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The Development of Motion Sensitivity During the First Year of Life

RUSSELL D. HAMER,* ANTHONY M. NORCIA*

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Using the sweep visual evoked potential (VEP), we have measured oscillatory displacement thresholds (OMTs) in 49 infants ranging in age from 7 to 54 weeks of age. The stimuli were high-contrast (80%), sine-wave gratings (1 c/deg) undergoing oscillatory displacements at 6 Hz. In addition to the motion thresholds, contrast thresholds for phase-reversing (6 Hz), 1 c/deg gratings were measured in the same session for 26 infants. In the main experiment, responses were recorded at the second harmonic (F2) of the stimulus frequency (12 Hz) under binocular viewing conditions. Our main finding is that, over the age range during which infants' peak contrast sensitivity (CS) first develops to within a factor of 2 of adult CS (9–12 weeks), infants' sensitivity to grating displacement is a factor of ~ 10 less than adults'. Moreover, infants' sensitivity to oscillatory motion undergoes relatively little development over the period between 2 and 15 months postnatal, gradually achieving a factor of 4.5 below adult values by 1 yr of age. Averaged over the entire age range tested, infants' OMTs were 167 sec arc, a factor of 6.4 times higher than the average OMT (26 sec arc) for 13 adults tested under identical conditions. In contrast, the infants' average CS for reversing gratings averaged only a factor of 2.5 less than the adults' average CS. In a second experiment, we took advantage of a developmental asymmetry in the monocular oscillatory motion VEP which allows for unambiguous identification of direction selective responses from very young infants. Monocular motion VEPs were measured in five infants (8–14 weeks) and their data analyzed at the fundamental frequency (F1). Responses at F1 were present in the monocular motion VEP from each infant and were 180 deg out of phase between the two eyes, identifying them as directional cortical responses with a nasalward/temporalward bias. These directional thresholds were equal to or lower than the symmetric (F2) thresholds. The presence of directional asymmetry in the motion VEP and the similarity of the monocular F1 and F2 OMTs support the notion that the OMTs measured in the main experiment were, in fact, derived from the responses of directionally selective cells in visual cortex. These data also imply that the OMTs are not derived from local contrast-reversal responses. Other models to explain infants' relative insensitivity to oscillatory motion are discussed.

Visual development   Direction selectivity   Motion VEP   Oscillatory motion threshold

INTRODUCTION

The study of the development of direction selective mechanisms provides a direct test of the maturation of a specifically cortical function, since direction selectivity is not thought to occur prior to visual cortex (e.g. Braddick, 1993; Wattam-Bell, 1991). Motion-based detection has been demonstrated behaviorally in 6- and 12-week-olds by Aslin and Shea (1990) and in 14-week-olds by Dannemiller and Freedland (1993). Direction selectivity in this same age group has been demonstrated electrophysiologically by Wattam-Bell (1991). The consensus of prior research is that direction selectivity may develop over the first few months of life, depending to some extent on the exact spatio-temporal parameters used to measure it.

In the present study, we have explored another measure of the developmental status of motion mechanisms, the oscillatory motion threshold (OMT) for sine-wave gratings as assessed by the visual evoked potential (VEP). In adults, psychophysically determined oscillatory motion thresholds can be as low as 10–20 sec arc and are relatively constant above ~ 8% contrast in the fovea (Johnston & Wright, 1985; Wright & Johnston, 1985; Nakayama & Silverman, 1985). At high contrast ($\geqslant 40\%$), OMTs fall off very gradually with increasing retinal eccentricity (Wesemann & Norcia, 1992). If infants, like adults, also had a relatively shallow falloff in motion sensitivity with retinal eccentricity, then foveal immaturities (Yuodelis & Hendrickson, 1986) might be less limiting to motion responses than in more foveally-dependent responses (such as grating or vernier acuity). This factor would tend to optimize our ability to measure a relatively high sensitivity to oscillatory grating motion by means of the steady-state VEP.

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*Smith-Kettlewell Eye Research Institute, 2232 Webster Street, San Francisco, CA 94115, U.S.A.

Vector contrast sensitivity and oscillatory motion thresholds

Previous psychophysical studies in adults have considered oscillatory motion thresholds in terms of a decomposition of the oscillatory stimulus into *static* (C_{stat}) and *phase-reversing* (C_{rev}) components (Nakayama & Silverman, 1985; Wesemann & Norcia, 1992). Infants are highly sensitive to low-spatial-frequency gratings undergoing counterphase modulation at 6 Hz (Norcia, Tyler & Allen, 1986; Norcia, Tyler & Hamer, 1990b). In adults, counterphase gratings of these spatio-temporal frequencies are known to be detected by *direction selective* mechanisms. For example, Levinson and Sekuler (1975) pointed out that a counterphase grating can be decomposed into two gratings, each at half contrast, drifting in opposite directions. They showed that detection thresholds for counterphase gratings were determined independently by the observers' thresholds for either of the drifting components, implying that direction selective mechanisms were underlying the detection of the counterphase gratings. Furthermore, over certain ranges of spatial and temporal frequency, observers are able to report the direction of grating motion at contrast threshold (Watson, Thompson, Murphy & Nachmias, 1980; Derrington & Henning, 1993). At other spatio-temporal frequencies, non-directionally selective mechanisms are most sensitive and the direction of motion is not available at contrast threshold (Watson *et al.*, 1980).

One can thus distinguish between contrast sensitivity as a vector quantity, when direction is encoded at threshold, as opposed to a scalar quantity, such as that measured with static targets or high spatial frequency counterphase gratings (Levinson & Sekuler, 1975). In this sense, contrast sensitivity measured with counterphase gratings under certain conditions is a measure of *vector*, or *motion contrast sensitivity*. It is possible that previous infant VEP contrast thresholds measured with low-frequency counterphase reversing gratings were also tapping directionally selective mechanisms, as has been suggested by others for the adult pattern reversal VEP (Kulikowski, 1977; Spekreijse, Dagnelie, Maier & Regan, 1985). Given their high sensitivity to low-frequency counterphase gratings, to the extent to which C_{rev} is also a controlling factor in determining infants' OMTs, infants might be expected to have high sensitivity to oscillatory motion. A natural question thus arises as to the relationship between the developmental sequences of contrast sensitivity for counterphase reversing targets and that of the OMT.

Relationship between the OMT and immaturities in direction selective mechanisms

While one might expect high sensitivity to oscillatory motion based on infants' high contrast sensitivity for counterphase modulation, other evidence suggests that neonatal motion mechanisms are immature. In both young human infants (Norcia, Hamer & Orel-Bixler, 1990a; Norcia, Garcia, Humphry, Holmes, Hamer & Orel-bixler, 1991) and young infant monkeys (Brown, Norcia, Hamer, Wilson & Boothe, 1993), motion VEPs in response to gratings undergoing oscillatory displacements show a striking immaturity under monocular testing conditions—the monocular MVEP is dominated by a strong response at the fundamental frequency (F1) of the stimulus frequency that is 180 deg out of phase between the two eyes. This pattern of response implies the presence of a *developmental motion asymmetry* in the response of directionally selective cortical cells during early infancy in both species. For stimuli similar to those used in the present study, normal human infants' MVEPs progress monotonically toward symmetry and approach an adult-like balance of F1 to second harmonic (F2) responses sometime between 5 and 7 months of age (Norcia *et al.*, 1990, 1991; Brown *et al.*, 1993). This developmental sequence implies that some aspects of motion processing remain immature over the first semester of life.

It is thus an open question as to whether the developmental motion asymmetry (Norcia *et al.*, 1990; Hamer, Norcia, Orel-Bixler & Hoyt, 1993; Brown *et al.*, 1993) is associated with a general immaturity of motion mechanisms, or if there is some dissociation between the maturation processes leading to the development of *symmetrical* motion responses and the maturation of mechanisms that determine the *absolute sensitivity* of directional mechanisms. If infants show high sensitivity to oscillatory motion during the period when the developmental motion asymmetry is still present, or low sensitivity when symmetrical responses to oscillatory motion have developed, this would imply such a dissociation. In fact, we find infants to be relatively *insensitive* to oscillatory motion over the entire first year of life in spite of their well-developed contrast sensitivity.

METHODS

Experiment 1

Observers

Infant observers ($N = 52$) were recruited from parent education classes at a local hospital. All infants were healthy and were born within 2 weeks of expected term. The infants were from 7 to 54 weeks of postnatal age. Recordings were made after informed consent was obtained from the parent(s). Motion thresholds were obtained from 49 of the 52 infants. Contrast thresholds were also measured in the same testing session in 26 of the infants. Thirteen adult observers, each free of ocular pathology and with acuity of 6/6 or better, also participated.

Apparatus

Display. Sinusoidal luminance gratings were generated on a video monitor equipped with a P4 phosphor. For 32 infants, horizontal gratings were used; for 17 infants, vertical gratings were used. Space-average luminance was 80 cd/m^2. z-Axis contrast linearity was obtained with a resistor/diode network and was verified to be within 2% of nominal contrast up to 80% contrast using a Spectra Pritchard 1980A photometer. The display measured 17.6 cm high and 23.6 cm wide, corresponding to 10 × 13.5 deg visual angle at a 1 m viewing distance. Oscillatory motion was created by square-wave modulation of a programmable delay-line which controlled the timing of the gate signal presented to a function generator synchronized to the horizontal scan-line. The device was programmable in 256 10-nsec steps, resulting in a resolution of 1 part in 6000. For the contrast sensitivity measurements, the gratings were square-wave alternated at 12 contrast reversals per sec (6 Hz). The spatial frequency of the gratings was 1 c/deg. Contrast sensitivity had been previously found to be similar for spatial frequencies of 1 c/deg and lower in both infants and adults (Norcia *et al.*, 1990b).

