Neurons that detect interocular conflict during binocular rivalry revealed with EEG

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When the two eyes view incompatible images, perception alternates between them. What neural computations underlie this binocular rivalry? Perceptual alternations may simply reflect competition between the sets of monocular neurons that respond to each image, with the stronger driving perception. Here, we test an alternative hypothesis, that the computations that resolve rivalry make use of an active signal that reflects interocular conflict. Images presented to each eye were flickered at different frequencies while we measured steady-state visually evoked potentials (SSVEP). Signals at frequencies that are combinations of the two input frequencies can arise only from binocular neurons. In a first experiment, we measured energy at these “intermodulation” frequencies during binocular rivalry and found it to be highest immediately before rivalry restarted following a period of incomplete resolution of rivalry (a “mixed” percept). This suggests that the intermodulation signals may arise from neurons important for resolving the conflict between the two eyes’ inputs. In a second experiment, we tested whether the intermodulation signal arose from neurons that measure interocular conflict by parametrically increasing conflict while simultaneously reducing image contrast. The activity of neurons that receive input from both eyes but are not sensitive to conflict should reduce monotonically as contrast decreases. The intermodulation response, however, peaked at intermediate levels of conflict, suggesting that it arises in part from neurons that respond to interocular conflict. Binocular rivalry appears to depend on an active mechanism that detects interocular conflict, whose levels of activity can be measured by the intermodulation frequencies of the SSVEP.

Introduction

The world is replete with situations in which the images reaching the two eyes conflict with each other. For example, the two images are grossly mismatched when one eye is partially occluded by an external object that the other eye can see past (e.g., Arnold, 2011). During such conflict, at least part of one image is often completely suppressed from visual awareness. In the laboratory, such interocular suppression can be observed during the striking phenomenon of binocular rivalry, in which substantially conflicting images are presented to the two eyes and perception alternates between the two. This article investigates the mechanisms that help the visual system to attain a unified percept in such situations. Specifically, we address the question of how the visual system detects the need to suppress one eye’s input.

In most current models of rivalry, suppression is an outcome of a “winner-take-all” mutual inhibition between monocular neural populations representing each eye’s image; alternations arise from noise and/or adaptation of the less inhibited population (Dayan, 1998; Lehky, 1988; Mueller, 1990; Tong, Meng, & Blake, 2006; Wilson, 2003). However, recent work suggested that explicit computations of interocular conflict might be a part of the neural mechanisms that...
produce binocular rivalry (Said & Heeger, 2013). This
work proposed that binocular “opponency” neurons
(Ohzawa & Freeman, 1986; Poggio & Talbot, 1981)
perform a difference computation between the two
eyes’ inputs and inhibit the weaker eye in proportion to
this measure of conflict. The role of the difference
computation in binocular rivalry was supported by
results from a psychophysical experiment (Said &
Heeger, 2013).

The goal of the present work is to more directly test for
the existence of an interocular conflict signal and its
relevance for rivalry. A previous study attempted to
address a similar question by measuring event-related
potentials (ERPs) while manipulating the angular dif-
ference of gratings in the two eyes (Roebel, 2012; see
Discussion). However, it was unable to distinguish
between signals arising from binocular and monocluar
neurons.

Here, the use of steady-state visually evoked
potentials (SSVEP) and frequency-tagged stimuli made
it possible to isolate electroencephalography (EEG)
signals that arise from binocular neurons. Presenting
stimuli dichoptically and tagging each eye’s stimulus
with its own temporal frequency allow for separate
measurement of the neural signals originating from
each eye (Brown & Norcia, 1997). If the two eyes are
tagged at frequencies \( f_1 \) and \( f_2 \), signals arising from
monocular neurons will be at those fundamental
frequencies and their harmonics, \( m^* f_1 \) and \( m^* f_2 \), where
\( m \) is an integer. Binocular neurons, which combine
input from the two eyes, will produce additional energy
at the nonlinear intermodulation frequencies
\( m^* f_1 \pm n^* f_2 \), if they possess nonlinearities such as
rectification, squaring, and/or divisive normalization
(Baich & Levi, 1988; Brown, Candy, & Norcia, 1999;
Regan & Regan, 1988; Sutoyo & Srinivasan, 2009;
Tsai, Wade, & Norcia, 2012; Victor & Conte, 2000).
Previous studies have observed these intermodulation
frequencies during rivalry but have not investigated
them in detail (Sutoyo & Srinivasan, 2009; Zhang,
Jamison, Engel, He, & He, 2011).

