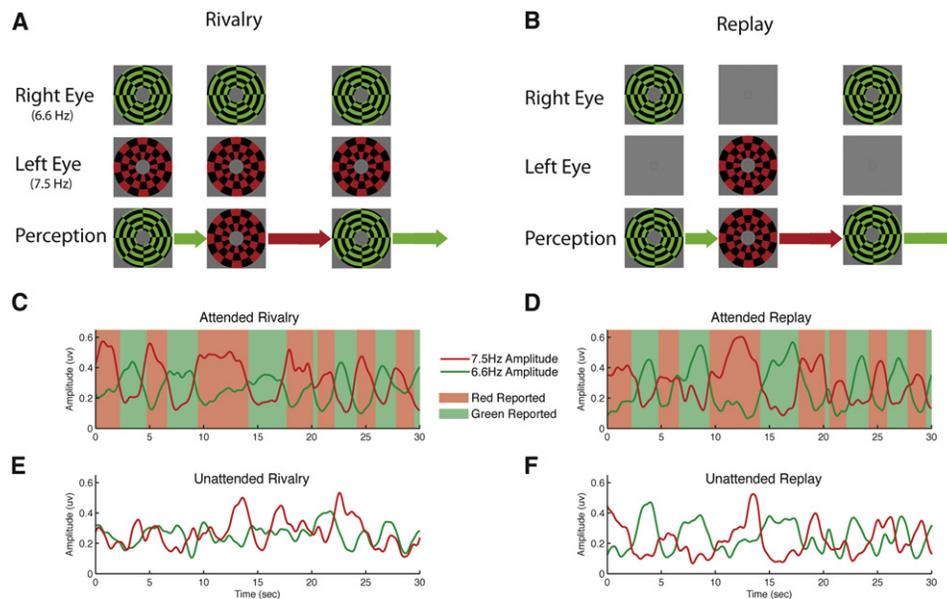
Figure 1. Methods and Sample Signals

(A) In the rivalry conditions, two checkerboards flickering at different frequencies were dichoptically presented, one to each eye. Despite the invariant physical stimulus, subjects perceived alternation between the two checkerboards when they attended to them.

(B) In the replay conditions, the alternating perception in the attended rivalry condition was simulated by presenting corresponding monocular stimuli one at a time.

(C–F) The time courses of amplitude of the two eyes' signals from an example participant in the attended rivalry (C), attended replay (D), unattended rivalry (E), and unattended replay (F) conditions. Red curves show the EEG amplitude corresponding to the red checkerboard (power at 7.5 Hz), and green curves show the amplitude corresponding to the green checkerboard (6.6 Hz). Red- and green-shaded areas in (C) and (D) indicate the phases during which the subject reported perceiving the red or the green checkerboard as the dominant percept. The curves were smoothed (Gaussian kernel, SD = 150 ms) for illustration purposes. See also Figure S1.

measured in a representative participant. When the observer attended to the checkerboard stimuli, the amplitudes of the two eyes' frequency-tagged signals were in a counterphase relationship, such that when one eye's signal rose, the other's fell (Figure 1C). This indicates that as the cortical response to one eye's stimulus increased in strength, its response to the other eye's stimulus weakened, which is a signature of binocular rivalry (Brown and Norcia, 1997). In contrast, the two signals in the unattended rivalry condition fluctuated randomly, without a systematic relationship between them (Figure 1E). In the replay conditions, however, the two eyes' signals modulated in counterphase, regardless of whether the observer's attention was on the stimulus, an expected result given that the stimuli were physically alternating (Figures 1D and 1E).

Figure 2A shows EEG signal amplitudes averaged across 13 subjects. The gray curves plot the average of six second epochs centered on all peaks (top rows) and troughs (bottom rows) of the time course of one eye's frequency-tagged signal amplitude. The black curves plot the time-locked average of the other eye's signal within the same time window. In the attended rivalry and the two replay conditions, the black curves modulated in counterphase to the gray curves, meaning that the peak of one eye's signal corresponded to a trough of the other eye's signal, the signature of sustained rivalry. In the unattended rivalry condition, this signature of rivalry was greatly diminished.

