

Analysis of the development of spatial contrast sensitivity in monkey and human infants

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Received May 31, 1988; accepted July 26, 1988

The development of spatial contrast sensitivity in human and monkey infants reveals changes in the properties of underlying contrast-detection mechanisms in the visual system. A reanalysis of published data shows that the development of the spatial contrast sensitivity function can be described satisfactorily by the simultaneous vertical and horizontal scaling of a template function whose shape on a log-log axis does not change during development. Because individuals differ in the point to which contrast sensitivity has developed at any particular time, the use of group-averaged data as a basis for estimating the course of the developmental process has two undesirable results. First, it provides estimates of spatial contrast sensitivity during development that do not reflect any individual's sensitivity. Second, it incorrectly suggests that the shape of the spatial contrast sensitivity function changes during development.

INTRODUCTION

The function relating an observer's contrast sensitivity to the spatial frequency of a sinusoidal grating test target is the spatial contrast sensitivity function. This function provides a measure of the spatial properties of contrast-detecting elements in the visual system.¹ It is widely believed that the contrast sensitivity function is in fact the envelope of the sensitivity functions for collections of neural channels that subserve the detection and discrimination of spatial patterns.^{2,3} In young monkeys and humans, spatial contrast sensitivity is poor: both the peak contrast sensitivity and the spatial resolution of the visual system are substantially lower in young humans and monkeys than they are in adults. Over a period covering roughly the first year of monkey life or the first five years of human life, spatial resolution and contrast sensitivity, as measured behaviorally, develop to adult levels.⁴⁻⁸

It is thought that changes in the contrast sensitivity function in early life are of two kinds. First, the function changes in both vertical and horizontal scales, reflecting development of the sensitivity and the refinement of the spatial scale of the visual system. Second, it changes in shape, reflecting a change, other than a simple change in scale, in the properties of the underlying contrast-detecting mechanisms.⁹ The reported change in shape is related to the reduction in sensitivity at spatial frequencies below the peak that is commonly seen in adult subjects; it is reported to be attenuated or absent in early life.^{4,5,10} This low-frequency sensitivity reduction is generally associated with lateral spatial antagonism (lateral inhibition) in the visual system, and its absence in young observers is thought to be related to the late development of this kind of spatial processing.^{4,5,9}

Because of the difficulties associated with testing human infants, it is often difficult to obtain enough data from indi-

vidual infants to characterize the developmental process fully. As a result, many studies combine data from a number of individuals tested at a particular age to obtain a group average and then use the group data to estimate the form of the developmental function. However, because there are differences in developmental level among individuals at any given age, the combination of data by age may result in a misleading representation of the developmental function. It is generally appreciated that it is appropriate to consider different methods for representing average developmental data. But when suitable methods do not present themselves, the consequences are not always fully explored. In the specific case that we consider in this paper, we show that group averaging can yield estimates of spatial contrast sensitivity that do not represent the sensitivity of any particular individual and can yield estimates of developmental time course that do not describe the time course of any individual's development.

We have reexamined the way that the spatial contrast sensitivity function changes over development by using a method that defines a template form for the contrast sensitivity function from individual data. We conclude that the function does not, in fact, change its shape importantly. Instead, it simply scales vertically and horizontally. Thus the development of spatial contrast sensitivity can be described by the change in the vertical and horizontal scales of a template function. The development of these scales progresses to different degrees in different individuals of a given age. The results of the analysis suggest that the sensitivity and the scale, but not the underlying spatial structure, of visual mechanisms subserving contrast detection change over development.

Data on spatial contrast sensitivity typically are plotted on double-logarithmic coordinates, and we follow that convention here. In these coordinates, changes in vertical and horizontal scales manifest themselves in rigid shifts in the

position of a standard function, and hereafter we refer to these shifts rather than to the scale changes that underlie them.

METHODS

We analyzed three sets of published data on the development of spatial contrast sensitivity. The first and most extensive data set comes from a study of normal macaque monkeys, tested between the ages of 5 and 52 weeks, that were trained by using operant techniques and studied longitudinally.⁷ We also examined behavioral data on the development of spatial contrast sensitivity in human infants, obtained by using a preferential looking paradigm,^{5,10} and another set of infant data obtained by using an evoked potential method.¹¹ In all cases, contrast sensitivity is taken as the inverse of the threshold Michelson contrast required for reliable detection of the grating target; specific details of the stimuli and the methods used in these studies can be obtained from the primary references.

