

DEVELOPMENT OF CONTRAST SENSITIVITY IN THE HUMAN INFANT

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Abstract—Contrast sensitivity and grating acuity were measured using the sweep VEP method in a group of 48 infants from 2 to 40 weeks of age and in a group of 10 adults. Sinusoidal gratings were reversed in contrast at 12 alternations per sec at a space-average luminance of 220 cd/m². During 10 sec trials, either the contrast or the spatial frequency was increased in a series of 19 steps. Thresholds were estimated by extrapolation of the VEP response functions to zero amplitude.

The contrast threshold at low spatial frequencies developed rapidly from 7% contrast at 2–3 weeks to an asymptote of 0.5% at 9 weeks. For adults, maximum sensitivity at low spatial frequencies was 0.32–0.22%. The sweep VEP estimate of grating acuity showed a gradual increase in spatial frequency with age, starting at 5 c/deg during the first month and reaching 16.3 c/deg at 8 months. The mean adult acuity was 31.9 c/deg.

There appeared to be two phases in the development of contrast sensitivity and acuity. Between 4 and 9 weeks overall contrast sensitivity increased by a factor of 4–5 at all spatial frequencies. Beyond 9 weeks, contrast sensitivity at low spatial frequencies remained constant, while sensitivity increased systematically at higher spatial frequencies.

Visual development Spatial vision Visual evoked potentials Contrast sensitivity Human infants

INTRODUCTION

Measurements of infant contrast sensitivity functions (CSFs) were first made over 15 yr ago (Atkinson, Braddick & Braddick, 1974; Harris, Atkinson & Braddick, 1976; Banks & Salapatek, 1976). In spite of this long history and the importance of the contrast sensitivity function for developmental theories of form vision (Banks & Salapatek, 1981; Gayl, Roberts & Werner, 1983; Banks & Ginsburg, 1985), surprisingly few data are available at any but the youngest ages. With the exception of the study by Pirchio, Spinelli, Fiorentini and Maffei (1978) and two eye movement studies (Meijler & Van den Berg, 1982; Hainline, Camenzuli, Abramov, Rawlick & Lemrise, 1986), previous reports have dealt mainly with single cross-sectional age groups or only the period up to 3 months. In general, sample sizes have been small, except in Atkinson, Braddick and French's (1979) large study of contrast sensitivity in the neonate and the eye movement study of Hainline et al.

The earliest measurements of contrast sensitivity in infants were made using behavioral methods based on the infant's preference for

pattern (Atkinson et al., 1974; Banks & Salapatek, 1976). Contrast sensitivity was found to be markedly lower than that of the adult, and the CSF of 1–2 month olds appeared to lack low spatial frequency attenuation which is characteristic of the adult CSF.

Infant CSFs have also been measured using the visual evoked potential (VEP). The most extensive VEP data are those of Pirchio et al. (1978) who measured contrast sensitivity in 13 infants tested on 20 occasions. Pirchio et al. (1978) used Campbell and Maffei's (1970) VEP extrapolation technique to measure contrast thresholds, but only in a limited number of cases. Most of the data presented were measurements of the amount of contrast needed to attain a criterion amplitude, rather than extrapolated threshold measurements. They found that peak contrast sensitivity and acuity developed over the same time course. Both log sensitivity and log acuity were linear functions of age up to at least 10 months of age, the oldest infants studied.

More recently CSFs for infants under 3 months have been measured using the preference or VEP techniques pioneered in earlier investigations (e.g. Banks & Stephens, 1982;

Fiorentini, Pirchio & Spinelli, 1983; Banks, Stephens & Hartmann, 1985).

Contrast sensitivity in infants has also been studied using techniques based on eye movements. Meijler and Van den Berg (1982) used the suppression of OKN by low contrast targets to measure contrast sensitivity and Hainline et al. (1986) used small-field OKN responses to drifting gratings to determine contrast thresholds.

Threshold measurements can be difficult in infants and the collection of a number of thresholds from the same infant can be a time-consuming process. Recent methodological innovations (Regan, 1973; Tyler, Apkarian, Nakayama & Levi, 1979; Norcia & Tyler, 1985) involving swept parameter displays and Fourier analysis of the evoked response have greatly increased the speed with which VEP threshold measurements can be made. We have demonstrated previously the utility of the sweep VEP technique in measuring CSF's in small groups of infants (Norcia, Allen & Tyler, 1986; Norcia, Tyler & Hamer, 1988). The present report discusses the development of contrast sensitivity in a large sample of infants between 2 and 40 weeks of age.

METHODS

Subjects

Infant observers ($n = 51$) 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 1 to 45 weeks of age. Nineteen infants were tested on more than one occasion, resulting in a total of 92 recording sessions. One infant, 1 week of age, failed to produce any criterion records and was thus excluded from further analysis.

The infants were refracted photographically using the system described in Day and Norcia (1986) and Norcia, Zadnick and Day (1986). Two infants were excluded from the study on the basis of their photographic refractions, one a high oblique astigmat and one a high hyperopic anisometropia. The sample yielding contrast sensitivity data thus consisted of 48 infants between 2 and 40 weeks of age. Ten adult observers, each free of ocular pathology and with acuity of 6/6 or better, also participated.

Apparatus

Display. Vertical sinusoidal luminance gratings were generated on a Joyce (Cambridge

Electronics) display scope. Space-average luminance was 220 cd/m^2 . z-Axis contrast linearity was verified to be within 2% of nominal contrast up to 90% contrast using a Spectra Pritchard 1980A photometer. Contrast remained within 70% of full contrast up to 4 c/cm as determined photometrically and psychophysically. The display measured 14 cm high and 28 cm wide. The gratings were square-wave alternated at 12 contrast reversals per sec.

