

Chapter Three

BEHAVIORAL ANALYSIS OF VISUAL DEVELOPMENT

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I INTRODUCTION

The previous two chapters have described in detail the many anatomical and physiological changes that occur in the visual system during the pre-natal and early postnatal weeks and months in several mammalian species.

In this chapter we describe the development of visual function as measured behaviorally. The majority of available data are from primates, both human and monkey; some data are also available for cats. Since the retina (Hendrickson and Kupfer, 1976; Abramov et al., 1982; Hendrickson and Yuodelis, 1984; Yuodelis and Hendrickson, 1986) and central visual pathways (LeVay et al., 1980; Blakemore and Vital-Durand, 1986) are immature in infant primates and undergo considerable postnatal development, it is not surprising that visual function as measured behaviorally undergoes substantial postnatal development. Although it is difficult to discern which level of the system underlies the development of any particular behaviorally measured visual function, there is some evidence to suggest that even the optical and early neural elements in the visual pathway undergo some postnatal development.

Our discussion begins with the development of the earliest elements in the visual system, that is, those that influence the quality of the visual image. Each subsequent visual function discussed reflects, as much as our present understanding permits, the maturation of successively higher levels of the visual pathway. We have excluded from this chapter a discussion of the development of color vision [a thorough recent review of the development of color vision in human infants is provided in Teller and Bornstein (1987)]; virtually nothing is known about the development of color vision in animals, either behaviorally or physiologically. It will become obvious that a great deal of work remains to be done to understand the development of visual behavior and the processes that underlie this development.

A Methodology

Before beginning to discuss the development of visual behavior, it is important to gain a sense for how one measures visual sensitivity in a young animal or human. Most successful assessment techniques make use of some natural behavior of the organism, so that data can be obtained relatively quickly and without extended periods of training. This is particularly true of methods used with human infants, which are usually based on either natural pattern preferences or eye movements elicited by moving patterns. The preferential looking technique, now the most commonly used method for assessing visual sensitivity, is based on the natural tendency for infants to fixate a high contrast pattern (e.g., Fantz, 1965; Teller, 1979). Preferential looking was transformed into a robust psychophysical technique called forced-choice preferential looking (FPL) in Davida Teller's laboratory, initially for the testing of grating acuity in human infants (Teller et al., 1974). Subsequently, this method has been applied to assessment of a variety of visual functions such as color vision (e.g., Peeples and Teller, 1975), depth perception (e.g., Atkinson and Braddick, 1976), spatial contrast sensitivity (e.g., Atkinson, et al., 1977a,b), and light and dark adaptation (e.g., Dannemiller and Banks, 1983; Dannemiller, 1985).

The FPL technique requires a human observer to make forced-choice judgments about the location of a visual pattern given two choices. The choice is usually between a left or right position within an otherwise uniform field, and the pattern stimulus is generally presented opposite a stimulus that is matched in luminance to the pattern. The judgments are made on the basis of the infant's looking behavior, including eye movements, changes in pupil size, and other fixation cues, or differences in interest between the two stimulus fields. It is important to note that in the *forced-choice* version of this technique, the observer's task is to judge—using any available cues—the *location* of the pattern stimulus, not necessarily the side the infant “prefers” or the side of first fixation. The FPL technique has also been adapted for use with monkey infants (e.g., Teller et al., 1978) and, in one case, kittens (Sireteanu, 1985). The FPL technique can be used to test infant monkeys from birth until about 12 weeks, whereas human infants can be tested from birth until about 18 months. Beyond the ages over which FPL data can be collected—that is, when the patterns cease to attract the infants' attention reliably—operant techniques are used.

The performance of human infants on discrimination tasks is sometimes studied using an habituation method that relies on the infants' tendency to fixate novel displays. The infant is habituated to repeated presentations of a particular target, and a new one is then substituted. If the infant reliably shows renewed attention to the display, it is assumed that the two targets can be discriminated (Fantz, 1964).