In our analysis we used an iterative minimization procedure¹² to provide estimates of the best-fitting contrast sensitivity function. The minimization was performed after the data were logarithmically transformed. The minimization was therefore designed to shift rigidly the curves measured for each individual until they all fit the chosen template function. The function that we used was a double exponential of the form

$$k_s(\omega k_\omega)^\alpha \exp(-\beta \omega k_\omega), \quad (1)$$

where ω is the spatial frequency. The four free parameters affect primarily the steepness of the low-frequency (α) and high-frequency (β) portions of the curve, lateral shifts along the frequency axis (k_ω), and vertical shifts along the sensitivity axis (k_s). This function is similar to one reported by Wilson¹³ to account well for his contrast sensitivity data from humans; we chose it because it also reliably provided better fits to the monkey data than did such plausible functions as a difference of exponentials.

In our major analysis we fitted expression (1) to as many as 54 sets of contrast sensitivity data. The procedure simultaneously provided a best-fitting shape for expression (1), by globally optimizing α and β across all the data sets, and the appropriate individual offset for each data set, by finding the optimal values for k_ω and k_s . This process may be thought of as first a series of shifts that bring all the contrast sensitivity data in a particular group into register by rigid translation of each individual set of data and then an estimation of the curve shape that best fits the combined data. In the calculation, of course, the two operations took place in parallel, rather than in series; the contrast sensitivity data were brought simultaneously into alignment with the template curve, and they also determined the form of that curve.

RESULTS

Monkey Infants

We first consider the data on contrast sensitivity development in pigtail macaque monkeys (*Macaca nemestrina*), measured by Boothe *et al.*,⁷ using operant techniques. These data are the most extensive available on contrast

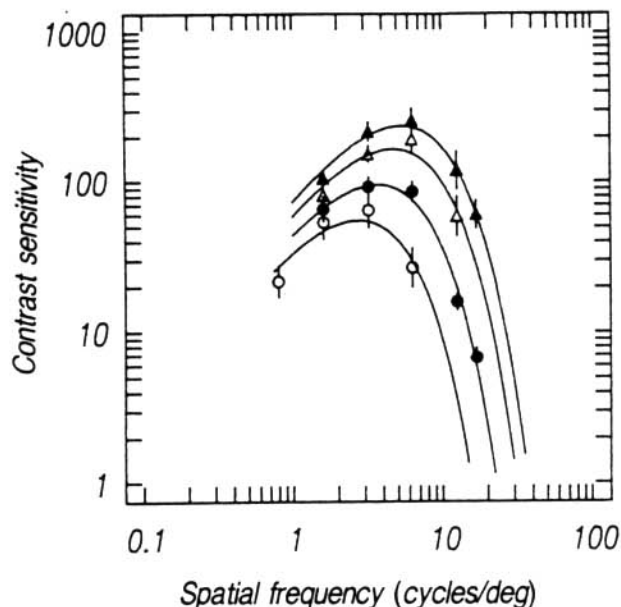


Fig. 1. Spatial contrast sensitivity functions obtained from a macaque monkey at four ages: 10 weeks (open circles), 17 weeks (filled circles), 24 weeks (open triangles), and 45 weeks (filled triangles). The error bars represent standard errors of the mean contrast sensitivity at each frequency. The smooth curves through the data show the best-fitting curve of the form of expression (1) for each data set, fitted under the constraint that the same average shape curve fit all 33 data sets obtained from the six monkeys included in the study. (Data were obtained from Ref. 7.)

sensitivity development in individual primates. Figure 1 shows spatial contrast sensitivity data obtained from a single monkey at four different ages between 10 and 45 weeks, showing the steady improvement in both sensitivity and resolution that is characteristic of development in monkey and human infants. It is evident that this monkey's changes in contrast sensitivity can be described well by rigid shifts up and to the right in an archetype contrast sensitivity function, as shown by the smooth curves in the figure. This function was in fact derived by the procedure described above (see the Methods section), from a total of 33 sets of contrast sensitivity data obtained from six normal monkeys between the ages of 5 and 52 weeks. The particular positions of the four functions illustrated were of course optimized for the four sets of data in the figure, but the shape represents the general shape of the monkey spatial contrast sensitivity function.

In order to show the reliability with which this function fits the data for different monkeys at different ages, in Fig. 2 we show three plots illustrating the scatter of the data about this function. Each plot was prepared by translating the actual contrast sensitivity data so that the best-fitting template function for each data set was superimposed upon all the others and then plotting the scatter of the data about the single resulting function. Figure 2A shows this scatter for all 33 data sets; notice that the total range of scatter of the data about the function is rarely larger than 50%, which is not much greater than the standard errors of the estimates of threshold (e.g., Fig. 1). We conclude that the single archetype function adequately describes the data from all the monkeys at all ages tested.