VEP recording. The EEG was pre-amplified by Grass P511J amplifiers equipped with isolation cables (Grass IG3/P511). Two bipolar placements of O_2 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 et al. (1989). Briefly, the amplitude and phase of the second-harmonic pattern reversal response were determined by a Discrete Fourier Transform. Contrast thresholds were estimated by linear extrapolation to zero amplitude of the function relating VEP amplitude to log stimulus contrast. Grating acuity was estimated by extrapolation to zero amplitude of the function relating VEP amplitude to linear spatial frequency.

Procedure

VEP recording. Infants were either seated comfortably in their parent's lap or held upright facing the monitor (if younger than about 8 weeks). Contrast thresholds and grating acuities were measured in loosely randomized blocks of two to five 10 sec trials. Contrast thresholds were measured using swept contrast gratings of fixed spatial frequency; grating acuity was measured by sweeping spatial frequency at fixed contrast. For the swept contrast measurements, the contrast of the grating was incremented every 0.5 sec in 19 equal logarithmic steps, starting at low contrast. Spatial frequencies of 0.25, 0.5, 1.0, 2.0, 4.0, 8.0 and 16.0 c/deg were used. The range of spatial frequencies actually presented was keyed to the infant's age, based on previous measurements of grating acuity (Norcia & Tyler, 1985). In the swept spatial frequency measurements, a series of 19 gratings of a fixed contrast of 80% were presented one every 0.5 sec in a sweep of linearly-spaced spatial frequencies, starting at a low spatial frequency.

We attempted at least two but no more than five trials in a given condition before moving to another condition. Acuity and contrast sensitivity measurements were intermingled. It was not possible to obtain thresholds for each condition from all infants.

Adult psychophysics. Psychophysical contrast sensitivity functions (CSFs) were obtained from 7 adult observers using the method of ascending and descending limits. An attempt was made to match the conditions of the psychophysical measurements to those used in the VEP recording. Thus, ascending and descending series spanning the threshold were presented using a sweep procedure similar to that described above. The range of the contrast sweeps covered approx. 2 octaves below threshold to two octaves above threshold in ascending and descending series of 7 trials each. Thresholds for each observer were taken as the median of the ascending and descending series at each spatial frequency. Trials lasted 10 sec and the observers were given a button to press to indicate their threshold. Mean luminance, temporal modulation and field sizes were the same as those used for the adult VEP studies. Field sizes and viewing distances for the adult psychophysics and VEP recordings were the same as those used for the infants, except for spatial frequencies of 8 c/deg and above, where somewhat longer viewing distances were used for the adults. Test distances thus ranged from 40 to 400 cm from the display, depending upon spatial frequency. The distances were chosen so that the resolution

limit of the monitor was not exceeded and so that there were always at least 10 cycles displayed at each spatial frequency.

RESULTS

Adult VEP and psychophysical thresholds

The CSF for seven observers obtained by the method of ascending and descending limits is presented in the left-hand panel of Fig. 1. Datum points plot the mean sensitivity ± 1 SEM for each spatial frequency. The VEP CSF for the same observers and 3 additional observers is shown in the right hand panel of Fig. 1. For each observer, the best sensitivity obtained on any individual trial or on the vector average of all trials at that spatial frequency was used. The vector average was calculated as the Pythagorean sum of the sine and cosine Fourier coefficients of all trials recorded in a given condition.

For the seven observers who participated in both VEP and psychophysical measurements, a repeated measures ANOVA indicated, in addition to a significant effect of spatial frequency on sensitivity, slightly higher psychophysical sensitivity ($F = 9.15$; $P = 0.023$) than VEP sensitivity, but no interaction between method and spatial frequency ($F = 1.88$; $P = 0.11$).

The use of "best" threshold for the VEP produces a CSF of similar shape to that obtained psychophysically and one that most closely approaches the psychophysical sensitivity. Choosing the "best" VEP sensitivity results

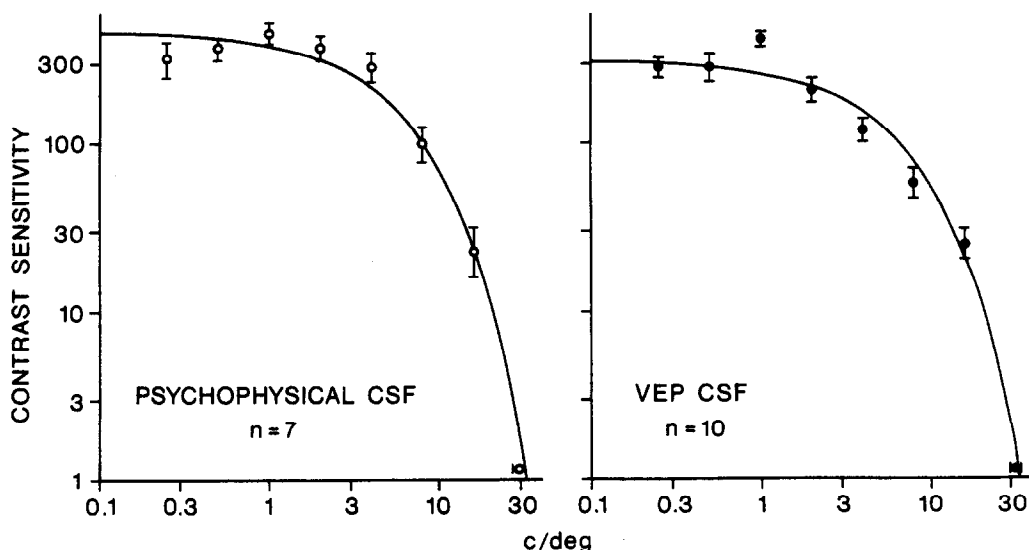


Fig. 1. Adult VEP and psychophysically determined CSFs. Lines indicate the best fit function $s = ce^{-a}$. Error bars are ± 1 SEM.

in a CSF which averaged 0.6 octaves lower than the psychophysical CSF. Central tendency measures, such as the mean or median of individual trial thresholds underestimated psychophysical sensitivity by an even larger amount.

