A Method for Investigating Binocular Rivalry in Real-time with the Steady-state VEP

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Under conditions in which the visual system cannot reconcile dissimilar images from the two eyes, perception typically alternates between the two half-images—a process known as binocular rivalry. We report a real-time, steady-state VEP method that is a sensitive detector of the continuous alternations in perceptual dominance across the eyes. This method works by labeling each half-image with a slightly different temporal frequency so that the record generated by each can be recovered from the EEG by spectrum analysis. In this way, one can track the "waxing" and "waning" of the VEP amplitudes for each eye simultaneously during spontaneous rivalry, permitting an analysis of the relative physiological dominance of each eye in real-time. Such alternations were clearly observed in the VEP amplitudes generated by each half-image during rivalry (the amplitudes for the two eyes correlated negatively). In contrast, VEP amplitudes for the two eyes varied either synchronously or randomly when the half-images were allowed to fuse. The instances of physiological dominance of each eye as evidenced by the VEP correlated well with the subjects' report of perceptual dominance. This purely electrophysiological method appears to be suitable for measuring rivalry in non-verbal human or animal subjects, as it does not require active participation from them. © 1997 Elsevier Science Ltd.

binocular rivalry   steady-state VEP   dichoptic viewing

INTRODUCTION

When the two eyes view dissimilar images that cannot be fused, subjects usually report a perceptual alternation between these images, a phenomenon known as binocular rivalry (von Helmholtz, 1910). Various hypotheses have been proposed to explain the phenomenon, most notably, as a default mechanism for fusion when the latter fails (Blake, 1989), or as a covert underlying process of binocular vision operating at all times, even during fusion (Kaufman, 1964; Wolfe, 1986). More recently, it has been proposed that the perceptual competition occurs between the two stimulus representations rather than between the eyes (Logothetis et al., 1996).

Binocular rivalry has been studied extensively using psychophysical methods (see Blake, 1989; Levelt, 1965; Wolfe, 1986). Some evidence of monocular suppression relating to binocular rivalry has been found at the single unit level (Sengpiel et al., 1994; Varela & Singer, 1987). The best evidence to date for single-unit correlates of binocular rivalry comes from the laboratory of Logothetis and co-workers. Using dichoptic gratings drifting in opposite directions, it was found that cellular responses in monkey MST reflected the animal's report of direction of

motion (Logothetis & Schall, 1989). Similar results were later found in monkey cortical areas V1, V2 and V4 (Leopold & Logothetis, 1996).

It has been known for many years that the suppressive phase of binocular rivalry manifests itself in the human VEP. Lansing (1964) was the first to report a periodic suppression of the EEG under conditions promoting rivalry. He found that the VEP at the flicker frequency of a monocular grating was periodically suppressed during the presentation of a steady grating in the other eye. This periodic physiological suppression also corresponded to the subject's perceived suppression of the flickering grating by the steady pattern. MacKay (1968) showed that transient VEP recordings were reduced in amplitude when a flashing blank field in one eye was perceptually suppressed by a noise pattern in the other. Wright et al. (1986) also reported a reduction in transient VEP amplitude when a temporally modulated checkerboard pattern was suppressed by a blank field. Cobb et al. (1967) used dichoptic orthogonal gratings that were temporally modulated in counterphase. Since the temporal modulation was 180 deg out of phase in the two eyes, it was expected that the VEP would have to average to zero as the responses for each stimuli should cancel electrically at the scalp. However, the VEP in the rivalry condition was found to be equivalent to, or greater than, the VEP of either eye obtained under monocular conditions, indicating that the response of the percep-

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tually dominant eye was uncontaminated by the other eye. It was concluded that the lack of response reduction in the rivalry condition was evidence for physiological suppression of one eye. Lawwill and Biersdorf (1968) used orthogonal gratings that were labeled at the scalp with slightly different temporal frequencies. In this way, they could recover eye-specific VEP responses at the electrodes. By having the observer gate the averaging based on the separate stimulus triggers, they found larger amplitudes and shorter latencies in the dominant, rather than in the suppressed phases, concluding that the observed effects were due to physiological rivalry.