It is thought that the attenuation of spatial contrast sensi-

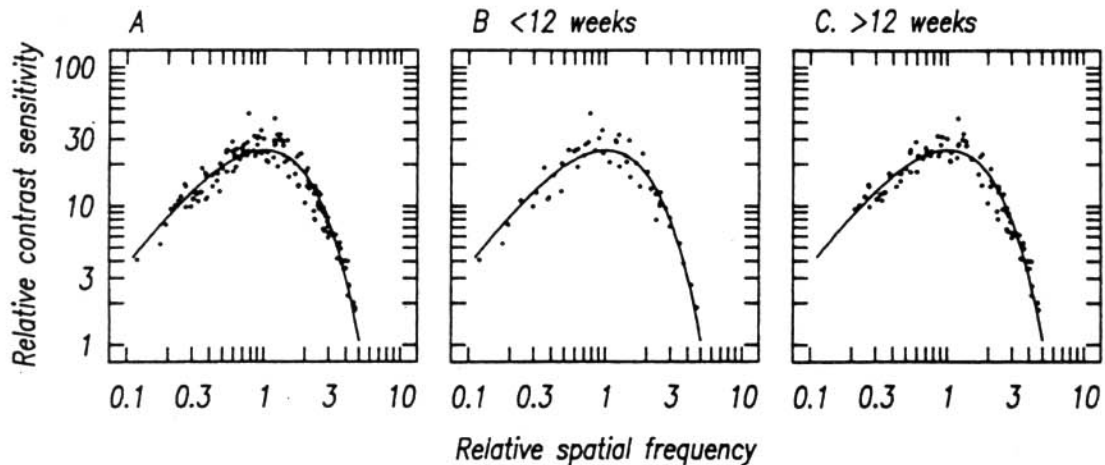


Fig. 2. Three graphs showing the scatter of contrast sensitivity data from infant monkeys around the best-shaped contrast sensitivity function described by expression (1) and fitted simultaneously to all the data by using the method described in the text. Each panel shows the best smooth curve and scattered data that have been shifted, set by set, by an appropriate amount to fit that curve. A, All 33 sets of contrast sensitivity data from all six monkeys. B, The 11 sets of data obtained from the monkeys below the age of 12 weeks. C, The 22 sets of data obtained from monkeys above the age of 12 weeks. (Data were obtained from Ref. 7.)

tivity at low spatial frequencies that characterizes measurements made by using stationary or slowly modulating targets in adult human observers is weaker or absent in young infants and develops over the first few months of life.^{4,5,10} If there were a similar pattern of development in monkey in-

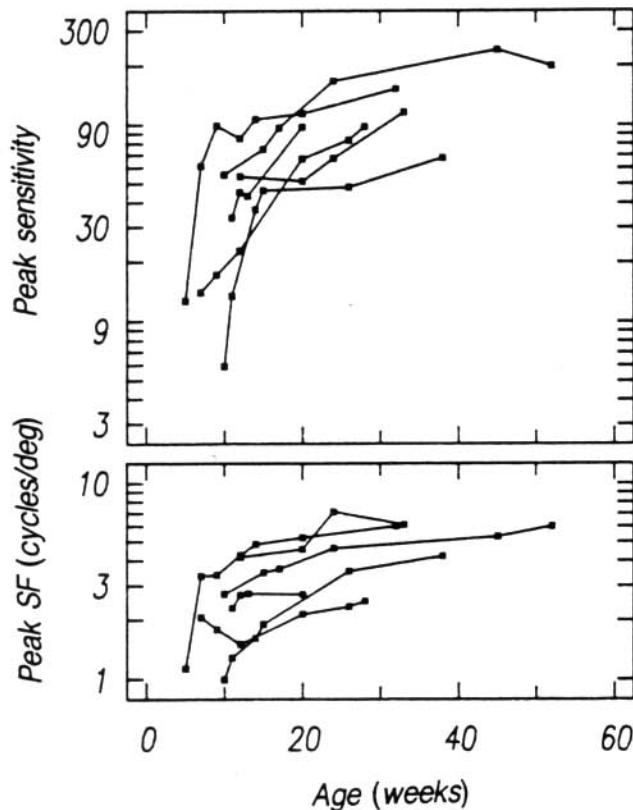


Fig. 3. Developmental time courses for spatial frequency and contrast sensitivity in monkeys. The upper panel plots the sensitivity at the peak of the best fitting template contrast sensitivity function for six monkeys studied at different ages. The lower panel plots the spatial frequency at which the peak sensitivity occurred. Note the substantial variation from animal to animal in the developmental time course for both parameters. (Data were obtained from Ref. 7.)

