Development of vernier acuity and grating acuity in normally reared monkeys

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Abstract

The developmental time courses for vernier acuity and grating acuity were measured longitudinally in infant *Macaca nemestrina* monkeys. Behavioral measurements of vernier and grating acuity were made at regular intervals during development. Near birth, grating acuity is relatively more mature than vernier acuity. The proportional rate of vernier acuity development is faster than that for grating acuity. During the course of development, grating acuity improves approximately 15-fold whereas vernier acuity improves about 60-fold. Both visual functions approach adult levels at about the same age, around 40 weeks postnatally. Although grating acuity develops about four times faster in monkeys than in humans, vernier acuity development in monkeys are about a factor of 2 poorer than are typically reported for humans. The differential development of vernier acuity and grating acuity does not necessarily reflect development at different levels of the visual system.

Keywords: Visual development, Vernier acuity, Grating acuity, Macaque monkey

Introduction

The development of spatial vision in primates has been characterized primarily by measures of grating acuity and spatial contrast sensitivity. In both humans and monkeys, grating acuity, as measured behaviorally, is poor near birth (0.5-1 cycle/deg) and develops over the succeeding weeks and months to around 30 cycle/deg. This process spans about the first 5 postnatal years in humans, but is essentially complete during the first year in macaque monkeys (see Boothe et al., 1985, for review). The relationship between the developmental time courses for macaque monkeys and humans has been described as "four-toone," that is, one week of monkey development is comparable to four weeks of human development (Teller & Boothe, 1979). The development of contrast sensitivity, as measured behaviorally, has been studied extensively in monkeys (Boothe et al., 1988) and less so in humans (e.g. Atkinson et al., 1977; Banks & Salapatek, 1978; Bradley & Freeman, 1982). Although most of the human data are from either very young infants or older children, it appears that the four-to-one relationship also holds for contrast sensitivity.

Relatively little is known about the development of spatial position sensitivity. Several studies of vernier acuity development in humans have been published showing that vernier acuity improves approximately 20-fold over the first 6 months (Manny & Klein, 1984, 1985; Shimojo et al., 1984; Shimojo & Held, 1987). Some additional improvement is seen between 6 and 14 months (Manny & Klein, 1985), however acuity at the oldest test ages was still considerably poorer than that shown by adults. Both Manny and Klein (1984) and Shimojo et al. (1984) found that the just-discriminable displacement on a vernier detection task was smaller than the just-discriminable bar width in a grating detection task at all test ages. Shimojo and Held (1987) later reported that prior to about 3 months, the just-discriminable displacement for the vernier task was larger than the just-discriminable bar width; this implies that the two developmental functions cross around 3-4 months postnatal. It is important to note that the crossing of the functions depends on the choice of scaling units for vernier and grating acuity; a different choice may result in a different age at crossing or no crossing at all. To avoid the issue of scaling in the present study, we measured the full developmental time courses for vernier and grating acuity in individual subjects and compared the sequences in terms of relative maturation.

It is important to establish the developmental time course for vernier acuity for several reasons. Psychophysical data from human adults have revealed that vernier acuity is finer than grating acuity in the central visual field. However, as targets are moved out toward the periphery, vernier acuity decreases more rapidly than does grating acuity (Westheimer, 1982; Levi et al., 1985). These studies have been taken as evidence that vernier and grating acuity may be limited by different neural mechanisms. Levi and others have suggested that the limits of grating resolution are determined by the retinal mosaic, that is, resolution is limited by the diameter and spacing of foveal cones,

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whereas positional sensitivity is limited by cortical magnification (the amount of cortical territory devoted to a particular location in the retina). If spatial resolution and positional sensitivity are indeed based on different underlying processes, then their developmental time courses may be different. If, by chance, the time period over which vernier acuity develops is not perfectly coincident with that for grating resolution, then knowledge of the relative developmental time courses may contribute to our understanding of the underlying mechanisms. Finally, psychophysical studies of human amblyopes suggest that vernier acuity is compromised to a greater degree than other measures of spatial vision by strabismus in early life. In this case, knowledge of the normal time course for development is important for establishing a baseline against which the effects of abnormal visual experience can be evaluated, and for understanding the neural basis of amblyopia.

