Development of Rivalry and Dichoptic Masking in Human Infants

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PURPOSE. To examine the development of rivalry, dichoptic masking, and binocular interactions in infants more than 5 months of age using the visual evoked potential (VEP).

METHODS. VEPs were recorded in 35 infants between 5 and 15 months of age and 23 adults between 13 and 59 years of age. Counterphasing, sinusoidal, 1 cycle/deg gratings were presented dichoptically. Responses from each eye were isolated by "tagging" each half-image with a different temporal frequency (5 or 7.5 Hz). Observers were presented with fixed 80% contrast gratings in each eye in experiment 1. Rivalry was detected on the basis of a negative correlation between the simultaneously measured response amplitudes at the second harmonics of the two eye-tagging frequencies. In a second analysis of the same data, response amplitudes recorded under dichoptic viewing conditions were compared to those obtained in a monocular control condition (dichoptic masking). In experiment 2, a 40% fixed-contrast grating was presented to one eye, whereas the other eye viewed a grating that was swept in contrast from 1% to 67%. Dichoptic masking was measured as the reduction in the fixed-grating response caused by the variable contrast grating.

RESULTS. Experiment 1: although adults showed evidence of VEP amplitude alternations between the eyes for cross-oriented half-images (physiological rivalry), infants did not. This immature response to rivalrous stimuli occurred despite the presence of responses at nonlinear combination frequencies recorded with gratings of the same orientation in each eye, a definitive indication of binocular interaction. In addition, both iso- and cross-oriented half-images produced less dichoptic masking in infants than in adults in this experiment. Experiment 2: dichoptic masking in the infants was equivalent to that seen in adults with parallel gratings in the two eyes; however, masking with cross-oriented configurations was approximately five times weaker in the infants relative to the adults.

CONCLUSIONS. The authors have identified a set of stimulus conditions under which infants between 5 and 15 months of age fail to demonstrate physiological rivalry despite the presence of binocular interactions. The observed lack of binocular rivalry may be the result of a specific immaturity in dichoptic, cross-orientation suppression. (*Invest Ophthalmol Vis Sci.* 1999;40:3324–3333)

There is good agreement that horizontal disparity and the sign or presence of interocular correlation begin to be detected by 3 to 5 months of age in the human infant.[1–8] By this age, infants prefer correlated over anticorrelated patterns, zero disparity patterns over very large disparities, and fusable targets versus ones with vertical disparities. The current literature on the development of binocular rivalry in human infants suggests that this process also develops rapidly during the same developmental time period.[2,3,9,10] Birch and coworkers[2] examined positive and negative preferences for disparate/anticorrelated stimuli

versus zero disparity stimuli. They found an increasing preference for a zero-disparity target compared to patterns of opposite contrast across the eyes. This preference for identical images in the two eyes had the same time course as the emergence of preference for a disparate stereogram versus a nondisparate control. Shimojo and coworkers[9,10] and Gwiazda and coworkers[3] examined discriminations between conventional rivalry targets and fusable ones. Infants were presented with a dichoptic stimulus comprised of superimposed horizontal and vertical bars, which appeared rivalrous to adults, and a stimulus comprised of identical bars in each eye, which appeared fused. They found that infants less than 3 months of age preferred the "rivalry" target, but that preference switched to the interocularly identical pattern after 4 months of age. Gwiazda and coworkers[3] found that the switch in preference was correlated with the age at which infants began to prefer a disparate target over a nondisparate target.

These preference studies indicate that rivalrous and superimposable stimuli are discriminated by 3 to 5 months of age. They do not, however, indicate the basis for the preference or why the preference should shift from one type of stimulus to another during development. Moreover, preference methods cannot indicate whether the defining feature of rivalry—spon-

taneous alternations between percepts—was experienced by the infants.

In this article, we asked whether infants beyond 5 months of age showed evidence of binocular rivalry alternations as measured with a new visual evoked potential (VEP) technique.[11] In adults, this technique has been shown to successfully record physiological alternations in dominance and suppression between the eyes that are correlated with the report of perceptual alternations that occur when viewing rivalrous stimuli. Like previous behavioral studies, we wanted to compare VEP responses to rivalrous stimuli with stimuli that tap the detection of interocular correlation. As a measure of the detection of interocular correlation, we used spectral analysis to detect nonlinear responses at the difference and/or sum frequencies in the VEP generated by the dichoptic presentation of two half-images modulated with different temporal frequencies.[12,13] The presence of so-called intermodulation components constitutes objective evidence for the neural detection of the state of interocular correlation.

We found no evidence of binocular rivalry in human infants between 5 and 15 months of age despite clear evidence of nonlinear binocular interactions associated with the detection of changes in interocular correlation. In a second experiment, infants of this age also were found to exhibit gross immaturities in their interocular masking for targets that adults perceive as rivalrous.

MATERIALS AND METHODS

Observers

A total of 35 infants and 23 adults participated. The infants ranged in age from 5 to 15 months in experiment 1, and 5 to 11 months in experiment 2. Twenty-seven infants participated in experiment 1, and 7 of these infants plus 8 additional infants participated in experiment 2. Adults ranged in age from 13 to 59 years in both experiments. All adult observers had Snellen acuity correctable to 6/6 or better in each eye and no prior history of strabismus or amblyopia. The research protocol was approved by the local Institutional Review Board and conformed to the tenets of the Declaration of Helsinki. Informed consent was obtained from the parents of the infants and the adult observers, after the VEP recording procedure was explained.