fants, we would expect a difference in the quality of the fits of the template curve to data from younger and older monkeys. In Figs. 2B and 2C this suggestion is examined for these data; scatter plots similar to that in Fig. 2A are shown for two groups of data representing animals younger than 12 weeks (Fig. 2B) and animals older than 12 weeks (Fig. 2C). There is no appreciable difference in the quality of the fit for the two groups, suggesting that the shape of the underlying contrast sensitivity function does not change, at least over the age range studied.

Because a single function can be used to fit all the data from the study of Boothe *et al.*,⁷ it follows that the course of spatial contrast sensitivity development for a particular individual can be described by the position of the function with time (see Fig. 1). In Fig. 3 this position is plotted as a function of age for each of the six monkeys in the study. The upper part of the figure shows the height of the peak of the contrast sensitivity function [proportional to k_s in Eq. (1)], and the lower part shows the spatial frequency at which the peak sensitivity occurs (inversely proportional to k_w). As noted in the analysis of the individual data that is given in the original report, there is considerable variation from monkey to monkey in the course over which the contrast sensitivity function develops. It has not escaped our notice that curves of this type, describing a developmental time course, could in principle be subjected themselves to a similar template analysis, which could provide good information about the average course of development. The most important missing ingredients are a function and a transformation rule that can be combined to describe individual variations in developmental time course. In addition, longitudinal data on human development are scarce.

As mentioned in the Introduction section, in studies of contrast sensitivity in human infants it is difficult to obtain enough data from an individual infant at a given age. It is therefore tempting to combine data from several individuals studied at a particular age with a particular stimulus condition. However, if there is substantial variation from individual to individual in the point to which development has progressed, there could be distortions in the shape of the

spatial contrast sensitivity function calculated from group-averaged data. To examine this possibility, we used the monkey data⁷ to calculate group-averaged contrast sensitivity functions by averaging the threshold value obtained for each infant tested at each spatial frequency for five different age groups. The results of this analysis are shown in Fig. 4. Figure 4A shows the means and the standard deviations of the contrast sensitivity values for each of five age groups. Represented this way, the group data suggest that the spatial contrast sensitivity function has a low-pass character in the youngest monkeys and becomes bandpass in older monkeys. Figure 4B shows the same data as in Fig. 4A, along with five individually fitted curves derived (without rigidity assumptions) from expression (1); the standard deviations have been omitted for clarity. These fits confirm the impression obtained from inspecting Fig. 4A that there is an important change in the shape of the function over development. Finally, Fig. 4C shows the group-averaged data from the youngest and oldest age groups, along with the best-fitting versions of the particular form of expression (1), which, when rigidly translated, provided the best fit to all the individual data (see Figs. 1 and 2). Notice that the template function derived from the individual data provides a poor fit to the group-averaged data from the youngest age group, despite the fact that individual spatial-contrast sensitivity functions measured at this age fit the template function well. Only in the oldest age group, in which the heterogeneity of the population is less, are the group-averaged data described adequately by the template function.

In considering these results, it should be noted that the consequences of horizontal scatter are more important for interpretation than are those of vertical scatter; that is, if all the variation from individual to individual were in peak sensitivity (k_s), the group-averaged curve would have the correct shape. Variation in the spatial scale (variation in k_w) must be present for the averaged curve to be distorted in shape.

Human Infants

Our analysis of the monkey contrast sensitivity data suggests that data on contrast sensitivity development obtained from human infants might also be described well by a rigidly translating template curve. We also were concerned that analyses of group-averaged data might distort the human infant data in much the same way as they distort the monkey data (Fig. 4). We therefore analyzed two sets of individual data obtained from human infants between the ages of 4 and 37 weeks. The first set of data was obtained by using stationary gratings, with performance monitored by a preferential looking technique.^{5,10} The second data set came from a recent study in which gratings whose contrast was modulated sinusoidally at 6 Hz were used and in which the swept-contrast visual evoked potential was used to estimate contrast sensitivity.¹¹