We derived an index of rivalry strength by dividing the amplitude of the counterphase modulation of the rival signal by the amplitude of the modulation of the aligned signal (Figure 2B; see Supplemental Experimental Procedures for a more detailed description of the index, and Figure S2A for analyses of rising phase and falling phases of the signal). Analysis of the rivalry index yielded a significant statistical interaction between stimulus types (rivalry/replay) and attention conditions (attended/unattended): $F_{(1,12)} = 22.7$; $p < 0.001$. In the rivalry conditions, removing attention reduced the rivalry index by nearly a factor of four. When attention was focused on the conflicting stimuli, the rivalry index reliably differed from zero (t [12] = 8.92; $p < 10^{-4}$), and when attention was focused away, it did not (t [12] = 1.88; $p > 0.05$). In the replay conditions, the attended and unattended rivalry indices were comparable and both reliably different from zero (t [12] = 22.9 and t [12] = 15.8, respectively, in both cases, $p < 10^{-6}$). As a complementary analysis, not dependent on finding peaks, we also computed the Pearson's r correlation coefficient between the left and right eye frequency-tagged amplitude time course (Figure S2B). We found strong negative correlations in the attended rivalry (r = −0.319), attended replay (r = −0.594), and unattended replay (r = −0.537) conditions, but not in the unattended rivalry condition (r = −0.078).

The fact that the rivalry index in the unattended rivalry condition was not statistically different from zero could not be attributed to generally weak EEG signal because the power of the tagged frequencies was actually stronger in that condition than in the unattended replay conditions, where counterphase modulation was readily detectable (Figure 3D). It is impossible, of
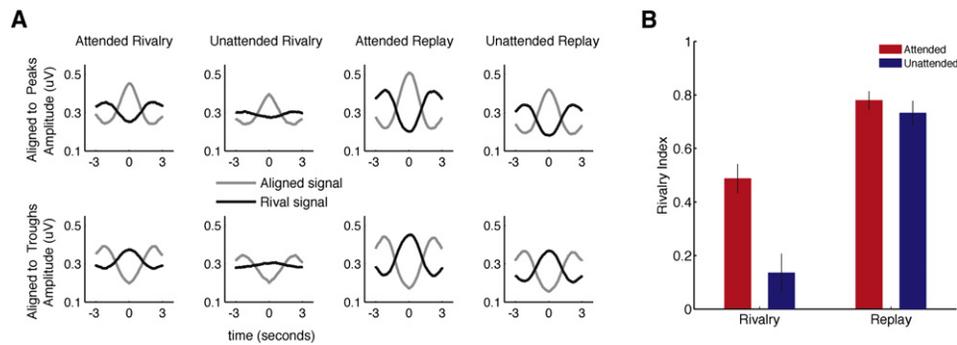
Figure 2. Averaged Time Course and Rivalry Indices in Experiment 1

(A) Gray curves show averaged EEG amplitude with one eye's signal aligned to the peaks (upper row), and troughs (lower row). Black curves show the time-locked average signal from the other eye. The columns from left to right correspond to the attended rivalry, unattended rivalry, attended replay, and unattended replay conditions. Note the strong counterphase modulation in all conditions except the unattended rivalry condition only.

(B) Rivalry indices calculated by dividing the amplitude of the rival signal by the amplitude of the aligned signal. Error bars in all figures indicate across-subject standard errors of the mean.

See also Figure S2.

course, to prove that the rivalry index was equal to zero in the unattended rivalry condition, but any small counterphase modulation that might have been present was likely due to some residual attention paid to the rivalry stimuli. Post hoc subjective reports (see below) suggested that subjects were largely, but not completely, unaware of the unattended rivalry stimuli.

Given the absence of a neurophysiological signature of rivalry when attention is directed away from the conflicting stimuli, a natural next question is: What is the state of the visual system when presented with unattended, conflicting dichoptic signals? In a pilot study, we gathered post hoc subjective reports from subjects viewing the same stimuli as used during the EEG recordings (for details, see Supplemental Experimental Procedures). Subjects were very uncertain about the nature of

their percepts in the unattended situation, confirming the effectiveness of the attentional manipulation, but at the same time providing very limited information about the state of the conflicting stimuli. Indeed, this uncertainty was the main reason we adopted the frequency-tagged SSVEP measure to begin with. Nevertheless, the data did suggest that perceptual alternations were greatly reduced when attention was withdrawn.

