



# Development of Contrast Sensitivity Across the Visual Field in Macaque Monkeys (*Macaca nemestrina*)

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**Interpretation of measurements of visual performance in infants must be based on knowledge of the locus of highest sensitivity in the infant retina. While we know that adult contrast sensitivity and spatial resolution is highest at the fovea, recent anatomical data show that the infant fovea is relatively immature. We have studied the variation of contrast sensitivity across the visual field during development in infant monkeys in order to investigate the behavioral consequences of this immaturity. The results show that, unlike adults, the sensitivity of the infant foveal region is similar to that of the near periphery. Central contrast sensitivity and spatial resolution improve substantially relative to the periphery over the first 20–40 postnatal weeks. Thus, contrast sensitivity in the periphery is relatively mature in infants with respect to more central regions of the visual field. The maturation pattern seen behaviorally is consistent with physiological and anatomical maturation patterns in macaque monkey.**

Contrast sensitivity Peripheral vision Macaque monkey

## INTRODUCTION

Spatial resolution in newborn primates, human and non-human, is on the order of 30 times poorer than in adults and approaches adult levels with a characteristic time course (see Boothe, Dobson & Teller, 1985; Kiorpes & Movshon, 1990). Sensitivity to contrast is also immature in newborns, as much as a factor of 10 poorer than in adults. These behaviorally characterized changes in the contrast sensitivity function during development provide a window into the anatomical and physiological processes that limit performance in infants.

To understand the developmental changes we see behaviorally in infants it is important to establish what locus (or loci) in the visual system is setting important limits on performance. For example, in adults visual acuity varies across the visual field, with the locus of highest acuity and contrast sensitivity at the fovea (see Graham, 1989; Robson & Graham, 1981). Thus adult free-viewing contrast sensitivity measurements typically reflect the capability of the central visual field. It is natural to assume that contrast sensitivity data collected from freely viewing infants also reflect the performance of the central visual field. However, recent anatomical

data show that in fact the infant fovea is underdeveloped (Abramov, Gordon, Hendrickson, Hainline, Dobson & LaBossiere, 1982; Yuodelis & Hendrickson, 1986). The density of cones in the central retina is low in newborns and increases dramatically during the early postnatal months; the degree of change in photoreceptor density with age is smaller in the periphery than in the fovea. Yuodelis and Hendrickson (1986) also reported morphological immaturities in human foveal cones that are likely to reduce the efficiency of light-capture. Foveal cones lag behind parafoveal cones and mid-peripheral photoreceptors in their maturation (Hendrickson & Drucker, 1992). The infant monkey retina, like the infant human retina, is underdeveloped at birth (Hendrickson & Kupfer, 1976; Packer, Hendrickson & Curcio, 1990). Although data on the morphology of infant macaque cones are scarce, organization of the fovea in macaque monkeys is relatively more mature than in human infants at birth.

Given the documented immaturities in the infant primate fovea, we suspected that contrast sensitivity in the central visual field in young primates might in fact not be superior to that of the peripheral visual field. If that is the case, it is important to know to what extent behaviorally-measured contrast sensitivity development reflects foveal development. Contrast sensitivity development has been fully characterized over the first postnatal year in macaque monkeys (Boothe, Kiorpes, Williams & Teller, 1988). There are a few behavioral studies of contrast sensitivity development in human infants. Most data are from infants ranging in age from

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1 to 4 months (Atkinson, Braddick & Moar, 1977; Banks & Salapatek, 1978, 1981; Peterzell, Werner & Kaplan, 1993) or children older than 2 years (Bradley & Freeman, 1982; Abramov, Hainline, Turkel, Lemerise, Smith, Gordon & Petry, 1984). In all of these studies the subjects were allowed to observe the stimuli freely (with no attempt to control retinal locus). It is of course assumed that the subjects used the retinal locus of highest sensitivity, whatever that may be.

A few studies have addressed the question of retinal locus specific sensitivity in human infants. Indirect evidence suggests that there exists a region of relatively higher sensitivity in the infant retina (Spinelli, Pirchio & Sandini, 1983). Threshold for detection of small, but not large, spots increases with eccentricity in 1 month old infants (Schneck, Hamer, Packer & Teller, 1984). Courage and Adams (1990) noted a change in acuity between 1 and 3 months at 20 deg eccentricity but did not compare that change with central acuity. Sireteanu and colleagues (Sireteanu, Kellerer & Boergen, 1984; Sireteanu, Fronius & Constantinescu, 1994) made behavioral measurements of acuity at 10, 20 and 30 deg eccentricity in infants during the first postnatal year. They found clear changes in acuity with age at all loci tested. Sireteanu *et al.* (1984) compared development of acuity at 10 deg peripheral with free-viewing acuity (from a different group of infants) and found the free-viewing acuity to be slightly superior at all ages but more so at the oldest test age (11 months). Only one study directly compared central and peripheral acuity in the same subjects. Allen, Tyler and Norcia (1989) measured acuity for phase-reversing gratings in the central and peripheral (8–16 deg) visual field simultaneously via sweep-VEP techniques. They also found foveal acuity to be superior to peripheral acuity at all ages, which ranged from 12 to about 30 weeks. They note, however, that peripheral acuity is relatively more mature than central acuity at the earliest ages (Tyler, 1993).