Whether or not these results can be attributed to processes underlying binocular rivalry needs to be considered carefully, as it is critical to show that any observable physiological signature of rivalry correlates with the perceptual alternations. Using a flickering grating in one eye and a steady orthogonal grating in the other, Riggs and Whittle (1967) found some reduction in amplitude and more pronounced frequency doubling in the rivalry condition compared with viewing the flickering pattern alone. Hence, there was evidence for specificity of response in the rivalry condition. However, the authors reported no observable difference in VEP amplitude as perceptual dominance shifted from the flickering to the steady pattern. Thus, they attributed the observed differences between the rivalry and monocular conditions to binocular interactions other than rivalry. Martin (1969) reached the same conclusion. Recording transient VEPs, the only potential candidate found in the EEG that might be evidence for physiological rivalry was the presence of a monocular signature in the binocular wave form during perceptual rivalry. However, these signatures appeared during fusion as well, implying that they only represented a general bias for one monocular representation under binocular stimulation. Also, the occurrence of these signatures during rivalry did not correlate with perceptual dominance of the corresponding stimulus. As a result, the author attributed these signatures to effects of physiological dominance other than rivalry (such as natural eye dominance).

The main reason why studies advocating the manifestation of binocular rivalry in the VEP have failed to convince the skeptics is that they do not provide evidence for the critical characteristic of rivalry: the real-time, ongoing alternations in dominance across the eyes. Instead, these studies focus on time-averaged physiological records of suppression or dominance not necessarily specific to binocular rivalry.

Establishing a method for the study of binocular rivalry with the VEP is crucial if one is to have a direct measure of the underpinnings of the perceptual shifts in dominance in non-verbal subjects, i.e., experimentally manipulated animals or human infants. Strong evidence for binocular rivalry in the VEP would require one to provide qualitative data on the continuous shifts of dominance and suppression in real-time and in both eyes simultaneously, i.e., an entire record of the interplay in dominance across the eyes; it is important to also show

that the physiological alternations mirror the perceptual alternations in stimulus dominance in the subject. This study had two goals: to establish a method for tracking rivalry alternations in real-time and to develop a purely electrophysiological indicator of rivalry that does not require the observer to direct the averaging process. We report a method based on the steady-state VEP that unambiguously registers the alternating shifts in physiological dominance for the two eyes simultaneously; these physiological shifts correlate with the subjective shifts of dominance in the subject. This method requires no participation on the part of the subject, which makes it ideal for studying the ongoing alternations in dominance in non-verbal infants or untrained animals.

METHODS

Subjects

Eight observers with no visual or other abnormalities between 12.9 and 52.4 years of age participated in this study. All had normal, or corrected vision to 20/20 or better Snellen acuity. Informed consent was obtained after the procedure was explained.

Stimuli and apparatus

Each half-image comprised a 2 c/deg cosine grating at 80% contrast. Spatial frequency and contrast were selected on the basis of the large VEP responses they generated in most observers. The gratings were generated on two monochrome monitors (Dotronix, New Brighton, MN) that were free to rotate 360 deg around their centers. These monitors faced each other so that the two gratings were reflected by front-surface mirrors and entered each eye dichoptically. Screens with circular apertures were used to mask the monitors. It was important that we obtained good signal-to-noise ratios on single trials because our technique did not permit signal averaging (see below), and it was empirically determined that stimuli subtending 12 deg (at 100 cm) yield acceptable signal-to-noise ratios; Smaller fields yielded signals that were seldom resolvable from noise. The observer's head was stabilized in a chin and head rest and the monitors were aligned for accurate centering independent of rotation angle. Gratings smoothly oscillated through 180 deg of spatial phase along the direction orthogonal to their orientation so as to produce an equivalent counterphase modulation. The temporal frequencies of these oscillations were 5.5 Hz for the grating viewed by the left eye and 6.6 Hz for the grating viewed by the right eye. Four recording conditions were used that produced rivalrous (two gratings oriented diagonally at 45 and 135 deg), fused (two diagonal gratings oriented similarly at 45 deg in both eyes), or monocular views (left or right eye viewing one stimulus presented in the rivalry condition, with the fellow eye occluded).