VEP recording. The EEG was pre-amplified by Grass P511J amplifiers equipped with isolation cables (Grass IG3/P511). Two bipolar placements of O_z vs O_1 and O_2 were used. The amplifier bandwidth was 1–100 Hz at − 3 dB and the EEG was digitized at 180 Hz.

Spectrum analysis and threshold estimation. Details of the spectrum analysis techniques and threshold estimation procedure are provided in Norcia, Clarke and Tyler (1985) and Norcia, Tyler, Hamer and Wesemann (1989). Briefly, the amplitude and phase of the second-harmonic (12 Hz) pattern response were determined by a discrete Fourier transform. Motion (or contrast) thresholds were estimated by linear extrapolation to zero amplitude of the function relating VEP amplitude to log stimulus displacement (or log contrast). The portion of the amplitude response used for the threshold extrapolation was determined according to amplitude, phase and noise criteria (see Norcia & Tyler, 1985; Norcia *et al*, 1989) insuring that statistically significant VEP was utilized for the estimation of a cortical threshold.

Procedure

VEP recording. Infants were either seated comfortably in their parent's lap or held upright facing the monitor. Contrast and motion thresholds were measured in separate blocks of trials in either the first or second half of a 1 hr test session. A minimum of 3 trials per condition were obtained. Infants viewed the video monitor with both eyes open.

In each trial, the displacement of the grating was incremented every 0.5 sec in 19 equal logarithmic steps generally spanning a range of 600 sec arc (60 deg of phase) to 1800 sec arc (180 deg, or full pattern-reversal). The sweep range was altered slightly in some cases in order to encompass the full response range of an individual infant with either unusually high or low sensitivity. The same procedure was used for contrast threshold measurements, with the contrast generally sweeping between 0.4% and 40%. The contrast range was extended (to 80%) or reduced somewhat (to 25%), depending on the age and/or sensitivity of the particular infant being tested.

The adults were tested using the same procedures and stimulus conditions as were used for the infants with the following exceptions. (i) Vertical sine-wave gratings were used in all cases. (ii) The sweep range was chosen to be commensurate with the greater sensitivity of the adults. For motion thresholds, the grating displacement swept between 12 (1.2 deg phase) and 180 sec arc (18 deg phase). For contrast thresholds, grating contrast swept between 0.1% and 25% contrast. (iii) A fixed number of trials was used (16 for motion, 12 for contrast). (iv) Finally, adults were tested at an additional, higher spatial frequency (3 c/deg) and at two temporal frequencies (6 and 10 Hz).

Experiment 2

In a second experiment, five additional young infants (8–14 weeks in age) were tested *monocularly*, as well as with both eyes viewing the monitor ("BE" trials). The stimulus conditions were identical to those of the main experiment. The gratings were presented in vertical orientation. The testing procedures were unchanged except for the use of an adhesive eye patch to achieve monocular viewing. For the monocular trials, the fundamental (F1, or 6 Hz) was also analyzed. A minimum of 5 trials were run for each eye. For BE trials, F2 was analyzed as in the larger group comprising the main study.

RESULTS

Experiment 1

Oscillatory motion and contrast response functions

Figure 1 displays sweep VEP data from individual infants for both oscillatory motion (left) and contrast (right) stimuli. Each panel represents the vector average, on a bin-by-bin basis, of 3–6 sweeps of grating displacement or grating contrast. Upper portions of the panels show the amplitude (in μV) of the second harmonic (12 Hz) response, plotted as solid curve. A cortical threshold was estimated by linear extrapolation (solid regression line) along the amplitude response to the displacement (or contrast) value corresponding to 0 μV. The vertical dashed lines demarcate the portion of the amplitude response that was used for the extrapolation. The noise estimate for each analysis bin is indicated by the open squares. The average noise for the entire 10-sec trial appears as a dotted line.

The phase of the response (in rad) appears as the solid curve in the lower portion of each panel. At the beginning of each sweep, before a significant VEP is generated, the phase changes rapidly, consistent with non-visually-driven activity. Once significant driving by the stimulus begins, the phase of the response stabilizes, changing more slowly from bin to bin, indicating that the response is time-locked to the stimulus. A phase function that slopes downward to the right represents a progressively *leading* phase response; if it slopes upward, it represents a progressively *lagging* phase response.

The response functions manifest a number of characteristic forms. For both oscillatory motion and contrast reversal, the amplitude function tends to take on one of two forms: either a *monotonic* (linear) function of log motion amplitude (or log% contrast); or a *non-monotonic* function of log stimulus amplitude. The non-monotonic responses tend to take on a step-like pattern [two monotonic, linear rising portions separated by a relatively constant portion; e.g. see Fig. 1 (c and f)]. However, some appear as a clear, two-peaked function [e.g. Fig. 1 (b and g)]. These non-monotonic response patterns are suggestive of a transition between two response mechanisms (e.g. Norcia *et al.*, 1989).

Overall, the phase of the response is generally either constant, or monotonically leading the stimulus phase over the range where the response amplitude is significant. Examples of constant phase functions are shown in Fig. 1(a) (motion sweep) and Fig. 1(d) (contrast sweep). For infant ZW, the driven phase response for oscillatory motion [Fig. 1(a)] begins at the first analysis cursor (at $+0.21\pi$) and ends at $+0.26\pi$ rad. This corresponds to a difference in VEP timing of ~ 2.1 msec (2.5% of the 12 Hz period). The total variation in phase within the driven response corresponds to a total timing variation

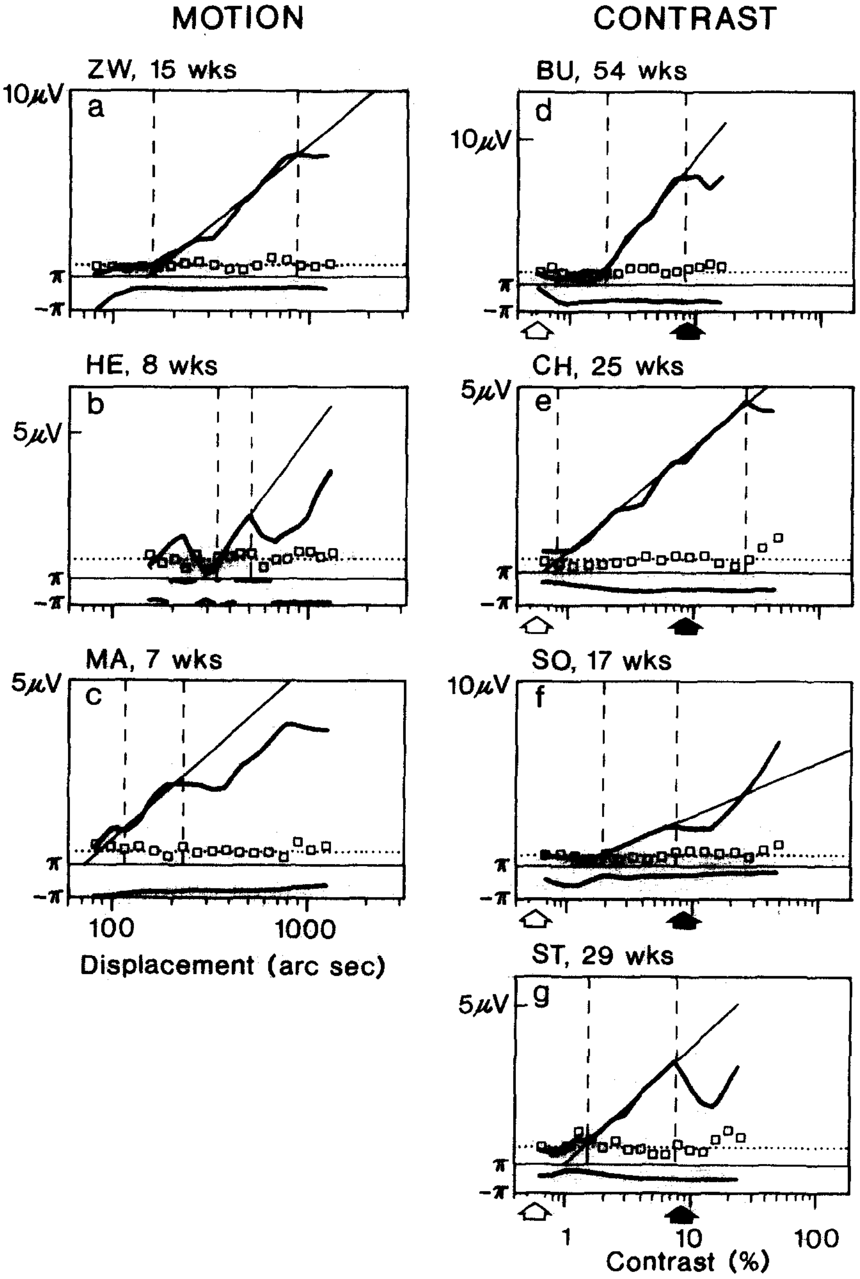

FIGURE 1. Sweep VEP data from individual infants for oscillatory motion (left column) and contrast reversal (right column). Each panel is divided into upper (amplitude responses) and lower (phase responses) portions. The VEP amplitude axes are linear, starting from $0\,\mu$V at the horizontal line marking a response phase of π. Bold curves indicate the VEP amplitude at the second harmonic of the stimulus (12 Hz). Linear extrapolation to threshold is indicated by the lines through the data. The small open squares show the average noise amplitude in each analysis bin. The noise amplitude averaged over a full 10-sec sweep is indicated by a horizontal dotted line. The bold curve in the lower portion of each panel represents the response phase, ranging from $-\pi$ to π. The large open arrows mark the average adult VEP threshold for contrast reversal. The large solid arrows mark the average C_{rev} (described in text and in Fig. 6) for 49 infants. For oscillatory motion, the maximum SNR ranges between 6.3 (b) to 13.5 (a). For contrast, the maximum SNR ranges between 5.6 (g) to 15.3 (f).