We made quantitative measurements of contrast sensitivity across the visual field in infant monkeys. We found that contrast sensitivity and acuity in the foveal region is not superior to that of the near periphery in young monkey infants. However, the sensitivity of the central visual field develops more quickly and to a greater extent than that of the peripheral visual field. Some of these data have been briefly presented elsewhere (Kiorpes & Kiper, 1991, 1992; Kiorpes, 1995).

## METHODS

### *Subjects*

Seven monkeys, *Macaca nemestrina*, were subjects in this experiment. Six monkeys were tested from infancy throughout the first postnatal year; the other one was tested as a juvenile for control purposes. All monkeys were supplied by the Washington Regional Primate Research Center and were hand-raised in our infant nursery. Care of the animals was provided in accordance with established, approved protocols which conform to

the guidelines of the *NIH Guide for the Care and Use of Laboratory Animals*.

### *Behavioral testing*

Peripheral contrast sensitivity was tested by training the monkeys to maintain fixation on a centrally-located square while grating stimuli were briefly presented in the periphery. The animals' task was to indicate the location at which the stimulus had been presented.

*Stimuli.* The stimuli were small patches of sinusoidal grating presented at specific locations in the visual field. The stimuli were displayed on a Barco CDCT 6551 19" monitor with a space-averaged luminance of 44 cd/m<sup>2</sup>, which subtended 39 deg at 60 cm. Stimulus contrast was vignettted in space by a two-dimensional Gaussian and was smoothly ramped on and off in time over approximately 150 msec. The standard deviation of the spatial Gaussian was normally 0.75–1 deg for stimuli of 1 cycle/degree (c/deg) or higher; for stimuli lower than 1 c/deg, the standard deviation was equal to one period of the grating in degrees. Grating patch size was kept approximately constant across spatial frequency, so that the number of cycles of the stimulus was proportional to the spatial frequency of the grating. Stimulus presentation and data collection were under computer control (Hertz 386 personal computer with a Microfield T8 graphics board).

*Eye position control.* Eye position was monitored using a Micromeasurements System 1200 video-based eye-tracker. The video camera was mounted above the display; a small beam splitter, positioned at a 45 deg angle in front of the fixation square, delivered the image of the monkey's eye to the camera. Initially, we used a large half-silvered mirror which was positioned in front of the display, covering the entire display, to deliver the image of the eye to the camera. This arrangement was cumbersome since it restricted the viewing distance and therefore the range of testable eccentricities, and reduced the luminance of the display to 25 cd/m<sup>2</sup>. In spite of the reduction in luminance, the measured effect of the mirror on infant contrast sensitivity was negligible. Free-viewing contrast sensitivity functions were virtually indistinguishable with and without the mirror. For peripheral viewing conditions, infants studied with the large mirror in place showed the same pattern of results as those studied without the mirror. There was a small effect of the mirror at high spatial frequencies in the oldest animals (30–50 weeks), as would be expected from human psychophysics (see Graham, 1989; Kiorpes & Movshon, 1989). Eye position was calibrated by recording horizontal output of the eye tracker while the monkey fixated targets sequentially presented at 4 deg increments along the nasal and temporal horizontal meridian.

*Behavioral task.* The monkeys were placed in a cage with a facemask mounted on one wall (see Boothe *et al.*, 1988), from which they could view the display. They were trained to fixate a small square, which subtended 1.5 deg at 60 cm, located in the center of the display. When the monkey placed its face in the mask and

maintained eye position within a 2 deg window, a sinusoidal grating patch was briefly presented on either side of the central square at a specified eccentricity along the horizontal meridian. The animals' task was a two-alternative forced-choice: the animal indicated whether the grating patch had appeared on the left or right side of the display. For testing the youngest animals (generally those younger than 12 weeks), we used a procedure which combines preferential looking and operant techniques (modelled after Schneck *et al.*, 1984). The monkeys were trained to fixate the central square and then make either a leftward or rightward saccade to indicate the direction of stimulus presentation. A human observer—who could not see the display—watched the movement of the eye on a video monitor and judged the side of stimulus presentation from the direction of the saccade. The monkeys were rewarded with a 0.5 ml squirt of milk for the observer's correct response. Older animals (generally those older than 12 weeks) were trained to pull one of two grab bars to indicate the side of stimulus presentation. At the termination of the stimulus presentation period, they had 300 msec within which to make a response. They were rewarded with a 0.25 ml squirt of diluted apple juice for correct responses; errors resulted in a time-out which was signalled by a tone (1000 Hz).