Form of the contrast sensitivity function

Previous investigators have shown that log sensitivity at high spatial frequencies declines linearly with linear spatial frequency on both psychophysical (Campbell & Green, 1965) and evoked potential measures (Allen, Norcia & Tyler, 1986). Under the temporal conditions used to record the steady-state VEP, the low spatial frequency roll-off of the CSF seen with static patterns is minimal (Robson, 1966). Sensitivity as a function of spatial frequency can thus be described by a single negative exponential function in log-log coordinates.

The negative exponential model, $s = ce^{-av}$ was fit to each set, excluding the acuity measurements, where s is the sensitivity at each spatial frequency v , and c and a are constants. The model fits are shown as the solid curves in Fig. 1. Asymptotic sensitivities (c) were 312 for the VEP and 466 for the psychophysics. The high spatial frequency roll-off parameter (a) was -0.17 and -0.18 for the VEP and psychophysical CSFs respectively. Predicted grating acuities obtained by extrapolating the model fits to a sensitivity of 1.25 (80% contrast) were 33.0 c/deg for the VEP and 32.0 c/deg for the

psychophysics, compared to measured values at 80% contrast of 31.9 and 29.0 c/deg, respectively. The model accounted for 92% of the variance in the VEP measurements and 96% of the variance in the psychophysical measurements.

Test-retest reliability of swept VEP CSFs

Figure 2 plots contrast sensitivity functions obtained from two infants, David and Hunter, who were each tested at 19 and 21 weeks of age. The data at each spatial frequency are from the single trial or vector average from either channel which yield the highest sensitivity. The functions were generally reproducible to within less than an octave across sessions, with the maximum discrepancy being 1.5 octaves of contrast. Peak sensitivity of the two infants was quite similar at 300, but David's grating acuity was nearly a factor of 2 higher than Hunter's. The grating acuities measured by swept spatial frequency are within 0.3 octaves of those predicted by an extrapolation of the CSF measured at and above 1 c/deg. The range above 1 c/deg was chosen for extrapolation since David had only one measurement below 1 c/deg and since Hunter's data are not well fit below 1 c/deg by a single negative exponential. For David the predicted acuity was 17.0 c/deg vs a mean of 20 c/deg observed over the two recordings. The corresponding values were 13.7 c/deg predicted vs 11 c/deg observed for Hunter.

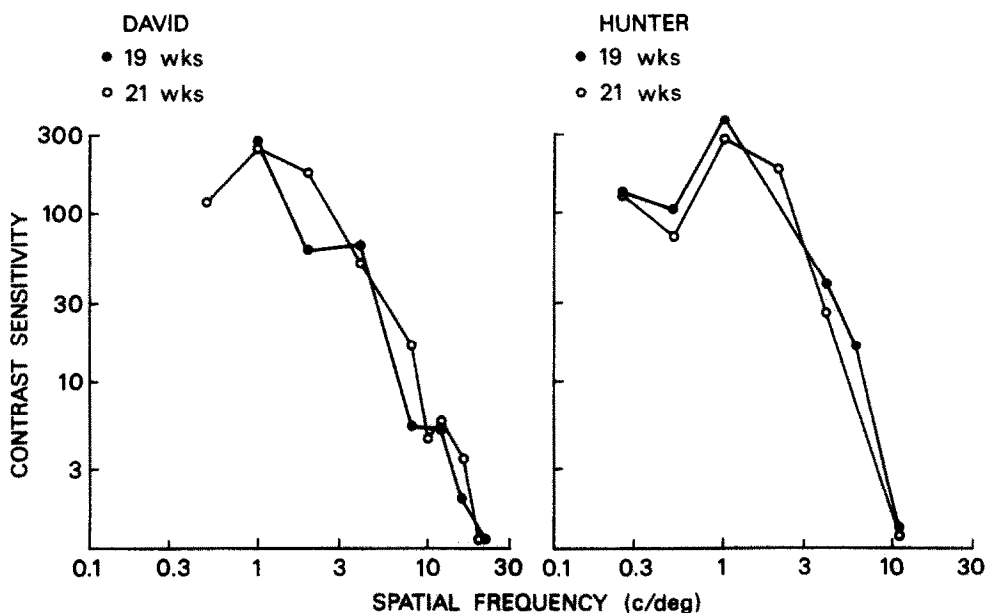


Fig. 2. Repeatability of the VEP CSFs for two infants. Open and solid symbols are from recording sessions separated by 2 weeks.

Longitudinal development of contrast sensitivity

Fifteen infants were tested longitudinally, with sessions being separated by at least 1 month. Data from one of these infants is shown in Fig. 3. For this infant, sensitivity at 0.25 c/deg was about 160 at 5 weeks and improved only slightly between 5 and 30 weeks. However, sensitivity for each of the higher spatial frequencies continued to increase up to 30 weeks.

Figure 4 shows the development of contrast sensitivity at low spatial frequencies for the group of 15 infants studied longitudinally. For each infant the best contrast sensitivity obtained from either a single sweep trial or from the vector average for the condition was used. Since not all the infants were tested at 0.25 c/deg or 0.5 c/deg, and since sensitivity was sometimes higher at 0.5 or 1 c/deg than at 0.25 c/deg, we used the following rule to select an infant's data: if thresholds were obtained at 0.25, 0.5 and 1.0 c/deg, or at 0.25 and 0.5 c/deg, the highest sensitivity was used; if thresholds were obtained only at 1.0 c/deg but not at 0.25 or 0.5 c/deg, the infant was not included; if only 0.25 or 0.5 c/deg produced a threshold, the best threshold was used.