Because of the limited utility of subjective reports, we examined the EEG measurements closely for additional clues regarding the nature of cortical processing during unattended rivalry. The reduced counterphase modulation could have been due to dramatically slowed rivalry of the two eyes' signals, in which one signal stays much stronger than the other for prolonged durations. However, this was not observed in the
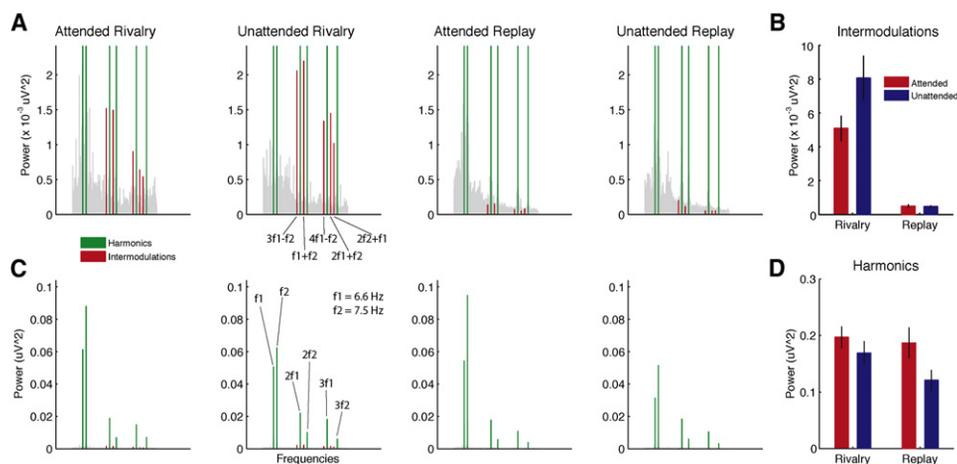

Figure 3. Power of the Intermodulation Products and Harmonics

(A) Red bars indicate the power at the intermodulation products in each condition, averaged across subjects: $3f1-f2$, $f1+f2$, $4f1-f2$, $2f1+f2$, $2f2+f1$ ($f1 = 6.6$ Hz, $f2 = 7.5$ Hz).

(B) The summed power of the five intermodulation frequencies in the four conditions, averaged across subjects.

(C) The same data as in (A), plotted on an expanded y axis. Green bars indicate the power of the first three harmonics: $f1$, $f2$, $2f1$, $2f2$, $3f1$, $3f2$.

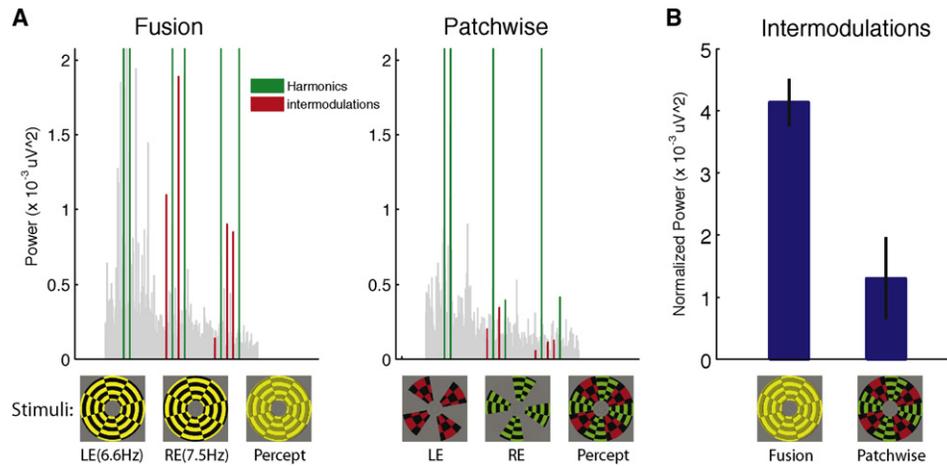(D) The summed power of the harmonics.

See also Figure S3.

Figure 4. Power of Intermodulation Frequencies in Simulated Fusion and Patchwise Conditions

(A) Power spectrum of the EEG signal in the two conditions, averaged across subjects. Red bars indicate the intermodulation frequencies. The fusion condition shows a pattern of intermodulation frequency terms that is very similar to that observed in the unattended rivalry condition of experiment 1. The bottom of the figure shows the stimuli used in experiment 2 (see Supplemental Experimental Procedures for more detailed descriptions). In the fusion simulation condition, the two eyes were presented with the same checkerboard pattern in the same color (yellow), but contrast reversing at different temporal frequencies. Because the dichoptic stimuli were pattern compatible, subjects did not perceive any rivalry of the two eyes' signals. In the patchwise simulation condition, four patches of red checkerboards were presented to one eye, and four green patches were presented in complimentary locations to the other eye. To simulate the dynamic property of the patchwise perception during binocular rivalry, the location of the occluders slowly rotated overtime (12°/s).

