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OPERANT MEASUREMENTS OF CONTRAST SENSITIVITY IN INFANT MACAQUE MONKEYS DURING NORMAL DEVELOPMENT*

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Abstract—The development of contrast sensitivity was measured longitudinally in seven *Macaca nemestrina* monkeys. Operant conditioning methods were used to train and then test infant monkeys from the ages of 1 to 12 months. Several changes were observed in the contrast sensitivity function, including an overall increase in sensitivity to contrast, a shift in the peak of the function toward higher spatial frequencies, and an increase in the cutoff spatial frequency. The time-courses for the changes in the contrast sensitivity function were characterized by rapid development during the first 10–20 weeks, followed by a gradual asymptotic development to adult levels over the remainder of the year. Sensitivity to contrast was found to develop with different time-courses for different spatial frequencies; sensitivity to low spatial frequencies reached adult levels much earlier than sensitivity to high spatial frequencies.

Visual development Macaque monkey Contrast sensitivity Spatial vision

INTRODUCTION

The development of spatial vision in human and nonhuman primates has been the subject of considerable research in the last 10 years. Spatial vision in primate infants is strikingly immature in comparison to that of adults. For example, grating acuity in newborns is about 50 times poorer than it is in adults (Dobson and Teller, 1978; Teller *et al.*, 1978; Lee and Boothe, 1981). This immaturity is not restricted to visual resolution. It has been demonstrated that human infants also show considerable immaturity in sensitivity to contrast at spatial frequencies below the resolution limit (Banks and Salapatek, 1976, 1978, 1981; Atkinson *et al.*, 1977; Pirchio *et al.*, 1978). There is a protracted period of postnatal development that extends over the first 3–5 years during which spatial vision develops to adult levels (see Boothe *et al.*, 1985, for review).

The specific factors that limit spatial vision in infants and subsequently allow for its development to adult levels are not fully understood. Determination of the factors that control the postnatal development of spatial vision is important in two respects. First, it is of theoretical interest to attempt to relate optical (Williams and Boothe, 1981; Howland *et al.*, 1982) and neural (Blakemore and Vital-Durand, 1981) changes that are known to occur during development in nonhuman primates to changes in behavioral sensitivity (Boothe, 1982). Correlations between neural and behavioral sensitivity could reveal the structures or neural systems that limit visual sensitivity at different ages. Second, there are clinically important disorders of visual development that are characterized by deficits in resolution and contrast sensitivity. In order to understand the neural bases of these deficits, or amblyopias, it is important to establish the natural time-course of development and its limiting factors.

Since the studies necessary to establish the factors that limit spatial vision in infants are by nature invasive it is necessary to rely on an animal model. It has been demonstrated that the infant macaque monkey provides a reasonable model for studying the development of spatial vision under both normal and abnormal conditions of visual experience (Teller and Boothe,

*All research described in this report was conducted at the Infant Primate Research Laboratory at the University of Washington in Seattle.

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1979; Boothe, 1981; Kiorpes and Boothe, 1981; Boothe *et al.*, 1985). Developmental data collected using infant *Macaca nemestrina* monkeys can be extrapolated to the human relatively safely with the approximate age conversion of weeks (in monkeys) to months (in humans). In this report we present a detailed description of the time-course for spatial contrast sensitivity development in normal infant monkeys. Preliminary data have been presented elsewhere (Boothe *et al.*, 1980; Boothe, 1984).

METHODS

Subjects in these experiments were seven infant *Macaca nemestrina* monkeys born at the Washington Regional Primate Research Center. The infants were separated from their mothers within a few days after birth and housed in the nursery facilities of the Infant Primate Laboratory. All care of the infants was conducted according to the protocols of the Washington Regional Primate Center and conformed to the NIH guidelines for research animal welfare.

Procedures for training and testing of infant monkeys on visual discrimination tasks have been detailed elsewhere (Williams *et al.*, 1981; Boothe, 1981). Essential procedures are described below.

The monkeys were trained to perform a spatial two-alternative forced-choice discrimination task. On each trial the monkey was required to discriminate a sinusoidal grating stimulus from a homogeneous field of equal space-average luminance. The monkey was trained to pull one of two grab bars to indicate which of two adjacent displays contained the grating stimulus. Correct responses were rewarded with liquid reinforcement (milk for young infants; apple juice for older monkeys). Incorrect responses resulted in a short time out period that was signalled by a tone.

During the testing sessions the monkeys roamed freely in a face-mask cage (Sackett *et al.*, 1971). Very young infants were housed continuously in these specially designed cages to facilitate training and were allowed access to the task at regular intervals during the day. To initiate a trial, the monkey placed its face in the facemask. Photocells imbedded in the mask were used to sense the presence of the face; the resulting signal was used to turn on the displays. This procedure served to control viewing distance without restraining the monkey.