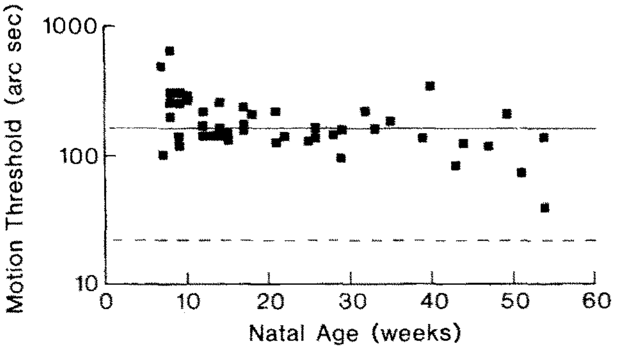

FIGURE 2. Oscillatory motion VEP thresholds (OMT) as a function of age for 49 infants. The horizontal solid line marks the geometric mean threshold for the infants (167 sec arc ±0.21 log units). The average motion threshold for 10 adults was 26 sec arc (±0.18 log units), a factor of 6.4 times lower than the infants' mean threshold (horizontal dashed line). A linear regression fit to the data [log OMT = 2.3664 − 0.00632(age), $r = -0.4764$] has a slope that is significantly less than 0 ($t = 3.711$, d.f. = 47, $P < 0.0005$, one-tailed test). Note that infants' motion thresholds decrease by only a factor of 2.3 over the entire first postnatal year.

of only 7.2 msec. For the contrast response [infant BU, Fig. 1(d)], the total variation in phase after the first analysis cursor was 0.17π rad, corresponding to a total variation in VEP timing of 6.9 msec (8.3% of the 12 Hz period).

In some instances, the phase slightly lags the stimulus. Unlike the amplitude functions, the phase responses tend to dichotomize between OMT and CS responses. Constant phase patterns are manifested in both the motion and contrast data. However, we find that phase lags are more common in response to oscillatory motion, whereas phase leads are more common for ordinary contrast reversal [e.g. Fig. 1(e, g)].

Developmental sequence for sensitivity to oscillatory grating motion

Figure 2 presents the oscillatory motion thresholds as a function of age for 49 infants. The geometric mean threshold was 167 sec arc (SD = ±0.21 log units) indicated by the horizontal solid line. Of the 13 adults, 10 yielded measurable motion-VEP thresholds for the 1 c/deg stimulus presented at 6 Hz. The geometric mean motion threshold for the 10 adults was 26 sec arc (dashed line; SD = ±0.18 log units). The adults' motion thresholds were virtually identical when tested at 3 c/deg (23 sec arc at 6 Hz, $N = 11$; 27 sec arc at 10 Hz, $N = 10$).

Most notable in this figure is that there is little improvement in the oscillatory motion threshold as a function of age over the entire first postnatal year. A linear regression fit to the data has a slope of −0.0063 log sec arc/week ($r = -0.476$). Although this slope is significantly less than zero (the 99% confidence limits for the regression slope using a one-tailed t-test range from −0.011 log sec arc/week to −0.002 log sec arc/week), it corresponds to an improvement in OMT by a factor of only 2.32 over the 47-week age range tested. Based on the shallow age trend, the motion thresholds for the infants range from ~10 times higher than adults for young infants (≤10 weeks), to ~4.5 times higher than adults for older infants (≥40 weeks). Averaged over the full age range, the infants' geometric mean threshold (horizontal solid line) was a factor of 6.4 times higher than the mean adult threshold.

Developmental sequence for contrast sensitivity

Contrast thresholds (CT) were also measured in the same session as the motion thresholds in 26 of the 49 infants. These are shown in Fig. 3. Except for the youngest infants, CT is relatively constant over the entire age range, similar to the motion VEP data (Fig. 2). The mean CT for all 26 infants was 1.5% (±0.36 log units) (i.e. a CS of 66). The average CT for the 20 infants older than 9 weeks of age was 1.19% (± 0.28 log units), only a factor of 2 less than the average adult CT of 0.6% (i.e. CS = 167 ± 0.23 log units, $N = 10$). These results are consistent with prior sweep VEP measures of CS in infants 9 weeks of age and older (Norcia *et al.*, 1986, 1990b; Norcia, Tyler & Hamer, 1988).

Unlike the motion responses, where infants were 5–10 times less sensitive than adults, the infants' mean CT (1.5%) is only a factor of 2.5 times less than the mean adult CT (0.6%, $N = 10$). If the infants under 10 weeks of age ($N = 6$) are excluded from the comparison, in order to restrict the comparison to the age range where infants' contrast responses are known to be relatively constant with age (Norcia *et al*, 1990b), then adult:infant ratios are 1.95 for CT and 5.3 for motion. It is clear that the infants' cortical motion responses are substantially less mature relative to adults' than are their pattern reversal responses.

Developmental sequence for response phase

The steady-state VEP allows for an independent evaluation of the developmental time–course of the relative timing of the evoked response by analysis of the phase at various ages. This is shown in Fig. 4. In Fig. 4(a), we have plotted the raw phase values (from 0 to 360 deg) for the oscillatory motion sweeps from 49 infants. The data from the left and right-hemisphere

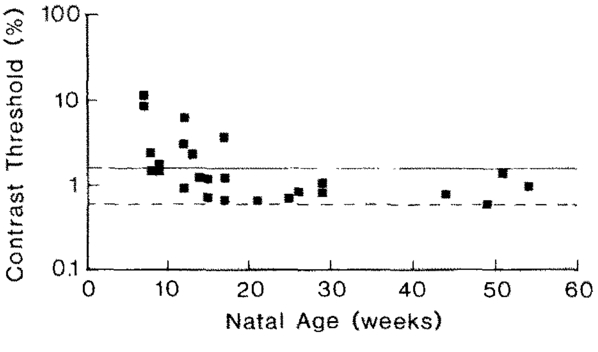

FIGURE 3. VEP contrast thresholds (CT), in% Michelson contrast, as a function of age for 26 of the 49 infants. All lines and symbols are as in Fig. 2. Except for the youngest infants, CT is relatively constant over the entire age range. Unlike the motion responses, where infants were 6.4 times less sensitive than adults, the infants' mean CT (1.5%) is only a factor of 2.5 less than the mean adult CT (0.6%, $N = 10$).

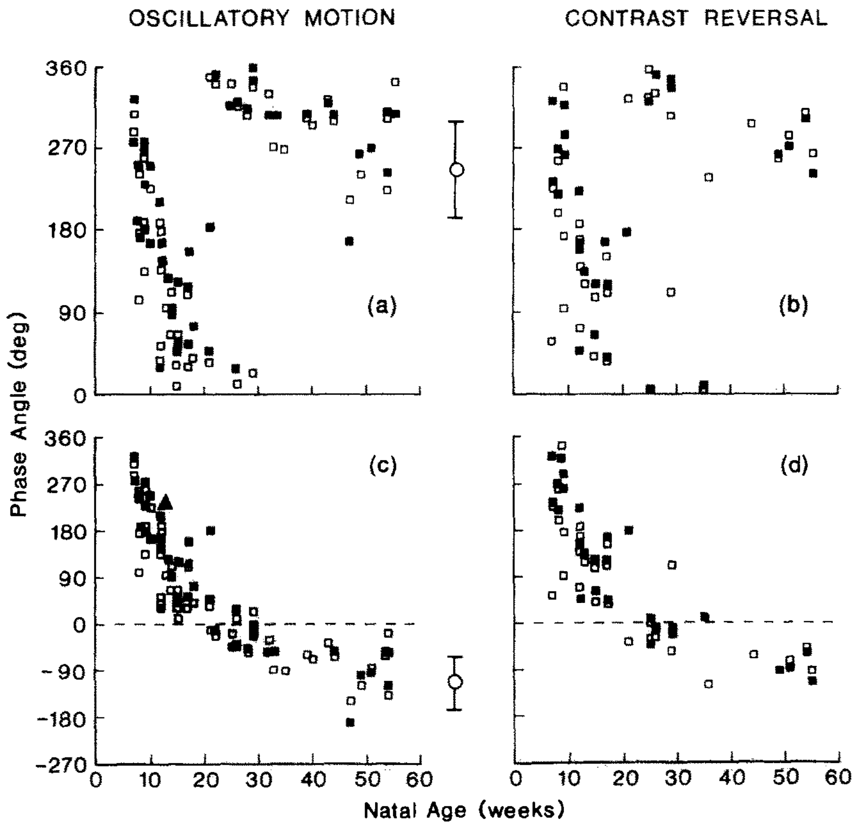

FIGURE 4. Development of steady-state VEP response phase. Top panels show the average phase for the final three bins of the oscillatory motion (a) and contrast (b) sweeps, on a 0–360 deg range. Open and solid squares are for the left and right hemisphere recording channels, respectively. In the bottom panels (c, d), the phase was "unwrapped" (i.e. 360 deg subtracted from the raw phase values) for the older infants (> 20 weeks of age). See text for details. Average phase for 10 adults (± 2SD) is indicated in each panel by the large open circle. Note that the VEP phase advances by ~ 300 deg between 7 and 18 weeks of age, corresponding to a VEP timing advance of ~ 69 msec, or an average of 6.3 msec per week.

channels are shown as open and solid symbols, respectively. Each point is the average of the phase values in the last three bins of the displacement sweep, encompassing displacements ranging from 600 to 1800 sec arc. These phase values were chosen because they were derived from the high-SNR (signal-to-noise-ratio) responses of the displacement sweep. The comparable, high-SNR phase data for contrast sweeps (26 infants) are shown in Fig 4(b). Average phase values (± 2SD) for 10 adults are shown in each panel by a large open circle.