In operant tasks, the subject makes the discrimination for itself in order to obtain a reward. These techniques require some period of training. The rewards are of course tailored to the species being studied. For example, a monkey may be rewarded with apple juice (Boothe et al., 1980) for correctly discriminating two stimuli, whereas a human infant may be rewarded with a Cheerio (Birch et al., 1983) or an attractive visual display (Mayer and Dobson, 1982). The tasks themselves must also be carefully chosen: a human infant can be asked to point to or touch the correct stimulus; a monkey infant can be trained to pull a grab-bar or touch one of several panels to indicate its choice; kittens are usually tested on a jumping stand (Mitchell et al., 1976). The jumping stand method requires the kitten to jump from a platform onto one of two surfaces; correct choices are rewarded with beef baby food or an equivalently palatable substance, while errors are punished by letting the animal fall a few inches through a trap door.

Most of the data discussed in this chapter were collected using one of these techniques. Absent from most of this discussion are data collected using the visual-evoked potential. The evoked potential provides an electrophysiological measure that, regrettably, does not have any clear quantitative relationship to behavioral data from individual infants (Sokol and Moskowitz, 1985). Furthermore, evoked potential data are available in quantity only for human infants and not for infants of nonhuman species. It is therefore difficult to correlate the origin of the evoked potential signal

with specific neural function. We have included evoked potential data only in a few important cases where no behavioral measures of function are available.

II PHYSIOLOGICAL OPTICS

In cats and monkeys, the optical quality of the eye is suboptimal at birth and develops to adult levels postnatally. At the time of eye opening in kittens, the ocular media are cloudy, degrading light transmission by about 1 logarithmic unit. In addition, the *tunica vasculosa lentis*, a vascular network that supplies the developing lens, is still present during the early postnatal weeks, causing considerable scatter of the incoming light. The media clear and the vascular membrane breaks down progressively over the next 2–3 weeks, during which time the apparent quality of the optics also improves. Over the first 5–7 postnatal weeks, there is a factor of 2 improvement in the quality of optical imaging based on the width of the line spread function (Bonds and Freeman, 1978; see also Chapter 2). The optical modulation transfer function, which describes the contrast transfer properties of the optics, derived for 7-week-old kittens is similar to that derived for adult cats, although there is some evidence even at this age for a continuing high level of light scatter within the eye.

Although the ocular media are clear at birth in primates, there is measurable improvement in the quality of the retinal image in the early postnatal weeks (Williams and Boothe, 1981). During the first 13 postnatal weeks in monkeys, image quality as measured by the width of the line spread function shows nearly a factor of 2 improvement. Figure 1 shows line spread functions obtained from a single infant monkey at each of three ages. A progressive narrowing of the function from 1 to 13 weeks is evident, particularly at the level for which retinal illuminance is one-tenth that at the peak (tenth-height). The corresponding optical modulation transfer functions shown in Figure 2A demonstrate the improvement in contrast transmission between 1 and 13 weeks for this monkey. Optical modulation transfer functions for older monkeys are within the same range as those from 13-week-old monkeys; therefore it is assumed that the optical quality of the monkey eye is adultlike by 13 weeks. It is possible, though, as in the cat that there is greater light scatter in the young monkey eye than in the adult that is not revealed by the methods used by Williams and Boothe.

Although there is measurable improvement in retinal image quality during the early postnatal weeks in cats and monkeys, the condition of the optics in the newborn is probably not a major limiting factor for the development of visual sensitivity. In both cats and monkeys, the time course for the development of visual resolution extends well beyond the time period over which changes in optical quality have been demonstrated (see Section IV). Moreover, comparison between behaviorally measured contrast sensitivity