The pair of displays was set at viewing distances ranging from 0.3 to 1.2 m depending on the spatial frequency range resolved by the animal. All testing was conducted binocularly with natural pupils and no optical correction. Refractive errors were evaluated for all animals. With the exception of one monkey, all were within 1.75 D of emmetropia and demonstrated no cylindrical error greater than 1 D. The one exception, Z.Z., had 5 D of hyperopia which is not outside the normal range of refractive errors for this species (Young, unpublished observations). The displays had a space-average luminance of 27 cd/m^2 and were surrounded by electroluminescent panels of approximately matching mean luminance and color. Photographic measurements of pupil size during testing revealed that pupil size remained relatively constant at 6 mm.

The stimuli were generated on Tektronix 602 CRT display units (P31 phosphor). The raster scan method developed by Campbell and Green (1965) was used to generate the sinusoidally modulated gratings. Inputs to the X and Y axes were provided by ramp waveform generators; input to the Z-axes were provided via a D/A converter controlled by a PDP11 computer. Look-up tables, generated from extensive calibrations, were used to compensate for the high spatial frequency falloff of the CRT and for some of the display nonlinearities. All aspects of stimulus presentation and data collection were computer controlled.

The method of constant stimuli was used to define threshold contrast for each of a number of spatial frequencies within the resolution limit of the monkey at each test age. For each spatial frequency, four or five contrast levels were chosen to span the psychometric function (that is, span the monkey's performance range from 50 to 100% correct). Generally, 40 trials were collected for each contrast condition, with the order of presentation of the various conditions randomized. The percent correct at each contrast level was plotted for each spatial frequency tested, as shown in Fig. 1 (top). Threshold contrast for each spatial frequency was determined by probit analysis (Finney, 1971), for which the upper and lower asymptotes were set to 99 and 50%, respectively. The slope and threshold were estimated by an iterative maximum likelihood estimation procedure. Threshold contrast was taken to be the level at which the function crossed the 75% correct level. Standard errors of the threshold estimates for