Stimuli and Apparatus

Dichoptic and monocular VEPs were recorded in response to contrast-reversing, 1 cycle/deg sine-wave gratings. In the dichoptic viewing conditions, each half-image was reversed in contrast at 5 Hz in one eye and 7.5 Hz in the other eye using a square-wave modulation profile. This difference in temporal frequency across the eyes made it possible to isolate and separately track the VEP from either eye in the electroencephalogram (EEG).[11] The dichoptically viewed gratings were either of the same orientation in each eye (parallel condition) or oriented orthogonally (cross-orientation condition). In addition, the gratings of each half-image were oriented in cardinal (vertical or horizontal) or oblique (diagonal at 45° or −45°) axes, to produce a total of four different stimulus conditions: cardinal-parallel and cross-oriented, and oblique-parallel and cross-oriented. In experiment 1, each eye viewed a fixed, 80% contrast grating in trials that lasted 8 seconds. In experiment 2,
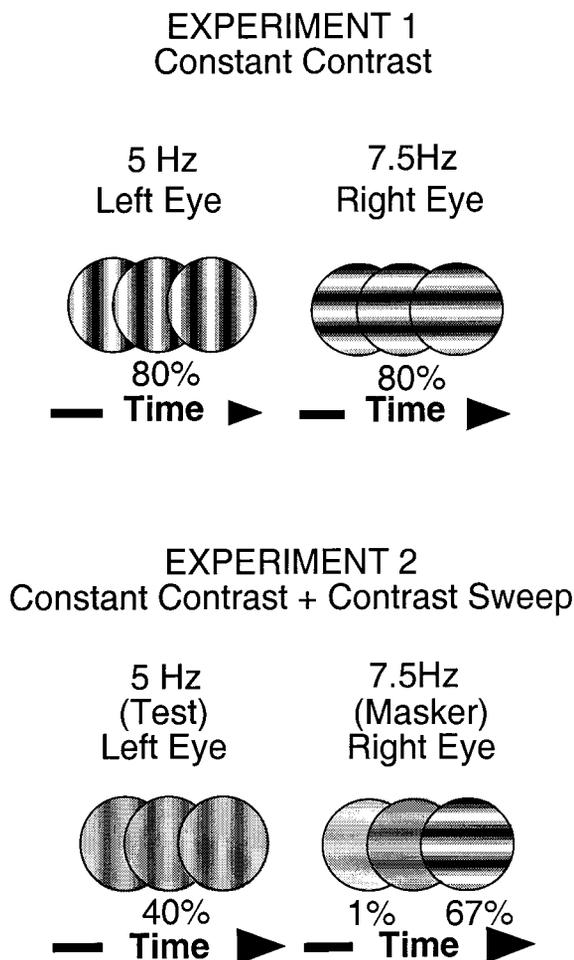
EXPERIMENT 1
Constant Contrast

5 Hz
Left Eye

7.5Hz
Right Eye

80%

80%

— Time ►   — Time ►

EXPERIMENT 2
Constant Contrast + Contrast Sweep

5 Hz
(Test)
Left Eye

7.5Hz
(Masker)
Right Eye

40%

1%   67%

— Time ►   — Time ►

FIGURE 1. Paradigms used in experiments 1 and 2 (only the cross-orientation condition is shown). In experiment 1, both gratings were kept fixed at 80% contrast over the trial period in both the parallel and cross-oriented conditions. In experiment 2, the test (5-Hz vertical grating) was kept fixed at 40% contrast and the masker (7.5-Hz vertical or horizontal grating) was swept from 1% to 67% contrast over each 10 seconds trial duration. See text for details.

one eye viewed a fixed 40% contrast grating reversing at 5.0 Hz, and the other eye viewed a 7.5-Hz reversing grating that was swept in contrast between 1% and 67% in 12 equal logarithmic steps presented over 10 seconds (Fig. 1). In the parallel conditions, the gratings cycle periodically through two correlated and two anticorrelated states, with the cycle repeating at the difference frequency (2.5 Hz). The correlated states arise when the gratings are in the same spatial phase in the two eyes and the anticorrelated states occur when the gratings are 180° out of phase between the two eyes.

The gratings were generated on a Dage-MTI multi-synch monitor positioned at distances of 70 or 100 cm for the infants and 100 cm for the adults, generating visual fields of 22° × 16° and 16° × 11.4°, respectively. Mean luminance was 40 cd/m². The half-images were temporally interleaved on alternate video frames at a frame rate of 60 Hz. Dichoptic separation of the two gratings was achieved with a combination of circularly polarized glasses worn by the observers (oppositely polarized across the left and right lens filters) and a Liquid Crystal shutter mechanism (NuVision SGS19S) placed over the video monitor. The shutter changed its direction of circular polarization syn-

chronously with the interleaving of the two half-images. Monocular control data were obtained by placing a patch over one eye during the parallel dichoptic viewing condition. This control condition was used for two purposes: to assess the amount of cross-talk between eyes in the dichoptic conditions and to serve as a reference for the dichoptic masking effects of parallel and cross-oriented gratings.

VEP Recording and Procedure

Infants were seated in their parent's lap in front of the monitor. The experimenter attracted the infant's attention to the stimulus with small toys centered on the monitor's display. Recordings were interrupted when the infant was judged not to be attending. Adults were instructed to simply fixate the center of the display. Recording sessions consisted of 5 to 8 trials per condition for infants and 10 trials per condition for adults. For the adults, trials were randomly interleaved across conditions in blocks of 5 trials. In half of the infants, the parallel and cross-oriented conditions were tested first, with the monocular control data collected last. This order was reversed for the other half of the infants.

The EEG was amplified at a gain of 50,000 for adults and 20,000 for infants, with amplitude bandpass-filter settings of 1 to 100 Hz (model 12A5; Grass Instruments, Quincy, MA). In the adults, the active electrode was placed over the occipital pole at the midline, 3 cm above the inion. The reference and ground electrodes were placed over the midline 3 and 6 cm above the active electrode, respectively. The same configuration was used in the infants, except that the relative distances between leads were adjusted in proportion to their smaller skull size. The primary data came from the second harmonics of each eye's input frequency, e.g., 10 and 15 Hz.