VEP recordings

Four active electrodes were positioned over the occipital pole in a "cross" configuration centered around

a reference placed 3 cm above the inion on the midline (Oz). The four electrodes at the extreme ends of the "cross" were 3 cm away from the reference. This bipolar configuration was chosen as it reduced background noise levels considerably in single trials compared with those in unipolar recordings. The EEG was amplified 100,000 times with a half-amplitude bandpass filter setting of 1 to 100 Hz (Grass Instruments, model P-511). A Recursive Least Squares (RLS) adaptive filter (Tang & Norcia, 1995) was used to extract the amplitude and phase of the signals generated by the two stimuli.

Periods of perceptual dominance for each eye during rivalry needed to be longer than the time-constant of the adaptive filter in order to be resolved. An appropriate value for the memory length of the adaptive filter was found to be in the order of 0.9 sec of raw EEG (1 bin). We therefore adjusted stimuli parameters such that periods of perceptual rivalry were no shorter than 0.9 sec. We found empirically that rivalry periods were satisfactorily lengthened by reducing luminance for the stimuli in both eyes. Thus, mean luminance was chosen to be low enough (20 cd/m^2) to produce an acceptably long period of perceptual rivalry while high enough to yield acceptably robust signals that could be extracted from noise in most subjects.

The two signals associated with the stimuli were uniquely labeled by the stimuli's temporal frequency of 5.5 Hz in one eye and 6.6 Hz in the other. Since there were two directions of movement for each complete oscillation of the stimulus, it was expected that each of these movements should generate a frequency-doubled evoked potential (see Norcia et al., 1985). Hence, the target frequencies at the scalp were the second harmonic components in the VEP that reflected processing of the two stimulus frequencies, i.e., 11 and 13.2 Hz. EEG amplitudes and phase values were also calculated at frequencies ±1.1 Hz distant from the driven response frequencies. There was no driven activity at these frequencies and they were used as experimental noise baselines.

Each recording condition comprised ten 12.7 sec trials of 14 bins each. Trials were interleaved across conditions by blocks of five, and the order of conditions was varied in a pseudo-random fashion across subjects.

Since the rivalrous stimuli often generated a "patchy" perceptual network of dominance of each eye in the relatively large dichoptic field, subjects were asked to report only on perceptual dominance in the center of the field (which was circumscribed by the experimenter as a disk approximately 2 deg in diameter). Targets for the two half-images were not reduced, as was previously done to achieve uniform suppression of one stimulus by the other (Leopold & Logothetis, 1996) because relatively small targets generated very weak or no VEP when the surrounding field was masked (see Discussion).

In the rivalry condition, subjects were instructed to press either of two buttons to report which stimulus was perceptually dominant, and to press neither when the stimuli perceptually overlapped or the dominance state

was otherwise ambiguous. Reports of dominance were done during the VEP recording in order to obtain a continuous record of perceptual shifts in dominance and suppression that could be directly compared with the alternations manifested in the VEP. The reports of dominance were represented as strings of 1's (left eye dominant), −1's (right eye dominant), or 0's (ambiguous, or the stimuli in both eyes perceptually overlapped). These button-press "states" were sampled at a rate of 397.4 Hz and later averaged into 0.9 sec time bins to make the perceptual report data similar to the VEP (see Results).

RESULTS

Signal strength

Monocular recordings of each eye (fellow eye blocked) showed that the signal was significantly phase-coherent across trials ($P < 0.0001$) as revealed by T^{2}circ (Victor & Mast, 1991). When the eye (either left or right) was blocked, the signal lost phase-coherence ($P > 0.1$), ruling out the existence of instrumentation artifacts during presentation of the stimuli. Signals in the channel with best signal-to-noise ratios (SNR) for both eyes when undergoing rivalry were separable from noise, with an SNR of 3.86 in the rivalry condition (SD = 1.5), 2.34 in the fusion condition (SD = 0.69) and 3.79 in the monocular conditions (SD = 1.45). These values reflect the average SNR available in individual 0.9 sec bins.