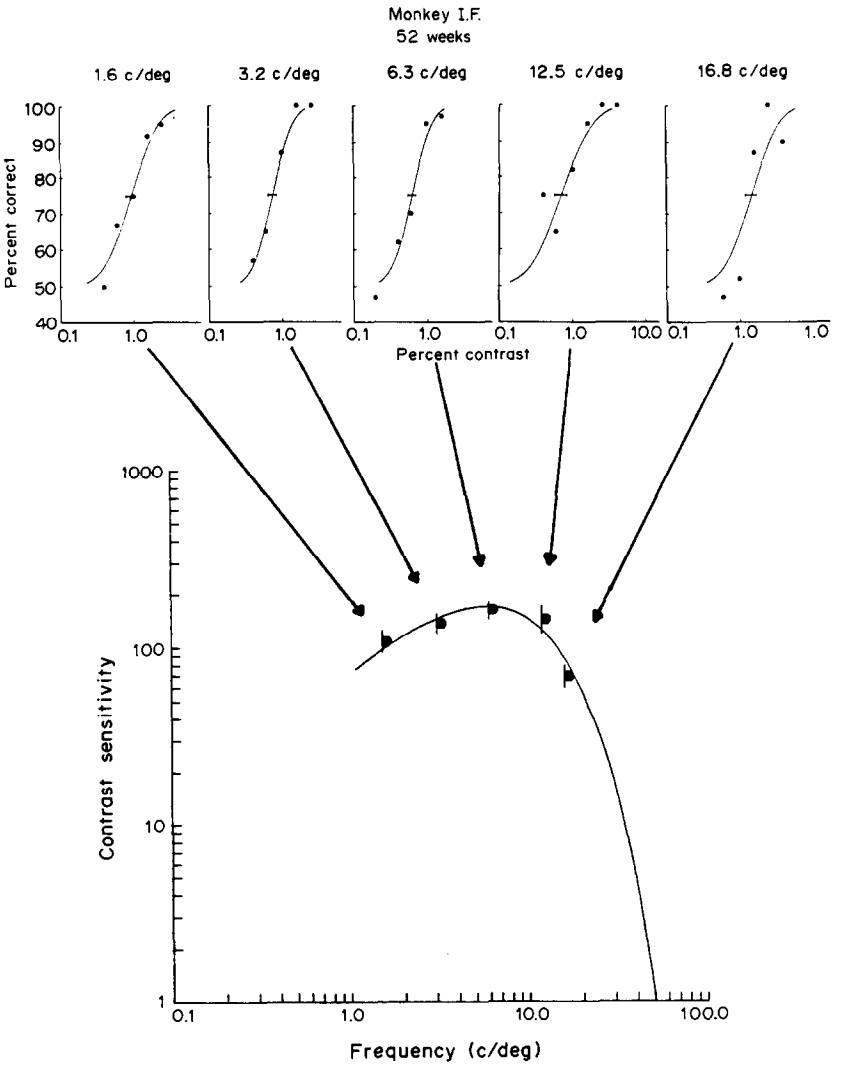


Fig. 1. (Top) Psychometric functions for each of five spatial frequencies for monkey I.F. at 52 weeks of age. For each frequency, monkey's percent correct is plotted against percent contrast. Contrast threshold and the standard error of estimation are designated on each function by the horizontal bar at the 75% correct level. (Bottom) Contrast sensitivity (the reciprocal of contrast threshold) is plotted as a function of spatial frequency. The smooth curve fit to the data describes the contrast sensitivity function (CSF). See methods for details of the curve-fitting and extrapolation procedure.

the functions in Fig. 1 (top) are indicated by the horizontal bars drawn at the 75% level; the standard errors are based on at least 160 trials per function.

Figure 1 (bottom) also illustrates the definition of the contrast sensitivity function (CSF). The reciprocal of threshold contrast and the standard error of estimate at each spatial frequency (from Fig. 1, top) are plotted as a function of spatial frequency on log–log coordinates. The smooth curve drawn through the data is a best-fitting double exponential function of the form

$$S = v(\omega f)^a e^{-b\omega f}$$

where S is contrast sensitivity and ω is spatial frequency. The four free parameters affect primarily the steepness of the low (a) and high frequency (b) portions of the curve, lateral shifts along the frequency axis (f), and vertical shifts along the sensitivity axis (v). This curve is similar to that suggested by Wilson (1978) for human adult CSF's. It was chosen over other commonly used functions because it reliably produced good fits to our data. An iterative computer program was used to adjust the parameters to yield a least squares fit to the data points. The spatial frequency at the point of maximum sensitivity for the fitted curve was taken to be the *peak frequency*. The contrast

sensitivity at the peak frequency was taken to be *peak sensitivity*. Extrapolation of the curve to a sensitivity of 1 (contrast of 100%) yielded the estimate of *cutoff frequency*. The CSF in Fig. 1 (bottom) has a peak frequency of about 6 c/deg, a peak sensitivity of about 150 and a cutoff frequency of 50 c/deg.

The estimates of cutoff frequency obtained by extrapolation can be used as an estimate of the resolution limit, or acuity, of the subject. There are two lines of evidence to suggest that these extrapolations provide reasonable estimates of acuity. First, when we attempted to measure contrast thresholds for spatial frequencies near the extrapolated cutoff the monkeys failed to achieve above-chance performance. Second, although the extrapolated cutoff frequencies are dependent upon the equation used for the fit, direct measurements of grating acuity, made in connection with other studies from our laboratory, are in good agreement with extrapolated cutoffs from the same animals. When compared with square-wave grating acuity data collected within a few weeks of CSF data in the same animals, the correlation between the two estimates of acuity was 0.99 (the contrast level of the square-wave gratings was 50%; the subjects' ages ranged from 15 weeks to adult). The mean difference between paired grating acuity and cutoff frequency estimates in log units was 0.075 (SD = 0.107; $n = 9$).

Each infant monkey was tested longitudinally so that CSF's were obtained repeatedly during the first postnatal year. Each function was based on 480–1200 trials (3–6 spatial frequencies, 4 or 5 contrasts per frequency, and 40 or more trials per contrast level). The data for each function were obtained within a maximum period of 4 days.

RESULTS

The development of the contrast sensitivity function (CSF) was characterized by an overall increase in sensitivity and a broadening of the range of spatial frequencies resolved. Figure 2(A) shows developmental data from one monkey, A.B., which illustrate these overall changes. All three of the measured aspects of the function, peak sensitivity, peak frequency, and cutoff frequency, showed considerable improvement with age. Comparison of the first function, obtained from A.B., at 10 weeks, with the last function, obtained at 38 weeks, reveals that the frequency at the peak increased by about a factor of 5 in the interim while the sensitivity at the peak and the cutoff frequency both increased by about a factor of 10. Data from a second monkey, T.M., are shown in Fig. 2(B). They exhibit changes that are qualitatively similar to those shown by A.B. but are somewhat larger in magnitude.