This paper presents a description of the normal time course for the development of vernier acuity relative to grating acuity in macaque monkeys. Macaque monkeys are particularly appropriate subjects because their visual system has been demonstrated to be structurally and functionally similar to humans, and they provide an excellent model for studying the development of amblyopia (see for example, Harwerth et al., 1983; Kiorpes et al., 1987; Kiorpes et al., 1989). Also, individual monkeys can be tested from infancy through adulthood, whereas it is difficult to test humans over the full developmental range.

The results of this study show that the two measured visual functions develop at different proportional rates, but approach adult levels at roughly the same postnatal age. Although these results could be taken to support the hypothesis that vernier and grating acuity depend on different neural mechanisms, it is possible that they reflect the development of a single mechanism. The development of these functions in strabismic animals is described in the following paper. A summary analysis of some of these data has been published previously (Kiorpes & Movshon, 1989*a*).

Methods

Subjects

Seven Macaca nemestrina monkeys were tested longitudinally beginning between 10 and 30 days postnatally. Data from an additional eight monkeys, tested cross sectionally, are also included. The infant monkeys, supplied by the Washington Regional Primate Center, were hand-raised in our infant nursery. Care and maintenance of the animals was provided in accordance with established, approved protocols, which conform to the NIH Guide for the Care and Use of Laboratory Animals.

Behavioral testing

Prior to 15 weeks of age the infants were tested using preferential looking methods. Beyond 15 weeks, operant methods were used. The procedures followed for preferential looking are described first, followed by those used for operant testing. The stimuli were of the same configuration in both cases.

The forced-choice preferential looking procedure developed by Teller (1979) was adapted for use with monkeys as has been described previously (Kiorpes et al., 1989). For this study, the technique was applied as follows. A human observer held the monkey in front of a blank white screen containing two $15 \times$ 20-cm apertures subtending 14-26 deg (horizontal extent) at viewing distances ranging from 40-80 cm. Behind each aperture was positioned a black-and-white video display monitor (Nanao 3030) on which patterns were presented under computer control. The holder observed the subject's face via a video camera and monitor. On the basis of the subject's looking behavior, the holder/observer made a forced-choice judgment on each trial as to whether a particular stimulus appeared in the right or left aperture. The observer was blind as to the position and identity of the stimulus, both of which were randomized from trial to trial. Feedback was provided as to whether each judgment was correct or wrong.

The stimuli for grating acuity were high-contrast (98%) square-wave gratings paired with a very high spatial-frequency grating that was beyond the resolution limit of the animal and appeared as a homogenous field that was matched in space-average luminance to the target grating (Fig. 1, top). The luminance of the displays was 30 cd/m². For vernier acuity, the stimuli were a pair of clearly visible square-wave grating; within one of the gratings, alternating sections of the grating were offset horizontally (Fig. 1, bottom) throughout the extent of the target. For preferential looking, the carrier spatial frequency of gratings used in the vernier task was 0.25 cycle/deg and the offset sections were 2.0 deg high; the offsets were always static. Since vernier acuity declines at high carrier spatial frequencies in both cats (Murphy & Mitchell, 1991) and humans



Fig. 1. An illustration of the stimuli used for testing grating and vernier acuity in monkeys. Top: Grating acuity was tested by pairing a high-contrast square-wave grating with a homogenous field of equal space-average luminance. (Note: the homogeneous field was in fact medium grey in color and not dark, as it appears in the figure.) Bottom: Vernier acuity was tested with a pair of low-frequency, high-contrast gratings within one of which alternating sections were offset horizontally; the offsets were always static. (Note: the white borders in the figure do not appear in the test situation.)