Evidence for physiological rivalry in the VEP

VEP data for a single subject (LN) are shown in Fig. 1. The top graph [Fig. 1(A)] is the VEP collected during dichoptic viewing of the orthogonal gratings (rivalry). Each trace plots the amplitude at the temporal frequency in the cortical EEG that reflects stimulation of one eye (see Methods). The amplitudes from each eye were plotted as a function of time for all 10 trials abutted together. This allowed a direct and continuous comparison of relative signal strength across the eyes in a viewing condition when the two monocular stimuli were reported to be competing perceptually. A portion of the record is expanded in the inset, as marked by the dashed lines. The plot underneath [Fig. 1(B)] depicts the corresponding VEP amplitudes under the viewing condition where the two stimuli were reported to fuse. Recall (see Methods) that this condition is identical to the rivalry condition except that one of the stimuli was rotated so that the two monocular targets had similar orientations. These plots illustrate the clear difference in the relationship between the two eyes' responses in the rivalry and fusion conditions: in the rivalry condition, each eye shows repetitive cycles of suppression and dominance in the VEP with the inverse effect in the fellow eye at any one time. In the fused condition, the VEPs from the two eyes have no such relationship. Figure 1(C) and Fig. 1(D) show the interocular relationships for the entire data set of VEP amplitudes for rivalry and
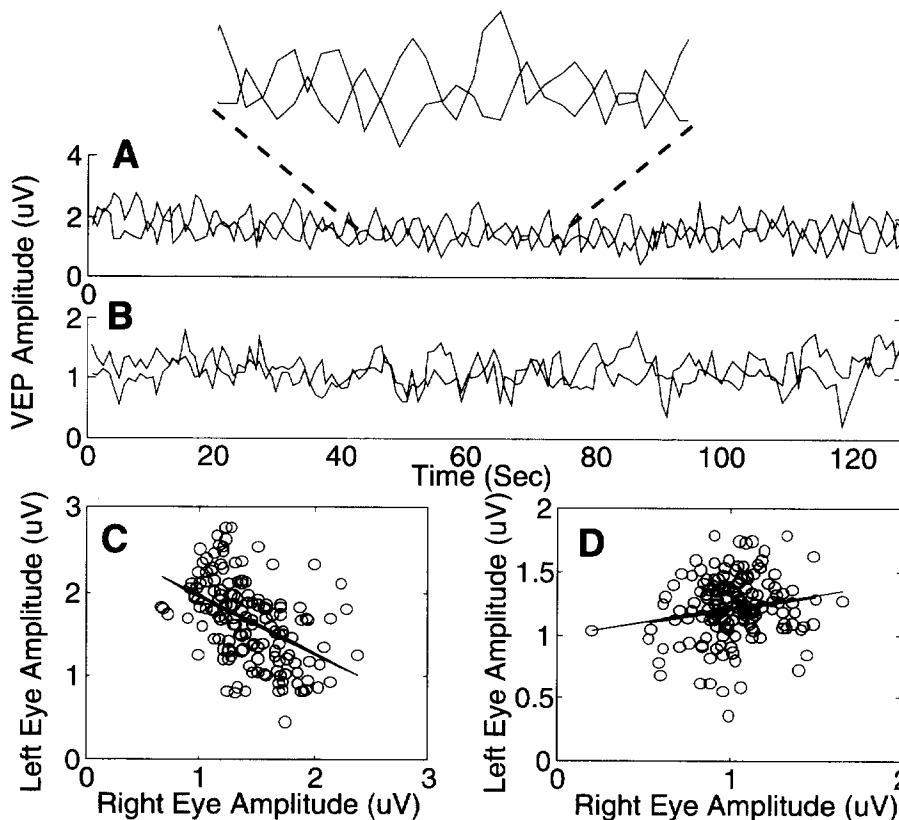
FIGURE 1. Alternation in VEP amplitudes in subject LN that are generated by the two half-images as they undergo rivalry (A), or fusion (B). Records were obtained during viewing over the entire duration of the test for each of these conditions (individual trials were abutted). In (A), a portion of the VEP from both eyes was enlarged to show how the two amplitudes clearly alternate in dominance over time. The correlations between the amplitudes of each eye are given for rivalry and fusion in (C) and (D), respectively. Note how the two eyes correlate negatively when undergoing rivalry. See Table 1 for a summary.

fusion, respectively (amplitudes from each of the 0.9 sec bins collected across the 10 trials).