The three CSF measures, peak frequency, peak sensitivity and cutoff frequency, appeared

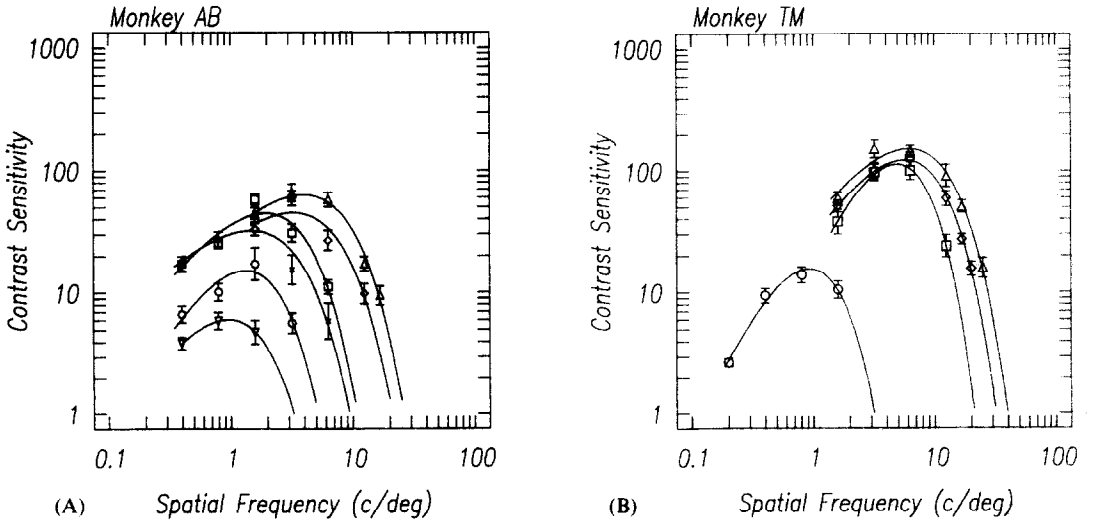


Fig. 2. Development of the spatial CSF for two monkey subjects. Contrast sensitivity is plotted as a function of spatial frequency at each of a number of ages. (A) Data for monkey A.B.: 10 weeks (▽), 11 weeks (○), 14 weeks (×), 15 weeks (□), 26 weeks (◇), 38 weeks (△). Patterns were always vertical; viewing distance varied from 30 cm at 10 weeks to 120 cm at 38 weeks. (B) Data for monkey T.M.: 5 weeks (○), 12 weeks (□), 20 weeks (◇), 32 weeks (△). Patterns were always vertical; viewing distance at 5 weeks was 15 cm, otherwise it was 120 cm.

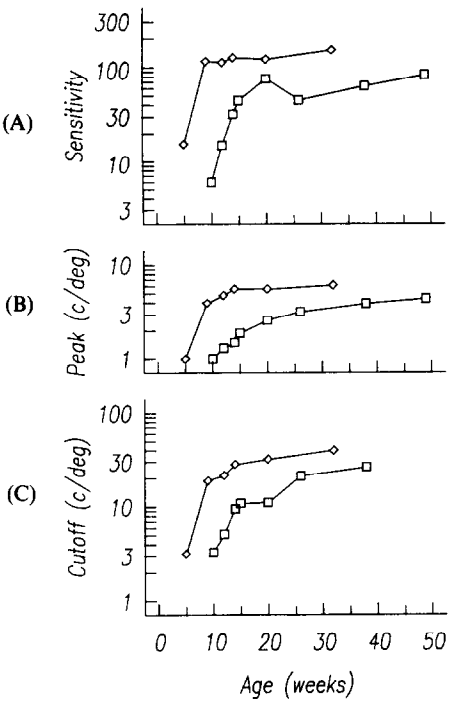


Fig. 3. Development of CSF parameters for two representative monkey subjects: the fastest to develop (◇, T.M.) and the slowest to develop (□, A.B.). The three measured CSF parameters are presented in separate plots: (A) peak sensitivity, (B) peak frequency, (C) cutoff frequency.

to improve simultaneously on average. In Fig. 3, the developmental time-course for each of the measured aspects of the CSF is plotted. In each case, data from two representative monkeys are presented: the monkey whose rate of development was the most rapid of the seven animals tested (T.M., diamonds), and the monkey whose rate of development was the slowest (A.B., squares). The data in Fig. 3 show an early period of rapid development for each of the CSF measures that extended over the first 10–20 postnatal weeks, or until the cutoff frequency reached about 20 c/deg. Thereafter, there was a continued gradual improvement on all of the CSF measures throughout the remainder of the first year. The extent of the residual development during this latter period was greatest for cutoff frequency and slightest for peak sensitivity. By the end of the first year, peak frequency had improved from near 1 to 3–6 c/deg, peak sensitivity had improved from about 10 to near 100 and cutoff frequency had improved from 1–3 to 30–50 c/deg.

The developmental time-courses from the individual subjects shown in Fig. 3 define the range of individual differences found in the study. Monkey T.M. (diamonds), who showed the fastest development, demonstrated a CSF that was adult-like in form by 20 weeks. An adult-like CSF is of the characteristic form shown by adult monkeys although the high-frequency portion of the curve undergoes further development. The slowest monkey, A.B. (squares), first demonstrated an adult-like CSF at 38 weeks.