Between 7 and 18 weeks of age, the response phase decreases rapidly by ~ 300 deg, corresponding to an average advance of VEP timing of ~ 69 msec for the 12 Hz second harmonic, or an average advance of ~ 6.3 msec per week. The VEP response phase continues to decrease, although its rate of change with age decreases after ~ 20 weeks of age. At this time, the raw phase data manifests a discontinuity, jumping back up to values near 360 deg. The steady-state VEP phase cannot distinguish between 2π cycles of phase (e.g. a 20 deg shift is indistinguishable from 380 deg shift). Hence, assuming that the developmental changes in VEP timing are continuous, we presume that the phase data for infants $\geqslant$20 weeks of age have "wrapped around", i.e. they have advanced by >360 deg relative to the phase data for young infants. The "unwrapped" phase data for motion and contrast sweeps are shown in the corresponding bottom panels of Fig. 4 (c, d). In these panels, 360 deg was subtracted from all the phase values for infants over 20 weeks of age.† The unwrapped phase data illustrate that the developmental time-course for phase is identical for both contrast and oscillatory motion stimuli.

Figure 5 compares our steady-state phase data for oscillatory motion [taken from Fig. 4(c)] with the implicit-time data [Fig. 5(b)] from an earlier study by Sokol and Jones (1979). For this comparison, our phase data have been converted to apparent latency (Regan, 1989) according to the relation,

$$\text{apparent latency (msec)} = n * T_2 + (T_2/360) * \phi + D$$

where ϕ is the steady-state phase in deg, T_2 is the period of the second harmonic stimulus (83.3 msec), n is an indeterminate positive integer ($n \geqslant 1$) and D is the total effective delay in the VEP apparatus at the output of the amplifiers. D was measured to be 42.6 msec, corresponding

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†Four infants > 20 weeks had unusually small phase advances relative to their age peers. Hence, the phase-wrapping procedure resulted in too great a shift for these infants and their data were thus left "unwrapped".

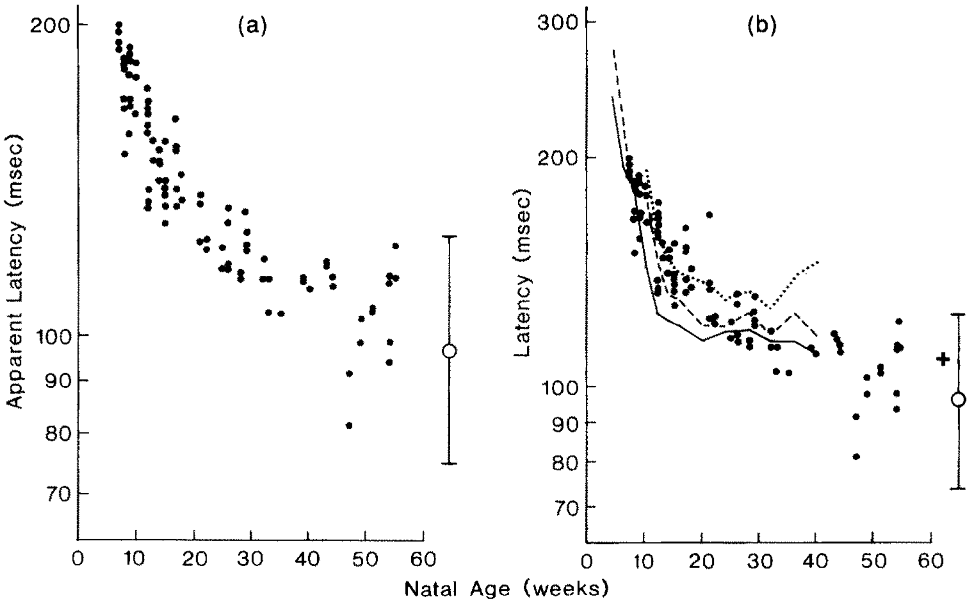

FIGURE 5. (a) Development of apparent latency of the steady-state MVEP. The steady-state phase data from Fig. 4(c) were converted to apparent latency according to the relation given in the text. Apparent latency is plotted on a logarithmic axis. The geometric mean apparent latency (± 2SD) for 10 adults is shown as a large open circle to the right of the graph. (b) Comparison of steady-state MVEP apparent latency with the developmental progression of VEP implicit time (from Fig. 7 in Sokol & Jones, 1979). The implicit-time data for transient pattern reversal of 15, 30 and 60 min arc checks are indicated by the three curves (dotted, dashed and solid, respectively). The + marks the mean implicit time for 20 adults tested by Sokol and Jones. Both steady-state and transient VEP measures indicate a decrease in latency of ~ 70 msec between 7 and 18 weeks of age. However, the implicit-time data manifest a marked knee between 10 and 20 weeks and exhibit little or no decrease thereafter. In contrast, our apparent latencies continue to develop between 10 weeks and the end of the first year.

to an absolute equipment phase of 184 deg at 12 Hz.† The term $n*T_2$ is required since the absolute delay in the nervous system can only be determined to within a 2π modulus based on steady-state VEP phase. It is unreasonable for n to equal 0, since, in this case, the unwrapped phase values for the older infants ($> \sim 20$ weeks) and adults would correspond to negative apparent latencies. We have set $n = 1$ since this yields adult apparent latency values (96.4 msec) that are close to the adult values for implicit time obtained by Sokol and Jones [see + in Fig. 5(b)] and by others (Moskowitz & Cook, 1983; McCulloch & Skarf, 1991; Fiorentini & Trimarchi, 1992).

Sokol and Jones (1979) measured VEP implicit times in infants in response to transiently presented checkerboard patterns (phase-reversed at 1.88 Hz) of various sizes. The implicit-time data for 15, 30 and 60 min arc checks are indicated by the three curves (dotted, dashed and solid, respectively) in Fig. 5(b). These data are representative of similar data obtained in three other studies (Moskowitz & Sokol, 1983; McCulloch & Skarf, 1991; Fiorentini & Trimarchi, 1992). The checkerboard patterns had fundamental spatial frequencies along the diagonal of 1.4, 0.7 and 0.35 c/deg, respectively.

The data in Fig. 5 are plotted on semi-logarithmic axes (log effective latency vs age) under the hypothesis that the neural delays might mature according to a simple exponential process. This hypothesis would predict that, on these axes, all the neural latency data would fall on a single line with a negative slope corresponding to the time constant of the process. Such a simple model is clearly inadequate to account for either Sokol and Jones' implicit-time data or our steady-state apparent latency data over the full age ranges tested. In both data sets, there is a steep, linear falloff of log latency in young infants ($<$ 10–16 weeks) and a transition to aymptotic performance where latencies approach adult values. In the implicit-time data, this transition is relatively sharp, in comparison to our apparent latencies which continue to decrease over the entire first postnatal year.

In fact, it is noteworthy that VEP phase continues to decrease both for oscillatory motion and contrast reversal (Figs 4 and 5) after 2 months of age, whereas infants' contrast sensitivity has reached nearly adult values by 9 weeks of age (Norcia *et al.*, 1990b). This indicates that increasing contrast sensitivity is not the basis of decreases in neural latency after 2 months of age.

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†The DFT analysis software calculates phase assuming the pattern-reversal stimulus to be in cosine phase. However, the stimulus always starts in sine phase with respect to the data collection. This factor contributes an absolute phase shift of 90 deg at the stimulus frequency, i.e. 180 deg for the second harmonic. An additional phase shift due to analog filtering in the VEP recording channels was determined to be negligible (4 deg). Hence the total equipment-related absolute phase was 184 deg, corresponding to an apparent latency of 42.6 msec at the second harmonic. This factor has been accounted for only in the data presented in Fig. 5, where absolute phase is important for comparison with prior studies.

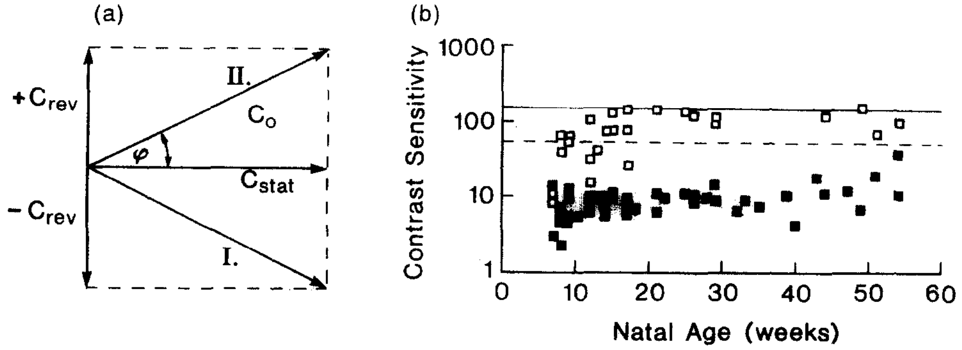

FIGURE 6. (a) Decomposition of an oscillating grating of contrast C_o into orthogonal static (C_{stat}) and counterphase-reversing (C_{rev}) components. In this decomposition, the two components are in fixed 90 deg spatial phase. $C_{stat} = C_o\cos(\phi)$ and $C_{rev} = C_o\sin(\phi)$, where 2ϕ is the change in spatial phase of the grating at threshold. During one-half cycle of displacement, the grating jumps from position I to position II, through a phase angle of 2ϕ. The static component, C_{stat}, does not change. The component, C_{rev}, however, undergoes a 180 deg phase-reversal. A full sweep of grating displacement corresponds to a sweep of ϕ from 0 to 90 deg, resulting in a sweep of the contrast of the counterphase component from 0 (all of the contrast in the static component, C_{stat}) to 1.0 (all of the contrast in C_{rev}). (b) CS data from 26 infants shown in Fig. 3 (open squares), along with the comparable motion-VEP data plotted in terms of the sensitivity to the modulating component ($100/C_{rev}$, solid squares) of the motion stimulus. Infants' cortical responses were much less sensitive to the phase-reversing component of the oscillating grating than they were to ordinary counterphase-reversing gratings: the average ratio of CS/C_{rev} for the 16 infants older than 10 weeks of age was 9.7 compared with 3.5 for adults.