Pearson-r correlation coefficients describing the interocular relationship were calculated for the rivalry and

fusion conditions for each trial, yielding a total of 10 coefficients for each of the two conditions. Table 1 lists the mean correlation coefficients for each subject in the rivalry and fusion conditions. An exact Wilcoxon sign

TABLE 1. Statistics for exact two-tailed Wilcoxon rank-sum test

Subject	Rivalry	Fusion	Riv/Fus	LE/Perc	RE/Perc	NLE/Perc	NRE/Perc
AG	**−0.37****	**0.09**	***	**0.50****	**−0.54****	**0.10**	**0.14**
	0.20	0.23		*0.12	0.13	0.22	0.29
DV	**−0.45****	**0.06**	***	**0.55****	**−0.54****	**−0.02**	**0.03**
	0.17	0.28		0.15	0.23	0.22	0.23
IL	**−0.44****	**0.1**	**	**0.43****	**−0.49****	**0.16**	**0.12**
	0.26	0.29		0.19	0.18	0.21	0.24
JB	**−0.46****	**0.20**	***	**0.55****	**−0.49****	**−0.08**	**−0.03**
	0.21	**0.29**		0.20	0.17	0.37	0.33
LN	**−0.73****	**0.17**	***	**0.72****	**−0.72****	**−0.11**	**−0.13**
	0.08	0.30		0.14	0.20	0.22	0.29
MP	**−0.58****	**0.18***	***	**0.64****	**−0.66****	**0.05**	**−0.02**
	0.28	0.32		0.18	0.13	0.77	0.33
NF	**−0.23**	**−0.05**		**0.09**	−0.08	**0.06**	**−0.02**
	0.42	0.31		0.22	0.26	0.24	0.27
SV	**−0.44****	**0.37****	***	**0.62****	**−0.60****	**−0.10**	**−0.09**
	0.23	0.01		0.12	0.11	0.29	0.28

$*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

Numbers in bold are the correlation coefficients; numbers beneath are the standard deviations, which are provided for information about variability even though significance testing was non-parametric. LE/Perc, left eye signal vs perceptual dominance; RE/Perc, right eye signal vs perceptual dominance; NLE/Perc, noise near left eye signal vs perceptual dominance; NRE, noise near right eye signal vs perceptual dominance.

rank test was used to test whether these sets were significantly different from a mean of zero, and from each other. Seven out of eight subjects (subject NF gave negative results for all data; see below) showed significant negative correlation coefficients for rivalry ($-0.37 > r > -0.73$), and significant positive or no significant correlation for fusion ($0.06 < r < 0.37$). In addition, each subject showed significant differences between the rivalry and the fusion correlation coefficients.

Evidence that physiological rivalry correlates with perceptual rivalry

Digitized data on the reports of perceptual dominance were binned similarly to the VEP data. The binning took into consideration the manual reaction time between the VEP onset for the stimulus coming through each eye and the button press signaling perception of that stimulus. Binning was performed by sliding the 0.9 sec averaging windows over the perceptual dominance report with 20 msec steps over a range of possible reaction times between -900 and 1700 msec. For each of these steps, the binned dominance report was correlated with the VEP amplitudes for the stimulus of each eye. This yielded cross-correlation functions as shown in Fig. 2. Each curve in Fig. 2(A) (left eye) and Fig. 2(C) (right eye) shows the cross-correlation function for a single 12.7 sec trial. Note that these cross-correlation curves are consistent in shape from trial to trial. Figure 2(B) and Fig. 2(D) show the two corresponding mean curves (bowing functions) obtained from averaging the 10 trials. The lower and upper curves around the mean are the ± 1 standard deviations (SD). Note that the cross-correlation functions for the left and right eyes peak in the expected positive and negative directions, respectively. That is, the left eye's VEP amplitudes should correlate positively with the 0 to +1 (left) button press data; similarly, the right eye's VEP amplitudes should correlate negatively with the 0 to -1 (right) button press data. Additionally, the two cross-correlation functions reach their peak at approximately the same reaction time value. The set of correlation coefficients (each of 10 trials) contributing to the mean value at the peak positive (left eye) and negative (right eye) points were found to be significantly different from zero in all cases, except for subject NF (see Table 1). The correlation coefficients were statistically significant even without correction with respect to reaction time ($P < 0.01$).