(Levi & Klein, 1982; Bradley & Skottun, 1987), we chose low carrier frequencies for all conditions.

Vernier and grating acuity were typically tested in an interleaved fashion, with order counterbalanced across ages so as to avoid order effects and maintain the interest of the animal. For each task, threshold was estimated based on four stimulus values (offsets or spatial frequencies) that were chosen to span the performance range of the observer from near chance to near perfection; 30 trials were collected per stimulus value in pseudorandom order. Most data were collected binocularly, and testing on the two tasks at each age was completed within a 3–5 day period. In some cases, monocular performance was compared to binocular performance. For monocular testing, data for each eye were collected in counterbalanced order over a period of not more than 7 days. The development of acuity was assessed by preferential looking at intervals of approximately 2 weeks, continuing up to 12–15 weeks of age.

Most animals older than 15 weeks were trained to perform an operant two-alternative forced-choice discrimination task so that development could be followed over the long term. The animals were trained to make the same discriminations that were used for preferential looking testing, using the same displays and stimuli. The training procedures used have been described in detail previously (Williams et al., 1981). For operant testing, viewing distances ranged from 2-10 m depending on the animals' acuity. The monkeys were rewarded with 0.25 ml of apple juice for correct discriminations; errors were followed by a time-out period, usually 5-10 s in duration, that was signalled by a tone. For operant vernier acuity testing, the carrier spatial frequency was 4.0 cycle/deg and the offset sections were 0.5 deg high. In two animals, we explored a range of carrier spatial frequencies and found little effect on threshold up to about 12 cycle/deg. The methods for threshold estimation were the same as for preferential looking except that the estimates were based on five stimulus values (spatial frequencies or offsets) and at least 50 trials per point.

Data analysis

All estimates of acuity were obtained using the method of constant stimuli. Threshold was defined as the spatial frequency (grating acuity) or offset (vernier acuity) supporting discrimination by the observer (monkey or human) at the 75% correct level. Threshold values and standard errors of estimate were obtained by probit analysis of the log transformed data sets (Finney, 1971), using a maximum-likelihood-ratio technique.

Individual analysis of these psychometric functions was occasionally problematic. While in most cases the functions rose lawfully from near chance to 100% correct, in some cases asymptotic performance was lower (although never less than 80%), or the data were nonmonotonic. Initially, individual analysis of such data sets was attempted by allowing the probit routine to fit the asymptotic performance value, but this proved unsatisfactory because the resulting thresholds were often unreliable and might have been biased by the addition of the free asymptote parameter. Another way to approach this analysis is to assume that the level of best performance for the data set is indeed the level obtained for the most visible stimulus, and use a lower asymptote for these probit calculations. But setting a lower asymptote underestimates the actual threshold, because threshold is defined as the median level between the asymptote and chance, and increases variability. Moreover, it is likely that the asymptotic level of performance is in fact close to 100% in all cases but, for certain data sets, the stimulus values chosen were below that needed to elicit such good performance.

The most satisfactory resolution of this problem is derived from the simplifying hypothesis that all of the psychometric functions for a particular task have the same underlying slope, and differ from one another only in position along the abscissa. In practical terms, this is done by fitting a single free parameter—the slope—to all of the data jointly, while allowing a second parameter—the threshold—to vary from data set to data set. We did this calculation using preferential looking data. We simultaneously fit all of the grating acuity data, and separately all vernier acuity data, for an individual monkey to determine representative psychometric function slopes for each monkey on each task. Thresholds were then obtained for individual data sets with the probit slope appropriately constrained.