Behavioral Data

Our analysis of the data of Banks and Salapatek^{5,10} is shown in Fig. 5, with a format similar to that used in Fig. 2. Banks and Salapatek reported group-averaged data from 20 infants in three age groups: 4, 8, and 12 weeks.⁵ We performed a single minimization that fitted a rigid curve to all the data from the 20 individual infants (the individual data were presented in a later report¹⁰). In Fig. 5 this fit is presented separately with the data from each of the three groups of infants. The first point that is evident from the figure is that the scatter of data about the fitted function is substantially greater for these data than for the data from monkeys shown in Fig. 2, especially for the data from younger human infants. This increase in variability is largely attributable to the smaller number of trials contributing to the human infant data. The difference in variability can be seen by comparing the individual infant data¹⁰ with the individual data from the monkeys (see Fig. 1 and also Ref. 7). The second point is that there is no apparent basis for rejecting the fit of the template function to any of the three sets of

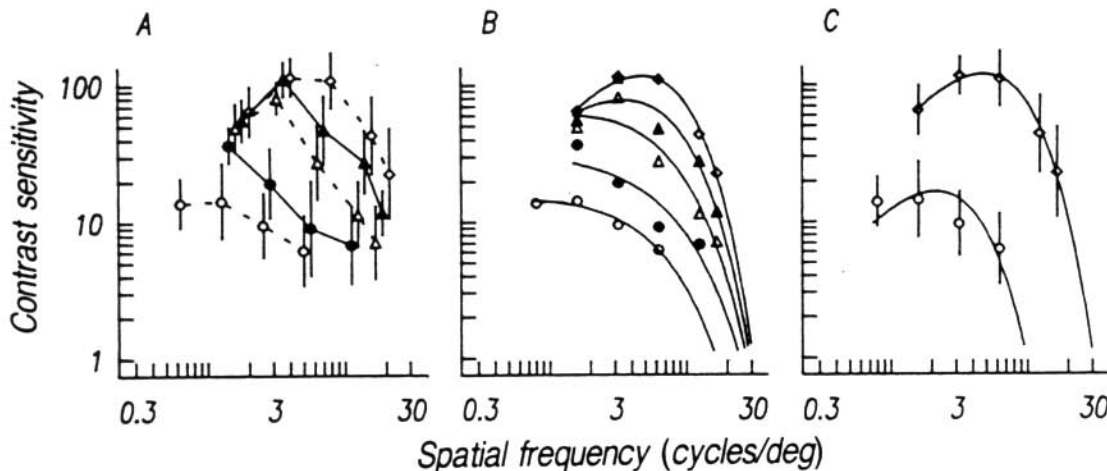


Fig. 4. Analysis of the effect of group averaging on the apparent development of contrast sensitivity. A, Pooled spatial contrast sensitivity data for monkeys in five age groups: near 10 weeks (open circles), 13 weeks (filled circles), 18 weeks (open triangles), 28 weeks (filled triangles), and 45 weeks (open diamonds). The error bars show the standard deviations of the distributions of sensitivity at each age and spatial frequency. The data have been displaced slightly laterally for clarity. B, The data shown in A are plotted again, with smooth curves representing the best-fitting form of expression (1) for each data set. Note that these curves were not fitted under the rigidity assumption but were optimized separately for each data set. The error bars have been omitted for clarity. C, Data for the 10-week and 45-week groups, plotted again against the best-fitting form of the template function shown in Figs. 2 and 3; the template is the function whose shape best describes all the individual contrast sensitivity data. Note that the template's fit is poor for the 10-week data but is reasonable for the 45-week data. (Data were obtained from Ref. 7.)