As a control for the numerical analysis, the same procedure used above was carried out by cross-correlating reports of dominance with EEG noise instead of VEP. Noise was calculated for each bin as the average of the
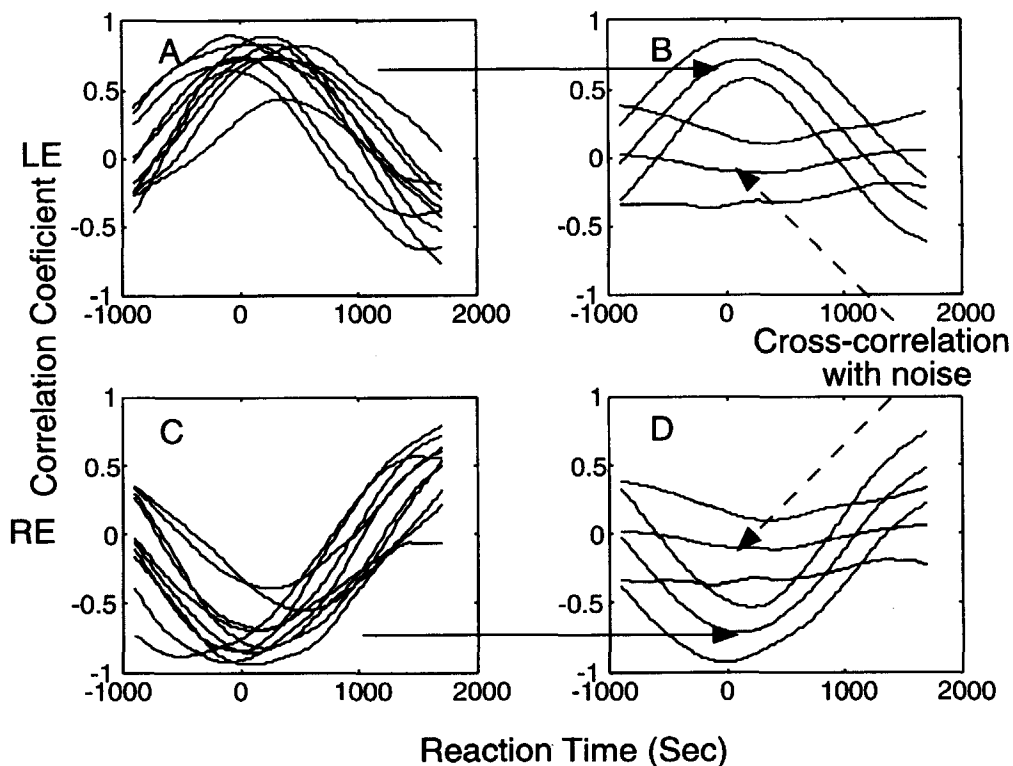

FIGURE 2. The curves for the cross-correlation functions between VEP amplitudes generated during rivalry and the corresponding report of perceptual rivalry. (A) and (C) in the left column are the cross-correlation functions for single trials. These were achieved by sliding the binning windows of the digitized perceptual reports with respect to the VEP data to account for manual reaction time. Note that individual curves peak at about the same reaction time. (B) and (C) are the means (middle bowing curve) with their corresponding 95% confidence interval. The correlation coefficients for both eyes were statistically significant even with a zero reaction time. The second set of curves in these panels (relatively flat) are the cross-correlation functions between EEG noise and the perceptual report (button press data). See text for details, and Table 1 for summary statistics.

two EEG amplitudes that were recorded near the signal frequency. e.g. 9.9 and 12.1 Hz for the 11 Hz second harmonic generated by the 5.5 Hz stimulus (see Norcia *et al.*, 1985). The mean cross-correlation coefficients across trials between dominance report and noise yield the center dotted curve (flat function) in Fig. 2(B) and Fig. 2(D). For each subject, a one-tailed exact Wilcoxon sum rank test indicated that the set of coefficients at the peak correlation coefficient for VEP/button press data was significantly greater (for left eye) and smaller (for right eye) than their corresponding correlation coefficients for noise/button press data (at matched reaction time value) (see Table 1).

Figure 3 shows how the VEP and the perceptual dominance report agree when the binning windows over the latter have been adjusted to account for reaction time. Figure 3(A) and Fig. 3(B) are the data for left and right eyes, respectively. The dominance report is shown beneath the VEP data. Again, a section of the data (for the left eye) was enlarged for clarity. Note how well the peaks of the VEP amplitudes for left eye line up with the reports of left eye dominance (positive peaks in button

press), while the peaks of the VEP amplitudes for the right eye line up with the reports of right eye dominance (negative peaks in button press). The relationship between the entire set of VEP amplitudes and perceptual reports of dominance are shown for both eyes in Fig. 3(C) and Fig. 3(D). Results for all subjects are shown in Table 1.