In a first experiment, we examined the temporal
dynamics of the intermodulation frequencies during
binocular rivalry. If the intermodulation frequencies
arise from neurons that signal the level of interocular
conflict and a need to resolve such a conflict, they
should be highest at the onset of binocular rivalry
alternations (i.e., immediately before either eye is
suppressed). When presenting a rivalrous stimulus,
there are often extended periods during which the
visual system fails to clearly resolve to one eye or the
other, resulting in a percept that is a mixture of the two
eyes’ inputs in either a fused or piecemeal fashion (e.g.,
Blake, O’Shea, & Mueller, 1992). Our data revealed
that during such mixed periods, the intermodulation
frequencies increased and then fell prior to normal
rivalry recommencing.

In a second experiment, we tested if the intermodula-
tion frequencies arose from neurons that signal the
level of interocular conflict, as opposed to binocular
neurons that combine nonconflicting input from the two
eyes. We did this by systematically varying the degree of
conflict. Our stimuli were plaid patterns made of
orthogonal 45° and −45° gratings presented to the two
eyes. By parametrically reducing the contrast of the 45°
grating in one eye and the −45° in the other, we induced
percepts that varied between fusion and rivalry, including
states intermediate between the two. Importantly, the
increase in interocular conflict was caused by a reduction
in contrast. Thus, if the intermodulation signals reflect
only binocular neurons that combine the inputs from the
two eyes in a straightforward manner (e.g., by summing
or averaging them), we would expect that signals from
these neurons should monotonically decrease as contrast
decreased (while the stimulus conflict increased). If, on the
other hand, the intermodulation signals contain a
component that reflects interocular conflict, then such a
component should increase as conflict increases. We
found that the intermodulation signals peaked at
intermediate states between fusion and rivalry, suggesting
that at least some part of them arise from neurons
sensitive to the difference between the two eyes’ inputs.
Altogether, our results suggest that human visual cortex
contains an interocular conflict detection mechanism that
may play a role in resolving interocular conflict and
thereby initiating binocular rivalry.

Methods

Subjects

Eight subjects participated in Experiment 1 (four
women; mean age: 24 ± 4 years). Three of these, and
nine new subjects, participated in Experiment 2 (four
women; mean age: 27 ± 7 years). All subjects had
normal or corrected-to-normal visual acuity and gave
written consent to participate according to a protocol
approved by Institutional Review Board at the
University of Minnesota.

For the second experiment, we discarded one
subject who did not experience clear rivalry at
interocular contrast difference (IODC) = 0.8
(>50% of the stimulus duration was spent in a
mixed percept), thereby bringing our sample size to
\( N = 11 \).

Display

Stimuli were generated and displayed using Psycho-
physics Toolbox (PTB–3; Brainard, 1997; Kleiner et al.,
2007; Pelli, 1997) in MATLAB on a Gateway VX1120 CRT monitor (refresh rate 85 Hz). The monitor luminance gamma curve was measured using a Photo-research PR-655 and corrected in software to ensure correct display of stimulus intensity. Subjects viewed stimuli using a custom-built mirror stereoscope.