In the event that fixation within the 2 deg window was not maintained throughout the stimulus presentation, the trial was immediately interrupted. Feedback was given to the animal as to when its eye was in the window via a low frequency tone (500 Hz). In the event that an animal failed to make a response following a stimulus presentation, the same stimulus was re-presented for up to three presentations (provided that the eye remained in the window). Failure to respond through three presentations of a single stimulus was scored an error. All testing was monocular; the animals were free to accommodate to the screen, the distance of which ranged from 30 to 75 cm.

Within a single session, contrast sensitivity at a given eccentricity was evaluated by interleaving trials of different spatial frequencies and contrasts in a randomized-block design. All contrast threshold estimates were obtained using the method of constant stimuli. We used 3–5 contrast levels per spatial frequency and collected 40–50 trials per condition. Threshold was defined as the contrast supporting discrimination at the 75% correct level. We did not separately analyze nasal/temporal field presentations. The range of spatial frequencies and contrasts tested were chosen to span the visible range for each monkey at each age and for each eccentricity. In some cases, we measured spatial resolution (acuity) by varying only spatial frequency; contrast was then held constant at 90%. Threshold values and standard errors of estimate were obtained by probit analysis (Finney, 1971) of the log transformed data sets using a maximum-likelihood-ratio technique.

We used eccentricities ranging from 4 to 24 deg. All data for eccentricities greater than 12 deg were collected at a viewing distance of 30 cm with the small beam

splitter arrangement (see above); the large mirror restricted the range of testable eccentricities to  $\pm 12$  deg. Our 0-deg data were collected under free-viewing conditions with the stimuli placed 3–6 deg from the center of the screen. The brief presentations used under fixation conditions were unsuitable for free-viewing conditions: either the monkey continued to fixate the center and detect the stimulus eccentrically or responded randomly since it could not search both sides of the display in the time available. We therefore extended the duration of stimulus presentation for 0 deg conditions to 2–4 sec to allow time for searching, although they typically responded within 500–1000 msec anyway. We cannot assert unconditionally that the monkey used the "fovea" under these conditions; we can only argue that the monkey used the locus of highest sensitivity. It is our impression that they used the foveal region under free-viewing conditions throughout development since they appeared to fixate centrally at the youngest ages and their fixation patterns did not change with age.

Because of the large number of conditions in this study (contrast sensitivity at multiple spatial frequencies at a series of eccentricities) it was extremely difficult to get data across all eccentricities from an individual animal at any given age. We therefore do not have longitudinal data for all animals at each eccentricity. For animals younger than 15 weeks, we accepted data collected within a single week as representative of a given age. For animals older than 15 weeks, when the rate of developmental change is slower in macaques, we accepted data collected within a 2-week period as representative of a given age.

We have previously shown that the shape of the spatial CSF does not vary during development for either monkeys or humans under free-viewing conditions; only the horizontal and vertical position of the function changes (Movshon & Kiorpes, 1988). This invariance of shape makes it possible to describe contrast sensitivity data at any age simply by the overall sensitivity and spatial scale (vertical and horizontal scale factors, respectively). We wanted to see if the same invariance of shape also held for data from different eccentricities, which would allow us to use the same fitting and data reduction technique with the measurements from the present study. Therefore we simultaneously fit all the data, collapsing across age, eccentricity, and animals. We used a double-exponential curve, which we know to fit free-viewing monkey contrast sensitivity data well (Williams, Boothe, Kiorpes & Teller, 1981; Boothe *et al.*, 1988; Movshon & Kiorpes, 1988).

$$k_s(\omega k_\omega)^\alpha e^{-\beta \omega k_\omega}$$

where  $\omega$  is spatial frequency. The four free parameters affect primarily the steepness of the low frequency ( $\alpha$ ) and high frequency ( $\beta$ ) portions of the curve, lateral scale along the frequency axis ( $k_\omega$ ), and vertical scale along the sensitivity axis ( $k_s$ ). All data sets were jointly fit with a function whose shape parameters ( $\alpha$  and  $\beta$ ) were the same, but whose scale parameters ( $k_\omega$  and  $k_s$ ) varied independently for each data set. We verified, using

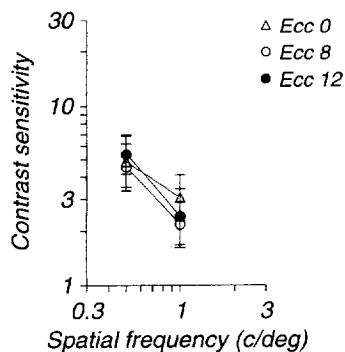


FIGURE 1. Contrast sensitivity for two spatial frequencies (0.5 and 1.0 c/deg) at three visual field locations (0, 8 and 12 deg) for 7-week-old monkey GD. Viewing distance was 60 cm.