Collective analysis of psychometric functions obtained at different ages is valid since there was no tendency for the slope of the psychometric function to change systematically with age for either acuity task. Regression analyses of individually fit psychometric function slopes failed to reveal a significant change with age. It therefore seemed reasonable to assume that the underlying psychometric function is similar for a given monkey and task regardless of age and can therefore be rigidly shifted along the abscissa. Examples of such logarithmically shifted psychometric functions for a single monkey are shown in Fig. 2A. Three grating and vernier data sets are shown for monkey VW, obtained at ages ranging from 22 to 82 days. The data points for each data set are plotted with error bars representing the standard deviation of the binomial distribution around each point. The dashed horizontal line shows chance performance. The psychometric function plotted with each of the data sets for grating acuity is the same function, calculated in the simultaneous analysis of all five grating acuity data sets obtained from VW, rigidly shifted horizontally in spatial scale. The same procedure was applied to the vernier acuity data; the function shown was calculated based on six data sets, and is rigidly shifted horizontally for the data sets shown. Clearly the function calculated using the fixed-slope procedure yields reasonable fits to individual data sets.

It is possible to evaluate the validity of this rigid-shift hypothesis using the methods of nested hypothesis testing (Mood et al., 1974). To do this, we compared the goodness of fit (in a chi-square sense) for each data set fit with the slope fixed and the slope free. For 12 of the 14 longitudinal data sets, the goodness of fit was no better with the slope free to vary for each function, suggesting that in general the apparent variation in slope from function to function is without statistical significance. Thus, the statistical analysis illustrates that the loss of one free parameter - slope - in the probit fits does not significantly reduce the quality of the fits. What is gained is an increase in robustness of threshold estimates and the elimination of variability due to variation in upper asymptote. All thresholds derived from longitudinally obtained preferential looking data were calculated in this way. It is important to note that the conclusions drawn from the data are unaltered by the fixedslope analysis.

Unlike the preferential looking data, operant data were not subject to variability in the level of best performance. Each operant data set was therefore analyzed separately. It is worth noting that the slope of the psychometric function for individual animals in operant testing was reasonably consistent from ses-



Fig. 2. Examples of individual data sets and probit fits. A: Data obtained by preferential looking with examples of fixed-slope fits. B: Data obtained by operant testing with psychometric functions fit separately. In the left panels, proportion correct as a function of spatial frequency is shown; in the right panels, proportion correct as a function of spatial offset is shown. In A, the psychometric functions for grating acuity are the same function, calculated as described in the text, rigidly shifted horizontally for each data set; similarly, the psychometric functions shown with the vernier acuity data are a single function rigidly shifted for each data set. All data in A are from a single monkey, VW, between the ages of 22 and 82 days; the open and filled symbols are used only to clarify to which data set the points belong. In B, the psychometric functions were fit separately to each data set with the slopes free to vary. All data in B are from a single monkey, TK, between the ages of 45 and 70 weeks. In this case, the data sets are placed arbitrarily with respect to the abscissa (they are separated for clarity), therefore the x axes are unlabeled.

sion to session for a particular task. This point is illustrated in Fig. 2B, which shows individual operant data sets for monkey TK obtained between 45 and 70 weeks of age. The slope of the fitted psychometric function was free to vary in each case. The slopes and levels of best performance are clearly similar for a given task. Although there are several differences in the testing conditions and data treatment between the preferential looking and operant methods, examination of the pattern of results shows that there are no consistent breaks in the data around 15 weeks. This supports the notion that these differences in methodology have no important effect on the outcome.

Results

All of the monkeys tested longitudinally showed essentially the same pattern of vernier acuity and grating acuity development. Vernier acuity improved over a greater range and at a faster rate than grating acuity, although adult levels were approached at similar ages for both functions. Longitudinal data from three individual animals are shown in Fig. 3. In the top panels, the development of vernier acuity is shown for each animal as a function of age in days. Vernier acuity is expressed in inverse minutes of arc so that improvement is always shown as an increasing rather than decreasing function of age. In the bottom panels, grating acuity development, in cycles/degree, is plotted on the same age scale. Grating acuity developed from initial levels in the range of 1-4 cycle/deg up to 20-30 cycle/deg over the first 40 weeks. Vernier acuity developed from initial levels in the range of 0.03-0.06 min⁻¹ up to 1.6-5.0 min⁻¹ over the same period of time. In every case, the proportional improvement in vernier acuity during development was greater than the proportional improvement in grating acuity during development.