Decomposition of oscillatory motion into phase-reversing and static components

A sinusoidal grating undergoing oscillatory motion can be decomposed analytically into the sum of a static sinusoidal grating and a counterphase-reversing grating that is in spatial quadrature (Nakayama & Silverman, 1985; Wesemann & Norcia, 1992). This decomposition provides a means to consider the oscillatory motion threshold in terms of *modulation sensitivity*, rather than in terms of a *spatial displacement*. Perhaps the difference between the motion and contrast data can be accounted for by comparing the responses to only the modulating components of the stimuli used.

Figure 6(a) depicts the decomposition of the motion stimulus onto its orthogonal static (C_{stat}) and counterphase-reversing (C_{rev}) contrast components. Given an oscillating grating of contrast C_o, the modulation amplitude of these two components may be derived from the following simple equations:

$$C_{stat} = C_o\cos(\phi); \quad C_{rev} = C_o\sin(\phi) \qquad (1)$$

where 2ϕ is the change in spatial phase of the grating at threshold. During one-half cycle of displacement, the grating jumps from position I to position II, i.e. through a phase angle of 2ϕ. The static component, C_{stat}, does not change. The component, C_{rev}, however, changes its sign, thus undergoing a 180 deg phase-reversal. A full sweep of grating displacement may be thought of as a sweep of ϕ from 0 to 90 deg, resulting in a sweep of the contrast of the phase-reversing component from 0 (all of the contrast in the static component, C_{stat}) to 1.0 (all of the contrast in C_{rev}).

Figure 6(b) shows the data from Fig. 3 plotted in terms of CS (open squares), along with the comparable motion-VEP data (solid squares) plotted in terms of the sensitivity to the modulating component ($100/C_{rev}$) of the motion stimulus. If the infants' motion VEPs could be accounted for entirely in terms of cortical responses to the contrast-reversing component of the stimulus, then the two data sets should have been congruent on this plot. However, the cortical responses from each of the 26 infants were more sensitive to counterphase reversal than to the reversing component of the oscillating grating: the average ratio of CS/C_{rev} for the 26 infants was 7.7. For infants older than 10 weeks of age, the ratio of CS to C_{rev} is a full factor of 10. For the adults ($N = 10$), sensitivity to the phase-reversing grating was also higher than to the reversing component of the oscillating grating. However, CS/C_{rev} was only 3.5 for the adults.

The relative insensitivity to C_{rev} may also be seen in individual infants' data in Fig. 1. The large solid arrows shown on the contrast abscissae of Fig. 1 indicate the geometric mean C_{rev} (8.6%) calculated from the OMTs for all 49 infants. In each case, the average C_{rev} falls well above the extrapolated contrast threshold.

Figure 7 illustrates a within-subjects comparison of VEPs for sweeps of contrast undergoing counterphase reversal (solid curves) and oscillatory motion sweeps (dashed curves), where the motion VEPs have been plotted in terms of the modulating component of the motion stimulus (C_{rev}) for each bin of the trial. Panel a shows the data from one adult observer (RDH). For this observer, the threshold value for C_{rev} was 1.6 times higher than the contrast threshold (1%). For infants JO [Fig. 7(b)] and EV [Fig. 7(c)], respectively, C_{rev} thresholds were 11.4 and 13.1 times higher than the contrast thresholds.

The data in Fig. 7 also allow for a within-subjects comparison of the forms of the amplitude and phase responses for the two types of sweeps. For adult RDH, once the driven response begins, the VEP amplitude increases linearly with log contrast with nearly the same slope for both motion and counterphase contrast reversal. Above ~4% contrast, the contrast VEP appears to shift to a second mechanism (VEP source), whereupon it becomes coincident with the motion response. The driven phase response is nearly identical for motion and counterphase reversal and is relatively constant over the entire driven response range.

For infant JO [Fig. 7(b)], the response patterns are also quite similar for the two tasks: the VEP amplitude in each case is monotonic, linearly increasing with log contrast for more than half the sweep range. The temporal phase pattern for the driven responses are also similar. In both instances, they are relatively constant. The driven phase response for oscillatory motion begins at -0.21π and ends at -0.23π rad, indicating strong time-locking of the VEP to the stimulus reversals. The total variation in VEP timing over the driven response is 8.8 msec (for oscillatory motion) and 11.6 msec (for counterphase reversal). The absolute temporal phase is nearly the same for the two tasks: the phase stabilizes at $\sim -0.2\pi$ rad for both motion and contrast sweeps. Note that the contrast VEP attains a peak SNR of 6.2 at $\sim$ 5% contrast and saturates thereafter. However, the motion VEP does not begin to emerge from the noise until after C_{rev} exceeds $\sim$ 10% contrast. The very first bin of the motion VEP corresponds to a C_{rev} of $\sim$ 5% contrast.

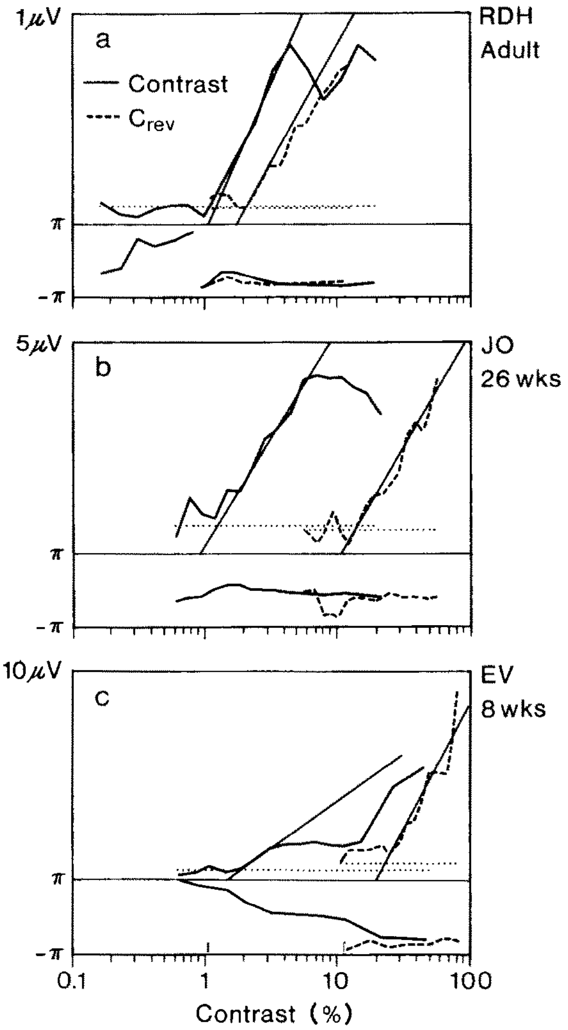

FIGURE 7. Within-subjects comparison of contrast reversal (solid curves) and oscillatory motion (dashed curves) VEPs for one adult (a) and two infants (b, c). Motion VEPs have been plotted in terms of the modulating component of the motion stimulus (C_{rev}) for each bin of the trial. For the infants, the VEP amplitude and phase records shown are the vector average of 4–5 stimulus sweeps. The horizontal dotted lines indicate the average noise amplitudes for the corresponding VEP records. Adult observer RDH (a) had an oscillatory motion threshold of 23.4 sec arc and a contrast threshold of 1%. In terms of C_{rev}, RDH's motion threshold was 1.6%, 1.6 times the contrast threshold. For infant JO (b), threshold C_{rev} was 9.5%, a factor of 11.4 times higher than the contrast reversal threshold (0.83%). For infant EV (c), the C_{rev} (19.5%) and contrast (1.49%) thresholds differed by a factor of 13.1. The oscillatory motion thresholds for the two infants in displacement units were 137 sec arc (JO) and 280 sec arc (EV).

For infant EV, the contrast VEP has two components, a low- and a high-contrast limb, with a horizontal transition between them. The high-contrast limb is similar to the initial rising portion of the motion VEP. The phase responses for motion and counterphase contrast reversal differ in form. A progressive phase lead is present in the initial rising portion of each of the limbs of the counterphase response, whereas the motion VEP has a driven phase response that is constant, or slightly lagging. The two phase responses stabilize at the highest contrasts at nearly the same absolute phase.

Experiment 2

The absolute sensitivity of directionally selective cortical mechanisms

The oscillatory motion thresholds shown in Fig. 2 were based on the symmetric (F2) component of the MVEP with BE viewing the stimulus. Both direction selective and non-direction selective mechanisms could contribute at F2. It would be important to determine the relative sensitivity of direction selective mechanisms compared to non-direction selective mechanisms, to determine which type is determining the OMT. We took advantage of the presence of the developmental motion asymmetry in young infants which allows for the unambiguous identification of direction selective cortical responses (Norcia *et al.*, 1991; Hamer *et al.*, 1993). If the threshold of these direction specific responses is comparable to or less than the binocular F2 thresholds, we can infer that there are not any non-directionally selective units with greater sensitivity. If we find F2 responses of grating displacements below the specifically directional response threshold, we would then have to conclude that the true motion threshold was in fact higher than that of other non-direction specific mechanisms manifesting themselves at F2.