(B) Summed power of the intermodulation products, normalized by the summed power of the harmonics. The plotted values have been scaled by the mean harmonic power to give meaningful units.

See also Figure S4.

amplitude time courses (e.g., Figure 1E). Two other possibilities are that the two eyes' signals either engaged in patchwise rivalry (i.e., two signals rivaled piecemeal, with local perceptual alternations not synchronized across space) or stayed in a fusion-like state (i.e., the two eyes' signals were combined without one suppressing the other).

In both patchwise rivalry and fusion, the two eyes' signals are concurrently processed in the visual pathways and thus have ample opportunity to interact with each other, for example as simultaneous input to binocular neurons or through lateral interactions between monocular neurons. Because of nonlinearities in the visual system (e.g., half- or full-wave rectification [Clynes, 1961]), such interactions should produce energy in a series of nonlinear intermodulation frequency components whose frequencies are $m \times f1 \pm n \times f2$, where f1 and f2 are the tagged frequencies, and m and n are positive integers (Baitch and Levi, 1988; Brown et al., 1999; Regan and Regan, 1988; Sutoyo and Srinivasan, 2009; Victor and Conte, 2000). Indeed, in our data we found substantial power at the intermodulation frequencies in the rivalry conditions, where the two eyes' signals have the potential to interact in cortex, but not in the two replay conditions, where they are presented separately in time without the opportunity to interact (Figures 3A and 3B). Furthermore, in the attended rivalry condition, we found greater intermodulation power during the transitions between reported dominance periods, a time during which patchwise rivalry and fusion are expected to occur, than during the dominance periods themselves (t [12] = 6.6; p < 0.0001; see Figure S3). Thus, the power of the intermodulation frequencies is a marker of cortical interactions between the two eyes' signals.

Importantly, the power of the intermodulation frequencies was significantly stronger in the unattended rivalry condition than in the attended rivalry condition (Figure 3B, t [12] = 2.37; p < 0.05). This indicates stronger interaction between the two eyes' signals, suggesting combination of the two eyes' signals in the visual cortex when attention is withdrawn. The difference between conditions was not simply due to greater overall power during unattended rivalry: in contrast to the intermodulation frequencies, the power of the harmonic frequencies was significantly weaker in the unattended conditions than in the attended conditions, for both rivalry and replay (Figure 3D, F [1,12] = 23.7; p < 0.001), consistent with a previous study of attentional effects on the SSVEP (Morgan et al., 1996).