nested hypothesis testing (Hoel, Port & Stone, 1971), that the fits obtained using this “multi-fit” method (90 simultaneously-fit data sets with 182 total free parameters) were not significantly different from individual curve fits (90 data sets each with 4 free parameters) ( $\chi^2 = 10.70$ ,  $df = 178$ ,  $P > 0.05$ ). We therefore used the measures of sensitivity and spatial scale derived for each data set from this joint fit for our subsequent analysis.

## RESULTS

### Individual data

In the youngest animals tested, we found little or no variation in contrast sensitivity within the central visual field. Figure 1 shows contrast sensitivity at several locations within the central 12 deg in a 7-week-old monkey. Sensitivity was similar at 0, 8 and 12 deg for both spatial frequencies tested. Variation in spatial resolution with eccentricity within the central 12 deg was noted in a few cases as early as 9–10 weeks. Figure 2 shows measured acuity for two young monkeys at 0, 8 and 12 deg eccentricity. While one monkey showed lower spatial resolution at 12 deg relative to 0 and 8 deg (Fig. 2A), the other showed no variation in acuity with eccentricity (Fig. 2B) as was generally the case in younger monkeys. We found substantial individual differences in the degree of variation of acuity and contrast sensitivity with eccentricity in the 9–12 week

range. Two of the four monkeys tested in this age range showed some decline in acuity and contrast sensitivity with eccentricity.

Although we found little evidence of variation in contrast sensitivity across different locations within the central 12 deg in the youngest monkeys, beyond 12 deg there was a fall-off in sensitivity with eccentricity in even the youngest animal tested. Figure 3A shows contrast sensitivity data at 12, 18 and 24 deg in the periphery for a 9-week-old monkey. There was a clear reduction in contrast sensitivity across spatial frequency with increasing eccentricity at 9 weeks, which was similar in form to that seen later, at 17 weeks, in the same animal (Fig. 3B).

Between 12 and 30 weeks, greater variation in contrast sensitivity developed within the central 12 deg. By about 15–18 weeks, all animals showed better contrast sensitivity at an eccentricity of 8 deg than at 12 deg. Figure 4A shows contrast sensitivity functions at 0, 8 and 12 deg for a 16-week-old monkey. This monkey showed better contrast sensitivity at 8 deg than at 12 deg for all spatial frequencies tested; some animals showed better sensitivity at 8 deg only for high spatial frequencies. Figure 4A also shows little difference in contrast sensitivity between 0 and 8 deg peripheral, as was typical of the age. Monkeys older than 30 weeks tended to show a systematic decline in contrast sensitivity with eccentricity across the central 8 deg (Fig. 4B), which was the typical pattern for adult monkeys. For comparison, data from a human adult (one of the authors) collected under the same visual conditions as the monkey data are shown in Fig. 4C.

Although it may be obvious, it seems worth pointing out that contrast sensitivity varies differently with eccentricity depending on the spatial frequency of the stimulus, as would be expected from human data (Robson & Graham, 1981). Sensitivity declines more steeply with eccentricity at high spatial frequencies than at low spatial frequencies. This pattern is illustrated in Fig. 5, where contrast sensitivity is plotted as a function of eccentricity for each of four spatial frequencies. These data, from a 40-week-old monkey, are typical in that there was very little variation in sensitivity with eccentricity at low spatial frequencies ( $sf < 4$  c/deg) within the central 8 deg.

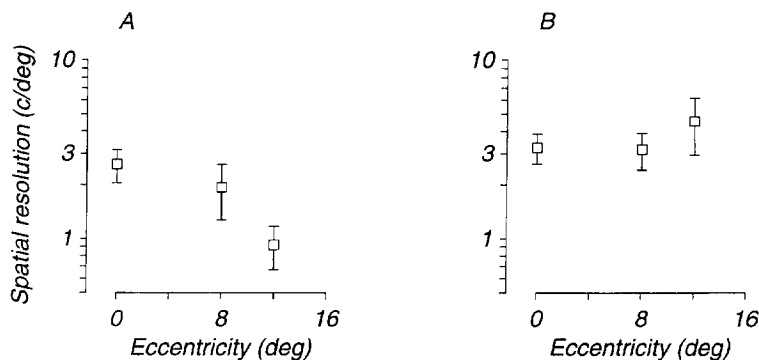


FIGURE 2. Spatial resolution at three visual field locations (0, 8 and 12 deg) for two young monkeys: (A) ZD, 10 weeks, and (B) SX, 11 weeks. For ZD, spatial resolution declined with eccentricity; for SX it did not. Viewing distance was 60 cm.