We tested five infants between 8 and 14 weeks of age monocularly and analyzed their VEPs at the fundamental frequency (F1). The amplitude responses for the three infants who completed LE, RE and BE testing are shown in three corresponding columns of data panels in Fig. 8. For each infant, the top two panels show the monocular motion VEPs analyzed at F1, with the F1 thresholds marked on the abscissa by a solid arrow. The monocular F2 thresholds in each case are shown by the open arrows. The third row of panels in Fig. 8 shows the BE data analyzed at F2. The large asterisk on each abscissa marks the geometric mean (204 sec arc) of the thresholds from $\leqslant$ 15 weeks of age these infants' age peers (i.e. 23 infants

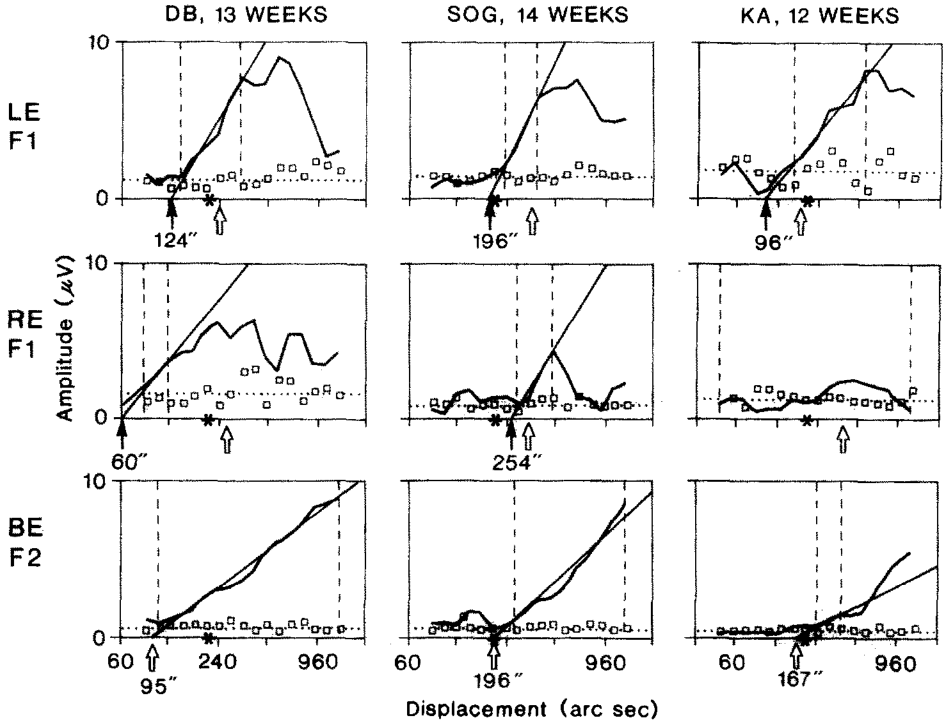

FIGURE 8. Monocular MVEPs from three infants (DB, 13 weeks; SOG, 14 weeks; KA, 12 weeks) based on the asymmetric (F1) responses (top two rows). Extrapolated thresholds are indicated by the solid arrows on the abscissa. The corresponding extrapolated thresholds for monocular MVEPs analyzed at F2 are indicated by the open arrows. Each record shown represents a vector average of 5–8 sweep trials. The bottom row shows the infants' BE motion VEPs analyzed at the symmetric component (F2). The tick marks on the abscissa indicate factors of 2 increases in stimulus displacement. The large asterisk on each abscissa marks the geometric mean of all the (BE, F2) thresholds shown in Fig. 2 for infants ≤ 15 weeks of age (204 sec arc, ± 0.21 log units, $N = 23$). Note that the lower of the two monocular motion thresholds based on F1 responses (solid arrows) are in each case less than or equal to the F2 threshold (open arrows).

from Fig. 2). The monocular response phase data for the three infants are shown in Fig. 9.

The amplitude responses from a 13-week-old infant (DB) are shown in the left column of panels in Fig. 8. DB's best monocular F1 threshold (RE ~ 60 sec arc) is slightly better than her BE (F2) threshold (95 sec arc). Moreover, DB's monocular phase data [Fig. 9(top)] maintain a nearly perfect 180-deg phase relationship throughout the entire portion of the trial in which the displacement exceeds the extrapolated threshold. DB's monocular F2 thresholds (open arrows, LE, 240 sec arc; RE, 260 sec arc) are higher than her monocular F1 and BE thresholds.

This pattern of response can be seen to hold in general for the other two infants (SOG, 14 weeks and KA, 12 weeks). In each case, the best monocular F1 thresholds are never worse than the BE F2 thresholds, and the monocular phase responses at F1 are in 180-deg phase relationship between the two eyes (Fig. 9). For infant SOG, the BE threshold was 196 sec arc, compared to monocular F1 thresholds that straddled this value (254 sec arc for the RE and 147 sec arc for the LE). For the youngest infant (KA), a criterion amplitude was not achieved in the RE F1 response. However, KA's F1 threshold for the LE (96 sec arc) was better than the BE F2 threshold (140 sec arc). The monocular F2 thresholds were also higher than the F1 thresholds for these two infants. These results indicate that directionally selective mechanisms are the most sensitive ones responding to the oscillatory motion stimulus.

Sensitivity to counterphase reversing gratings (CS) was also measured in the three infants shown in Figs 8 and 9 in order to ensure that their CS was neither inordinately high nor low. Their CSs were, in fact, typical of the larger group of infants whose data are shown in Fig. 3, i.e. 78 (DB), 68 (SOG) and 33 (KA). Their binocular F2 thresholds were also typical of the larger group (asterisks).

It is important to note that the monocular F1 responses for all five infants manifested the developmental motion asymmetry at all but the smallest grating displacements, including those at the extrapolated threshold (Fig. 9). This implies that the extrapolated F1 thresholds were, indeed, based on the responses of directionally selective cortical cells. The similarity between the F1 thresholds and BE (F2) thresholds within infants is consistent with the hypothesis that OMTs in the main experiment, including those from older infants, reflect the responses from direction selective cortical cells.

DISCUSSION

We have found that infants are relatively insensitive to oscillatory grating motion, requiring on average nearly 3 min arc of displacement before significant motion

VEPs are generated. Under the same testing conditions, adult motion thresholds were < 0.5 min arc. Most striking are the findings that infants' motion sensitivity increases by only a factor of 2.3 between 7 weeks of age to the end of the first postnatal year. Over this age range, infants' motion thresholds mature from a factor of 10 higher than adults to within a factor of 5 of adult motion sensitivity. Averaged over the full age range tested, infants are a factor of 6.4 less sensitive to oscillatory motion than the adults. Yet, over the same age range, infants' sensitivity for counterphase-reversing gratings of the same spatio-temporal frequency is, on average, within a factor of ~ 2 of adult CS, based on the combined results from the present study and a more extensive prior investigation of CS development (Norcia *et al.*, 1990b).

Motion-based detection of oscillatory grating displacements in infants

The developmental motion asymmetry is a unique signature that can be used to unambiguously identify responses from cortical motion mechanisms in young infants. Previously Norcia *et al.* (1990a, 1991) have shown that monocular oscillatory motion VEPs in infants under ~ 20 weeks of age exhibit a striking nasalward/temporalward asymmetry for the stimuli used in the present study. The asymmetry is manifested in the form of a strong response at F1, biased towards *opposite physical directions of motion in the two eyes* (i.e. the LE and RE motion VEPs are 180 deg out of phase). The monocular F1 responses cannot derive from local (unsigned) contrast responses since these would generate a VEP dominated by even harmonics. Imbalances between ON- and OFF-channels could, in principle, produce odd harmonics, but these would not be expected to differ by 180 deg of temporal phase between the two eyes. Thus, an asymmetric response pattern in the monocular motion VEPs such as observed in Expt 2 *can only occur as a result of a directionally encoded response* (Norcia *et al.*, 1991; Hamer *et al.*, 1993) and can be used to infer the presence of directionally selective response components. Unfortunately, the test cannot be applied to older infants (or normal adults) because once symmetrical responses have developed, the monocular motion VEP is dominated by the even (symmetric) harmonics and significant F1 responses are generally no longer present.

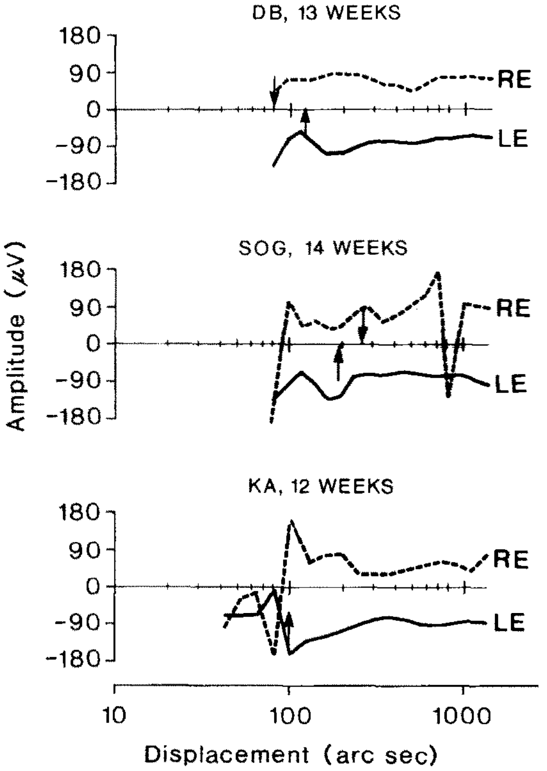

FIGURE 9. Monocular motion VEP response phases corresponding to the monocular amplitude data shown in Fig. 8. Note that the LE and RE responses are 180 deg out of phase, indicating the presence of the developmental motion asymmetry. This pattern of response unambiguoulsy identifies the MVEPs shown in the top two panels of Fig. 8 as deriving from direction selective cortical cells with a nasalward/temporalward direction bias. The developmental motion asymmetry is present starting at displacement amplitudes as small as the extrapolated motion threshold (arrows) and continues out to the largest grating displacements presented (nearly full counterphase reversal).