Signal Processing and Data Analysis Methods

Real-Time Binocular Rivalry Detector. A recursive least square (RLS) adaptive filter[14] was used to determine VEP amplitude and phase over 0.8-second epochs. The RLS filter is an adaptive, matched-filter that is more effective than the discrete Fourier transform (DFT) for detecting time-varying signals occurring in short data records.[14] Analyses were performed separately for the second harmonic components ($2F_L$, $2F_R$) generated by the distinct left and right eye stimulation frequencies. In experiment 1, these short-time analysis epochs were used to detect rivalry using the method described previously.[11] Briefly, rivalry alternations cause the VEP amplitudes in the two eyes to be negatively correlated over time. By labeling each eye's output with a different temporal frequency, rivalry alternations can be detected objectively and in real-time using only the cortical response record. The bin length was such that it contained an exact integer number of response cycles at all analysis frequencies used. It was also short enough to track adult rivalry, but long enough to provide adequate signal-to-noise (SNR) ratio. For each observer, a composite data record was constructed by abutting all trials recorded in either cross-oriented (rivalry) or parallel (binocular correlation/anti-correlation) conditions. A Pearson product moment correlation was calculated between the left and right eye response amplitudes from the entire composite record for a given observer. This measure of rivalry has been shown to correlate with perceptual alternation in adults.[11]

Intermodulation Analysis. Complete spectra for the parallel and cross-oriented conditions were calculated using a mixed-radix DFT (MATLAB; The MathWorks, Inc., Natick, MA). These spectra were used to determine response amplitudes at all the harmonics of the two eye stimulation frequencies and at all the nth-order sum and difference frequencies. Spectra were first obtained from a 40-second composite record made by abutting the first five 8-second trials recorded from an observer in a given stimulus condition. The individual observer spectra were then coherently averaged across the infant and adult groups separately. Each individual thus contributed equally to the grand averages. All records contained exact integer multiples of both the 10- and 15-Hz response frequencies. Coherent averaging uses both phase and amplitude information, which emphasizes response components that are consistent in phase across observers. This method is thus conservative in identifying the presence of response components. Additional components that are random in phase across observers (but phase coherent within an individual observer) will not be represented in the coherent average.

Fixed Contrast Dichoptic Masking Analysis. Amplitude and phase values from the 10 individual 0.8-second epochs were coherently averaged over each trial, and these values were then coherently-averaged across the 5 to 8 trials per condition generated by the infants and for the 10 trials per condition for the adults, using methods described in detail elsewhere.[14,15]

Swept Contrast Dichoptic Masking Analysis. In the second experiment, which used swept contrast maskers, the 12 individual 0.8-second epochs comprising each trial were coherently averaged, epoch-by-epoch across all trials in a given recording condition. These average records for each observer were then coherently averaged across observers within infant and adult groups for the parallel, cross-orientation, and monocular control conditions.

RESULTS

Experiment 1

Real-Time Rivalry. Adult and infant observer responses to cross-oriented dichoptic gratings were first compared using the real-time rivalry detector described previously.[11] The rivalry detector is based on the correlation between $2F_L$ and $2F_R$ amplitudes. A negative correlation is indicative of the ongoing, opposing fluctuations in dominance and suppression between the eyes, the fundamental characteristic of rivalry alternation. Figure 2 plots the group mean correlations ($\pm$ 1 SEM) for three SNR criteria for the cardinal (left subpanels) and oblique axes configurations (right subpanel) for infants (left) and adults (right). The horizontal lines above and below each bar indicate the range of individual correlations for the corresponding data inclusion criterion. The numbers inside the bars indicate the sample sizes.

Rivalry alternations produce fluctuations in amplitude and thus SNR. The real-time detector requires that the VEP amplitude be above the EEG noise level at least some of the time. We computed average interocular correlations for three progressively more stringent SNR criteria. The first criterion included all the data. The second two criteria required that the average SNR in the eye with the lowest SNR exceed either 2:1 or 3:1, with SNR defined on the basis of amplitudes at the response frequency, relative to adjacent EEG frequencies that were free of driven activity. Previous work has indicated that a SNR of 3:1
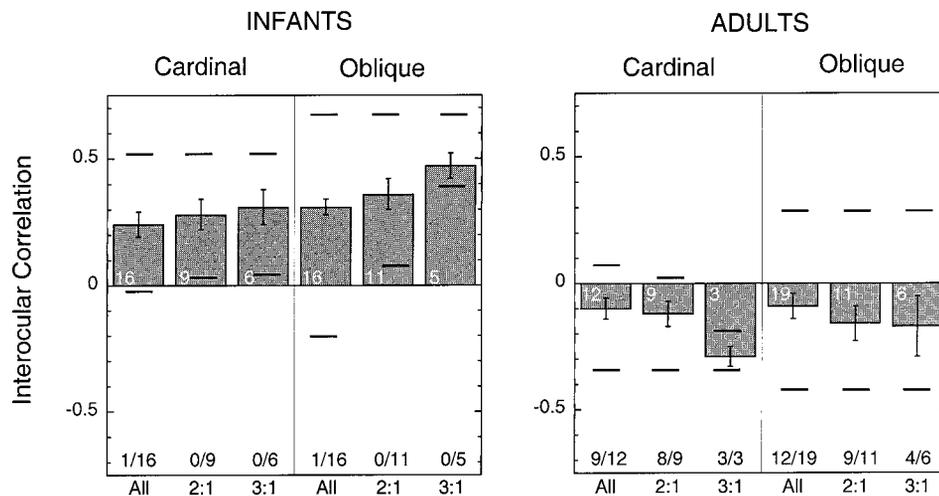
FIGURE 2. Mean correlation between the VEP amplitudes of the two eyes for three data inclusion criteria. Error bars are standard errors, and the *horizontal lines* indicate the range of individual observer correlations. Sample sizes for each comparison are shown inside the bars. The ratio below each bar indicates the number of observers with negative correlations in the corresponding comparison group. The data inclusion criteria were based on the signal-to-noise ratio (SNR), defined as the average signal amplitude at the response frequency divided by the average noise amplitude measured simultaneously at two frequencies immediately above and below the response frequency. Infants' amplitudes are positively correlated regardless of the viewing condition. Adults show significant negative correlations in five of six of parametric comparisons.