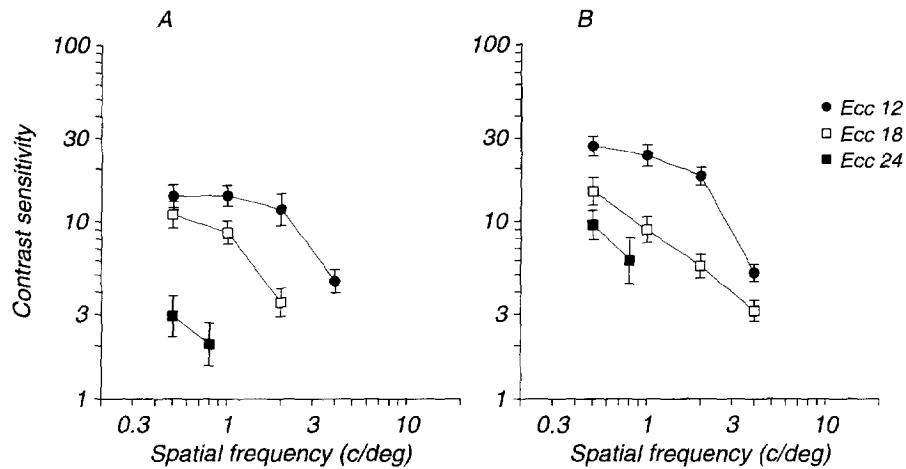


FIGURE 3. Contrast sensitivity functions at three locations in the periphery (12, 18 and 24 deg). The data are from monkey HG at 9 weeks (A) and 17 weeks (B). Viewing distance was 30 cm.

### Summary data

The developmental data from individual monkeys suggest that central contrast sensitivity is similar to that of the near periphery in young monkeys but develops to a greater degree than the periphery during maturation. The relationship between contrast sensitivity at central and peripheral locations appeared to be different at different ages. To better understand the course of maturation we quantified the way in which the contrast sensitivity function shifts in location with age and eccentricity. As described in the Methods, we determined a representative contrast sensitivity function for the viewing conditions of this study and extracted horizontal and vertical location parameters for each data set. Figure 6 illustrates this process. Three data sets from one animal at a single age are plotted; the smooth curves are a single curve of constant shape shifted in location to fit each data set. The vertical position of the curve is sensitivity at the peak; horizontal position is the spatial frequency at which sensitivity falls to one-half of the maximum sensitivity. The vertical bars through each of the three curves indicate the derived horizontal position for each curve, which we term characteristic spatial frequency.

The derived measures, peak contrast sensitivity and characteristic spatial frequency, are plotted as a function of age for four eccentricities (0, 8, 12 and 24 deg) in Fig. 7. Data from all seven monkeys are included. Note that only three monkeys were tested at 24 deg so there are relatively few data points for that eccentricity. Each point represents one data set. Peak sensitivity (Fig. 7A) improves steadily up to about 20 weeks at eccentricities of 0 and 8 deg, then remains fairly constant thereafter. There is less overall change at 12 deg but the pattern is similar to that at more central locations. The few data points we have at 24 deg suggest that there is rather little change in overall sensitivity at this location over the age range tested. Figure 7B shows the variation in characteristic frequency with age. There is clearly a shift in characteristic frequency with age at all four locations in the visual field. As we found with peak sensitivity, there is a rather dramatic change over the first 20 weeks; the extent of the developmental change is greatest in the central visual field. Beyond 20 weeks, there is continued gradual improvement in characteristic frequency for free-viewing that does not continue in the periphery. This result is consistent with our impression from the individual data sets that most of the change later in development appears as increased sensitivity to high