Stimuli

Stimuli were composed of orthogonal square-wave gratings (orientations: ±45°, spatial frequency: 0.7 cycles/degree, eccentricity: 1–8° of visual angle in radius) presented to the two eyes (Figure 1). Each eye viewed the sum of the two orthogonal component gratings with contrast of one grating in each eye manipulated to induce percepts ranging along a spectrum of fusion to rivalry. In the “fusion” condition, each grating had a Michelson contrast of 0.5 on a gray background (18.5 cd/m²). In other conditions, the contrast value of the +45° grating in the left eye and the −45° grating in the right eye was reduced, whereas that of the orthogonal grating in each eye remained at 0.5. The reduced contrast
gratings were set to contrast of 0.5*(1 – \( f_c \)), where the factor \( f_c \) parameterized different levels of IOCD. Thus, for the IOCD at \( f_c = 0 \) (from here on referred to as IOCD = 0), both eyes viewed identical plaids, which resulted in a fused percept. For IOCD = 1, the left eye viewed a single −45° grating, whereas the right eye viewed a single +45° grating, resulting in binocular rivalry. For intermediate IOCDs, a different grating in each eye had a reduced contrast, producing interocular conflict. As the IOCD increased, the perception gradually changed, starting from clear fused plaids at an IOCD of 0 to fused plaids with binocular luster (Levelt, 1965; Wolfe & Franzel, 1988) for intermediate IOCDs (IOCD ∼0.5) and rivalry for high IOCDs (IOCD >0.7).

In Experiment 1, IOCDs of 0.8 and 1 were used, with each IOCD presented in 30-s runs and a total of 30–40 runs/condition for each subject. Both of these conditions yielded either a piecemeal mixed percept or rivalry. Very similar patterns of results obtained for both IOCDs in Experiment 1, and so results were averaged across the two types of run. Experiment 2 used IOCDs of 0, 0.2, 0.4, and 0.8. These conditions induced fused binocular plaid percepts for IOCDs 0–0.4, with increasing amounts of binocular luster for 0.2 and 0.4 and rivalry at 0.8. Even at an IOCD of 0, subjects occasionally reported dominance of one or the other grating, consistent with monocular rivalry (Wade, 1975). The stimulus at each IOCD was presented in 50-s runs, with each subject participating in 3–10 runs/condition randomly ordered within one to three separate EEG recording sessions. During all runs in both experiments, subjects fixated a central mark and with their right hand pressed three buttons to indicate their percept. Two buttons indicated that they saw predominantly a top-left tilted grating (−45°) or predominantly a top-right (+45°) tilted grating, and a third button indicated that the percept was a fused plaid or piecemeal rivalry. For all sessions, the stimulus alternated between the gratings and a mean gray field at 4.72 Hz (\( f_1 \)) in the right eye and 8.5 Hz in the left eye (\( f_2 \)). The stimulus frequencies were not counterbalanced between the eyes, as we were concerned only with the intermodulation frequencies that arose out of a combination of the two eyes’ input frequencies and not the individual frequencies or eyes themselves.

**EEG data acquisition and analysis**

EEG data were acquired using a 64-channel Advanced Neuro Technology system with a sampling frequency of 1024 Hz. Analysis was conducted using EEGLAB routines and customized MATLAB code. Raw EEG data were down-sampled to 256 Hz and band-pass filtered between 1 and 30 Hz. Experiment 1 was conducted with 64 channels in the standard international 10/20 system. Experiment 2 was conducted with 10 channels: \( O_1, O_2, O_Z, PO_Z, PO_3, PO_4, PO_5, PO_6, PO_7, \) and \( PO_8 \).

The EEG data were manually inspected for transient artifacts. In case of such artifacts, the entire run was removed from analysis (a total of 63 such runs were discarded for the eight subjects in Experiment 1 and none for Experiment 2). For each session, we determined maximally responsive electrodes at four frequencies: the two expected stimulus frequencies, \( f_1 \) and \( f_2 \), and the two intermodulation frequencies, \( f_2-f_1 = 3.79 \) Hz and \( f_2+f_1 = 13.22 \) Hz (Figure 2A). On average, these frequencies had similar scalp distributions, around \( O_Z \) (Figure 2B), with some differences across sessions. All analysis was done using the electrodes for which the binocular \( f_2-f_1 \) signal was maximal for that session (for sessions that had multiple electrodes with comparable responses, signals were averaged across them). Using the other electrodes generated very similar results.