Analysis of contrast sensitivity development at individual spatial frequencies reveals that development proceeds at a different rate for different spatial frequencies. Low spatial frequencies reached maximal sensitivity earlier

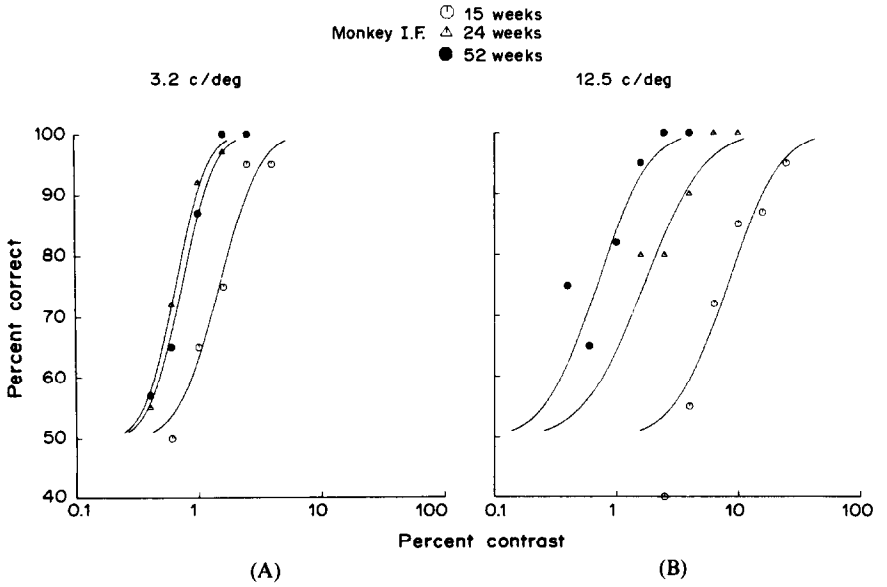
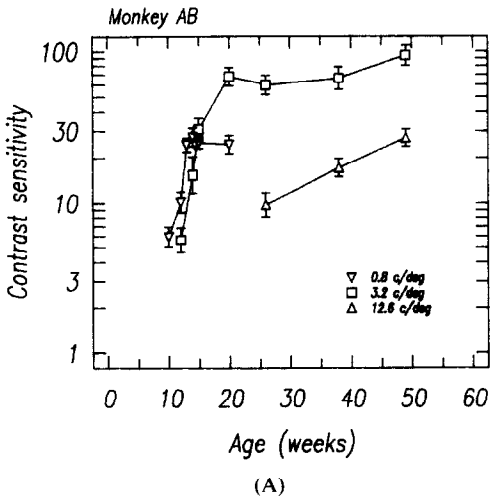


Fig. 4. Psychometric functions for a low (3.2 c/deg) and a high (12.5 c/deg) spatial frequency at each of three ages for monkey I.F.: 15 weeks (○), 24 weeks (△), 52 weeks (●).

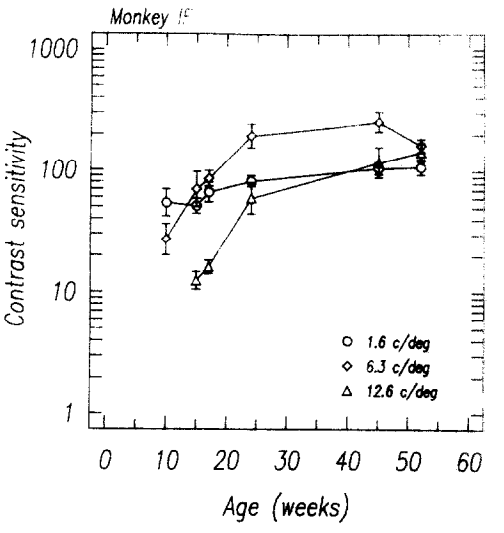
than middle and high spatial frequencies. Figure 4 shows psychometric functions obtained at three ages for each of two spatial frequencies from monkey I.F. Sensitivity for both frequencies, 3.2 c/deg [Fig. 4(A)] and 12.5 c/deg [Fig. 4(B)], improved between 15 weeks (open circles) and 24 weeks (open triangles). This improvement is apparent from the leftward shift of the functions along the abscissa. Contrast sensitivity for the lower frequency, 3.2 c/deg, changed little between 24 weeks and 52 weeks (solid circles) whereas sensitivity at 12.5 c/deg showed considerable improvement during the same period of time.

The time-courses for development of sensitivity to contrast at different spatial frequencies are summarized in Fig. 5 for each of three representative monkeys. The data suggest a progressive maturation of sensitivity with increasing spatial frequency. For each of the monkeys, developmental functions for three representative spatial frequencies are plotted. The data plotted for each monkey include sensitivity to a low, a middle and a high frequency. Sensitivity to the lowest frequencies approached an asymptote prior to the middle frequencies, which in turn approached asymptotic levels before the highest frequencies. Also, the highest frequencies were continuing to show improvement even at the oldest ages tested. These basic findings were consistent for all of our subjects.