Thus, the shifts in dominance and suppression observed for each eye in the VEP correlated well with the shifts in perceptual dominance and suppression that were reported to occur by the subject when experiencing binocular rivalry.

DISCUSSION

Using the present technique, we have obtained evidence for a VEP correlate of perceptual rivalry: perceptual dominance in the two eyes occurs with a corresponding shift in the cortical signals, the amplitudes of which correlated negatively across the two half-images. Adjusting for reaction time increased the correlation between the VEP and perceptual report,
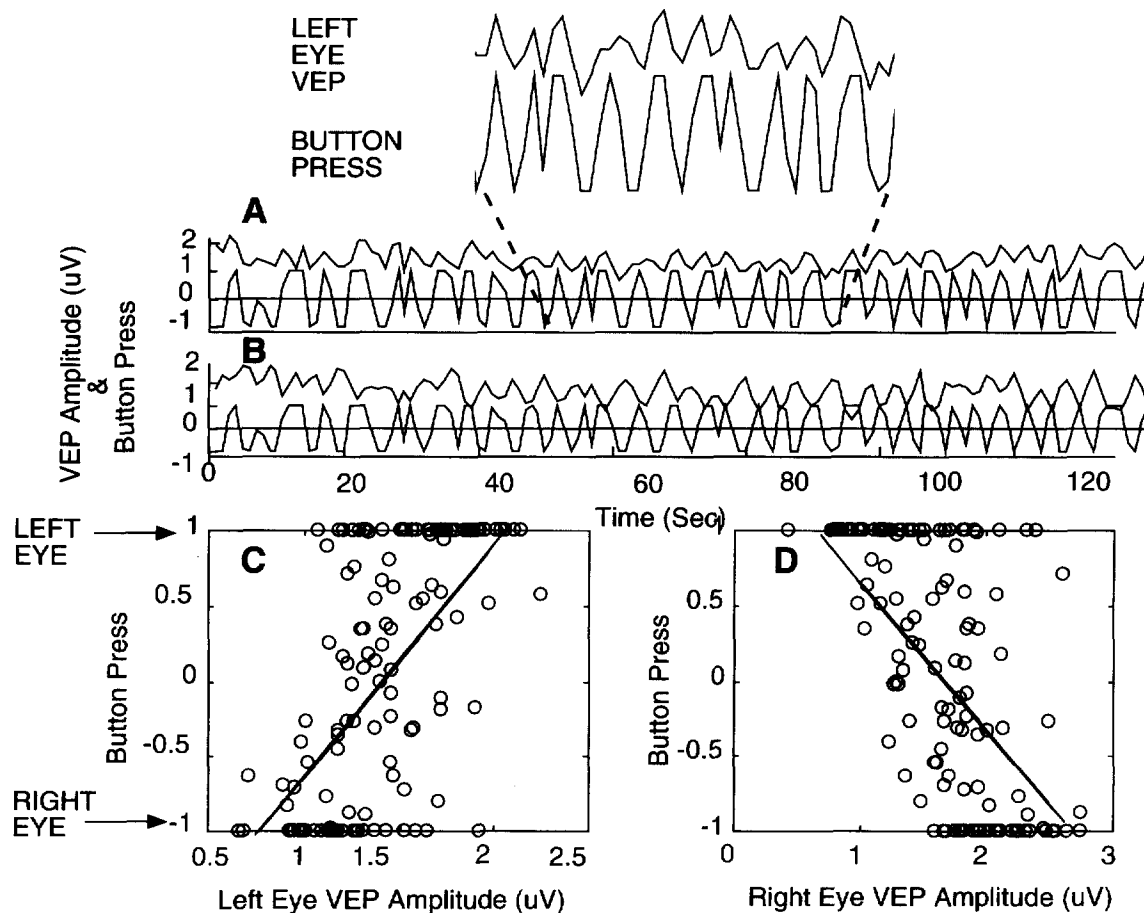