places an individual bin reliably above the EEG noise level.[11] Beginning with the most inclusive criterion (all data), the infant correlations were both significantly positive (0.24 ± 0.05; $P < 0.05$ and 0.31 ± 0.06) for the cardinal and oblique configurations, respectively. The adult values were both negative (-0.10 ± 0.04; $P < 0.05$ and -0.09 ± 0.05; $P < 0.10$) for the corresponding conditions. The SNR > 2:1 criterion resulted in significantly positive average correlations for the infants of 0.28 ± 0.06; $P < 0.01$ and 0.36 ± 0.06; $P < 0.01$ for the cardinal and oblique configurations, respectively. Comparable values for the adults were both significantly negative (-0.13 ± 0.05; $P < 0.05$ and -0.17 ± 0.07; $P < 0.05$). Infant correlations remained significantly positive for the 3:1 criterion (0.31 ± 0.07; $P < 0.01$; 0.47 ± 0.05; $P < 0.01$) for the cardinal and oblique configurations, respectively. Comparable values for the adults were -0.29 ± 0.04 ($P < 0.02$) and -0.17 ± 0.12 ($P < 0.20$). Nonparametric testing of the distribution of the signs of the correlations indicated that the adult correlations were significantly negative in the cardinal condition for the "all data included" criterion (9/12 negative: $P < 0.05$; sign test) and 2:1 SNR criterion (8/9 negative: $P < 0.01$). In the oblique condition, the adult correlations were significantly negative for the 2:1 criterion (9/11 negative: $P < 0.02$). All three adult observers showed negative correlations in the cardinal axis condition under the 3:1 SNR criterion. However, the sign test is not applicable with this sample size, so no significance values can be reported. The other nonparametric comparisons were not significant at the 0.05 level. Each distribution of infant correlations was significantly skewed to positive correlations ($P < 0.01$) due to the fact that only one interocular correlation was negative in each of the two cross-oriented conditions. These two negative correlations occurred at less than the 2:1 criterion and were small enough to be individually not significantly different from 0. Therefore, while the adults showed physiological alternations characteristic of binocular

rivalry in the cross-oriented conditions, infants did not. This led us to ask whether the apparent lack of binocular rivalry could be attributed to a general immaturity of binocular interactions under our stimulus conditions.

Intact Nonlinear Binocular Interactions in Infants: DFT Intermodulation Analysis. The two-frequency stimulation paradigm can be used to determine whether the input from the two eyes has been combined at a central binocular site. There are two manifestations of binocular interaction present in the data. One is the occurrence of significant response amplitudes at frequencies corresponding to nonlinear combinations of the two input frequencies.[12,13,16] The other is the presence of dichoptic masking—the reduction of signal amplitude at $2F_L$ or $2F_R$ relative to the monocular control condition by a grating presented to the other eye (see below). Figure 3 displays the DFTs of the VEP averaged coherently across observers for the two cardinal axes viewing conditions using the first five trials per observer from the real-time rivalry analysis. The infant data were averaged across all infants, regardless of age. Before averaging, we tested for significant age trends using correlations between age $2F_L$ and $2F_R$ amplitudes in the dichoptic viewing conditions. Pearson product moment correlations between the amplitude of the half-image second harmonics ($2F_L$, $2F_R$) and age in the parallel or cross-oriented conditions for cardinal or oblique axes were nonsignificant and ranged between 0.22 and 0.63 ($t_{(8)}$ lay between -1.32 and 1.00). The DFTs of both adults and infants showed clear second harmonic responses generated by the two half-images at $2F_1 = 10$ Hz and $2F_2 = 15$ Hz in both the parallel and crossed-oriented configurations (Fig. 3A). Adults and infants in the parallel condition also produced peaks at twice the difference frequency ($2F_2 - 2F_1 = 5$ Hz) and at the sum frequency ($F_1 + F_2 = 12.5$ Hz). Infants also generated a response at the difference frequency $F_2 - F_1 = 2.5$ Hz. No intermodulation components appeared in the cross-oriented condition for ei-
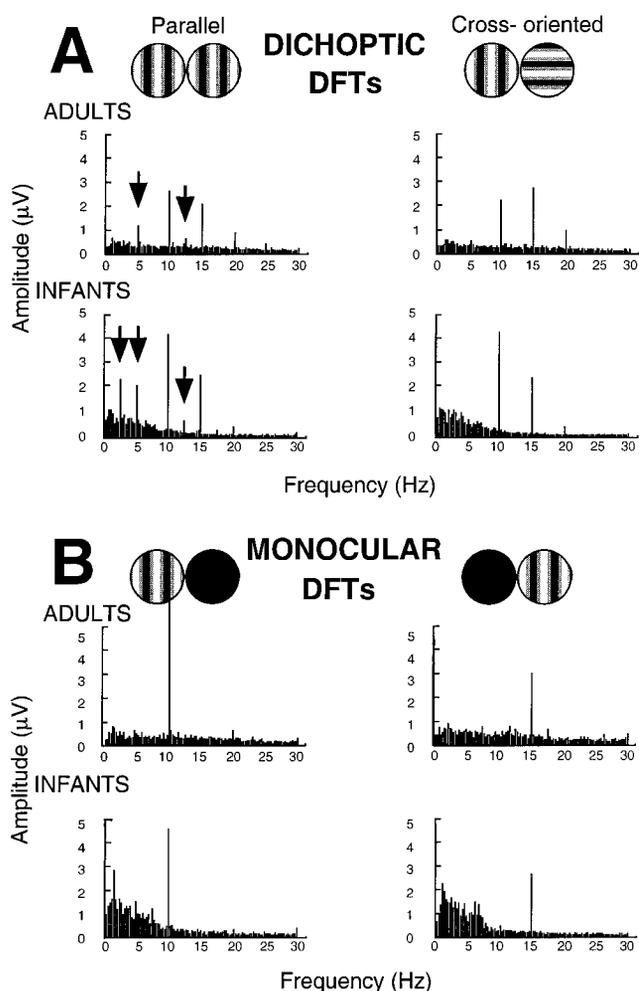
it is absent in the monocular control condition. The infants' responses to dichoptic gratings are similar to those of the adult, with the exception of the additional component at $F_2 - F_1$.