Developmental functions for all animals tested longitudinally on both measures are plotted together in Fig. 4 for comparison. Solid lines represent grating acuity development and dashed lines represent vernier acuity development. The ordinates for the two sets of data are aligned at adult performance levels so that acuity at any age is represented in terms of relative level of maturity. Adult performance is estimated using the best performance achieved over the course of the study. Other criteria could be chosen, such as taking an average, but the pattern of results would be the same. Several important features of the data are revealed by Fig. 4. First, grating acuity is relatively more mature near birth than vernier acuity. Second, the slopes of the two sets of functions are different. The slopes of the vernier development functions are steeper than those for grating development, thus vernier acuity develops at a faster proportional rate than grating acuity. Finally, both sets of functions approach adult levels at about the same age, 40-60 weeks.

The developmental functions for each type of acuity show striking similarity across animals. Regression lines fit to the individual data, log age vs. log acuity, have similar slopes within each set of acuity measures. Thus, two developmental functions can be determined that describe *in general* the time courses for grating acuity and vernier acuity in pigtailed monkeys. Fig. 5, using the same format as Fig. 4, shows data for the individual monkeys tested longitudinally and cross sectionally along with the calculated regression lines. The slopes of the regression lines are 0.79 and 1.30 for grating and vernier acuity, respectively. Statistical analysis showed the regression slopes to be significantly different: t = 86.9, df = 106, P < 0.001, for samples with unequal variances.

That two different developmental functions can be defined for vernier and grating acuity reinforces the notion that there might be different mechanisms underlying their development.



Fig. 3. Longitudinal data for three individual animals showing the developmental time courses for grating and vernier acuity. A: TJ; B: VY; and C: XX. Grating acuity (bottom; filled circles) in cycles per degree is shown as a function of age in days on log-log coordinates; vernier acuity (top; open circles) is shown in inverse minutes of arc on the same age scale as grating acuity (10 in inverse minutes is equal to 6 s).



Fig. 4. Developmental functions for grating and vernier acuity plotted together for the animals tested longitudinally. Solid lines show grating acuity functions, which relate to the left ordinate; dashed lines show vernier acuity functions, which relate to the right ordinate. The ordinates are aligned at adult performance levels, as measured for monkey TJ: 26.7 cycle/deg for grating acuity and 5 min⁻¹ (12.6 s) for vernier acuity. Both are plotted on the same age axis.

However, the finding that both types of acuity achieve adult levels at roughly the same age suggests that their development may actually depend on a similar mechanism. One way to approach the question of whether these functions depend on similar or separate mechanisms is to directly evaluate the relationship between them. Fig. 6 illustrates the relationship between grating and vernier acuity over the course of development. The two measures are plotted against one another, for all animals of all ages. The region containing the data, the normal sequence, defines the expected vernier acuity for a particular value of grating acuity regardless of the age of the animal. The sequence captures the general relationship between these two measures developmentally, although different animals may develop at different rates. Since vernier acuity and grating acuity each develop monotonically and at different rates, the relationship between them changes with age. Although the normal sequence does not reveal a proportional relationship, it does reveal a reliable, orderly relationship between these measures over the course of development.

As mentioned earlier, several studies of human infants have compared vernier and grating acuity development. Shimojo and Held (1987) found that, as in monkeys, the rates of development for these two visual functions were different in human infants. To compare monkeys and humans, we used the four-to-one rule described above equating monkey age in weeks with human age in months (Teller & Boothe, 1979) and plotted human and monkey grating acuity development and human and monkey vernier acuity development together in Fig. 7. 30

10

3

1

0.3

0.1

10

30

Grating acuity (c/deg)

Age (days) Fig. 5. Developmental grating (filled circles) and vernier (open circles) acuity data for all monkeys tested. Regression lines corresponding to each data set are also shown: the solid and dashed lines represent the general developmental time courses for grating acuity and vernier acuity, respectively. The axes are the same as in Fig. 4.