Stronger interaction between the two eye's signals in the unattended rivalry condition could arise for multiple reasons. One possible cause is patchwise rivalry, in which the intermodulation terms could arise from neurons with large receptive field in later visual areas that integrate responses from adjacent patches with different dominant frequencies. Lateral interactions between neurons responding to adjacent patches could also produce large intermodulation terms. Another possibility is that rivalry ceased without attention, and the two eyes' signals were locally combined by binocular neurons in early visual areas, resulting in a neural state similar to that produced by perceptual fusion. This would also generate strong intermodulation terms. To evaluate the likelihood of these two possibilities (while acknowledging that other accounts could still exist), we ran a second experiment that simulated them (Figure 4 and Figure S4). We then examined whether either simulation produced a power distribution across
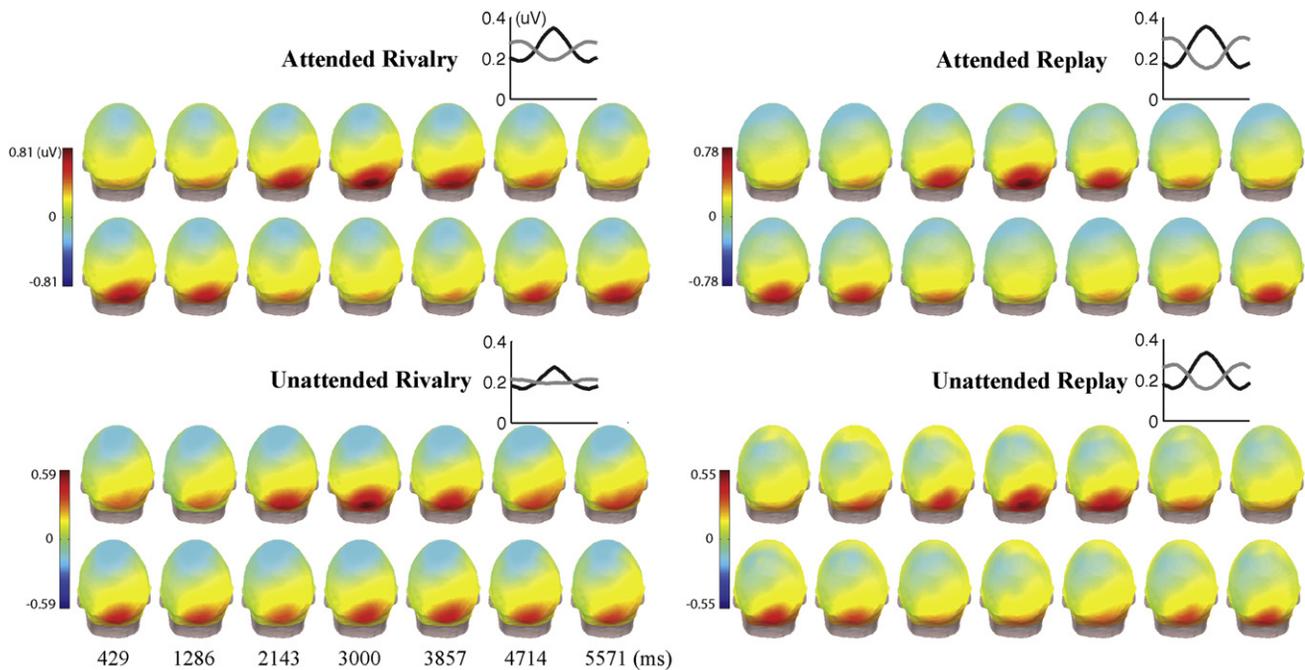
Figure 5. Time Courses of EEG Power Topography

These scalp topographies show power at the tagged frequencies at each electrode. Data have been aligned centered on peaks in one eye's time course and then averaged across four subjects. Seven maps were drawn for each 6 s epoch (each map represents the mean during an 857 ms window). In each of the four panels, the upper row shows power for the aligned eye's frequency and lower row shows power for the time-locked signal from the other eye. Inset line graphs show the results from occipital electrodes as in Figure 2A. Both line graphs and topographies show strong counterphase modulations, except in the unattended rivalry condition. See also Figure S5.

intermodulation terms that resembled the one observed in unattended rivalry.

In this second experiment, the relative power of the intermodulation frequencies was much stronger in the simulated fusion condition than that in the simulated patchwise condition. Because the binocular contrast reversal in the simulated fusion condition was a stronger physical stimulus than the locally monocular contrast reversal in the simulated patchwise condition, the fusion stimulus generated slightly more power overall for some subjects (two out of four). To correct for this difference in stimulus strength, we normalized the intermodulation power by the summed power of the harmonics in each condition. This normalized intermodulation power was much greater in the fusion condition than in the patchwise condition (Figure 4B, t [3] = 3.55; p < 0.05). Indeed, the intermodulation power was not significantly different from the noise level in the simulated patchwise condition. The intermodulation components found in the simulated fusion condition and those found in the unattended rivalry condition resembled each other in terms of frequency and the strength of power (Figure 3B), suggesting that the two eyes' signals are likely combined in some way, producing a neural state similar to that underlying perceptual fusion. The failure to observe significant intermodulation terms in the simulated patchwise condition suggests that patchwise rivalry is a poor model of cortical processing when attention is withdrawn.

To investigate the topography of the frequency-tagged EEG signal, and also to reveal its underlying neural sources, we replicated our first experiment using high-density (128 channels) EEG

recordings. Figure 5 shows the mean SSVEP topographies for each condition, averaged over 6 s epochs centered on peaks in one eye's frequency-tagged signal (as in Figure 2A; see Supplemental Experimental Procedures and Figure S5 for analysis details). Energy is mainly present at posterior electrodes, shows a clear peak for the eye's signal that was used to select peaks (aligned signal, upper rows), and demonstrates the characteristic counterphase modulation in the other eye's signal (rival signal, lower rows) for the attended rivalry condition. The counterphase modulation is also present in the two replay conditions but is again absent in the unattended rivalry condition. The inset line graphs in Figure 5 show the data analyzed as in Figure 2A. The results are in very good agreement with the first experiment, showing near-absent counterphase modulation of the VEP signals in the unattended rivalry condition.