MATLAB (MathWorks) was used for power spectrum analysis. For Experiment 1, to provide ongoing measures of EEG power, an adaptive recursive least square (RLS) filter (Brown & Norcia, 1997; Tang & Norcia, 1995) was used to extract the amplitude of the four frequencies over time. The RLS time series was smoothed with a Gaussian kernel of 66 ms and then high-pass filtered at 0.1 Hz to obtain frequency envelopes. For Experiment 2, power was calculated for entire individual runs at the two fundamental frequencies \( f_1 \) and \( f_2 \) and the two nonlinear frequencies \( f_2-f_1 \) and \( f_2+f_1 \) using the fast Fourier transform (FFT).

**Response-triggered envelopes**

In Experiment 1, RLS envelopes were averaged ±4 s around subjects’ reported perceptual transitions to yield triggered envelopes. Because of the stochastic nature of rivalry alternations, we chose transitions that satisfied a minimum duration criterion in which subjects’ reported perception remained constant (either eye dominant or mixed). For fundamental frequency transitions (Figure 3), we chose trials in which subjects reported the same dominant eye for >2 s before and after the button press (similar results were obtained for 0.5–3 s). For intermodulation frequencies (Figure 4), we chose the transitions in which the percept stayed mixed >2 s and the same eye remained dominant for >1 s (durations were chosen to maximize the number of transitions while having sufficient time to observe the intermodulation frequency correlates of mixed percepts).
Quadratic fits to FFT amplitudes and bootstrapping

For Experiment 2, quadratic polynomial fitting was performed on power versus IOCD curves across subjects. Bootstrap statistics were calculated by repeatedly (n = 10,000) sampling with replacement, from the 11 subjects, the power of the component frequencies as well as of the two intermodulation frequencies. These resampled data points were averaged and fitted with a quadratic polynomial. From this quadratic fit, we extracted the IOCD value at which the fit was maximum within the IOCD interval 0–0.8.

Results

In Experiment 1, subjects viewed rivaling, frequency-tagged patterns, while we measured EEG signals at both fundamental and intermodulation frequencies. The two eyes’ inputs flickered at different frequencies (4.72 and 8.5 Hz), which we label f₁ and f₂. Figure 2A (upper) shows a spectral plot of the EEG response for a single representative subject at the occipital electrodes O₂, O₁, and O₂. Figure 2A (lower) shows the average spectrum for all subjects. The response was maximal at the fundamental frequencies f₁ and f₂, with smaller responses at their second harmonics 2*f₁ and 2*f₂. Some previous SSVEP studies have used contrast-reversing stimuli, which produce the largest responses at the second harmonic (Brown & Norcia, 1997). Our stimuli alternated with a mean field (“on-off” flicker), and the dominance of the “on” response produced substantial energy at f₁ and f₂.

The spectra also show peaks at the f₂–f₁ and f₂+f₁ intermodulation frequencies, with higher energy at f₂–f₁ than f₂+f₁. Higher-order intermodulation frequencies (e.g., 3*f₁–f₂, 2*f₂–f₁) could be seen in some but not all subjects; they are not reported in subsequent results but when analyzed showed similar effects to the ones reported below. Figure 2C shows the averaged topographies of the fundamental (upper) and intermodulation (lower) frequencies. Both sets of frequencies were observed predominantly at the occipital and parieto-occipital electrodes with peaks near O₂, indicating that they emerged from early visual cortex.

Figure 2. (A) Power spectrum of the EEG signal in a single subject (upper) and averaged for eight subjects (lower) in Experiment 1. Fundamental frequencies with harmonics (blue) and intermodulation frequencies (magenta) are highlighted. Response was maximal at fundamental frequencies. Intermodulation frequencies used in analysis are labeled in large font. (B) Sixty-four–channel averaged topographies of the fundamental and intermodulation frequencies used in the analysis. All four frequencies responded maximally at occipital electrodes.
Figure 3. Average response triggered fundamental frequency envelopes for perceptual switches from (A) left to right eye dominance, (B) right to left eye dominance, (C) mixed percept to right eye dominance, (D) mixed percept to left eye dominance, (E) left eye dominance to mixed percept, and (F) right eye dominance to mixed percept. $f_1$, right eye: blue; $f_2$, left eye: red. Shaded regions span one standard error of the mean ($N = 8$).