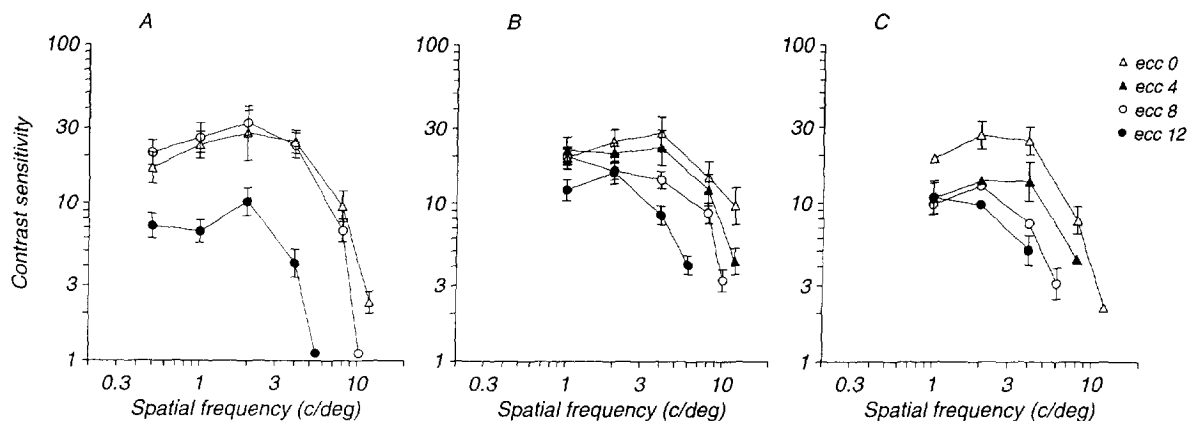


FIGURE 4. Contrast sensitivity functions at several locations within the central visual field for a 16-week-old monkey (A), a 34-week-old monkey (B), and an adult human (C). Viewing distance was 60 cm for the monkeys and 45 cm for the human.

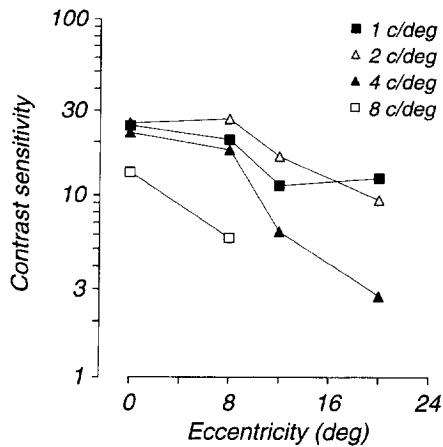


FIGURE 5. Contrast sensitivity as a function of eccentricity for 4 spatial frequencies (1, 2, 4 and 8 c/deg). Contrast sensitivity at high spatial frequencies declines with eccentricity more rapidly than at low spatial frequencies. The data are from a 43-week-old monkey at a viewing distance of 60 cm.

spatial frequencies, which manifests itself as a rightward shift in the contrast sensitivity function and a corresponding increase in characteristic spatial frequency.

Figure 8 summarizes in another form the important aspects of the data. Here, spatial resolution is plotted as a function of eccentricity for three age ranges: 8–12 weeks, 15–19 weeks, and older than 30 weeks. These resolution data are either actual measured grating acuities or extrapolated cut-offs of contrast sensitivity functions (from the multi-fits; see Methods); the error bars are standard deviations for the group data at each point. The youngest animals showed little reliable variation in acuity with eccentricity. As evidenced by the large standard deviations, the amount of overall variation in acuity and contrast sensitivity was large in the youngest group and there was no consistent pattern of variation in either measure with eccentricity within the

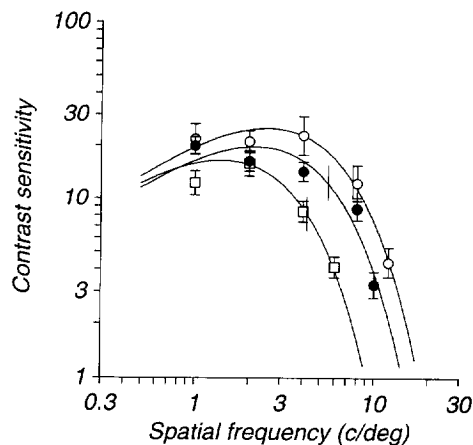


FIGURE 6. Representative curve fits resulting from the multifit method described in the text. The data are three data sets from a single animal (TE) at 34 weeks (see Fig. 4B; 4, 8 and 12 deg). The curve shown with each data set is the template curve, shifted by an amount determined during the multifit computation. The vertical bar through each curve marks the location of the characteristic spatial frequency for that data set.

central 12 deg. The superiority of the central visual field in acuity is clear in the older groups.

## DISCUSSION

The general pattern of contrast sensitivity development showed that in the youngest monkeys (7–10 weeks) sensitivity was similar across the central visual field. There was an overall rapid increase in sensitivity to contrast between 10 and 20 weeks, followed by a continued gradual improvement in sensitivity at high spatial frequencies to at least 40 weeks. The greatest degree of change in contrast sensitivity across spatial frequency was in the central 12 deg, with progressively less developmental change at greater eccentricity over the age range tested. This implies that contrast sensitivity in the peripheral visual field is relatively more mature with respect to the central visual field in infants.

There was no apparent superiority of “foveal” or free-viewing contrast sensitivity or acuity over the near periphery in the youngest animals, nor was there another obvious locus of highest sensitivity. Our results therefore differ from those reported for human infants. Studies of young human infants found slightly higher acuity for central as compared to peripheral (10–12 deg on average) visual field (Sireteanu *et al.*, 1984; Allen *et al.*, 1989). This difference could represent a real species difference, but it is more likely that this difference is in large part dependent on methodological differences. The stimuli in the human infant studies were larger (4–15 deg), brighter (75–80 cd/m<sup>2</sup>), and were not vignetted. Also, in the preferential looking studies, the stimuli were available for an unlimited duration under all conditions (Sireteanu *et al.*, 1984, 1994).