The results of Expt 2 (Figs 8 and 9) are consistent with the hypothesis that the oscillatory motion VEP thresholds in both experiments were based on the responses of directionally selective cells in visual cortex. In the five young infants tested in Expt 2, the F1 thresholds were clearly those of directional mechanisms, since the signature of directional selectivity, the developmental motion asymmetry, was present for all grating displacements, even at *the extrapolated threshold* (Fig. 9). In addition, the best of these directional thresholds were never worse than either the monocular or binocular OMTs based on the F2 component. This implies that direction selective mechanisms were the most sensitive mechanisms responding to the oscillatory motion stimulus. Moreover, unless the sensitivity of directional mechanisms were to *decrease* with development, it is reasonable to infer that they remain the most sensitive mechanism responding to the oscillatory stimulus at the older ages, where the developmental motion asymmetry cannot be measured. The relationship between the sensitivities of directional mechanisms and those controlling sensitivity to local contrast cannot change since both the OMTs and VEP contrast-reversal thresholds are nearly constant after 3 months of age (Figs 2 and 3).

The BE F2 responses measured in both experiments may thus be interpreted according to the following notion. For older infants (with symmetrical motion responses), BE F2 responses derive from either binocular (symmetric) motion mechanisms, or the sum of in-phase RE and LE mechanisms with symmetric motion responses. For young infants, who still have the developmental motion asymmetry, the interpretation of the BE data is more complicated. F1 signals generated from each eye add out-of-phase, yielding no net signal to record at the electrode locus.

The evoked response is a record of mass activity that reflects population biases in the relative number of units with a particular direction bias. It is unlikely that the population would be entirely comprised of units selective to one direction of motion. One would thus expect some response to each direction of motion to occur from a combination of direction specific mechanisms and also non-direction specific mechanisms. Components of the directional population response would appear at F2, as well as at F1. The symmetric component of the directional response will be enhanced as the proportion of cells capable of responding to each direction becomes equal.

We interpret the BE F2 responses observed Expt 2 (Figs 8 and 9) as reflecting the net symmetric response of directional and non-directional mechanisms. However, we note that the monocular F2 thresholds were higher than the BE F2 thresholds. This suggests that at under the spatio-temporal conditions used in the present experiments, the BE responses may have been reflecting facilitative interactions between the LE and RE responses. To the extent that the symmetric response components are associated with binocular processes, it is not unreasonable to expect non-linear interactions to occur under binocular stimulation.

Are counterphase-reversing gratings detected by motion mechanisms in infants?

In adults it is generally considered that under some spatio-temporal conditions, counterphase reversing gratings are detected on the basis of directionally selective mechanisms. Levinson and Sekuler (1975) showed that reversing gratings can be considered to be the sum of two gratings drifting in opposite directions. Detection threshold was reached when the contrast of the drifting components were at their independent threshold. Whether the same situation holds in infants is unknown at this time. In our data, direction selective mechanisms are demonstrably present at 6 Hz, 1 c/deg: the developmental motion asymmetry is apparent over the entire range of displacements from threshold up to nearly 180 deg (see Fig. 9; the response in the last bin plotted occurred at an average displacement of 23 minutes; reversal occurred during the last 0.5 sec of the trial). It is thus quite possible that the pattern reversal response is tapping direction selective mechanisms at 6 Hz, 1 c/deg in infants.

Development of response dynamics

We have found contrast sensitivity to be constant after about 10 weeks of age, replicating our prior results (Norcia *et al.*, 1990a,b). However, response phase continues to change throughout the first postnatal year for both contrast reversal and oscillatory motion stimuli (Figs 4 and 5). Between 12 weeks and the asymptotic adult value, phase decreases by about 270 deg (Fig. 4), corresponding to an apparent latency decrease of 62.5 msec (Fig. 5). Our results differ in this respect from previous studies which have found that VEP implicit time for the checkerboard reversal VEP develops much more slowly after 10–15 weeks of age (Sokol & Jones, 1979; Moskowitz & Sokol, 1983; McCulloch & Skarf, 1991). For example, pattern reversal implicit time decreases by only 22 msec (McCulloch & Skarf, 1991) to 36 msec (Sokol & Jones, 1979) between 12 weeks and adulthood for 30 min arc checks. The reason for this difference between our results and prior work is unclear. However, there are significant stimulus differences between transient checkerboard reversal and steady-state grating reversal paradigms which may account for the difference in observed results. Fiorentini and Trimarchi (1992), compared transient VEP implicit time for grating reversal and steady-state apparent latency using stimuli more similar to ours. They found that apparent latency and implicit time were well correlated, but they did not study enough older infants to make a quantitative comparison with our results.

VEP response latency is known to be a function of subjective contrast (Kulikowski, 1977). However, since contrast threshold is constant after 10 weeks of age, subsequent phase changes must arise from mechanisms other than those that control contrast sensitivity. These could include myelinization or synaptic efficiency but are unlikely to be due to changes in receptoral quantal efficiency (Banks & Bennett, 1988), since the phase of the response changes dramatically during a period of time during which the contrast threshold is nearly constant.

Possible mechanisms for selective immaturity of the OMT

In the following section, we consider several possible mechanisms which might lead to a dissociation between the developmental sequences for the OMT and contrast sensitivity for counterphase gratings. The discussion is organized around a schematic model of motion processing (Fig. 10) which is comprised of four stages: transduction of the stimulus, setting the dynamic range, spatio-temporal filtering and directional selectivity. We will consider the likely role of immaturities lying at each stage of processing in this admittedly simplified view of motion processing with a goal of suggesting why *infants are insensitive to the oscillatory motion of gratings motion when their sensitivity to counterphase modulation is so high* and *why oscillatory motion thresholds undergo such little development over the first postnatal year.*

Transduction efficiency

Considered on the basis of infants' contrast sensitivity for counterphase gratings (cf. Fig. 3; Norcia *et al.*, 1986, 1988, 1990b), the infants' motion VEP thresholds ought to have been about 20 sec arc (instead of 166 sec arc). That is, if the MVEP were driven solely by the contrast-reversing component of the oscillating grating, 20 sec arc of motion of a 1 c/deg grating would generate a reversing component of ~ 1.4% contrast, which is close to the 26 infants' average contrast threshold (1.46%) for counterphase gratings.* Clearly, the infants'

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*According to the same analysis applied to the adults' data, based on their geometric mean threshold for counterphase gratings (0.59%), their OMT ought to have been 8.6 instead of 26 sec arc. Apparently, the adult visual system is also not capable of utilizing all the available information regarding the modulating component of the oscillatory motion stimulus. However, it should be noted that for both infants and adults, at OMT, the static component was at nearly full (80%) contrast. The possibility that this component was interfering with (masking) the responses to the modulating component will be considered in the following sections.

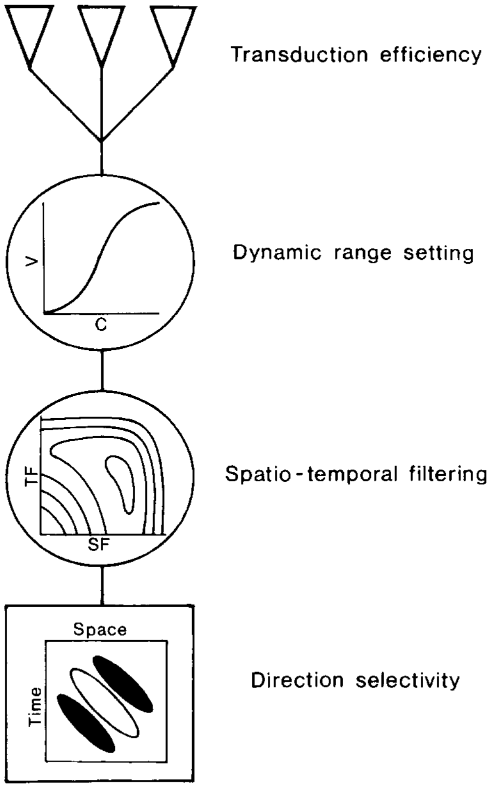

FIGURE 10. Schematic diagram of motion-processing pathway in the visual system. This simplified depiction is intended to aid the reader in the Discussion section entitled Possible Mechanisms for Selective Immaturity of the OMT. Four main stages are characterized. The OMT may be limited by immaturities in front-end mechanisms, such as transduction efficiency, or in the mechanisms that determine the dynamic response range in the distal visual pathway, such as contrast saturation, contrast masking and contrast gain control, or in early spatio-temporal filters, or in specifically cortical motion-sensitive mechanisms. See text for details.

visual system was not utilizing the available modulation information equally efficiently in the two tasks.

Sensitivity to both oscillatory motion and counterphase is ultimately limited by constraints imposed early in the visual system by the optics of the infant eye and by the quantum efficiency of the infant retinal mosaic (Banks & Bennett, 1988). Limitations at this level of processing cannot explain the poor OMTs, since the counterphase thresholds—which are subject to the same constraints at this early stage of processing—are so much more adult-like. The explanation for the dissociation must thus lie higher than the level of the photoreceptors. However, relative synaptic efficiency after the receptors cannot explain the deficit, since the counterphase thresholds measured from cortex would also reflect such immaturities.

Mechanisms responsible for setting response range

Contrast saturation. The most obvious stimulus-related difference between the counterphase thresholds and the OMTs is that the latter utilizes a strongly suprathreshold grating that is present throughout each 10-sec trial. At the mean OMT for the infants (167 sec arc), the static component is at 79.2% contrast, whereas, in the measurement of contrast sensitivity, the overall contrast presented to the visual system in the vicinity of contrast threshold ($\sim$ 1.5%) is quite low. It is possible that the developing visual system, though relatively mature in terms of absolute contrast sensitivity to low spatial frequency stimuli, has a restricted dynamic range relative to adults and is driven out of its operating range by the high-contrast stimulus used in the oscillatory motion task. Such contrast saturation could result from at least two non-mutually exclusive mechanisms: (1) contrast gain control mechanisms that are either temporally sluggish or incomplete relative to adult mechanisms; or (2) the presence of a greater degree of compressive non-linearity in the immature visual pathway. These two mechanisms could interact, in that contrast gain control may act to protect the nervous system from saturation, keeping neural responses in their linear operating range. If gain control is incomplete, incoming signals may be subject to subsequent compressive non-linearities.