Dichoptic Masking: Fixed Contrast Half-Images. Another manifestation of binocular interaction, dichoptic masking, is also apparent in Figures 3 and 4—the amplitudes at $2F_1$ are smaller in the dichoptic viewing conditions than in the monocular control condition (cf. adult 10-Hz amplitudes in Figs. 3B and 4B to the 10-Hz amplitudes in the corresponding A panels and to the infant data in Fig. 4B to the infant data in 4A). To quantify masking strength in infants and adults, we normalized each observer's mean response at $2F_1$ in the parallel and crossed-orientation conditions to that obtained in the monocular control condition. The data were first processed as coherent averages within an observer and then averaged incoherently (without phase) across observers, regardless of whether the half-image was a 5-Hz vertical or 7.5-Hz horizontal grating. Incoherent averaging was used to focus the measure on amplitude reductions in the masking condition, independent of possible phase differences across observers. Only observers who had data for monocular, dichoptic parallel, and
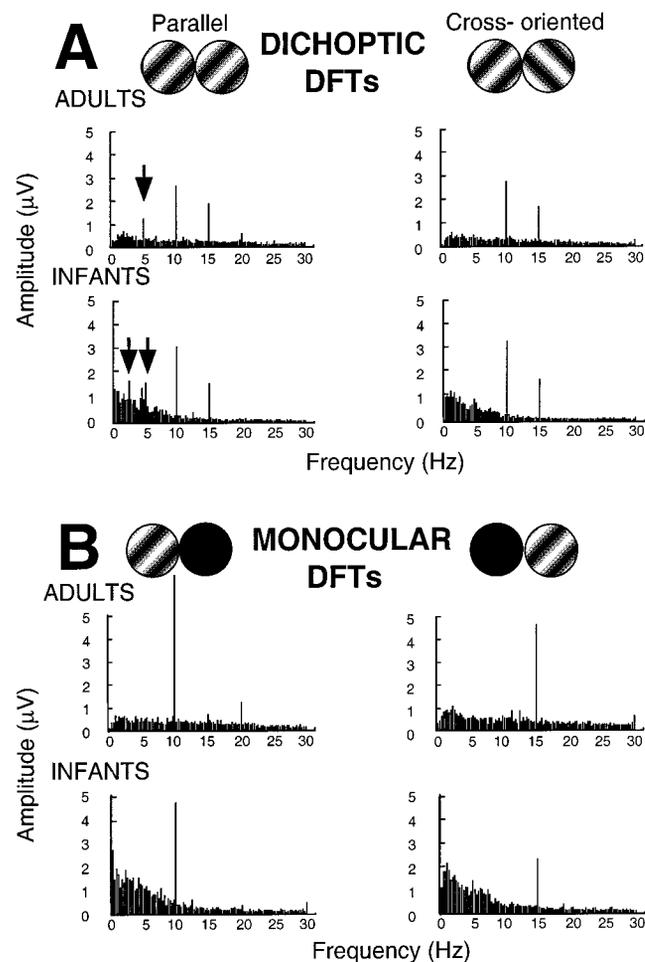
FIGURE 3. Group average discrete Fourier transforms for cardinal axes conditions. (A) Response to the dichoptic viewing conditions; (B) monocular responses to each grating. The dominant response to each half-image occurs at twice the frequency of stimulation, e.g., 10 and 15 Hz. The intermodulation components (*arrows*) present in adults in the parallel viewing condition also are present in infants, demonstrating that the latter have at least some form of binocularity. Group sizes for the monocular conditions: 5-Hz stimulus: infants, 5; adults, 8; 7.5-Hz stimulus: infants, 5; adults, 4.

ther group. Note that no frequency components related to the occluded eye (either second harmonic or intermodulation terms) appeared in the monocular controls (Fig. 3B), indicating that cross-talk between half-images was not sufficient to generate measurable response components.

VEPs recorded from the oblique axes configurations (Fig. 4) generated similar DFTs in infants and adults. Note that the absolute amplitudes of the intermodulation terms have decreased somewhat, as did the two second harmonic half-image responses. Hence, moving from the parallel cardinal to the parallel oblique viewing condition does not affect the relative proportion of intermodulation distortion to total response amplitude. The presence of VEP intermodulation components for parallel half-images indicates that the images from the two eyes have been combined at a nonlinear binocular site. This site is orientation selective in both infants and adults, since intermodulation is not seen with the cross-oriented configurations. The intermodulation is not due to stimulus cross-talk, because

FIGURE 4. Group average discrete Fourier transforms for oblique axes conditions. (A) Response to the dichoptic viewing conditions; (B) monocular responses to each grating. The intermodulation components (*arrows*) present in adults in the parallel viewing condition are also present in infants, demonstrating that the latter have at least some form of binocularity. Groups sizes for the monocular conditions: 50-Hz stimulus: infants, 5; adults, 8; 7.5-Hz stimulus: infants, 4; adults, 5.
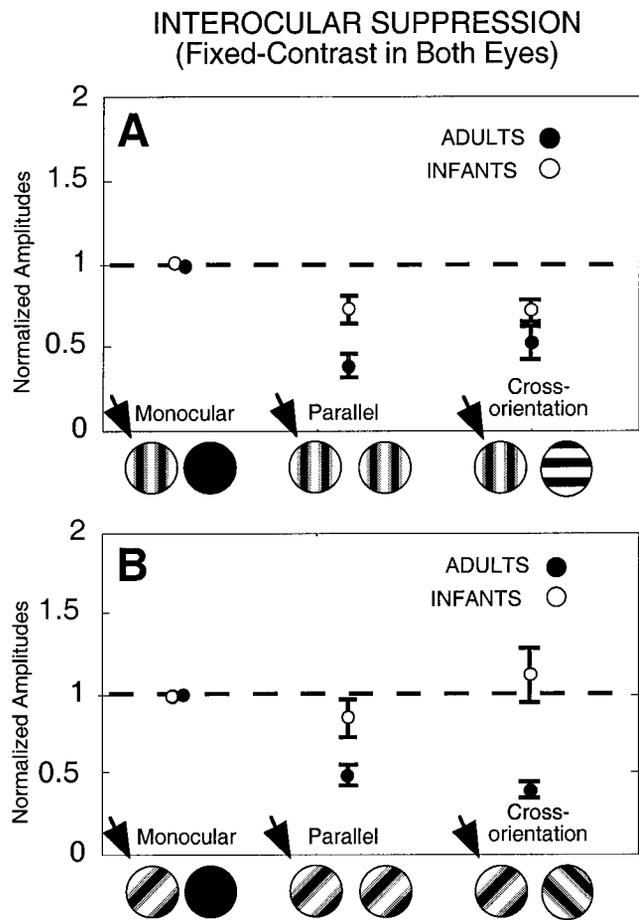
INTEROCULAR SUPPRESSION
(Fixed-Contrast in Both Eyes)

FIGURE 5. Mean VEP amplitudes generated for one half-image (*arrows*) in the parallel and cross-oriented viewing conditions for cardinal (**A**) and oblique (**B**) configurations. The data shown are the amplitude for the half-image responses collapsed across the vertical, 5-Hz grating and the horizontal, 7.5-Hz grating, both normalized to the monocular response for each grating. Normalization was applied for a given observer with a full set of monocular, parallel, and cross-oriented viewing conditions, before collapsing across observers. Error bars are standard errors. Group sizes: cardinal axes: infants, 10; adults, 9; oblique axes: infants, 9; adults, 12. Infants showed less dichoptic masking than adults, particularly in the oblique axis conditions.

dichoptic cross-oriented conditions were entered into the analysis, which is summarized in Figure 5. Approximately two thirds of all the infants (16/27) and two thirds of all the adults included in the previous figures qualified for this analysis (see Fig. 5 legend for additional details).