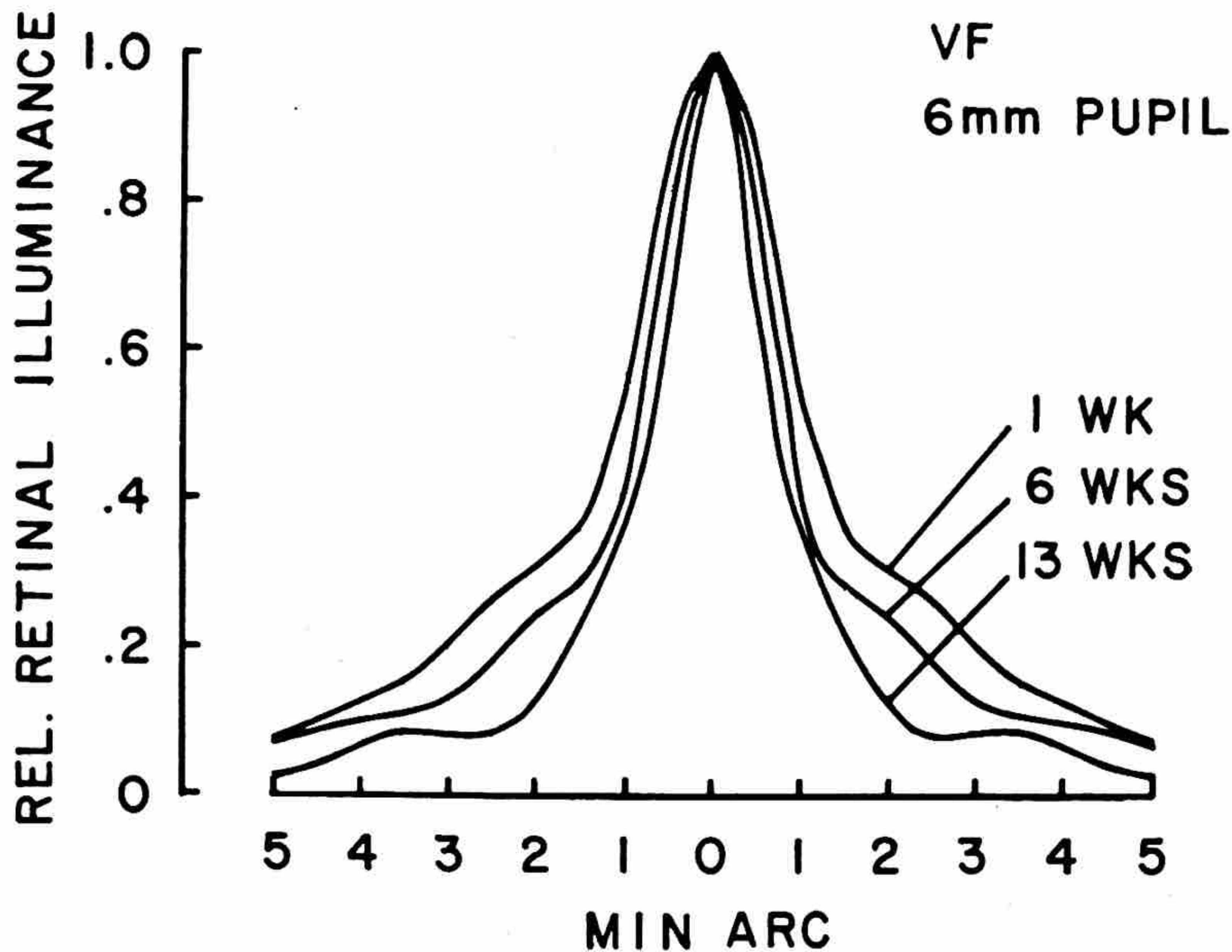


FIGURE 1. Retinal line spread functions for a single monkey infant measured at three ages. The three curves are normalized to 1 at 0 min arc. The data were collected using a double-pass optical technique. The line spread function is the distribution of light across the retinal image of a well focused thin bright line. (From Williams and Boothe, 1981.)

functions and derived optical modulation transfer functions in infant monkeys demonstrates that the behaviorally measured sensitivity is much poorer than the limit imposed by the optics. The data in Figure 2B show contrast sensitivity for an individual infant monkey at 5 and 13 weeks of age measured behaviorally (open squares; see Section IV for a more detailed consideration of contrast sensitivity measurements); the solid curves represent a numerical fit to these data. The dashed curves show—based on optical data from a different monkey taken at corresponding ages—the effect of correcting the fits for the contrast attenuation produced by the optics. The small differences at each age between the corrected and uncorrected curves are much less than the difference between the behavioral performance at the two ages, revealing that the development of the optics is not sufficient to account for more than a small part of the development of contrast sensitivity between 5 and 13 weeks. It is also obvious from a comparison of Figures 2A and 2B that the optics are capable of relaying information about spatial frequencies that the young monkey cannot resolve.