Collectively, these data suggest that the majority of CSF development occurs during the first half of the first postnatal year. Development during the second half of the year constitutes primarily a filling out of the high frequency portion of the function. There is a continued increase in sensitivity across the high frequency range and a resultant increase in cutoff frequency. Overall, the time period over which the CSF develops in monkeys covers at least the first 50 weeks after birth.



(A)



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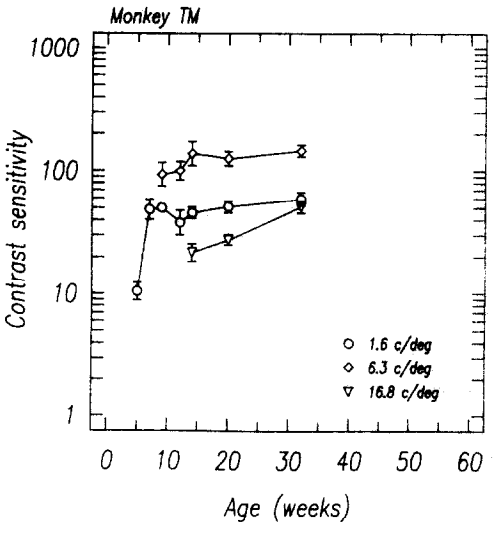

(C)

Fig. 5. Contrast sensitivity as a function of age at each of three spatial frequencies for three monkey subjects. (A) Monkey A.B.: 0.8 c/deg (▽), 3.2 c/deg (□), 12.6 c/deg (△). Note that in (A) 3 data points on the 0.8 c/deg function are clustered together between 10 and 15 weeks. (B) Monkey I.F.: 1.6 c/deg (○), 6.3 c/deg (◇), 12.6 c/deg (△). (C) Monkey T.M.: 1.6 c/deg (○), 6.3 c/deg (◇), 16.8 c/deg (▽). Contrast sensitivity approaches asymptotic levels at the lowest frequencies prior to sensitivity at middle and higher frequencies.

One indicator of the reliability of a subject's performance is the slope of the psychometric function. The slope (β) of an individual psychometric function is equivalent to the reciprocal of

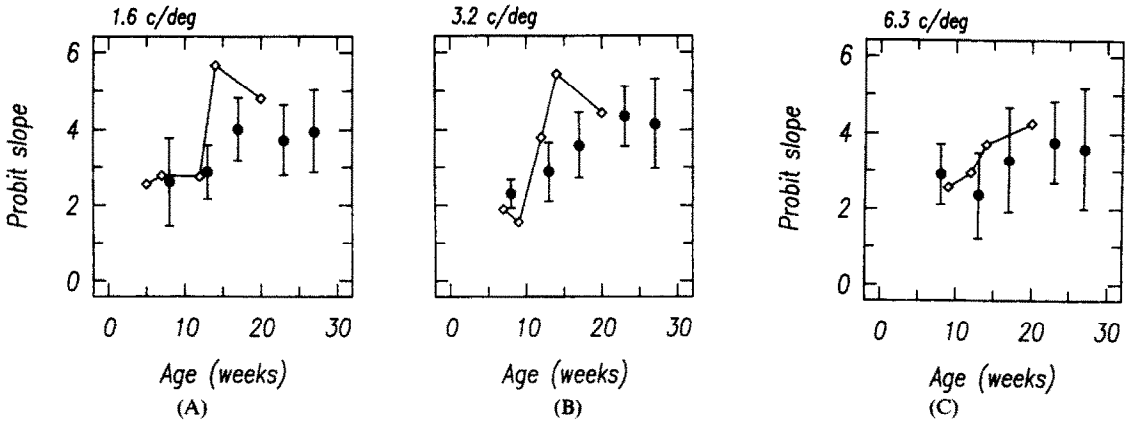

Fig. 6. Slope (β) of the probit fits as a function of age for three spatial frequencies: (A) 1.6 c/deg, (B) 3.2 c/deg, (C) 6.3 c/deg. Solid circles are averages of the probit slopes for all monkeys tested at each age (± 2 weeks). The error bars indicate ± 1 SD from the group mean. Squares are data for a single monkey, T.M.

the standard deviation of the best-fitting cumulative normal curve ($1/\sigma$). Although the probit slopes showed little overall change during the period of time studied, there is some suggestion of a progressive increase in the steepness of the slopes during the very early weeks. Figure 6 shows average probit slopes (solid circles) for all psychometric functions at each of three spatial frequencies for ages up to 30 weeks. Also included in Fig. 6 are individual data from monkey T.M. (diamonds), from whom we collected extensive data during the early weeks. Probit slopes for monkey T.M. showed a clear increase between 10 and 20 weeks at all three frequencies. The average probit slopes also showed this effect clearly at 1.6 and 3.2 c/deg [Fig. 6(A) and (B)], but the data for 6.3 c/deg [Fig. 6(C)] were much more variable. This variability is due, at least in part, to the individual differences in rate of development. The animals who developed fastest could resolve higher frequencies at earlier ages and showed changes in slope; no consistent changes were shown in the slower developing animals at the higher frequencies.