Figure 4. Average response triggered intermodulation frequency envelopes for perceptual switches from (A) mixed percept to eye dominance (right eye, dashed blue; left eye, dashed red; combined eyes, green), (B) one eye dominant to the other (left eye to right eye, dashed blue; right eye to left eye, dashed red, combined eyes, green), (C) eye dominance to mixed percept (colors as in [A]). Shaded regions span one standard error of the mean for ($N = 8$). *$p < 0.002$. 

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The fundamental frequencies reflected each eye’s perceptual dominance and suppression. Figure 3A, B shows \( f_1 \) and \( f_2 \) signals averaged around button responses that indicated “normal” rivalry transitions, in which first one eye then the other is relatively completely suppressed. Because subjects reported the state of the nonsuppressed eye, we term such events dominance-to-dominance transitions (reported transition at 0 s; error bars, ±1 standard error of the mean; \( N = 8 \)). Because the time courses had their means and very low frequency trends removed (see the Methods section), they are centered around 0 on the y-axis. As in previous results (Brown & Norcia, 1997; Zhang et al., 2011), when subjects reported perceived dominance transitioning from the left to right eye (Figure 3A), energy at the frequency of the left eye’s stimulus (\( f_2 \), red) decreased, and energy at the right eye’s frequency (\( f_1 \), blue) increased. The opposite pattern of response was observed for transitions from right to left eye (Figure 3B).

The curves in Figures 3A and B crossed each other about 690 ms before subjects pressed the button to indicate that their percept had changed. This difference likely reflects the time required to make a perceptual decision and generate and execute the button press. Previous SSVEP studies have not reported this number (Brown & Norcia, 1997), and the latency is slightly longer than estimates based on other techniques (~500 ms; Alais, Cass, O’Shea, & Blake, 2010; Einhäuser, Stout, Koch, & Carter, 2008). This difference may be due to greater perceptual and decision uncertainty in our work, owing to the relatively large number of ambiguous, “mixed” percepts.

Indeed, our stimulus possessed various features, such as a large aperture (~16° diameter), nonchromatic checks, and rapid flicker that particularly prolonged mixed percepts, in which neither eye reaches complete dominance (Blake et al., 1992; Kovács, Paphathomas, Yang, & Fehér, 1996). Figure 3C, D show fundamental frequency envelopes as subjects reported their perception transitioning from such mixed percepts to rivalry when one eye is dominant. As in dominance-to-dominance transitions, the frequency envelope corresponding to the right eye (\( f_1 \), blue) increased as subjects went from a mixed percept to right eye—dominant percept (Figure 3C). The opposite pattern was observed as subjects transitioned from mixed to the left eye dominance, but with a lower magnitude (Figure 3D). The diverging point between the two frequencies as the subjects transitioned from a mixed to dominance percept occurred 1.25 s before the button press (\( t = 0 \)). Figures 3E, F plot the envelopes for dominance to mixed transitions. The stimulus frequencies that corresponded to the dominant eyes had a larger response as compared with the suppressed eyes about 3 s prior to button press. At about 1.25 s prior to button press, the two frequency responses converged, reflecting the subjects’ transition into mixed percepts.

Figure 4 plots the intermodulation frequencies around perceptual transitions, averaged for the two largest intermodulation terms, \( f_1-f_1 \) and \( f_2+f_1 \). For the transitions from a mixed perceptual state to normal rivalry in which the image from one eye is dominant (Figure 4A), the intermodulation signals peaked at about 2.2 s before the button press and then dropped below baseline as rivalry dominance restarted. The pattern of intermodulation energy was almost identical for transitions to each of the two eyes’ dominance (dotted blue and red lines). The decrease in signal amplitude was completed by 1.1 s before the button press.

The decrease in intermodulation frequencies during transitions from mixed to dominance is consistent with the idea that they arise from neurons that are active during resolution of interocular conflict. To evaluate the statistical significance of the decrease, we performed \( t \) tests between two 1-s epochs starting at 3 s and 1 s before the reported transition. There was a marked decrease in the intermodulation signal between these epochs \((p < 0.002; \text{Figure 4A})\).