Our 0-deg, free-viewing contrast sensitivity and spatial resolution values are lower overall than would be expected based on other studies of free-viewing spatial vision in infant monkeys (Boothe *et al.*, 1988; Kiorpes, 1992), although the developmental time-course is similar to previous studies. Also, Merigan and Katz (1990) measured the variation in acuity across the visual field in adult macaque monkeys. Our acuity data are consistent with theirs for peripheral locations, while central acuity for their monkeys was about a factor of two better than ours. It is important to note that the infants in our study when tested under standard preferential looking conditions with large square-wave grating stimuli and unlimited viewing duration, showed higher free-viewing acuity than we measured under the conditions of this study; their acuity measured in that way was consistent with “normal” acuity development (see Kiorpes, 1992). It is likely that by using the small, vignetted grating patches and brief stimulus presentations we restricted central performance. However, it was important to maintain viewing conditions for central and peripheral testing to be as consistent as possible. Increasing the size and the duration of the stimulus improves contrast sensitivity in the peripheral as well as the central visual field. In fact these small spatially localized stimuli may reflect the activity of localized neural mechanisms better

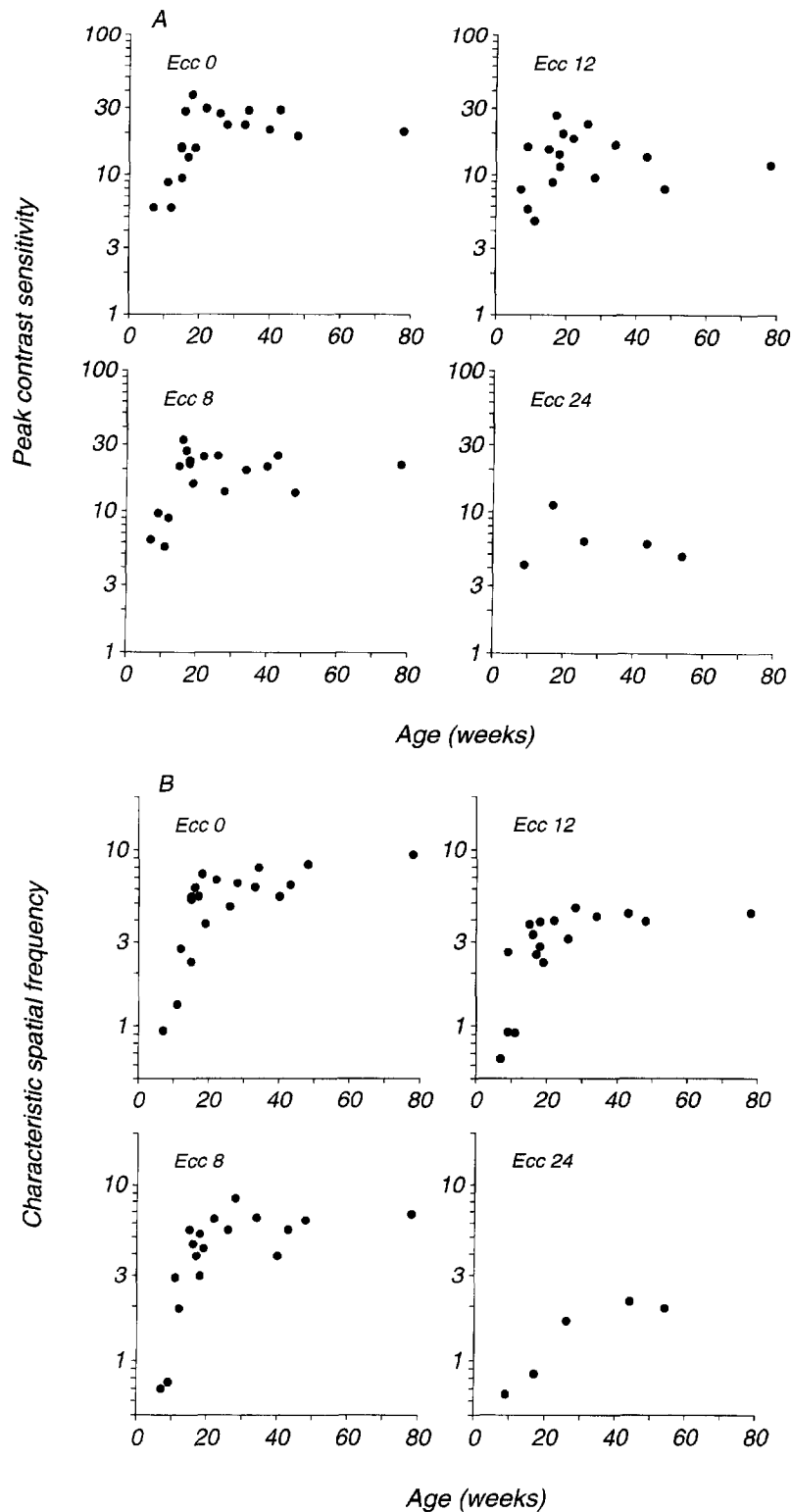


FIGURE 7. Derived measures, peak contrast sensitivity (A) and characteristic spatial frequency (B), as a function of age for four locations across the visual field (0, 8, 12 and 24 deg). Each point represents one data set.

than the typical, larger spatially extensive grating acuity targets. Frisen (1995) has reported a close correspondence between MAR and cone and ganglion cell spacing using small, localized spatially filtered targets which in general yield poorer foveal acuity estimates than more conventional targets. Therefore, we believe that the pattern of our results is an accurate representation of relative contrast sensitivity across the visual field.

The time-course of contrast sensitivity maturation varied somewhat with eccentricity. At all visual field locations out to 24 deg, there was some change in peak sensitivity and characteristic frequency during the first 20 weeks. However, the extent of the change was greatest for free-viewing conditions and declined progressively with eccentricity (see Fig. 7). There was gradual continued change in high spatial frequency sensitivity

thereafter, which was once again most evident centrally. This pattern of results shows that contrast sensitivity at low spatial frequencies develops consistently across the visual field in young monkeys. Sensitivity to high spatial frequencies, which is of course the domain of the central visual field, continues to develop to a greater extent and over a longer period of time than sensitivity to low spatial frequencies.