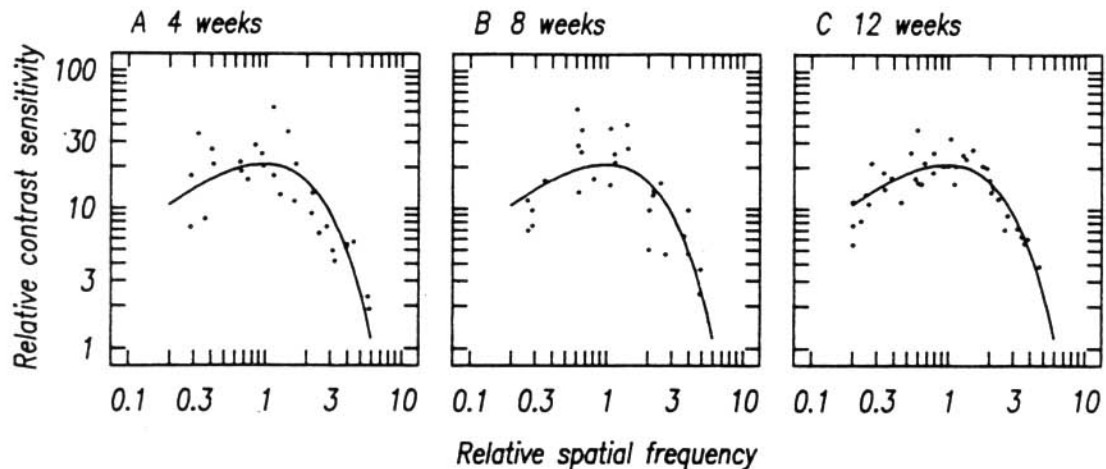


Fig. 5. Analysis of the contrast sensitivity of human infants, measured by using a preferential looking method. The three panels present an analysis of the shape of the contrast sensitivity functions for three age groups, using the format of Fig. 2. A, Data from six 4-week-old infants. B, Data from six 8-week-old infants. C, Data from eight 12-week-old infants. (Data were obtained from Refs. 5 and 10.)

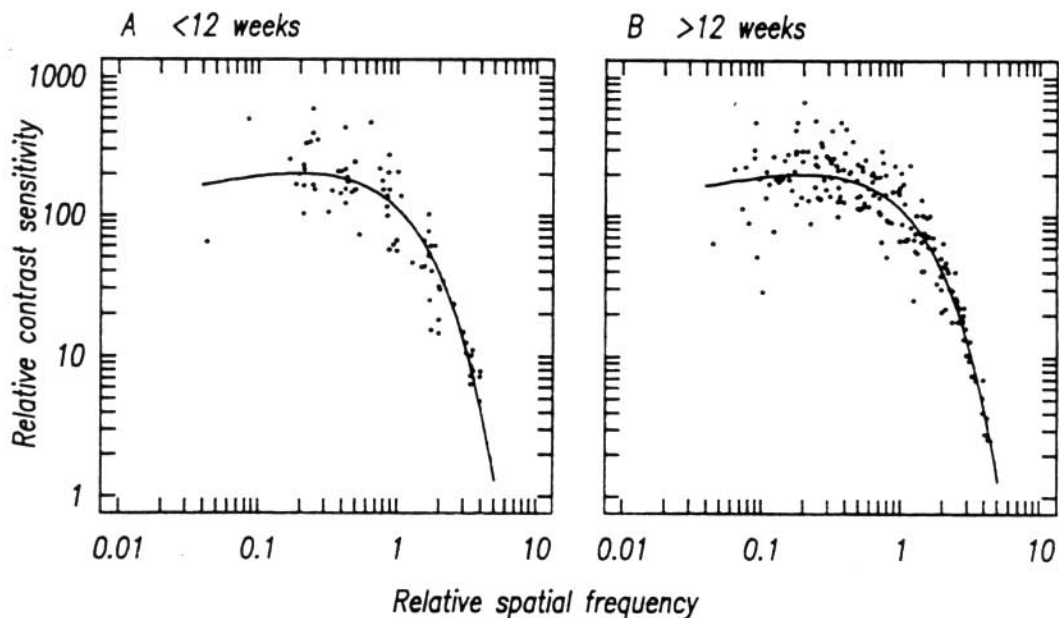


Fig. 6. Analysis of the contrast sensitivity of human infants, measured by using an evoked-potential method. The two panels present an analysis similar to that shown in Figs. 2 and 5, for two groups of infants. A, Data from 17 measurements with infants aged 12 weeks or less. B, Data from 37 measurements on infants aged 13 weeks or more. (Data were obtained from Ref. 11.)

data or for arguing convincingly for a change in the shape of the underlying function. This stands in contrast to the analysis of the group averages of these data presented by Banks and Salapatek.⁵ Their analysis, as does our own group-averaged analysis of the monkey data (Fig. 3), suggested that the low-frequency slope of the spatial contrast sensitivity function increases in the course of development.

The only other study of which we are aware in which spatial contrast sensitivity data from individual human infants are presented is that of Atkinson *et al.*,⁴ whose data and conclusions broadly resemble those of Banks and Salapatek. We did not subject these data to the template analysis because the relevant figure presents data from only 12 cases, for 8 of whom the published curves contain only two measured contrast sensitivity values. Nonetheless, inspection of the curves suggests that, if the data set were rich

enough to warrant a template analysis, the results would be similar to those that we have described for the data of Banks and Salapatek. In particular, the data that fail to reveal an attenuation at low spatial frequencies were all obtained at frequencies too high to reveal that attenuation if a template model were correct.