The intermodulation signal at the dominance-to-dominance transitions (Figure 4B) did not follow a consistent trend. It is likely that these transitions were too rapid to produce measurable signals in the EEG (see Discussion). At dominance-to-mixed transitions (Figure 4C), only inconsistent trends were seen in the intermodulation terms. This suggests that conflict is not signaled strongly until some time into the mixed percept, occurring at variable durations after the transition. It is possible that the intermodulation signals arise from neurons active only immediately before the perceptual conflict is resolved. The trend for a late increase (4-s posttransition) may reflect a rise preceding the subsequent mixed-to-dominance transition.

Although generally supporting the presence of neurons that signal conflict, our results are also consistent with an alternative hypothesis. During mixed percepts, neurons receiving input from each eye are active, and so the intermodulation signals may have been produced by other neurons that sum or integrate information from the two eyes. These may have been more active during mixed percepts than during rivalry, in which one eye was suppressed.

In Experiment 2, we attempted to rule out this alternative, by parametrically increasing interocular conflict while simultaneously decreasing total stimulus contrast. Neurons that integrate information from the two eyes should reduce their activity as stimulus contrast decreases (and conflict increases). Neurons that signal interocular conflict should show the opposite pattern.
We presented plaid patterns in which the contrast of a different one of the two component gratings was reduced in each eye. The contrast reduction induced interocular conflict, and the parameter controlling it was termed the IOCD (see Methods). Flickering plaid patterns with each IOCD were presented for 50 s at a time, with 3–10 presentations per IOCD for each subject.

For all four IOCD conditions, subjects reported which eye was dominant or whether they saw a mixed or a fused percept. The percentage of time spent in dominance increased with IOCD (Figure 5), with some rivalry present at each level. During fusion (IOCD of 0), the residual dominance periods were due to monocular pattern rivalry (Wade, 1975). For the highest IOCD, clear rivalry alternations were perceptually reported and were also visible in the counterphase modulation of the EEG fundamental frequency envelopes (as in Figure 3; data not shown).

Figure 6A plots the averaged power of the two fundamental frequencies, \( f_1 \) and \( f_2 \), and the intermodulation frequencies, \( f_2-f_1 \) and \( f_2+f_1 \), as a function of IOCD. The power of the fundamental frequencies fell monotonically across conditions. This pattern suggests that those frequencies reflected activity in neurons whose response was determined by stimulus contrast.

The intermodulation signals, however, showed an inverted-U shape as a function of increasing interocular conflict, parameterized by IOCD. This result is consistent with the hypothesis that a subset of neurons responsive to conflict increased their activity as IOCD increased, causing the intermodulation signal to rise initially. At higher IOCDs, however, this rise was apparently outweighed by the overall reduction of population activity with decreasing stimulus contrast, which caused the curve to decline (see below).

To test whether the intermodulation frequencies showed a different pattern than the fundamental frequencies, we performed a 2 × 2 repeated-measures analysis of variance across subjects with factors frequency type (two levels: fundamental and intermodulation frequencies) and IOCD (four levels). There was a significant main effect of IOCD \( (p < 10^{-10}) \), which is clearly evident in the decrease in FFT power with overall stimulus contrast. There was also a significant interaction between frequency type and IOCD \( (p < 0.019) \), showing that the fundamental and intermodulation frequencies had different patterns as a function of IOCD (i.e., monotonic decrease vs inverted-U, respectively). To test specifically for effects at the first two IOCD levels, we conducted a t test between the ratio of FFT power of the averaged

Figure 5. Percentage of time in perceptual dominance at each IOCD. Error bars show standard error of the means. *\( p < 0.05; ***p < 0.005; ****p < 0.001.\)

Figure 6. (A) FFT power at the two fundamental \( (f_1, f_2) \) and intermodulation frequencies \( (f_2-f_1, f_2+f_1) \) as a function of IOCD. Thin colored lines are individual subject data, and bold blue lines are the mean. (B) Histograms of bootstrapped peaks of quadratic fits to the averaged fundamental (left) and intermodulation frequencies (right; \( N = 11 \)).
intermodulation frequencies to the averaged fundamental frequencies at IOCDs 0 and 0.2. This difference was significant ($p < 0.04$).