Contrast sensitivity at low spatial frequencies developed rapidly over the first 10 weeks of age. Between 10 and 40 weeks thresholds remained approximately constant, with most of the sensi-

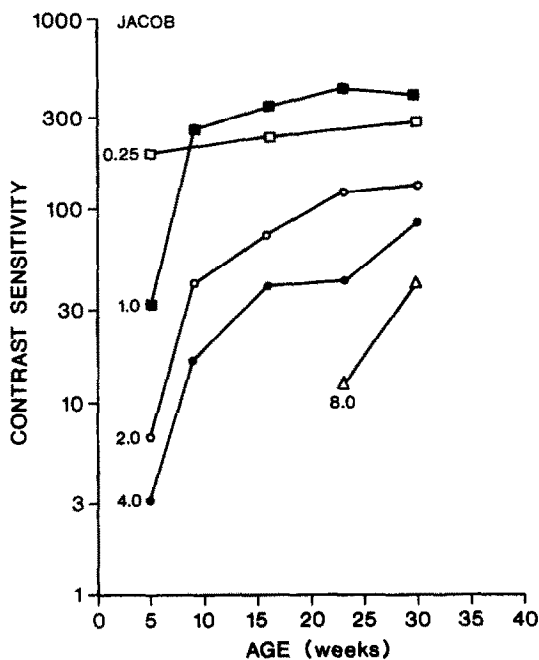


Fig. 3. Longitudinal measurements of contrast sensitivity vs age for one infant (Jacob). The parameter is spatial frequency in c/deg.

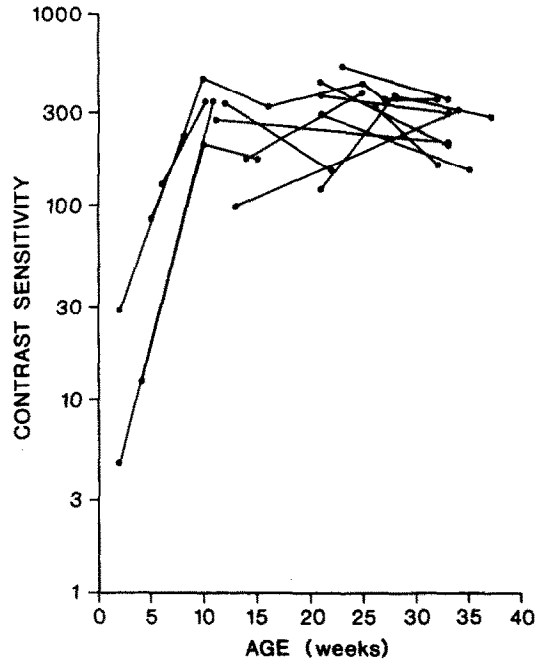


Fig. 4. Longitudinal growth of contrast sensitivity at low spatial frequencies. Each curve represents data obtained from an individual infant. The best contrast sensitivity value, either from a single trial or from the vector average, over the range of 0.25 to 1 c/deg was plotted. Contrast sensitivity develops rapidly before 10 weeks and shows little improvement thereafter.

tivity values lying between 200 and 400. The earliest sensitivities, obtained between 2 and 4 weeks, ranged from 4.7 to nearly 30. Each infant's data is represented by a curve connecting the points collected at different ages. Since the sensitivity development appears to have a sharp corner near 10 weeks of age, we did not interconnect points that were obtained in sessions at less than 9 weeks of age with those obtained after 12 weeks unless there was a datum point taken between 9 and 12 weeks.

Longitudinal development of grating acuity

A measure for grating acuity was obtained in 11 of the 15 infants tested longitudinally. These data are shown in Fig. 5. Unlike the development of contrast sensitivity at low spatial frequencies, which asymptoted by 10 weeks, grating acuity developed continuously over the entire age range. Acuity in the youngest infants ranged from 2.5 to 9 c/deg during the first 2 months to between about 10 and 20 c/deg after 30 weeks.

Cross-sectional development of contrast sensitivity

Figure 6 plots the mean values of low spatial frequency contrast sensitivity (as defined for

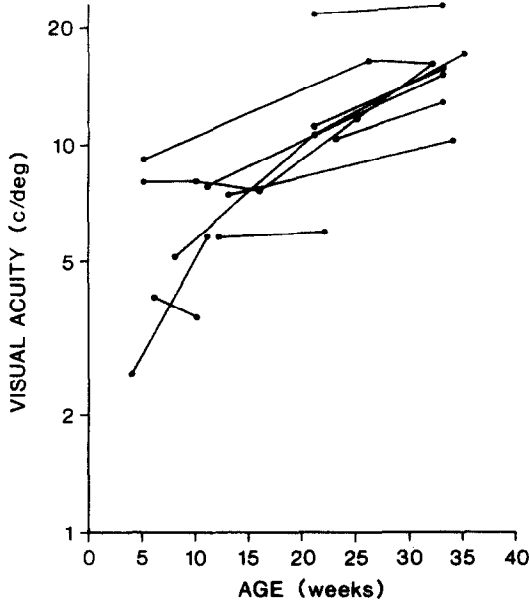


Fig. 5. Longitudinal growth of acuity. Each curve represents data obtained from an individual infant. The best acuity for a single sweep trial or from the vector average is plotted. Acuity does not asymptote at 10 weeks, but continues to develop over the entire age range.