Adult responses to the F_1 (test) half-image in the dichoptic condition were reduced in amplitude by an average of approximately 50% relative to the monocular response across the four stimulus configurations. Infants masked less than adults, especially in the cross-oriented, oblique configuration. In the oblique configuration, the infant amplitudes in the parallel masking condition were 1.77 ± 0.10 times larger than the adults, but in the cross-oriented condition they were 2.7 ± 0.07 times larger. In the cardinal axes parallel condition, the infant amplitudes were 1.82 ± 0.12 times larger than the adults and in the cross-oriented condition they were 1.4 ± 0.15 times larger. To test whether the infants showed significant dichoptic masking, independent-sample, two-tailed *t*-tests were per-

formed to test for significant differences between measured responses and a null hypothesis of no masking (a ratio of 1.0). Infants showed significant masking in both the parallel and cross-oriented conditions for the cardinal axes ($t_{(9)}$; $P = 0.01$), but masking was not observed for either of the oblique axes conditions ($t_{(8)}$; $P = 0.21$; parallel and $t_{(8)}$; $P = 0.63$; cross-oriented).

Experiment 2: Dichoptic Masking: Swept Contrast Maskers

The previous analysis of dichoptic masking quantified masking as a reduction of VEP amplitude. Amplitude reductions are difficult to interpret in terms of visibility or visual sensitivity. Therefore, in the second experiment, a different measure of dichoptic masking strength was introduced that quantifies dichoptic masking in terms of the strength of masker required to produce a criterion reduction in response amplitude. This measure was recorded in 15 infants, 7 of whom had participated in the first experiment.

When one of the half-images is swept up in contrast while the other remains fixed, the amplitude of the test (fixed contrast) response is reduced at the higher contrast values of the masker (swept contrast half-image). Individual examples of suppression of the test by the masker are shown for four infants in Figure 6, for the parallel (solid line) and cross-oriented (dotted line) viewing conditions. The masker was swept logarithmically in contrast from 1% to 67%. The top left and bottom graphs are representative of the 10 infants recorded in the cardinal axes conditions, while the upper right graph is representative of the 5 infants recorded in the oblique axes conditions. The left column represents young infants (22 and 26 weeks of age), and the right column the two oldest infants from the oblique and cardinal axes groups (44 and 42 weeks of age, respectively). Note that the cross-oriented masker is much less efficient in suppressing the fixed contrast half-image than the parallel masker, even for the older infants.

The functions in Figure 6 were fit using a nonlinear regression to the following equation:

$$V = R_{max} - R_{min}(C^S)/(C^S + K^S)$$

where R_{max} is the maximum VEP response; R_{min} the minimum VEP response; C, the masker contrast in percent; s a parameter controlling the rate of transition between R_{max} and R_{min}, and K the contrast at which VEP response is 50% reduced from the curve's maximum. The curve is derived from the hyperbolic-ratio function, which is a good description of cortical-cell contrast response functions.[17] Figure 7 shows the mean response to the test half-image as a function of masker contrast for infants and adults, directly comparing the cross-oriented and the parallel conditions for in each group in the right and left panels, respectively. Amplitudes (*V*) were normalized to the first bin for each subject before coherent averaging across observers.

For adults and infants, the test response was reduced to 50% of R_{max} by the parallel grating between 30 and 40% masker contrast in both cardinal (Fig. 7A) and oblique (Fig. 7B) conditions. When the masker was cross-oriented with respect to the test, adults showed strong masking, while infants showed little or no masking even at 67% masker contrast. At the highest masker contrast, infant and adult normalized am-
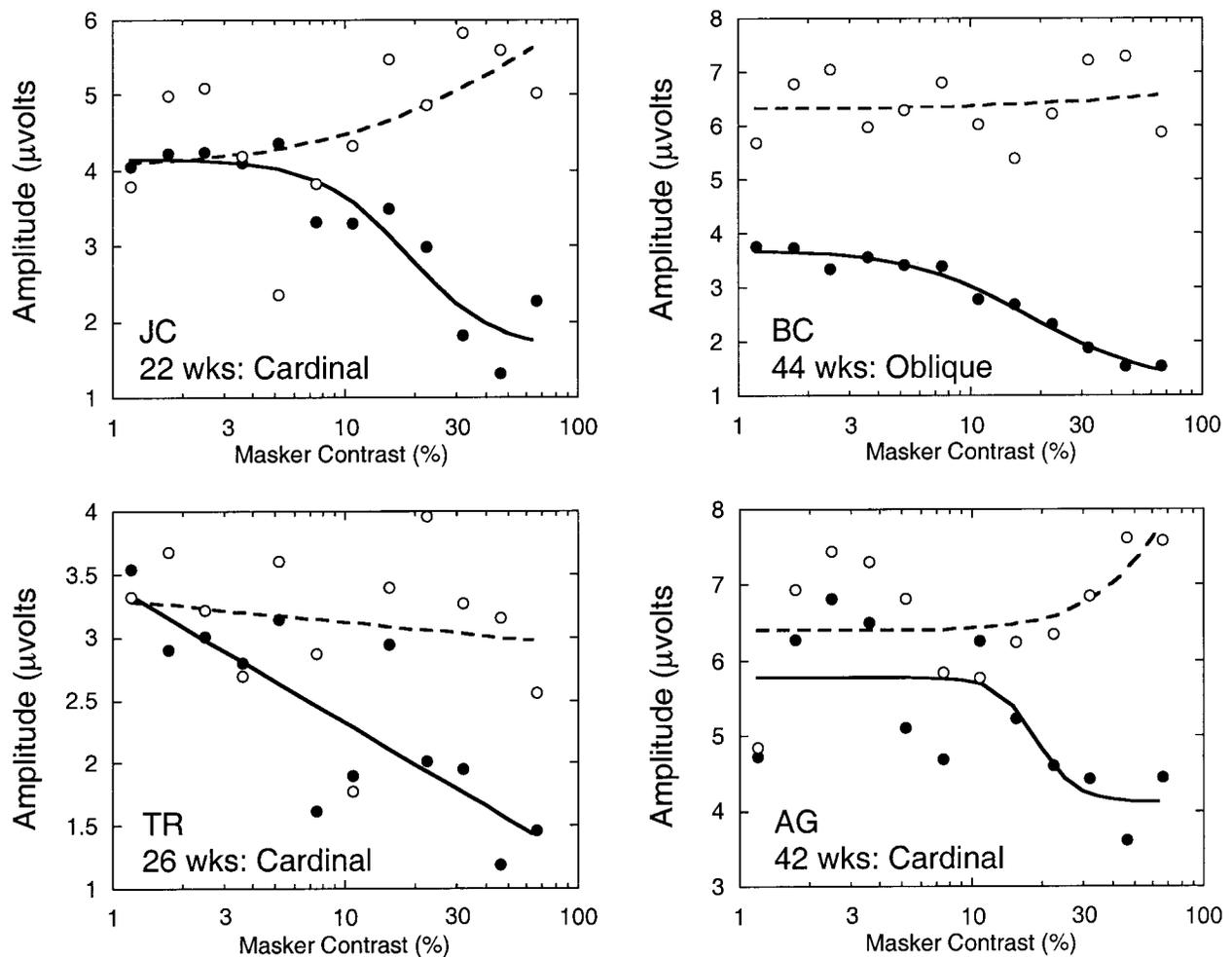
FIGURE 6. VEP amplitudes for the test half-image (fixed-contrast) as a function of the masker half-image contrast presented to the fellow eye. Individual data are shown for 4 infants in the parallel (*solid line*) and cross-oriented (*dotted line*) viewing conditions. The masker was swept logarithmically in contrast from 1% to 67%. The *top left* and *bottom* graphs are representative of the 10 infants in the cardinal axes conditions, whereas the *top right* graph is representative of the 5 infants in the oblique axes conditions. The *left* panels represent young infants (22 and 26 weeks of age), and the *right* panels the two oldest infants from the oblique and cardinal axes groups (44 and 42 weeks of age, respectively). Note that the cross-oriented masker is much less efficient in suppressing the fixed contrast half-image than is the parallel masker, even for the older infants.