One aspect of optical development that is quantitatively important in considering the development of spatial properties in the visual system is the change in retinal image magnification that accompanies the growth of the eye. For example, the axial length of the eye in primates roughly doubles

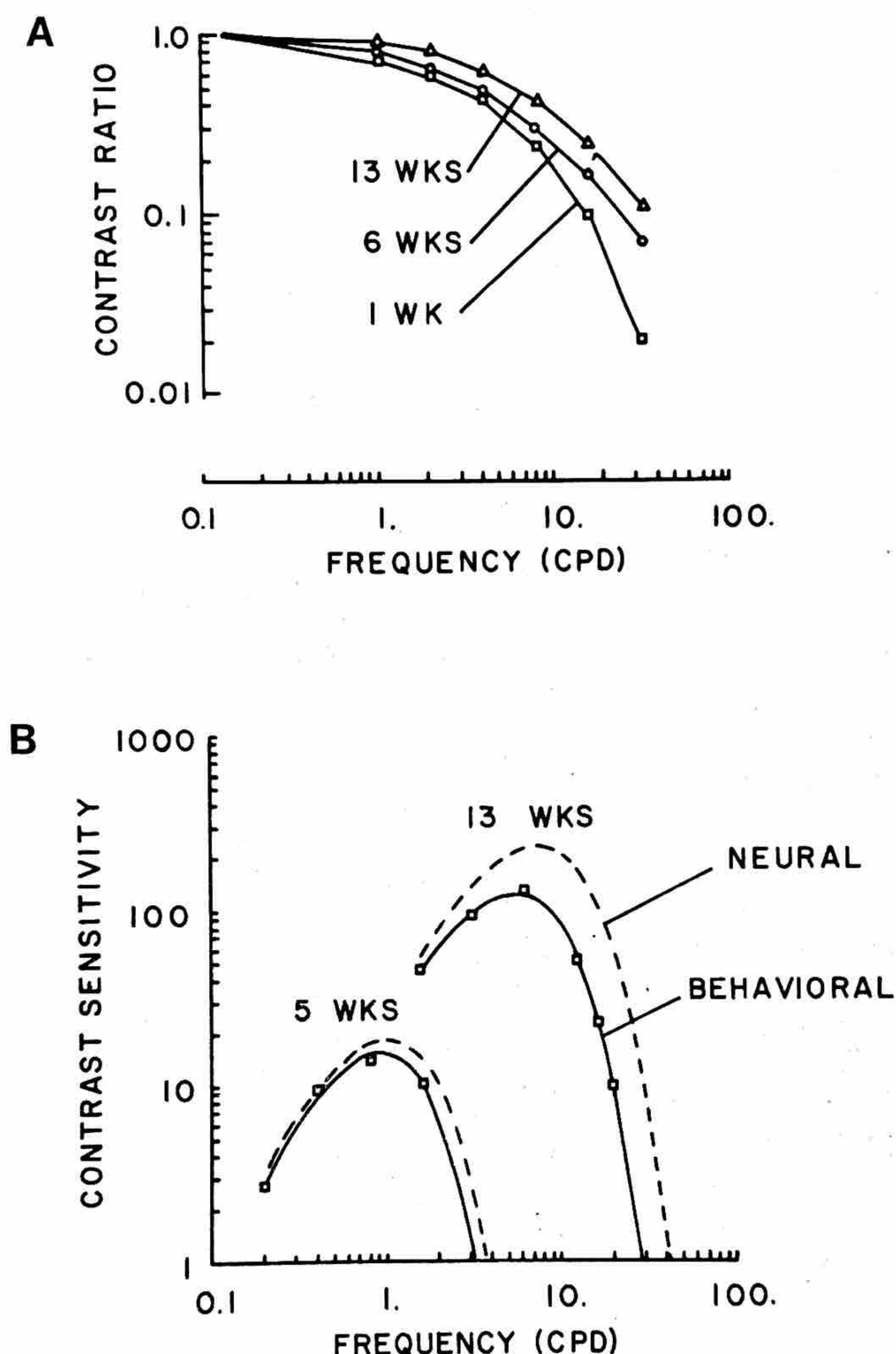


FIGURE 2. (A) Optical modulation transfer functions calculated by Fourier transformation of the line spread functions shown in Figure 1. (B) Behavioral contrast sensitivity functions obtained at two ages from a different infant monkey (solid curves and data points). The dashed curves show the theoretical effect of removing the spatial filtering produced by the optics of the eye measured at comparable ages [shown in (A)]. The improvement in contrast sensitivity produced by eliminating the optical contrast attenuation at either age is far less than the improvement in measured contrast sensitivity. (From Williams and Boothe, 1981.)

between birth and adulthood. This has no direct simple effect on the quality of the retinal image per se, but it alters the effect of that image on the subsequent neural elements of the visual system. All other things being equal, the visual resolution should double as the eye grows simply because the size of the retinal image doubles while the size of the neural elements used to analyze the image does not.

The determination of optical quality is accomplished experimentally by measuring the quality of the retinal image for a pattern that is in the best possible focus. Under natural viewing conditions, the accommodation control system is responsible for providing the retina with a well-focused image. The accommodation control system in primates is functionally immature at birth (see Aslin, 1987, for recent review). Human infants fail to accommodate accurately to targets presented at different distances (25–150 cm) prior to about 4 months postnatally. The closest distances measured correspond to four diopters (D) of accommodation for an emmetropic infant. Although younger infants often demonstrate the ability to accommodate correctly to a range of target distances, they do so less consistently than older infants. A similar trend is apparent in infant monkeys (Howland et al. 1982). Accommodative accuracy is poor in infant monkeys prior to about 5 postnatal weeks. Infants older than 5 weeks show consistently high accommodative accuracy over a range of target distances from 20 to 100 cm, corresponding to a 1–5-D range of accommodative power.