In addition to the parametric tests, we also formally tested the inverted-U shape of the intermodulation curve by fitting quadratic functions to the FFT power versus IOCD curve across 10,000 bootstrapped averages (resampling with replacement across subjects). These fits were used to estimate the IOCD at which the power was maximal in the interval 0–0.8. The location of the peak response for the intermodulation frequencies had a median between IOCD of 0.1 and 0.2. The fundamental frequencies’ median peak fell at 0, and the difference in peak location between the two sets of frequencies was highly reliable ($p < 0.005$).

The shape of the curves suggests that the intermodulation signals contain contributions from both binocular integration neurons, whose response depends on total stimulus contrast, and interocular conflict neurons, whose response increases with IOCD, with each type possessing a saturating output function. If this were the case, then the small reduction in contrast as IOCD increases from 0 to 0.2 would be expected to change the response of integrating neurons only very little, as the high contrasts at those IOCDs place them at a flat part of their response curve. The fact that the fundamental signals are relatively flat across low values of IOCD is consistent with this account. However, the increase in IOCD from 0 to 0.2 may have had a relatively large effect on neurons that signal conflict, as this change would be in the steep portion of their output function. Combining signals from the two types of neurons would thus yield a prediction of increasing intermodulation signals from IOCD 0 to 0.2. At higher values, the effects of IOCD should reverse, with the response of integrating neurons falling rapidly and responses of conflict detecting neurons increasing only a little. Combining signals from the two types of neurons would then yield a function that decreases from IOCD 0.2 to 1.0.

We simulated such a model using two neural populations, one that increased its response with the overall stimulus contrast (binocular summation/integration neurons), $R_i$, and another that increased its response with increasing interocular conflict, $R_c$. Response saturation was implemented using a normalization nonlinearity (e.g., Albrecht & Hamilton, 1982; Carandini, Heeger, & Movshon, 1997; Heeger, 1992) according to the equation $\sum_{k=1,c} R_k = \frac{A_k C_k}{\sigma_k + C_k}$, where $k$ indexes over the two types of neurons ($\sigma_i, \sigma_c$) determined the saturation point of each curve, and $A_i, A_c, C_i$ determined the amplitude of each curve. $C_i$ was the total contrast of the two gratings summed across both plaid (2, 1.8, 1.6, 1.2), and $C_c$ was the contrast difference between the two gratings summed across both plaid (0, 0.4, 0.8, 1.6). Using a grid search, we found many values of saturation constants and amplitudes for which the model showed an inverted-U shape behavior, similar to what was observed in our data. One example is plotted in Figure 7.

![Figure 7. Two-ensemble model with binocular integration (green) and interocular conflict (maroon) contributing to intermodulation signal (solid black). $A_i = 0.8, \sigma_i = 1.7, A_c = 0.1, \sigma_c = 0.3, n = 3$.](image)

**Discussion**

The most parsimonious explanation of the results from our two experiments is that human cortex contains neurons that detect interocular conflict and play a role in the resolution of binocular rivalry. Activity of these neurons contributes to the intermodulation frequencies in the SSVEP.

In the first experiment, intermodulation signals were relatively high at a time at which a need to resolve conflict was expected to be greatest (i.e., prior to the onset of strong suppression in rivalry). The intermodulation signals then decreased and stayed low for ~2 s as a period of one eye’s dominance began.

In the second experiment, we parametrically varied interocular conflict and total stimulus contrast in opposition to each other; as conflict increased, contrast fell. Our results indicate that the intermodulation signals did not simply reflect contrast. They rose to a peak when the IOCD was between 0.1 and 0.2, and then fell as the IOCD increased further. This is consistent with the intermodulation frequencies being generated by neurons that respond to interocular conflict and at the same time sensitive to contrasts of stimuli. A formal model, containing one neural population that detected conflict
between the two eyes and another that integrated signals between the two eyes, was able to reproduce the pattern of data we observed.