Fig. 4 above) for 38 infants up to 30 weeks of age. Data from the first recording session for each of the 15 infants tested longitudinally are also included. (There are no points plotted

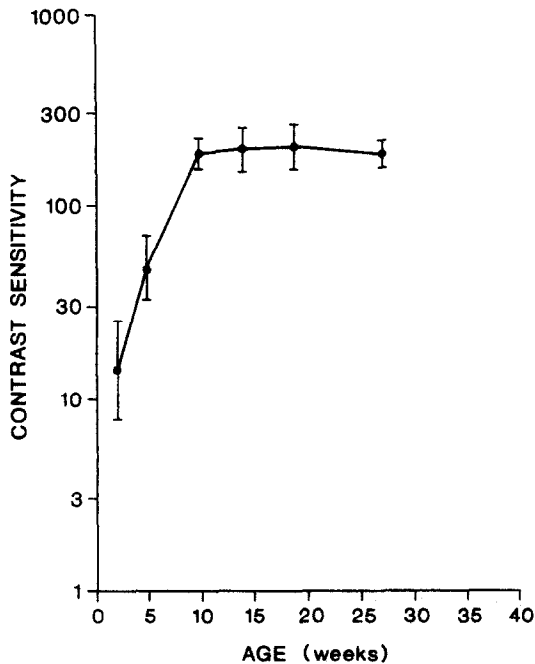


Fig. 6. Cross-sectional growth of contrast sensitivity at low spatial frequencies. Each symbol plots the mean sensitivity as a function of age, with the error bars indicating 1 SEM. Sensitivity develops rapidly, reaching a plateau of nearly 200 by 10 weeks.

beyond 25 weeks, since all but 3 of the infants we tested after 25 weeks had also been tested at least once before.) Each point represents the mean sensitivity, with the error bars indicating one standard error of the mean.

Contrast sensitivity developed rapidly between 2 and 10 weeks of age. Beyond 10 weeks there appears to be no consistent trend in development of contrast sensitivity at low spatial frequencies, with mean sensitivity being about 200. Adult sensitivity, using the Fig. 4 selection criteria, has a median value of 450.

Cross-sectional development of grating acuity

Figure 7 plots mean acuity data for the cross-sectional data set. The highest acuity value obtained on either a single sweep trial or on the vector average of all spatial sweeps was selected for calculation of the group mean. Grating acuity developed monotonically from 5 c/deg at 4 weeks to 16.4 c/deg at 31 weeks. Thirty-seven infants contributed acuity sweeps to this data set. Acuity development shows a gradual increase well beyond 10 weeks of age.

Fitting of the negative exponential model of infant CSFs

The goodness of fit of the single negative exponential model was examined in the group of infants who yielded an acuity measure as well as sensitivity measurements at a minimum of four

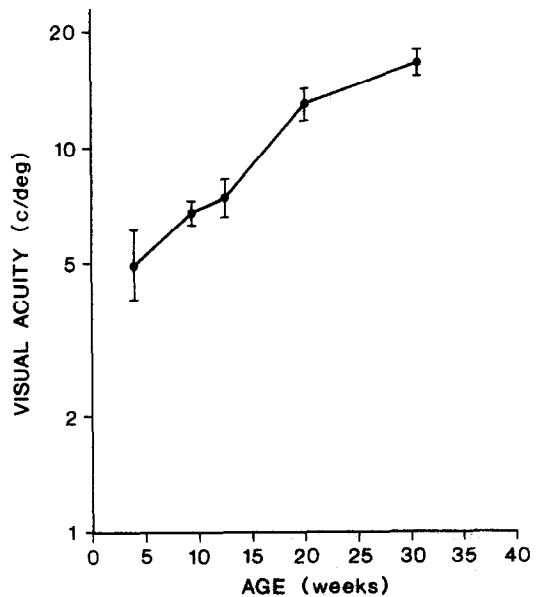


Fig. 7. Cross-sectional growth of acuity. Each symbol plots the mean acuity as a function of age, with the error bars indicating 1 SEM. Acuity growth is an approximately linear function of age when plotted on these semi-log coordinates.

spatial frequencies. This group was selected with two goals in mind; the first was to evaluate the appropriateness of the model for infant CSFs; the second was to examine how well the acuity limit obtained by sweeping spatial frequency matches the acuity predicted by extrapolation of the contrast sensitivity measurements for lower spatial frequencies.

Out of the 92 recording sessions 49 produced CSFs with five or more points. The negative exponential model was fitted to each session's data (excluding the acuity measure). On average, the negative exponential model accounted for 82% of the variance in these CSFs from individual infants. The model fit was then used to predict grating acuity at 80% contrast. The average discrepancy between the acuity predicted from extrapolation of the CSF and the acuity measured by sweeping spatial frequency was negligible at 0.4 octaves. This analysis indicates that individual infant CSFs are well

fitted by a simple negative exponential form, as are adult CSFs. Furthermore, the acuity value predicted from swept contrast measurements is consistent with the acuity obtained by swept spatial frequency.

Contrast development as a function of spatial frequency

Figure 8 plots the development of mean contrast sensitivity at 0.25, 0.5, 1, 2, 4 and 8 c/deg. Data were included only from the first session for any given infant who contributed one or more criterion threshold. As in previous figures, the highest sensitivity on either a single trial or on the vector average of all trials taken at the same spatial frequency was chosen as the estimate of contrast sensitivity for each infant at each spatial frequency. A total of 176 contrast thresholds are represented in the figure.

Contrast sensitivity at each spatial frequency increased substantially as a function of age.