There was no systematic variation in the upper asymptotes of the psychometric functions, which were usually between 90 and 100% correct. Thus it is probably not the case that the infants were generally less attentive or motivated at younger test ages. However, as a consequence of the changing slope without concurrent increase in the upper asymptote, the shapes of the CSFs would be influenced by the choice of criterion for scoring threshold from the psychometric functions. We used a 75% criterion; choice of a higher or lower criterion would have a subtle effect on the apparent rate of development for the low and middle frequencies. However, such an effect would be small compared to the developmental trends shown in Fig. 5 and would not influence the conclusions. It is worth noting that an increase in the steepness of the slope of the cumulative normal curve has also been reported to occur in human infants during the first 30 months (Mayer and Dobson, 1982).

Because our subjects were tested longitudinally, age is confounded with amount of practice on the psychophysical task. It is therefore possible that practice effects contribute to the overall pattern of development found for these infant monkeys. In order to assess the effects of practice on CSF development, we

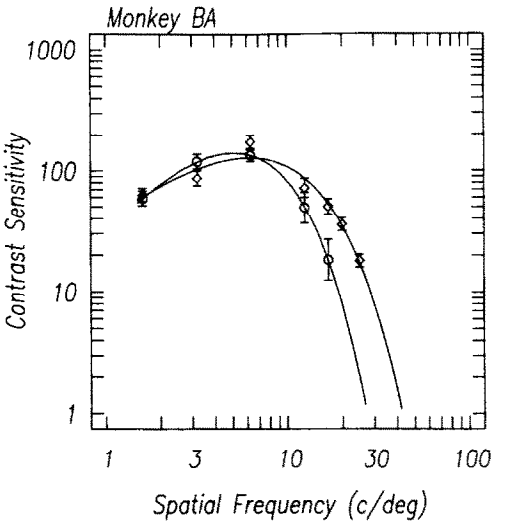

Fig. 7. Contrast sensitivity functions for monkey B.A., whose training was not begun until age 6 months. CSF data at 29 weeks are represented by the circles: data for 39 weeks are represented by the diamonds.

studied one monkey who began testing at 6 months rather than during infancy. Figure 7 shows CSFs from this monkey, B.A., whose first function (circles) was obtained at age 29 weeks. The 29 week CSF exhibits a form which is similar, in terms of peak sensitivity and frequency and cutoff frequency, to CSFs obtained from other monkeys of this age who have been tested since infancy. Continued testing (diamonds) revealed improvement only in the high frequency portion of the function with no concurrent improvement at the low and middle frequencies. This pattern is similar to what would be expected based on data from the other monkeys, all of whom were tested throughout infancy as well as during this age period. Thus, it seems unlikely that practice effects contribute greatly to the observed pattern of CSF development.

DISCUSSION

The development of sensitivity to contrast in infant monkeys was found to progress to a greater or lesser degree throughout the first postnatal year. A period of rapid development of sensitivity to all spatial frequencies extended through the first 10–20 weeks. The resulting changes in the CSF can be described qualitatively as shifts upward, that is, increased sensitivity, and shifts to higher spatial frequency ranges. In most cases, the form of the CSF was adult-like by 30 weeks in the sense that the peak sensitivity and frequency of the function were near adult levels. This initial rapid development was followed by a more gradual increase in sensitivity primarily at high spatial frequencies that was apparent through at least 50 weeks. We have described these changes quantitatively in terms of progressive improvements in peak sensitivity, peak frequency and cutoff frequency.

We found a large range of individual differences in the rates of CSF development among the individual animals in the study. This variability makes it difficult to precisely characterize the "average" developmental time-course. However, several aspects of CSF development were consistent among all animals. First is the essentially simultaneous development of all three of the measured aspects of the CSF for individual animals (see Fig. 3). The time-courses for development of these features were strikingly similar to each other suggesting that the changes underlying their development are unlikely to be comprised of a series of independent events. Second, the development of low, middle and high spatial frequencies progressed at different rates (see Fig. 5). This differential development suggests that a single mechanism gradually improving in sensitivity is unlikely to be responsible for the observed changes in the CSF.