100

300

10

3

0.3

0.1

0.03

1000

Vernier acuity (1/min)

Fig. 7 is similar in format to Figs. 4 and 5; the regression lines and small points are the monkey data from Fig. 5 that describe the general developmental time courses for these functions. Superimposed on the monkey grating data (upper cloud of points and solid line) are two sets of human grating acuity data: open squares are data from Shimojo et al. (1984); open circles are data from Shimojo and Held (1987). Clearly, the



Fig. 6. The changing relationship between vernier and grating acuity over the course of development. Vernier acuity (1/min) is plotted against grating acuity (cycle/deg) for all monkeys tested, collapsed across age. The region containing the data defines the *normal sequence*.



Fig. 7. Comparison between the development of vernier and grating acuity in humans and monkeys. The axes, small data points, and regression lines are the same as in Fig. 5 except that age is expressed in weeks for monkeys and months for humans. Human grating and vernier acuity data are shown by the large symbols: open squares represent data from Shimojo et al. (1984); open circles represent development as reported by Shimojo and Held (1987); filled triangles represent vernier acuity development as measured by Manny and Klein (1985).

four-to-one rule is a reasonable description of the relationship between the human and monkey data in this case. However, this age translation may not be appropriate for vernier acuity development. Three sets of human vernier acuity data are plotted along with the monkey vernier acuity data (lower cloud of points and broken line). The open symbols are as described above for grating acuity; the filled triangles represent data from Manny and Klein (1985). Although the human and monkey data appear to be in reasonable correspondence at the earliest ages (open circles), the slope of the human developmental function as described by Shimojo and Held (1987) is considerably steeper than that for the monkeys (3.1 compared to 1.3 for the monkeys). However, this developmental function for human infants was also much steeper than that reported in the other human studies. Vernier acuity development as described by Shimojo et al. (1984; open squares) and Manny and Klein (1985; filled triangles) is similar in rate to the monkey data: 1.49 and 1.27, respectively, keeping in mind that age is in months for humans and weeks for monkeys. Thus, while the slopes of the developmental functions from these human studies and from the monkeys are similar, the data do not seem to lend themselves quantitatively to a four-to-one translation; the human infants seem to have slightly better vernier acuity than the monkeys when their grating acuity data show correspondence.

Although the developmental comparison between humans and monkeys appears to be difficult to quantify, the comparison between adult performance levels is straightforward. Vernier thresholds for adult humans tend to be in the range of $12-50 \text{ min}^{-1}$ (see, for example, Westheimer & McKee, 1977). The best thresholds for the monkey observers in this study were about 6 min⁻¹. It is unlikely that the task itself is more difficult than those used in the human studies; one human observer tested with our stimuli performed in the range of other human studies: 16 min⁻¹ (Kiorpes & Movshon, 1989b).

Discussion

The present study shows that the development of vernier acuity follows a different course than the development of grating acuity in normally reared monkeys. The major difference between the developmental functions is that vernier acuity is less mature at birth and subsequently develops faster than grating acuity. From the age of the first measurement, grating acuity improves about 15-fold whereas vernier acuity improves about 60-fold. These data appear to be consistent with the suggestion that vernier and grating acuity are limited by different neural mechanisms. However, two features of the development data suggest that they may in fact be limited by similar mechanisms. First, vernier and grating acuity approach adult levels at similar ages. Second, vernier and grating acuity are related to each other in an orderly manner over the course of development. I will review the basis for each position and argue that it is more likely that vernier and grating acuity are limited by similar mechanisms during development.