plitudes did not differ in the parallel condition, as tested by an independent sample two-tailed t-test ($t_{(17)} = 0.18$, $P > 0.85$ for cardinal axes and $t_{(8)} = -0.13$, $P > 0.89$ for oblique axes) but did differ significantly in both cross-oriented grating configurations ($t_{(17)} = 2.85$, $P = 0.01$ for cardinal axes and $t_{(8)} = 2.2893$, $P = 0.05$ for oblique axes). Averaging the raw data in Figure 7 over the oblique and cardinal axes yielded a ratio of parallel to crossed K values of 1.77 for adults and 0.36 for the infants, respectively. Cross-orientation dichoptic masking was thus about a factor of 5 less potent relative to parallel masking in infants than in adults.

DISCUSSION

Infants' VEP amplitudes between 5 and 15 months of age did not vary across the eyes in a manner consistent with physiological rivalry for dichoptic, orthogonal 1 cycle/deg gratings undergoing pattern reversal at 5 and 7.5 Hz. Infants also showed weaker dichoptic masking than adults, particularly in

the second experiment where cross-orientation dichoptic masking was about a factor of 5 less potent relative to iso-orientation masking in infants than adults. The apparent lack of physiological rivalry may be due to a number of factors, such as general or specific immaturities in binocular or orientation-domain masking or immaturities in the spatio-temporal dynamics of rivalry. We will consider each of these factors and several others in the following discussion.

Although our method has proven to be a sensitive detector of rivalry in adults, it may have failed to detect rivalry in infants if some of the basic properties of rivalry differ between infants and adults. First, we used a relatively wide visual field for our stimulus (see Materials and Methods), which is known to induce piecemeal rivalry. In adults, this perceptual "patchiness" does not preclude the detection of rivalry, and the VEP is well-correlated with perceptual report.[11] However, our method may not detect rivalry in infants if their rivalry is even more piecemeal. A finer mosaic of the representation of the two half-images in the cortical area under the active electrode
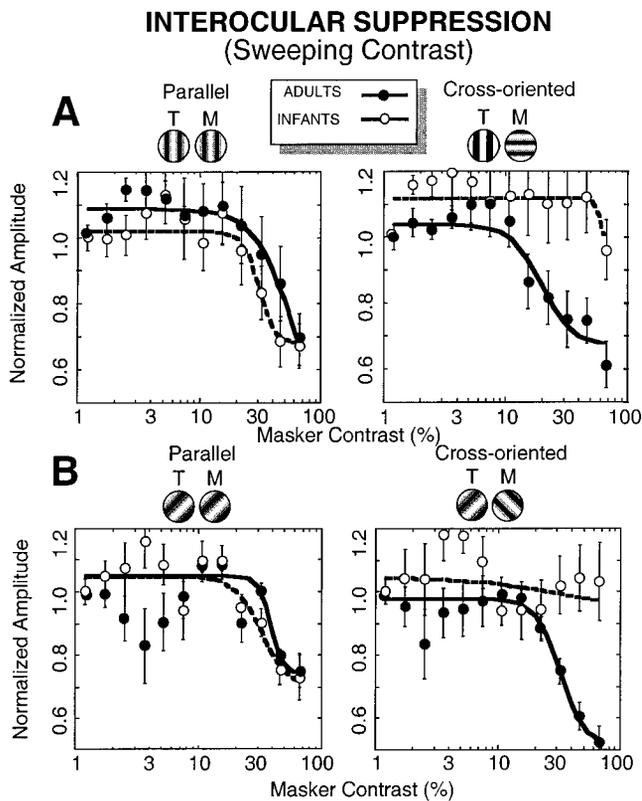
INTEROCULAR SUPPRESSION
(Sweeping Contrast)