Although the degree of accommodative inaccuracy demonstrated by young primate infants would provide sufficient defocus in an adult eye to degrade visual performance, it is unlikely that this amount of defocus limits infant visual resolution. Green et al. (1980) have analyzed the relationship between eye size, visual acuity, and depth of focus. They show that in a small eye of low visual acuity (like that of a young infant) it is necessary to defocus an image substantially before the blur can be detected—the eye has a large depth of focus. This makes the accommodative inaccuracy of infants irrelevant to their vision. As the eye grows and visual acuity improves, the depth of focus decreases and accommodative accuracy improves concurrently. It therefore appears that accommodative control in infants is no worse than is needed to maintain an image of good apparent quality. It is also worth noting that, like optical quality, accommodative accuracy approaches adult levels much earlier than visual resolution and therefore probably does not impose a consistent limit to the development of visual resolution.

III EYE MOVEMENTS

It seems that the infant's visual system is provided with a reasonably clear and adequately focused retinal image. However, in order to make effective use of this image, the infant must have an oculomotor control system that is capable of positioning the image of the object of regard on the fovea with reliability and stability good enough to allow proper visual function. Fixational instability could effectively degrade visual resolution even in the presence of a clear and well-focused retinal image. It is therefore necessary to consider the development of eye movements and oculomotor control. Little is known about this development in any species. However, a recent

quantitative study of human infants suggests that the oculomotor system can provide stable fixation and can produce rapid (saccadic) eye movements that are mature in speed, accuracy, and latency. Saccades are rapid, ballistically programmed movements that provide for the rapid foveation of visual targets. In a study of infants aged 2 weeks to 5 months, Hainline et al. (1984) found that under conditions of free viewing, infants produced many saccades that were adultlike in form and speed, along with two types of eye movements that were slower than any seen in the adult. The relative proportion of normal velocity to slow eye movements depended upon the type of visual stimulus presented to the infant; textured patterns elicited a higher proportion of adultlike eye movements than simple geometric forms. These results suggest that the attentional level of the infant is important for evaluating the form of the eye movements but that given appropriate stimuli, infants can produce rapid and well-controlled fixational eye movements.