Source localization analysis on the high-density recordings revealed that the scalp topographies could be accounted for by one major source near the medial occipital pole with small contributions from two bilateral occipital sources. These locations, near visual areas V1 and hMT+, had been identified in previous work (Di Russo et al., 2007) as sources of the EEG signal in conditions similar to ours (i.e., the SSVEP produced by medium frequency contrast reversal of a simple pattern). The contribution from the two bilateral (near hMT+) sources was relatively minor; a single source near V1 explained over 93% of the variance, whereas the three-dipole solution explained over 95% of the variance in the peak topographies for each subject. Figure 6 shows the reconstructed topographies from these sources and
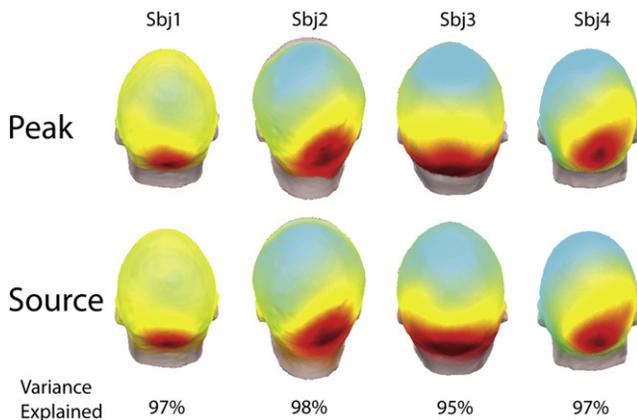
Figure 6. Peak Topography and Reconstructed Topography from V1 and hMT+ Sources

The three-dipole model explained at least 95% of the variance in the peak topography in each subject. See also Figure S6.

the original topographies for comparison. Principal component analysis also demonstrated that the topography time course (Figure 5) can be well explained as temporal modulations of a single spatial pattern that resembles the pattern seen at the peak (see Figure S6).

Conclusions

When subjects attended to our competing, dichoptic stimuli, their conscious perception spontaneously alternated between the two stimuli. When the image in one eye became dominant perceptually, that eye's frequency-tagged EEG signal gained strength, and the other eye's signal fell. This counterphase modulation is a physiological marker for binocular rivalry (Brown and Norcia, 1997). When attention was withdrawn from the competing stimuli, the marker for rivalry essentially disappeared, suggesting that binocular rivalry requires visual attention to operate. Source localization on the SSVEP topographies suggested a dominant source from medial occipital lobe (V1/V2) near the posterior pole and minor contributing sources from bilateral areas near MT, consistent with previous studies (Di Russo et al., 2007; Fawcett et al., 2004; Müller et al., 1997). These results suggest that attention is necessary to resolve the interocular conflict in early stages of visual processing.

Although previous studies found that attention could determine the initial dominance (Chong and Blake, 2006; Hancock and Andrews, 2007; Mitchell et al., 2004; Ooi and He, 1999), modulate the temporal dynamics of binocular rivalry to some degree (Chong et al., 2005; Paffen et al., 2006), and enhance the strength of suppressed signals (Bahrami et al., 2008; Kanai et al., 2006; Zhang et al., 2008, J. Vis., abstract), it remained unknown whether binocular rivalry could occur at all when attention was strongly diverted. In previous attempts to address this question, subjects were allowed to attend to the stimuli during brief intervals interspersed with longer periods of unattended rivalry (Cavanagh and Holcombe, 2006, J. Vis., abstract; He et al., 2007, J. Vis., abstract). Under these limited sampling conditions, it was inferred that perceptual alternation significantly slowed down or even stabilized, which might suggest

that rivalry did not occur during the intervals between attentional sampling. The interpretation of this work, however, is limited by the fact that attention was applied to the stimuli immediately before each perceptual report. Our experiment measured the status of rivalry when attention was continuously diverted from the competing stimuli.

Our conclusions may seem at odds with a previous fMRI study (Lee et al., 2007) that observed a propagating wave of binocular rivalry resolution even when attention was diverted. The nature of the dynamic change in V1 BOLD signal measured in that study was ambiguous, however, and could have arisen from other neural events besides the resolution of rivalry. Indeed, using similar stimuli, a more recent fMRI study from the same group failed to find evidence of interocular suppression with dichoptic stimuli when attention was diverted (Moradi and Heeger, 2009). Instead, the authors suggested that the V1 BOLD signal change observed in Lee et al. (2007) likely reflected cross-orientation suppression rather than binocular rivalry. The ability of the frequency-tagging method to identify signals originating from each eye makes our results less susceptible to such alternative explanations.