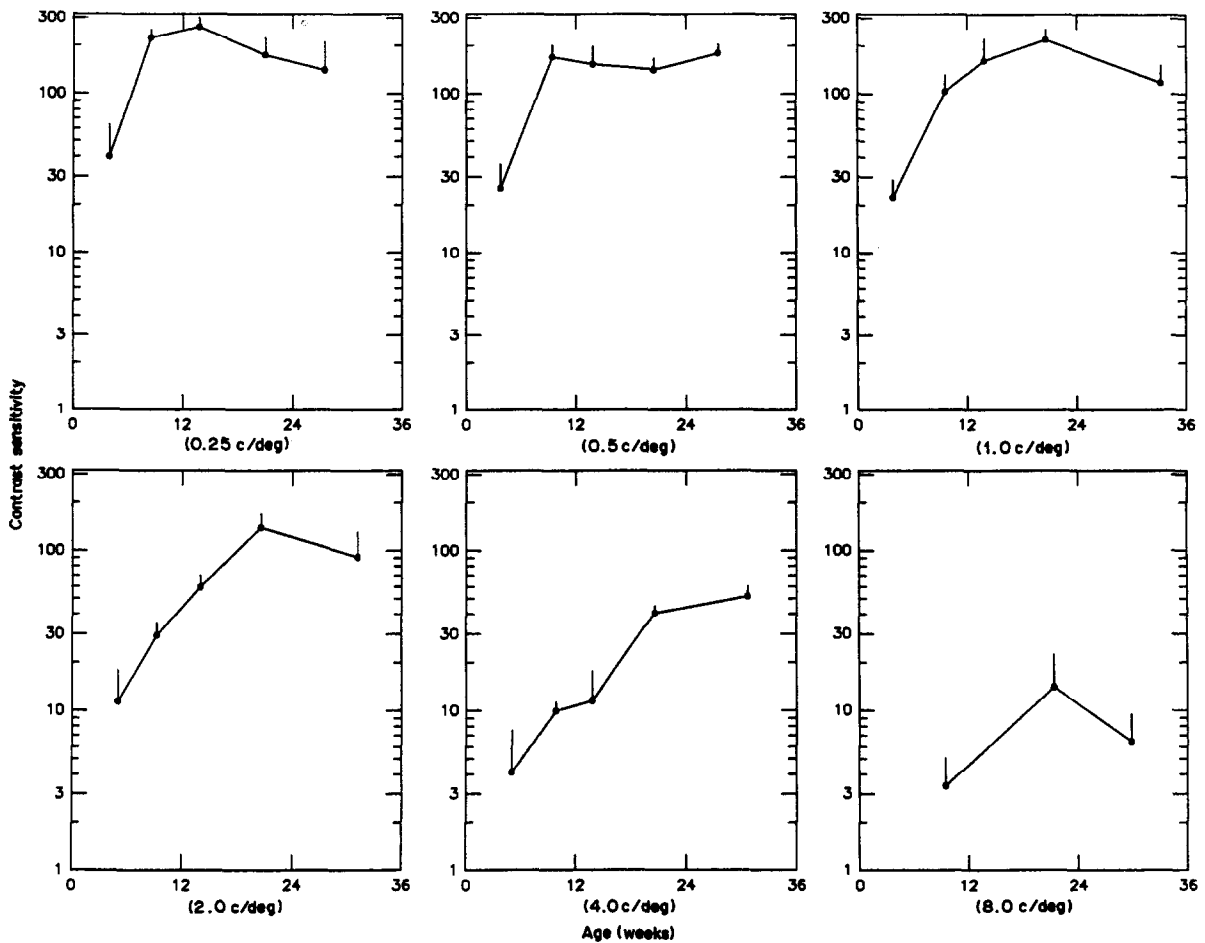


Fig. 8. Contrast sensitivity vs. age. Sensitivity at 0.25, 0.5, 1.0, 2.0, 4.0 and 8.0 c/deg is plotted. Contrast sensitivity develops at all spatial frequencies with development continuing longer at the higher spatial frequencies.

There is a progressive shift from low to high spatial frequency in the age at which contrast sensitivity reaches an asymptotic value, with low spatial frequencies reaching asymptote earlier than high spatial frequencies. The slight decline in contrast sensitivity in oldest age group at 8 c/deg is probably due to a small sample at this spatial frequency. The decline was not apparent when the last session of the longitudinally-tested infants was selected rather than the first session.

DISCUSSION

The present results indicate that contrast sensitivity development can be characterized by increases in both peak sensitivity and in spatial resolution. Contrast sensitivity at low spatial frequencies develops rapidly up to about 10 weeks of age. This can be seen both in the infants studied longitudinally (Fig. 4) and in the cross-sectional data set (Fig. 6). Little development of contrast sensitivity after 10 weeks is apparent in either the longitudinal or cross-sectional contrast sensitivity data obtained after 10 weeks. Peak (low spatial frequency) contrast sensitivity after 10 weeks was nearly 200, compared to 450 for adults.

The development of high spatial frequency sensitivity and grating acuity, on the other hand continues until at least 30 weeks. Continuous growth is apparent both in the grating acuity of infants studied longitudinally (Fig. 5), and in cross-sectional acuity data (Fig. 7). The longitudinal and cross-sectional acuity growth functions are similar in form to one another and to our previous sweep VEP measurements of the same function (Norcia & Tyler, 1985; Orel-Bixler & Norcia, 1987; Hamer, Norcia, Tyler & Hsu-Winges, 1989).

Both infant and adult CSFs were well-fitted by a single negative exponential. Our CSFs from individual infants were also fitted by Movshon and Kiorpes (1988), who used a double exponential model. The double exponential model can account for CSFs with low spatial frequency roll-off. Their fits indicate, as do ours, that the 6 Hz CSF has the same shape before and after 12 weeks of age. They found that very little low spatial frequency roll-off was present in their fitted CSFs. The lack of significant low spatial frequency roll-off validates our use of the single exponential model at high temporal frequencies.

Extrapolation of the contrast threshold estimates obtained from swept contrast measurements made at lower spatial frequencies

results in an acuity estimate which is consistent with the acuity measured by sweeping spatial frequency. Measurement of the CSF by different kinds of sweeps thus provides internally consistent values. A similar conclusion was drawn by Allen et al. (1986) who found that the CSF had the same form when measured by a series of contrast sweeps at different spatial frequencies or when measured by a series of spatial frequency sweeps at different contrasts.

Two processes underly the development of the CSF

To highlight the presence of two different developmental processes inherent in our data, contrast sensitivities for younger and older infants are plotted versus linear spatial frequency in Figs 9 and 10. The lines fitted to each set correspond to the negative exponential model, but now plotted on semi-log axes. Between 4 and 9 weeks, contrast sensitivity improves by a factor of about 4 at all spatial frequencies (Fig. 9). The increase in acuity from 5 to 7 c/deg can be accounted for mainly by increased contrast sensitivity (a vertical shift of the CSF).