FIGURE 3. The VEP amplitudes generated by each half-image undergoing rivalry plotted simultaneously with the digitized perceptual report (A) left eye; (B) right eye. Data from the perceptual report of dominance varies between −1 (right eye half-image dominant) and +1 (left eye half-image dominant), with the intermediate values resulting from the binning at peak reaction time. A section of the left eye plot was enlarged in (A) for a clear comparison between VEP and perception. Note how the left eye's VEP amplitude peaks with the report of dominance for that eye, and does so at the same rate. The same is true for the right eye: peaks in the VEP amplitudes for the right eye occur during report of dominance for the right eye. (C) and (D) show the respective correlation coefficients. See Table 1 for summary statistics.

although the two measures were well-correlated without the shift. By simply changing the orientation of one of the two gratings by 90 deg (changing the viewing condition from dichoptic to dioptic), the alternations in VEP stimulus dominance completely disappeared; in this case, the amplitudes for the two eyes either did not correlate, or correlated positively.

Limitations of the current technique

There is a fundamental trade-off between SNR and memory length (bin size)—longer memory lengths improve the SNR but decrease the temporal resolution. Rivalry would be difficult to detect if the half-images' responses were too small or if the rivalry phases became shorter than twice the memory length. Dominance phases of one eye can be controlled by changing the stimulus strength of that eye (Levelt, 1965), and we observed that the alternation rate can be slowed down by reducing luminance in both eyes. It appears that there is a sufficiently wide range of stimulus parameters available in human adults to make measurements practical. Applications to other subject groups or species may require other parameter values than have been used in the present study. SNR can usually be improved by signal-averaging over several trials, which is typically done in VEP analysis (see Regan, 1989). However, this signal-extracting procedure cannot be carried out with this method because the phases of the "waxing" and "waning" of the amplitudes during rivalry observed from trial to trial are determined by an arbitrary recording onset and would cancel out when averaged. Subject NF, who gave the negative results in this study had signals that were resolvable in that his SNR was generally above 2.9, but his SNRs were still below all subjects with resolvable signals. Thus, the limitation of this technique may not be restricted to unresolvable signals, but also to relatively low signals, making it impossible or difficult to detect how signals modulate as they are overcome by high noise levels. However, it was observed that signals in relatively young subjects are generally well-discriminated from noise, making this subject group ideal (incidently, NF was the oldest subject tested). Also, increasing the number of samples in the analysis will improve the chances of detecting the negative correlation between the amplitudes of each eye (our marker for rivalry) that is weakened by low SNR.

There is a second trade-off between SNR and the spatial "completeness" of the dominance phases of the half-images. It is known that rivalry is complete only in relatively small target fields, such as 1 deg or less (see Blake, 1989), but becomes piecemeal in larger fields. Unfortunately, we observed empirically that signals generated in small 2-deg fields were not resolvable from noise. We further observed that moving to a larger 12-deg field produced resolvable signals and alternations in their amplitudes that were consistent with relatively complete rivalry. This occurred even though subjects confirmed that they perceived rivalry as complete over the central region but not in the periphery. These results are

consistent with the VEP being chiefly sensitive to foveal stimulation owing to magnification of the foveal representation in the cortex (Cowey & Rolls, 1974; Virsu & Rovamo, 1979). The weak responses from the small targets may have been due to suppression from edge effects (Vassilev, 1973).

Usefulness of the technique

A major technical advantage of the present method is that (under appropriate conditions) it is a purely electrophysiological measure of rivalry. Previous investigations relied on the observer to provide signals to control the averaging process used to extract the VEP from the EEG. This is not necessary with our method since the sorting of the two eyes is done by spectrum analysis—which is also a highly effective method of signal extraction. Other workers (e.g. Lansing, 1964) have observed waxing and waning of the steady-state VEP during rivalry. However, in these studies, it would be difficult to distinguish spontaneous amplitude variations from rivalry. In our method, negative correlation between the two eyes' responses is a unique marker of physiological rivalry. Hence, the current method is an appropriate tool that can assess the nature of binocular rivalry in non-verbal human infants who cannot follow instructions and in experimental animals for whom the necessity of training is reduced, and perhaps eliminated. It also enables one to examine the behavior of both eyes simultaneously and in real-time.

The present technique is expected to be useful for studies focusing on developmental issues concerning binocular rivalry in the infant—a task which we have currently undertaken.

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