Evoked-Potential Data

Norcia *et al.*¹¹ used a swept-contrast modulating grating target to elicit a visual evoked potential whose amplitude profile determines an estimate of contrast threshold for the target. Because the gratings were contrast modulated, the spatial contrast sensitivity functions resulting from this stimulus configuration tend to be much more low pass than bandpass in character.¹⁴ This accounts for the difference in shape between the curves shown in earlier figures and the

two curves shown in Fig. 6. The curves shown in Fig. 6 are identical and were derived from a single minimization that fitted a rigid curve to 54 individual evoked-potential data sets. The two panels in Fig. 6 separately present the scatter of the data about the fitted template for data obtained from infants younger (Fig. 6A) and older (Fig. 6B) than 12 weeks. Although these data, too, are more scattered about the fitted curve than are the data from infant monkeys, there is no suggestion that the shape of the spatial contrast sensitivity function representing the two groups of data ought to be different. However, it is worth noting that, since the data were obtained at relatively high temporal frequencies, there is little low-frequency falloff in sensitivity.¹⁴ Therefore it is reasonable to conclude that a single template curve can be derived from these evoked-potential data and translated rigidly to describe the progression of the development of contrast sensitivity. The particular test conditions used in this study, however, make it difficult to draw firm conclusions about the development of low-spatial-frequency attenuation.

DISCUSSION

Analysis of Group-Averaged Developmental Data

The results of this analysis convince us that the widely held belief that spatial-contrast sensitivity functions change shape as infants develop is probably incorrect; instead, the apparent existence of this change may be a result of the method of data analysis used in studies of shifting infant populations.^{4,5} Although this procedure is not used universally in studies of infant visual development, it seems particularly common in studies of resolution and contrast sensitivity (see, for example, Refs. 5, 6, 8, 15, and 16). It is often acknowledged that the use of group averages may blur fine distinctions across the population being pooled, but in this paper we have exemplified the more-serious problems that arise when this pooling produces an apparently significant but artifactual result. With this case in mind, it is possible to imagine other situations in which group averaging could lead to similar misinterpretations of the underlying data, and it is natural to wonder whether some other method of data reduction and analysis might be more appropriate for this sort of situation.

Another possible method would be not to use the data from each individual simply in a group average but rather to combine all the data and perform an analysis like the one that we have done. It would then be possible to extract the appropriate scale factors for each individual's data. By averaging the scale factors (i.e., the average positions of the shifted functions) across individuals of a given age, one could then calculate the average template function for a given age group. This averaged function would more faithfully represent the spatial contrast sensitivity of the average individual than would a simple grouped-data average. In other words, in representing average spatial contrast sensitivity for a particular age, it is more representative to show the contrast sensitivity of the average individual than it is to show the average of the contrast sensitivity across all individuals.

One difficulty with generalizing this approach to other kinds of measurement may lie in the choice of a suitable template function. The problem can be avoided in those

unusual cases in which a canonical form for the function under study can be specified independently, as in the study by Powers *et al.* of the dark-adapted spectral sensitivity of human infants.¹⁷ In other cases, such as the ones we have analyzed in this paper, it is necessary to seek and to validate a particular functional form before applying it to data. In cases in which this proves difficult, a reasonably faithful rendition of the results may be obtained from the measured range of the data or by showing data from the best, the worst, and a typical subject.^{6,7,18} The goal remains the same, to represent the data of the average individual.

Neural Mechanisms

The absence of a change in the shape of the spatial contrast sensitivity function suggests that the different neural channels subserving contrast detection develop roughly in synchrony and that no subset of channels develops especially early or late. Moreover, because the low- and high-spatial-frequency limbs of the function preserve their shapes during development, there is no reason to suppose that low-level processes such as lateral inhibition are of late onset (cf. Refs. 9 and 10). This is in good general agreement with electrophysiological data on receptive-field development in primates, which show that both in the lateral geniculate nucleus and in the visual cortex, receptive fields have qualitatively normal properties in young animals.^{19,20} During development, there are, of course, important quantitative changes in the visual sensitivity and resolution of these receptive fields, but there is no reason to suppose that these reflect specific changes in neural processing, because the limits on visual performance are likely to be set by the development of peripheral mechanisms. By providing evidence for a lack of neural reorganization, our analysis reaffirms the suggestion that the normal development of visual performance is not limited by the development of mechanisms in the central visual pathways. Instead the key factors are likely to be changes in the organization and the sensitivity of mechanisms in the periphery, perhaps originating in the photoreceptors themselves.^{21,22}