To date there have been no studies that have specifically investigated contrast saturation or contrast gain in infants. Stephens and Banks (1987) measured contrast discrimination in 6- and 12-week-old infants using a behavioral technique (forced-choice preferential looking, or FPL). Although their data are consistent with the hypothesis that infants have an effectively lower contrast at the input to the visual system, the data are not adequate to evaluate infants' contrast gain since only one of the background contrasts used was sufficient to elevate the infants' thresholds.

Contrast masking: supra-Weberian masking by the static component of the oscillatory motion stimulus? In addition to saturation, it is possible that the modulating component of the stimulus is determining the responses and that this component is effectively masked by the static component to a relatively greater degree than in adults. Wesemann and Norcia (1992) measured psychophysical grating displacement thresholds in adults as a function of grating contrast and retinal eccentricity. When displacement thresholds were plotted in terms of their static and modulating components, the effect of increasing C_{stat} on C_{rev} conformed closely to Weber's law once C_{stat} was increased beyond a critical value. Thus, they argued that detection of oscillatory grating displacements is more akin to a traditional masking paradigm in which detection of the modulating component is made in the presence of a static masking component. However, since the infants' counterphase sensitivity is close to that of adults, the large loss in motion sensitivity at high contrasts would imply that the static component was exerting substantially more masking than in adults, i.e. exceeding Weber's law. Both contrast saturation or gain control failures could be examined by measuring contrast threshold for a reversing grating as a function of the contrast of a static mask of the same spatial phase as the test.

Spatio-temporal interactions during development

It is possible that infants' insensitivity to oscillatory motion is the result of the spatio-temporal tuning of the immature visual system. Perhaps higher sensitivities would have been obtained if we had used different temporal or spatial frequencies. Although this is a reasonable consideration, the data do not appear to support such an explanation. Psychophysical studies of OMTs in adults have shown that sensitivity does not vary over a wide range of spatial and temporal frequencies (Johnston & Wright, 1985; Wright & Johnston, 1985). Moreover, our data from both infants and adults suggest that little spatio-temporal tuning is present in the MVEP over the range that we have tested (Norcia *et al.*, 1990a).

While it is true that the infants showed high sensitivity in the contrast task, which utilized the same temporal and spatial frequencies as were used in the motion task, it is possible that the channel detecting the 6 Hz reversing component may be more broadly tuned in infants and thus be more susceptible to masking by the static component.

Specific immaturities in direction selective or positional mechanisms

Insensitivity to low velocities. A number of studies have explored the influence of stimulus velocity in infants' responses to moving patterns (e.g. Dannemiller & Banks, 1983; Kaufmann, Stucki & Kaufmann-Hayoz, 1985; Freedland & Dannemiller, 1987; Dannemiller & Freedland, 1989, 1991a, b, 1993; Aslin & Shea, 1990; Wattam-Bell, 1991). The general consensus has been that young infants are quite insensitive to slow stimulus velocities. Below 12 weeks of age, these studies indicate that infants require minimum velocities of 3 deg/sec (Kaufmann *et al.*, 1985)* to 9 deg/sec (Aslin & Shea, 1990) before reliable velocity-based responses could be measured. By 3–5 months of age, the estimated lower velocity decreased to a range of ~ 2 deg/sec (Kaufmann *et al.*, 1985) to 4 deg/sec (Aslin & Shea, 1990). These values are about two orders of magnitude greater than lower velocity limits for detection of motion by adults (Johnston & Wright, 1985; Wright & Johnston, 1985; Nakayama & Tyler, 1981).

In the present experiments, sweeps of spatial displacement also present sweeps of apparent stimulus velocity. For the 6 Hz stimulus, an average displacement threshold of 167 sec arc would correspond to a velocity threshold of 0.56 deg/sec, assuming that the infants' MVEPs in the vicinity of threshold reflect motion responses. [Such an assumption is supported by the data from Expt 2 (Figs 8 and 9) which demonstrates directional selective responses in young infants over the entire sweep range, all the way down to oscillatory displacement threshold.] If our data are restricted to young infants ($\leqslant 12$ weeks, $N = 16$) whose average OMT is 221 sec arc, the effective velocity threshold is only 0.74 deg/sec, a factor of 4–12 less than previous estimates.

If velocity-sensitive mechanisms were determining the MVEP, we would expect oscillatory motion threshold to depend directly on the temporal frequency of the stimulus. Of the 49 infants, 13 were also tested at 10 Hz. Their geometric mean OMT at 6 Hz was 195 sec arc (SEM = ± 0.062 log sec arc). Based on a strict velocity prediction, at 10 Hz their mean OMT should have been 60% (ratio of 6 to 10 Hz) of this value, or 117 sec arc. In fact, their 10-Hz OMT was 156 sec arc (SEM = ± 0.085 log sec arc). The threshold is lower at 10 Hz by an amount that is consistent with a velocity limit, within our experimental error. However, this test is not a strong one, since the predicted velocity difference is relatively small and since our experimental error is relatively large. A much stronger test for velocity-based responses could be achieved if a wider range of temporal frequencies were used.

Responses to position information. In addition to contrast information, grating displacement carries spatial position information. In adult vision, positional information has been argued to underlie hyperacuity tasks (such as detection of vernier displacements), in which stimulus displacements can be detected with very high precision (e.g. see Barlow, 1979; Westheimer, 1979). However, Wesemann and Norcia's (1992) results in adults argue against the OMT being a position acuity since they found that the relationship between displacement thresholds and *retinal eccentricity* was highly dependent on grating contrast, which would not be expected of a positional acuity. Thus, although a number of studies have attempted to study positional acuities in infants (Shimojo, Birch, Gwiazda & Held, 1984; Manny & Klein, 1984, 1985; Shimojo & Held, 1987; Manny, 1988; Zanker, Mohn, Weber, Zeitler-Dreiss & Fahle, 1992; Skoczenski & Aslin, 1992), these are not strictly comparable to the present study.

Moreover, the motion asymmetries displayed in Figs 8 and 9 argue strongly against the VEP being a strict position signal as opposed to a motion signal. The presence of significant F1 responses, concomitant with a 180-deg LE:RE phase difference cannot be accounted for by responses from purely positional mechanisms. In order for positional mechanisms to generate the VEP data shown in Fig 7, each eye would have to be able to differentially encode positional sequences (L:R:L:R vs R:L:R:L) within the stimulus presented to each eye.

Phase sensitivity and the development of directional selectivity. Oscillatory motion can also be thought of as spatial phase modulation. Sensitivity to phase information connotes either sensitivity to the absolute phase (position of a pattern) or more simply to relative changes in pattern phase or position. We have already

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*Kaufmann *et al.* (1985) used a rotary-motion stimulus which contains relative shear velocities twice those reported. Hence, their reported velocity thresholds have been doubled for comparison with the other data.

argued that the OMT is unlikely to be controlled by position sensitivity and we would thus expect that development of absolute phase sensitivity does not play a role in determining OMT. However, there is a close relationship between *relative* phase sensitivity and direction sensitivity/selectivity. Direction sensitivity can be thought of as a form of sensitivity to relative spatial phase in which ordinal spatial relationships are preserved over time. Most contemporary models of direction selectivity involve an initial spatio-temporal filtering stage comprised of two spatially displaced subunits with different neural delays, the outputs of which are nonlinearly combined (Reichardt, 1961; Adelson & Bergen, 1985; Watson & Ahumada, 1985). The sensitivity of these models to stimulus motion depends in large part on the degree of decorrelation between the subunits. Some motion models posit pairs of orthogonal, quadrature spatial filters, i.e. filters that are tuned to the same spatial frequency, but to phases separated by 90 deg (Adelson & Bergen, 1985; Watson & Ahumada, 1985; Nakayama & Silverman, 1985). Although complete orthogonality probably never occurs in real biological systems, evidence for spatial quadrature pairs has been found in adults (e.g. Bennett & Banks, 1987) and in cat cortex (Pollen & Ronner, 1981).

If the outputs from the two directionally selective spatial subunits have extensive spatial overlap, their outputs will be correlated and will produce less modulation for a given displacement than spatially distinct subunits. The decorrelation of such subunits, i.e. development of spatially separate quadrature pairs, may be a process that develops during infancy. Thus motion sensitivity and relative phase sensitivity may be poor early in infancy because of a relative lack of orthogonal spatial filters. On the other hand, pattern reversal responses may not be limited by immaturities in spatial quadrature pairs since sensitivity to this stimulus can be carried by ON- and OFF-channels which may be relatively more well segregated early in infancy. Thus, contrast sensitivity could remain relatively higher than motion sensitivity until phase/direction selectivity mediated by putatively orthogonal spatial filters develops.

SUMMARY

We have used the oscillatory motion VEP to measure the absolute sensitivity of motion mechanisms during the first year of postnatal development. After consideration of a number of alternative explanations, our data are most consistent with the hypothesis that the oscillatory motion VEP reflects the activity of directionally selective cortical cells. We have found that the thresholds based on the MVEP are relatively poor, both in comparison to the high sensitivity of infants to counterphase (Norcia *et al.*, 1990b) and in comparison to adult OMTs measured under identical conditions. Moreover, the infants' OMTs undergo surprisingly little development over the entire first postnatal year, in spite of significant maturation of motion mechanisms along other dimensions, such as the development of motion symmetry and response temporal dynamics. This suggests a dissociation between the developmental mechanisms underlying maturation of motion symmetry and those that determine or limit the apparent maturation of oscillatory motion thresholds. The low oscillatory motion sensitivity observed in infants over the entire first year of life may reflect prolonged insensitivity of a variety of post-receptoral mechanisms including the directionally selective cells in visual cortex themselves. Alternatively the sensitivity of cortical direction selective units may be limited by an unusual (immature) susceptibility of these cells to masking or by immaturities in gain control mechanisms.

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