A recent study suggested that such an inverted-U shape in the intermodulation frequencies could potentially arise simply from a normalization computation between two components present in a stimulus (Tsai et al., 2012). In this work, subjects viewed two superimposed binocular noise patterns that were frequency tagged. The observed intermodulation signals reached a maximum when the contrasts of the two stimuli were equal and grew smaller as contrast differences between the two patterns increased. For our stimulus, however, the two component patterns and the two eyes had equal contrast at an IOCD of 0, and our intermodulation frequencies peaked at higher IOCDs. Hence, contrast normalization alone appears unlikely to explain our data.

Said and Heeger (2013) proposed a model that contains both neurons that sum information from the two eyes and neurons that compute differences between the two eyes to signal interocular conflict. In their model, these different neurons drive binocular rivalry. Prior behavioral (Cohn, Leong, & Lasley, 1981; May, Zhaoping, & Hibbard, 2012), computational (Li & Atick, 1994), and some neurophysiological (Ohzawa & Freeman, 1986; Poggio & Talbot, 1981; Smith, Chino, Ni, Ridder, & Crawford 1997) work support the existence of such ocular opponency neurons, although Said and Heeger (2013) were the first to propose that they had a role in binocular rivalry. Our results provide physiological support for the existence of a mechanism that explicitly registers interocular conflict and its potential role in rivalry.

Our results did not show an increase in energy at the intermodulation frequencies near dominance-to-dominance transitions, as has been reported previously (Zhang et al., 2011). However, this previous study did not encourage subjects to report mixed percepts; it is possible that some long mixed percepts were present in their reported dominance-to-dominance transitions and that these may have produced the increase in intermodulation signals. The more rapid dominance-to-dominance transitions in the present work likely did not last long enough to produce responses in conflict detecting neurons that were measurable with SSVEP. Consistent with this explanation, in the present study, mixed-to-dominance transitions, which showed clear trends for longer mixed periods (>2 s), produced little to no change in the intermodulation frequency envelopes for short mixed periods (<1 s; data not shown).

Our results are also in general agreement with a recent report that found that the N170 component of the ERP first decreases and then increases in amplitude as interocular conflict in a stimulus increases (Roeber, 2012). The paper argued that the N170 reflects an interocular conflict signal during rivalry. Our method has the advantage of being able to segregate monocular from binocular signals in the SSVEP. Three earlier studies (Harter, Conder, & Towle, 1980; Jakobsson, 1985; Tyler & Apkarian, 1985) also measured ERPs during various levels of interocular conflict, but these were not aimed at mechanisms of rivalry and yielded conflicting results.

Whether the resolution of binocular rivalry requires top-down signals from higher visual or nonvisual cortical regions is an ongoing debate in the field (Frässle, Sommer, Jansen, Naber, & Einhäuser, 2014; Knapen, Brascamp, Pearson, van Ee, & Blake, 2011; Lumer, Friston, & Rees, 1998). Our data do not directly address this question: It is certainly possible that the SSVEP results we observed originated from neural computations that were gated by top-down activity. For example, the computations may be quite different in the absence of visual attention (Brascamp & Blake, 2012; Roeber et al., 2011; Zhang et al., 2011). Resolving this issue is an important question for future research.

Our results support the hypothesis that the computations underlying binocular rivalry make use of neural populations that signal the degree of interocular conflict. Two experiments using the intermodulation frequencies in the SSVEP provided evidence for such a conflict signal. Future work should be able to use the intermodulation frequencies to reveal additional aspects of the computations that induce binocular rivalry.

Keywords: binocular rivalry, binocular fusion, SSVEP, intermodulation frequencies

Acknowledgments

This work was supported by NIH R01 EY02301. We thank Keith Jamison for providing the code for the RLS filter and Daniel Neren and Isaac Hatch-Gillette for data collection. We also thank the anonymous reviewers whose useful comments helped to improve this manuscript substantially.

Commercial relationships: none.
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