Figure 10 replots the 9 week old data, along with data from 32 week olds and adults. After 9 weeks of age, maximum contrast sensitivity is changing only by a small amount, while sensitivity at higher spatial frequencies continues to increase dramatically. Thus, development of the CSF between 9 and 32 weeks is characterized by a nearly pure change in resolution, that is, an increase in the high frequency slope of the CSF without a change in its asymptotic sensitivity.

Low spatial frequency contrast sensitivity thus appears to reach an early asymptote of around 200 by 10 weeks of age. This value is about a factor of 2 lower than adult sensitivity. Acuity development reaches its first asymptote much later, at or shortly after 8 months (see Norcia & Tyler, 1985). Acuity at 8 months is about half that of the adult. An acuity difference of a factor of 2 between 7-9 month old infants and adults corresponds to a 20-fold difference in contrast sensitivity at 16 c/deg. It is likely that contrast sensitivity development after 9 months parallels the second, *slow* phase of VEP acuity development reported by de Vries-Khoe and Spekereijsse (1982), the beginning of which was apparent in the Norcia and Tyler (1985) data.

Comparison with previous VEP results

The present results differ in several respects from those obtained by Pirchio et al. (1978).

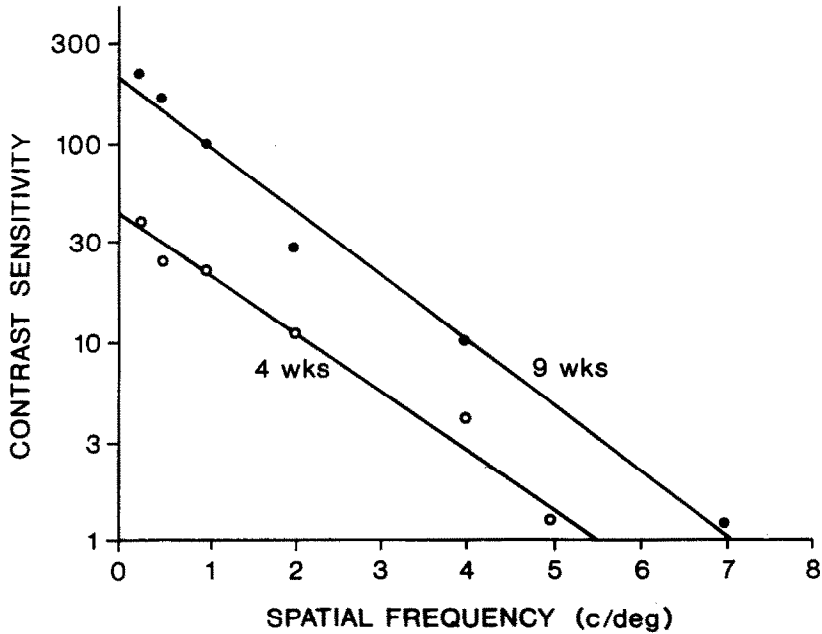


Fig. 9. Contrast sensitivity of 4 and 9 week old infants plotted on a linear spatial frequency axis. Changes in acuity are determined mainly by an overall increase in contrast sensitivity, i.e. a vertical shift of the CSF.

First, our absolute contrast sensitivities, both for infants and adults, are substantially higher. At least part of this difference may be explained by the nearly 50 times higher luminance used in the present study. However, we find that 10 week olds, for example, have a peak sensitivity which is only a factor of 2 lower than that

of the adult, while Pirchio et al. (1978) found a factor of 10 difference for this age group. The difference in luminance is therefore unlikely to explain this discrepancy, especially in light of the report by Fiorentini et al. (1983) that infant peak sensitivity becomes *more* similar to that of the adult as luminance decreases.

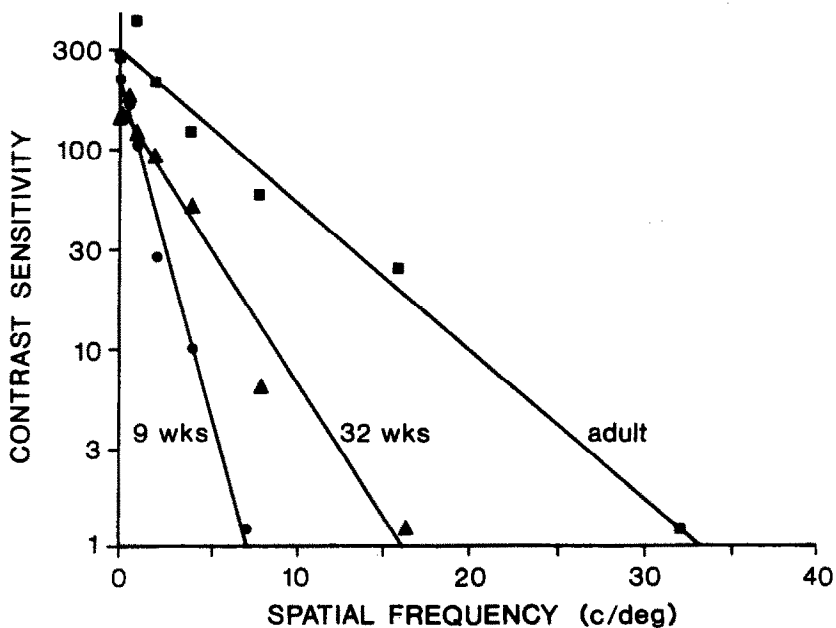


Fig. 10. Contrast sensitivity at 9 weeks, 32 weeks and for adults plotted on a linear spatial frequency axis. Sensitivity increases are restricted to the higher spatial frequencies, indicating that a change in spatial resolution, not sensitivity, dominates the development of the CSF after 9 weeks.