Most recent analyses implicate primarily receptoral factors in the maturation of grating acuity, but do not discount additional contributions by neural maturation at the level of the LGN and cortex (Banks & Bennett, 1988; Jacobs & Blakemore, 1988; Wilson, 1988; but cf. Brown et al., 1987). Recent advances in technology have provided the opportunity for careful quantification of the development of photoreceptors and changes in photoreceptor topography with age (Hendrickson & Yuodelis, 1984; Yuodelis & Hendrickson, 1986; Curcio et al., 1987). These studies have documented substantial changes in the morphology of foveal cones between birth and 4 years in humans, along with a graded increase in cone density over the same period of time. The human fovea is apparently not fully mature even at 4 years. A similar progression of changes in photoreceptor topography has been reported for the macaque monkey (Packer et al., 1990), who found a graded change in peak cone density between 2 and 25 weeks although the age at which adult cone densities are reached was difficult to establish with certainty. It seems likely that these changes in photoreceptor morphology and topography contribute in some way to the postnatal development of visual resolution. However, even taking into consideration these changes, the sampling limit appears to be well above behaviorally measured resolution in young primate infants (Brown et al., 1987; Banks & Bennett, 1988; Wilson, 1988; Jacobs & Blakemore, 1988).

Behaviorally measured changes in spatial resolution during development are mirrored in the development of LGN cell resolution. Blakemore and Vital-Durand (1986) demonstrated a progression in the development of spatial resolution in foveal LGN cells that was quite similar to the progression of acuity development in a single infant macaque, although the resolution of the best LGN cell at each recording age was about an octave better than the monkey's resolution. To extend this comparison for the present sample of monkeys, the LGN data from Blakemore and Vital-Durand (1986), as well as similar data for macaque striate cortical cells (Blakemore, personal communication; see also, Jacobs & Blakemore, 1988) are replotted along with the behavioral data from the present study. Fig. 8 shows that



Fig. 8. Comparison between spatial resolution of macaque neurons and monkey behavior as a function of age. Open circles are the grating acuity data from the present study. Physiological data represent the cell with the highest spatial resolution encountered by Blakemore and Vital-Durand (1986; Blakemore, 1990) in the LGN (filled triangles) or striate cortex (open triangles) of macaques at each age plotted.

the youngest monkeys perform well below the resolution levels of the best neurons. However, the progression of development beyond the youngest ages follows a similar time course to that measured physiologically. As Blakemore and Vital-Durand (1986) point out, this similarity does not necessarily suggest that LGN cells are setting limits on visual development; the developmental progression may be a manifestation of more peripheral changes like those seen at the level of the photoreceptors.

Psychophysical studies of adult performance suggest that vernier acuity, on the other hand, is related to cortical magnification (Westheimer, 1982; Levi et al., 1985; Fahle & Schmid, 1988). Vernier acuity declines in a manner consistent with cortical magnification as stimuli are moved from fovea to periphery. The suggestion is that optimal vernier performance depends on the relatively greater cortical territory devoted to the foveal representation in the striate cortex. However, recent data from Wässle et al. (1990) show that the greater cortical territory devoted to the foveal representation relative to the periphery can be related to a change in ganglion cell density from fovea to periphery, and is therefore not an amplification generated at the level of the cortex. Schein and de Monasterio (1987) reported a particular correspondence between ganglion cell afferents of the parvocellular pathway and cortical magnification. The similarity between ganglion cell density as a function of eccentricity and cortical magnification suggests that the decline in vernier acuity with eccentricity can be accounted for at the level of the ganglion cells. These data argue against the idea of a cortical limitation on vernier performance, and support the idea of retinal limitations on both vernier and grating acuity.