ACKNOWLEDGMENTS

This study was supported by National Institutes of Health grants EY 02017 and EY 05864. We are grateful to Anthony Norcia for supplying us with data from the individual infants in his study.¹¹

REFERENCES

1. F. W. Campbell and D. G. Green, "Optical and retinal factors affecting visual resolution," *J. Physiol. (London)* **181**, 576-593 (1965).
2. O. Braddick, F. W. Campbell, and J. Atkinson, "Channels in vision: basic aspects," in *Handbook of Sensory Physiology*, R. Held, H. W. Leibowitz, and H.-L. Teuber, eds. (Springer-Verlag, New York, 1978), Vol. 8.
3. N. Graham, "Spatial-frequency channels in human vision: detecting edges without edge-detectors," in *Visual Coding and Adaptability*, C. S. Harris, ed. (Erlbaum, Hillsdale, N.J., 1980).
4. J. Atkinson, O. Braddick, and K. Moar, "Development of contrast sensitivity over the first 3 months of life in the human infant," *Vision Res.* **17**, 1037-1044 (1977).
5. M. S. Banks and P. Salapatek, "Acuity and contrast sensitivity

- in 1-, 2-, and 3-month-old human infants," *Invest. Ophthalmol. Vis. Sci.* **17**, 361-365 (1978).
6. D. L. Mayer and M. V. Dobson, "Visual acuity development in infants and young children, as assessed by operant preferential looking," *Vision Res.* **22**, 1141-1151 (1982).
 7. R. G. Boothe, L. Kiorpes, R. A. Williams, and D. Y. Teller, "Operant measurements of spatial contrast sensitivity in infant macaque monkeys during normal development," *Vision Res.* **28**, 387-396 (1988).
 8. A. Bradley and R. D. Freeman, "Contrast sensitivity in children," *Vision Res.* **22**, 953-959 (1982).
 9. H. R. Wilson, "Development of spatiotemporal mechanisms in infant vision," *Vision Res.* **28**, 611-628 (1988).
 10. M. S. Banks and P. Salapatek, "Infant pattern vision: a new approach based on the contrast sensitivity function," *J. Exp. Child Psychol.* **31**, 1-45 (1981).
 11. A. M. Norcia, C. W. Tyler, and R. M. Hamer, "Development of contrast sensitivity in human infants," *Invest. Ophthalmol. Vis. Sci. Suppl.* **28**, 5 (1987).
 12. J. P. Chandler, "STEPIT," Indiana University Quantum Chemistry Program Exchange (Indiana University, Bloomington, Ind., 1965).
 13. H. R. Wilson, "Quantitative prediction of line spread function measurements: implications for channel bandwidths," *Vision Res.* **18**, 493-496 (1978).
 14. J. G. Robson, "Spatial and temporal contrast-sensitivity functions of the visual system," *J. Opt. Soc. Am.* **56**, 1141-1142 (1966).
 15. E. E. Birch, J. Gwiazda, J. A. Bauer, J. Naegele, and R. Held, "Visual acuity and its meridional variation in children aged 7-60 months," *Vision Res.* **23**, 1019-1024 (1983).
 16. S. Shimojo, E. E. Birch, J. Gwiazda, and R. Held, "Development of vernier acuity in infants," *Vision Res.* **24**, 721-728 (1984).
 17. M. K. Powers, M. Schneck, and D. Y. Teller, "Spectral sensitivity of human infants at absolute visual threshold," *Vision Res.* **21**, 1005-1016 (1981).
 18. D. Y. Teller, D. M. Regal, T. O. Videen, and E. Pulos, "Development of visual acuity in infant monkeys (*Macaca nemestrina*) during the early postnatal weeks," *Vision Res.* **18**, 561-566 (1978).
 19. C. Blakemore and F. Vital-Durand, "Organization and postnatal development of the monkey's lateral geniculate nucleus," *J. Physiol. (London)* **380**, 453-491 (1986).
 20. T. N. Wiesel and D. H. Hubel, "Ordered arrangement of orientation columns in monkeys lacking visual experience," *J. Comp. Neurol.* **158**, 307-318 (1974).
 21. A. M. Brown, M. V. Dobson, and J. Maier, "Visual acuity of human infants at scotopic, mesopic and photopic luminances," *Vision Res.* **27**, 1845-1858 (1987).
 22. M. S. Banks, P. J. Bennett, and B. Scheffrin, "Foveal cones and spatial vision in human neonates," *Invest. Ophthalmol. Vis. Sci. Suppl.* **28**, 4 (1987).