The form of the contrast sensitivity function we have observed is different from that reported by Pirchio et al. (1978). Our CSFs show less low spatial frequency attenuation in both infants and adults than in the Pirchio et al. (1978) data. Again, it is unlikely that luminance differences could account for the greater low frequency attenuation than they reported, since lateral interactions tend to be weaker rather than stronger at low luminances (Enroth-Cugell & Robson, 1966).

Since Pirchio et al. did not report adult psychophysical thresholds, it is unclear whether their VEP technique was producing optimal threshold estimates at low spatial frequencies. Two-lobed contrast functions are more common at low spatial frequencies (Campbell & Maffei, 1970; Tyler, Norcia & Hamer, 1987; Norcia, Tyler, Hamer & Wesemann, 1989) and it is sometimes difficult to record the low contrast lobe, which is almost always of lower amplitude than the high contrast lobe. This may also account for the stronger roll-off at low spatial frequency seen in our adult VEP data compared to the psychophysics. Difficulties in recording the low contrast lobe may also account for the low frequency attenuation in Fig. 2 for infants Hunter and for the tendency of the oldest age groups to show lower sensitivity in some conditions in Fig. 8.

The most important difference between our results and those of Pirchio et al. (1978) is the fact that we find peak sensitivity to develop at a more rapid rate than does acuity, while they reported that peak sensitivity and acuity develop at the same rate. In our data, sensitivity and acuity are dissociated after 9 or 10 weeks, suggesting that different processes underlie the development of peak sensitivity and acuity.

If the present results (Fig. 6) on peak sensitivity are extrapolated to the time of birth, a peak sensitivity between 2 and 6 would be obtained, which is in general agreement with Atkinson et al.'s (1979) estimate of 2 for the contrast sensitivity of the neonate. Our results at 6 months are also consistent with Harris et al.'s (1976) data obtained from a single subject.

Norcia et al. (1986) reported on a small sample of infants tested with the sweep technique. In that study, asymptotic sensitivity, c , was 1.26 times higher for adults than for 25–28 week olds (173 vs 137). For the present data, c is a factor of 1.20 higher for adults than for 27 week olds. The high frequency attenuation

parameter, a , was -0.46 for infants and -0.19 for adults in Norcia et al. (1986) compared to -0.38 and -0.17 for the same groups in the present data.

The peak contrast sensitivity for adults was somewhat lower in the Norcia et al. (1986) study than in the present study (173 vs 312). However, they recorded at a mean luminance of 80 cd/m^2 or 2.75 times lower luminance than used in the present study. Peak sensitivity has been found to increase with the square root of luminance (Van Nes & Bouman, 1967). The adult peak sensitivity of 312 observed in the present study is comparable to within measurement error with the Norcia et al. (1986) value corrected by 2.75, that is, a value of 287.

Possible anatomical constraints on contrast sensitivity development

Developmental changes in any of several possible mechanisms could be involved in the growth of peak sensitivity and acuity. Increases in cone outer segment length and changes in the waveguide properties of infant photoreceptors will increase the quantum efficiency of the infant photoreceptor array (Banks, Bennett & Shefrin, 1987; Banks & Bennett, 1988; Wilson, 1988). However, there is simply not enough anatomical data available to determine whether the time course of changes in retinal quantum efficiency matches that of the time course of peak sensitivity development.

Changes in the density of foveal cone packing will increase the spatial sampling limit of the infant photoreceptor array. Substantial developmental changes in foveal cone density have been reported by Hendrickson and Youdelis (1984). By 15 months foveal cone density is one half that of the adult. It is conceivable that the retina of Hendrickson and Youdelis' 15 month old is also typical of substantially younger infants and that foveal cone density changes most rapidly during the first 8 months when VEP acuity undergoes its initial developmental phase (Marg, Freeman, Peltzman & Goldstein, 1976; Sokol, 1978; de Vries-Khoe & Spekrijse, 1982; Norcia & Tyler, 1985).

A number of authors have remarked on the immaturity of the fovea of neonates relative to the rest of the retina (Mann, 1964; Abramov, Gordon, Hendrickson, Hainline, Dobson & La Boissiere, 1982; Hendrickson & Youdelis, 1984). Given the immaturity of the fovea and the observation that VEP contrast sensitivity at low

spatial frequencies is unaffected by exclusion of the fovea (Campbell & Maffei, 1970), it is likely that it is the near periphery in young infants which demonstrates the highest contrast sensitivity. The question as to which retinal region has the highest acuity in very young infants remains elusive (Spinelli, Pirchio & Sandini, 1983); but it is likely that contrast sensitivity development beyond 9 weeks is dominated by changes in the fovea (cf. Wilson, 1988).

In addition to the pre-neuronal retinal factors mentioned above, it is also possible that immaturities in neural processing also limit contrast sensitivity. Developmental changes may occur in the mechanisms responsible for effective light adaptation, which may in turn affect differential sensitivity. Myelination of the optic nerve or changes in synaptic efficiency may also play a role. It has been suggested on the basis of the prolonged developmental changes in VEP waveform that cortical mechanisms may play a role in contrast sensitivity development, particularly in the later phases of development beyond 8 months (de Vries-Khoe & Spekreijse, 1982). Finally, one cannot rule out effects due to differences in attention and cooperation between infants and adults.

The present measurements of contrast sensitivity development cover only a limited portion of the spatio-temporal domain. If significant spatio-temporal interactions exist, the picture could be quite different for different stimulus conditions or response measures (Moskowitz & Sokol, 1980; Orel-Bixler & Norcia, 1987). Because of this, it is difficult to compare our results immediately with previous behavioral data (e.g. Banks & Salapatek, 1976, 1978; Atkinson, Braddick & Moar, 1977) other than to say that markedly higher sensitivity can be demonstrated in infants using the VEP and/or with the targets we have used. For this reason and many others, it will be of great interest in the future to explore the remainder of the spatio-temporal domain using a range of targets differing not only in temporal frequency, but temporal waveform, luminance, color and retinal eccentricity.

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