There are many aspects of optical and ocular development that may contribute to the overall improvement in contrast sensitivity and visual resolution during infancy. Some of these factors are eye growth (Blakemore and Vital-Durand, 1986), refinement of the retinal receptors and their distribution across the visual field (Hendrickson and Kupfer, 1976), and improvement in optical quality (Williams and Boothe, 1981) and accommodative accuracy (Howland *et al.*, 1982). However, previous analyses of these factors have suggested that, separately or in combination, they probably do not provide the major limitation for visual resolution in infancy (Boothe, 1982; Blakemore and Vital-Durand, 1986).

Although little is known about the physiological development of neural elements in the visual pathways of primates, it is informative to consider the data that do exist. Blakemore and Vital-Durand (1986), in a recent study of the development of neural properties in the lateral geniclate nucleus (LGN), described several important developmental changes which appeared to occur over an age range comparable to that during which the major behavioral changes occur. LGN *X* cells, both magnocellular and parvocellular, demonstrated a maturation of surround strength, an increase in overall responsiveness, and a decrease in the size of the receptive field centers. The apparent maturation of surround strength occurred very early in postnatal life; strong antagonistic surrounds were found to be present, and seemingly adult-like, by 3–5 weeks. Since the earliest data collected in the present study were obtained at 5 weeks, it is unlikely that this factor affected the CSF changes observed in the present study. However, the changes in the overall responsiveness of single LGN *X* cells and the size of the receptive field centers could be important for CSF development. The increase in responsiveness of the individual neurons and the decrease in the size of the receptive field centers occurred over time-courses which were similar to each other. Major development of these features occured between 3 and 28 postnatal weeks, the same period during which the major

changes in the CSF as measured in the present study occurred. It is reasonable to postulate that the combined increase in responsiveness and decrease in receptive field center size in individual LGN *X* cells could underlie the combined increase in sensitivity and the shift toward higher spatial frequencies of the behaviorally measured CSF (Enroth-Cugell and Robson, 1966).

Unfortunately no studies of ganglion cell development in primates have been reported. It is therefore impossible to know whether the changes observed by Blakemore and Vital-Durand (1986) at the level of the LGN are primary in nature or secondary to changes occurring at the level of the ganglion cells.

The CSFs measured for our oldest monkeys appear to be quite similar to those found for both adult humans and monkeys (e.g. Williams *et al.*, 1981). Comparison between our infant monkey CSF's and those measured for human infants is difficult due to the differences in age ranges tested. CSF development has been studied most extensively in human infants from birth to 3 months, during which time there are changes in the overall sensitivity and the cutoff frequency (Atkinson *et al.*, 1977; Banks and Salapatek, 1976; 1978, 1981). We have no data over a comparable age range, which would be equivalent to the age range from birth to 3 weeks in infant monkeys (Teller and Boothe, 1979). There also appears to be a period in the early postnatal weeks, between 1 and 2 months, in humans during which the low frequency falloff develops. In our preliminary report (Boothe *et al.*, 1980) we had not noted a low frequency falloff in our youngest monkeys, however we had not tested frequencies below 1.5 c/deg at that time. Our present data show that the low frequency falloff was present at the earliest ages in the monkeys for whom we tested frequencies below 1 c/deg [see Fig. 2(A) and (B)]. We would need to look at younger ages (1–2 weeks) in order to determine whether or not the low frequency falloff is absent in neonatal monkeys.

With the exception of data from one infant, reported by Harris *et al.*, 1976, there are no behavioral data on CSF development between the ages of 3 months and 2.5 years. However, VEP data suggest a progression of CSF development in human infants that is similar to our monkey data. Norcia *et al.*, 1986, report contrast sensitivity at low frequencies to be near adult levels in 6 month old infants, whereas sensitivity to higher frequencies is still immature at that age. The overall pattern of change in the CSF is also similar in that there is an early period of rapid development followed by a later more gradual improvement in sensitivity and acuity (Norcia *et al.*, 1987).

A developmental period of 50 weeks for the monkey CSF correlates reasonably well with what is known about the human developmental time-course. On the basis of the age conversion of weeks to months for monkeys and humans for grating acuity development, our data suggest that human CSF development should continue up to at least 50 months. Bradley and Freeman (1982) studied contrast sensitivity in children between the ages of 2.5 and 8 years. They found that CSF development continued up to about 5 years (60 months) in children.

It is likely that the sensitive period for visual resolution extends at least throughout the period of normal development and possibly beyond. Since the development of the contrast sensitivity function in infant monkeys proceeds throughout at least the first postnatal year, the visual system would be vulnerable to the adverse effects of visual deprivation and other forms of abnormal visual input to a greater or lesser extent over at least the first postnatal year as well. This suggestion is consistent with the findings of Harwerth *et al.* (1986) that the sensitive period for deprivation amblyopia in the macaque monkey extends over the first two postnatal years. Further studies of normative development, both behavioral and physiological, will hopefully reveal the structures and functions concerned with this vulnerability.

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