Regardless of whether vernier acuity and grating acuity are limited by similar or different mechanisms in adults, it is worth realizing that the limits on infant visual performance are not necessarily the same as those in adults. As discussed above, the distribution of photoreceptors across the retina changes postnatally in both humans and monkeys (Hendrickson & Yuodelis, 1984; Yuodelis & Hendrickson, 1986; Packer et al., 1990). It is likely that the topography of ganglion cells also changes postnatally. The relationship between ganglion cell density and cortical magnification has not been studied in infants, so whether or not this relationship changes developmentally is not known. It is known that striate cortical cells improve developmentally in both spatial resolution and contrast sensitivity (Blakemore & Vital-Durand, 1986; Blakemore, 1990) and the development spatial resolution in cortical cells parallels development at the level of the LGN (see Fig. 8). Since developmental trends measured at the level of the LGN and cortex may well depend on changes at the level of the photoreceptors, it is at least plausible that the developmental functions described for vernier and grating acuity depend on the development of similar mechanisms that may be quite early in the visual system.

Banks and Bennett (1988) have described a developmental process that could serve as a limiting factor for both vernier and grating acuity. They developed an infant ideal observer model that demonstrates many of the behaviorally documented features of human visual development. By their analysis, changes in cone morphology and spacing between birth and adulthood can account for much of the improvement in contrast sensitivity. Although receptoral (including pre-receptoral) factors cannot account quantitatively for the degree of change seen behaviorally, the patterns of change predicted from the ideal observer analysis are qualitatively similar to developmental trends. In particular, the Banks and Bennett (1988) analysis predicts different rates of development for vernier and grating acuity based on changes in the quantum efficiency of cones as a function of age. The precise nature of the differences depends on a number of assumptions including summation area and the relationship between quantum efficiency and vernier acuity. However, it seems that developmental changes at the level of the photoreceptors could underlie different rates of development for vernier and grating acuity and it is therefore not necessary to postulate different underlying mechanisms.

Comparison between human and monkey developmental profiles is difficult. There are inconsistencies among the human studies that are without obvious cause. For example, Shimojo et al. (1984) and Manny and Klein (1985) show developmental functions for vernier acuity that are similar in slope to each other and to the monkeys, whereas Shimojo and Held (1987) report a considerably steeper function using apparently identical methods. Although the spatial frequency of the grating target in the Shimojo and Held (1987) and Shimojo et al. (1984) studies were slightly different, it seems unlikely that this difference is a major factor. Whatever the case, the four-to-one rule relating the development of grating acuity, and contrast sensitivity, in human and monkey infants may not be quantitatively appropriate for the development of vernier acuity. While plotting human age in months and monkey age in weeks allows the grating acuity data to superimpose, the vernier acuity data do not: beyond the earliest test ages, human vernier acuity is superior to monkey vernier acuity (refer to Fig. 7).

It would appear that vernier acuity develops relatively more quickly in humans suggesting that there is a different relationship between vernier and grating acuity in humans than in monkeys. However, it is important to note that all of the human studies were conducted with stimuli containing a dynamic cue to vernier offset, while in the present study, the stimuli were always static. It is possible that these studies reflect infants' sensitivity to motion rather than to vernier offset. Recent preliminary reports suggest that the temporal properties of the stimulus affect vernier threshold in infants (Aslin & Skoczenski, 1990; Carkeet et al., 1990). In particular, adding motion to the stimulus improves vernier thresholds in infants (Skoczenski, personal communication; Shimojo, personal communication).

This study shows that vernier and grating acuity follow different developmental time courses in normal infant primates. However, the mechanisms underlying these time courses are difficult to discern. These data could be taken to support the initial position that these two visual functions depend on different neural mechanisms. But two aspects of the data argue against their development being wholly independent: (1) vernier and grating acuity reach adult levels at similar ages, and (2) vernier and grating acuity are related to each other in an orderly manner over the course of development. These findings suggest that vernier and grating acuity are limited by the development of similar mechanisms that affect them differentially. In an attempt to disentangle these possibilities, we studied the development of vernier and grating performance in strabismic monkeys. The following paper (Kiorpes, 1992) describes the pattern of disruption of these two types of acuity in strabismic monkeys. The data provide greater insight into the processes that are important for acuity development and the nature of amblyopia.

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