Our behavioral data are consistent with findings on physiological and anatomical maturation of the macaque monkey visual system. Blakemore and Vital-Durand (1986) measured the spatial resolution of cells in the monkey lateral geniculate nucleus at different stages of development. They found spatial resolution to vary much less across a wide range of eccentricities in the newborn than in the adult; cells with receptive fields near the fovea had similar spatial resolution to those with receptive fields at eccentricities of 10 and 20 deg. Foveal superiority in spatial resolution for LGN cells emerged between 10 and 30 weeks.

Packer *et al.* (1990) measured the density of cones across the retina in *Macaca nemestrina* at several pre- and post-natal ages. They found cone density to be relatively flat across the central retina up to about 13 weeks. Over the following months, foveal cone density increased to near adult levels, with some continued increase even beyond the first postnatal year. Packer *et al.*'s density measurements predict that spatial resolution in mature animals should fall with a slope of roughly a factor of 4 over the central 24 deg, which is similar to that for our oldest animals (see Fig. 8, ○). While this agreement is gratifying, their data for younger animals predict more variation in acuity with eccentricity than we observed in our youngest animals. Predicted spatial resolution for their 6 and 13 week cases falls by about a factor of 2 over this eccentricity range, while our youngest animals showed no consistent variation (Fig. 8, □). It is therefore possible that factors other than the

maturation of foveal cone density, perhaps neuronal maturation later in the visual pathways (Movshon & Kiorpes, 1993), contribute to the changes we observed in this study.

In summary, we have shown that the central visual field in the infant monkey is similar in terms of contrast sensitivity to the near periphery and undergoes substantial postnatal development relative to the periphery. These behavioral changes are qualitatively consistent with anatomical changes in photoreceptor density and physiological changes in spatial resolution of cells in the lateral geniculate nucleus in macaque monkeys over the same range of ages.

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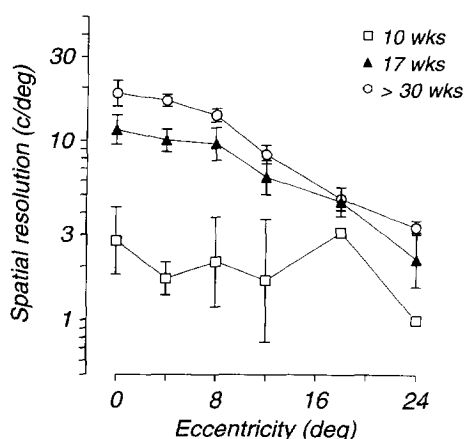


FIGURE 8. Group data showing spatial resolution as a function of eccentricity for three age groups: 10 weeks (range 8–12), 17 weeks (range 15–19), and older than 30 weeks. The data plotted are geometric means,  $\pm 1$  SD, of either measured spatial resolutions or cutoff spatial frequencies derived from the multifits. Note that the data points at 18 and 24 deg in the 10 week group were contributed by the same, single monkey (data shown in Fig. 3A).



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