In addition, we found that unattended conflicting dichoptic stimuli produced large amplitudes at intermodulation frequencies, and that such frequencies are more consistent with the neural state produced by binocular fusion than the state produced by patchwise rivalry. The simplest interpretation of these results is that, without attention, rivalry ceases, and the two eyes' signals locally combine in the visual cortex. One possible mechanism that may contribute to this fusion-like neural state is that orientation tuning may broaden without attention (Saproo and Serences, 2010), with the consequence being that cells become more permissive in the orientation domain.

In sum, binocular rivalry, seemingly automatic, is in fact highly dependent on attention. Rivalry ceases when observers are not attending to and interrogating the information at a location. These results argue for a specific role of visual attention in binocular rivalry that is consistent with its general role in object perception. Attention may be required to bind features together into an object (Treisman, 1998), perhaps by biasing and resolving competition in neurons between features that belong to different objects. Our data suggest that attention is similarly required to resolve competition between features arising from different eyes. Without attention, the competition between features appears to be suspended, with binocular neurons being driven by features from both eyes.

EXPERIMENTAL PROCEDURES

Participants

A total of 17 observers (13 naive to the purposes of the experiment) participated in experiment 1. Four naive observers participated in experiment 2. Four observers (two naive) participated in experiment 3. All subjects had normal or corrected to normal vision. In experiment 1, one subject was tested twice, and four subjects were eliminated from analysis due to low SNR, poor rivalry quality, or failure to follow task instructions. Thirteen subjects' data (nine naive) were included for analysis. The experimental protocol was approved by the Institutional Review Board of the University of Minnesota.

Tasks

Each trial lasted 30 s, and data were collected from 12 trials in each condition. In the attended conditions, subjects reported their perception by pressing one of two buttons corresponding to the dominance of the red or the green checkerboard. In the unattended conditions, subjects ignored the checkerboards and performed a demanding color-shape conjunction detection task on the central fixation point. Left and right eye stimuli were dichoptically presented using a mirror stereoscope for all three experiments. A chinrest was used to minimize subjects' head movement.

EEG Data Acquisition and Analysis

For experiments 1 and 2, EEG data were recorded using a 64-channel Neuroscan SynAmps RT system (Compumedics Neuroscan) with a band-pass filter from DC to 200 Hz, and digitized at 1000 Hz. A 64-channel Ag-AgCl electrode cap was used, but only six posterior channels were used for analysis (for some subjects, we only collected data from these six electrodes), including Oz, POz, O1, O2, CB1, and CB2. A surface Laplacian spatial filter was applied on the continuous EEG data to minimize common noise (Hjorth, 1975); signals from the five electrodes surrounding Oz were averaged then subtracted from the signal from Oz. The resultant was band-pass filtered from 1 to 30 Hz.

An adaptive RLS filter (Tang and Norcia, 1995) was used to extract the amplitude of the tagged frequencies over time. The rivalry index was computed by dividing the peak amplitude of the counterphase signal by the amplitude of the aligned signal. This was done separately for alignment at peaks and troughs, and the results were averaged. MATLAB (MathWorks) was used for power spectrum analysis.

In experiment 3, a 128-channel electrode cap and two 64-channel SynAmps RT amplifiers were used, with the same recording parameters as experiments 1 and 2. Source localization was performed using CURRY 6 (Compumedics Neuroscan) and custom MATLAB scripts. Structural MR images were collected on a 3T Siemens Trio scanner (T1 MPRAGE, 1 mm isotropic voxels), and three-layer boundary element models (Hämäläinen and Sarvas, 1989; He et al., 1987) (inner skull, outer skull, and scalp) were created from each subject's structural MR images using CURRY. Three current dipoles were initialized in seed locations consistent with sources identified in a previous study (Di Russo et al., 2007). Simultaneous least-square fitting was then applied to determine positions and moments of the dipoles that best explained the scalp EEG topography at the averaged rivalry peak. All dipoles were allowed free rotation, scaling, and motion within 1 cm of the initial seed location. See Supplemental Experimental Procedures for details of stimuli and data analysis.

SUPPLEMENTAL INFORMATION

Supplemental Information includes six figures and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.neuron.2011.05.035.

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