FIGURE 7. Group mean VEP amplitudes for the test half-image (T) plotted as a function of masker half-image contrast (M) in the fellow eye. Data were normalized to the bin corresponding to the lowest masker contrast (first bin) before collapsing across observers. The infants' data are shown with *open symbols* and *dotted lines*. The adults' data are shown with *filled symbols* and *solid lines*. The smooth curves were fit to a version of the hyperbolic ratio function, as described in the text. Error bars are standard errors. Note that, compared to adults, in both the cardinal or oblique conditions, infants suppress at the same or less masker contrast for the parallel condition, but suppress at much higher masker contrast values in the two cross-oriented conditions.

may result in equal signals for each half-image at the scalp, in spite of suppression within local regions of the representation. Second, infants may have faster rivalry alternation rates than adults, with much shorter periods of dominance and suppression in either eye. Due to signal-to-noise requirements, our method cannot use time resolutions that are much shorter than 0.8 to 0.9 seconds.[11] This translates into a resolution of approximately 1.6- to 1.8-second periods from dominance to suppression in each eye. Thus, if infants had half-image "waxing and waning" periods shorter than these lower limits, we would have failed to detect them. Third, infants may show evidence of physiological rivalry for stimuli other than those used in this study, e.g., at lower/higher spatial or temporal frequencies. If this is true, then rivalry may not have a unique developmental time course, and we happened to use parameters at which rivalry has not yet developed to maturity. All three of these explanations for our inability to demonstrate rivalry in infants are themselves evidence of immaturities in rivalry. That is, compared to adults, rivalry may be either much patchier, faster, or lacking at specific stimulus values.

Another explanation for our results is that infants may have had more attentional fluctuations during the trials than

adults. Wavering attention may significantly diminish the expected negative correlation between the amplitudes for the two half-images. Attentional fluctuations should affect both eyes simultaneously, resulting in a positive correlation between the two half-images that could overcome a smaller negative correlation from rivalry. Attentional fluctuations could explain why we found positively correlated amplitudes across the eyes in the infants. Attentional fluctuations are however an unlikely explanation for the immature dichoptic masking results. It is unlike that attentional fluctuations in both eyes of infants in the sweeping-contrast experiment could have differential effects between the parallel and cross-oriented viewing conditions, especially given that masking strength in the parallel condition is adultlike.

Finally, it is possible that there are differences in the pattern or process of VEP generation in infants that preclude measuring a functional rivalry generator. An alternative methodology that also may signal perceptual alternation, such as the eye movement method developed for alert behaving primates[18,19] could be used in future studies to decide whether the lack of alternation in the VEP is correlated with eye movement behavior.

Could the Immaturity of Physiological Rivalry Be due to Immature Binocularity?

Previous studies have linked the emergence of rivalry to the detection of interocular correlation.[2–4] Both infants and adults had clear intermodulation components in their dichoptic VEPs when the gratings were parallel but not when the gratings were cross-oriented. The presence of intermodulation components in the infant's VEP indicates that their cortex is capable of detecting the state of interocular correlation of the two half-images (e.g., correlated versus anticorrelated). However, the infant response to interocular correlation changes may not be fully adult, because the infants had an additional component at the difference frequency, which the adults did not.

Dichoptic masking under some of our stimulation conditions is not fully adultlike (e.g., parallel conditions in Fig. 5). However, results from experiment 2 where infants' immaturity for interocular suppression was shown to be selective for cross-oriented half-images, compared to parallel half-images, suggests that immature orientation-domain interactions, not immature binocular mechanisms, are primarily responsible for the observed lack of rivalry in infants.

Does the Site of Rivalry Lie Beyond Binocular Convergence?

Unlike stereopsis, rivalry does not require separate eye-of-origin information.[20–22] There is now compelling evidence that rivalry is not solely a competition between the eyes, but rather the stimulus representations that arise beyond binocular convergence. This evidence comes from observations that different half-images with congruent sections will often combine into two single images formed by the congruent parts, and rivalry may occur between the resulting percepts, as opposed to the half-images.[20,22] There is also recent evidence that human observers continue to perceive a grating at a particular orientation even when it and its cross-oriented partner half-image are switched rapidly between the eyes,[21] arguing against rivalry across the eyes and for rivalry across percepts.

Neural Basis of Configural Competition

A minimum requirement for rivalry is the presence of suppressive neural interactions between neurons tuned to different stimulus dimensions such as spatial frequency or orientation. Evidence for monocular cross-orientation suppression is plentiful. Single-unit studies in cats have shown that there is strong inhibition between cells tuned to different orientations.[23–28] However, this inhibition is not orientation specific, as it can occur for any orientation of the masker.[24,28] Cross-orientation suppression becomes adultlike in terms of cortical receptive field properties such as spatial frequency and orientation tuning as early as 4 weeks postnatal age in kittens.[29] Dichoptic cross-orientation inhibition also can be demonstrated in striate cortex of adult animals. However, the effect is not strong and has not always been detected.[30–36]

Cross-orientation Interactions Are a Likely Prerequisite for Rivalry Competition

If dichoptic cross-orientation interactions are weak or absent, it is possible that the perceptual outcome may be transparency or superposition rather than rivalry alternation. Rivalry could be absent even in a visual system with fully segregated ocular dominance columns, if that system does not have the necessary configural competition mechanisms. In line with this reasoning, Logothetis and coworkers[18,37,38] have shown that rivalry alternations grow progressively more prominent as one ascends the hierarchy of extra-striate areas in the alert behaving monkey. Of major importance for the present discussion, rivalry in monkey cortical cells was shown to occur predominantly in cells that are binocularly innervated[37,38] and not between monocular representations. Rivalry in human cortex is undetectable with functional magnetic resonance imaging in Broadman areas 17 and 18, is weak in Broadman's area 19, and becomes progressively more prominent in the fronto-parietal cortex.[39] Taken together, these recent results point to rivalry being a higher level perceptual process that occurs after convergence of the input from the two eyes.

The tight association previously reported between the development of disparity detection, correlation detection, and rivalry detection[2,3,9,10] may all reflect the emergence of a relatively low-level, interocular-difference detection mechanism. Higher level mechanisms, however, may be needed to produce the fundamental feature of rivalry—periods of alternating physiological and perceptual dominance and suppression. As the mechanisms underlying rivalry appear to be located predominantly in extra-striate cortex, these mechanisms may also take longer to develop.

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