Earlier studies of human infant eye movements suggested that saccades directed to targets in the peripheral visual field are less effective than in adults (Aslin and Salapatek, 1975; Salapatek et al., 1980; see also Aslin, 1987). Infants were presented with small targets at one of several distances away from the point of fixation, ranging from 10° to 30° . While adults would acquire the target in a single saccade or with one large saccade followed by a small corrective saccade, infants acquired the targets with a series of small saccades that were approximately equal in amplitude for a given target distance. This unusual pattern of eye movements was evident until about 2 months postnatally. In addition, the infants' latency for generating a saccadic eye movement was about five times longer than the latency for an adult saccade.

It is therefore not clear when saccadic eye movements actually become adultlike in both form and speed, although they appear to become at least grossly mature in humans between 2 and 5 months. Similarly, visual tracking behavior, or smooth pursuit, seems to become adultlike in the early postnatal months. Aslin (1981) studied smooth tracking behavior in young infants and found that newborns do not demonstrate smooth pursuit eye movements. Over the subsequent 2 months, infants gradually develop the ability to track smoothly moving targets, with characteristic accurate foveal pursuit for slowly moving targets developing before that for faster target movement. By 2 months, the infants tracked at a wide range of speeds, with a velocity gain of close to unity.

It is generally believed that the observed early development of infant oculomotor behavior reflects improvement in the visual control of eye movements rather than a purely mechanical or motor development. In this case, the development of oculomotor control would depend on calibration and integration of sensory and motor information during the first few postnatal months. Although sophisticated and elaborate methods exist for studying the basis of oculomotor control in nonhuman primates, no studies

of the development of eye movement control in infant monkeys have been conducted.

The results of studies on the development of reflexive eye movements are consistent with the suggestion that sensory control of eye movements develops later than the motor aspects of oculomotor control. Optokinetic nystagmus (OKN) is a characteristic reflex pattern of eye movements elicited by large moving fields (see Figure 3A) and consists of slow phases in which the eye moves with a direction and speed roughly matching the stimulus interspersed with rapid saccadelike fast phases that bring the visual axis back in the opposite direction. Newborn infants (human, monkey, and cat) show a directional asymmetry in the production of monocular OKN (Atkinson, 1979; van Hof-van Duin, 1978). The asymmetry is characterized by a more vigorous optokinetic response to stimuli moving from the temporal visual field toward the nasal visual field as compared to that for stimuli moving from the nasal field toward the temporal field (Figure 3B). The asymmetry, as would be expected from a visual rather than a motor limit, is specific to the slow phase of the nystagmus. Naegele and Held (1982) demonstrated that the velocity of the slow phase component of OKN was higher for nasally directed stimuli than for temporally directed stimuli. This asymmetry gradually decreases in extent over the first 3–5 months in humans.

In monkeys and cats, the directional asymmetry is maintained only through the first 3–5 postnatal weeks. There is ample evidence from the cat to suggest that the following response for temporally directed stimuli depends on the integrity of the ipsilateral pathway from the retina to the nucleus of the optic tract via the striate cortex, which develops over a similar postnatal period (Cynader and Harris, 1980; Harris et al., 1980; Cynader and Hoffmann, 1981). Data from strabismic humans suggest further that the integrity of cortical binocularity is important for development and maintenance of symmetrical OKN (Atkinson, 1979; van Hof-van Duin and Mohn, 1986).

A possibly related asymmetry has been noted in the development of visual sensitivity in the nasal and temporal visual fields. Kittens (Sireteanu and Maurer, 1982) and human infants (Lewis, et al., 1985) younger than 8 weeks show poorer detection performance for stimuli presented in the nasal visual field than for stimuli presented in the temporal visual field. After 8 weeks, the ability to detect stimuli presented in the nasal and temporal fields appears to be similar. The delayed development of sensitivity in the nasal field is consistent with a relatively slow development of the ipsilateral pathway from the retina through the visual cortex to the superior colliculus, which is thought to contribute importantly to the process of orientation to visual stimuli. These data taken together suggest that the postnatal development of visual orienting behavior depends more on the maturation of sensory aspects of oculomotor control than on purely motor factors.

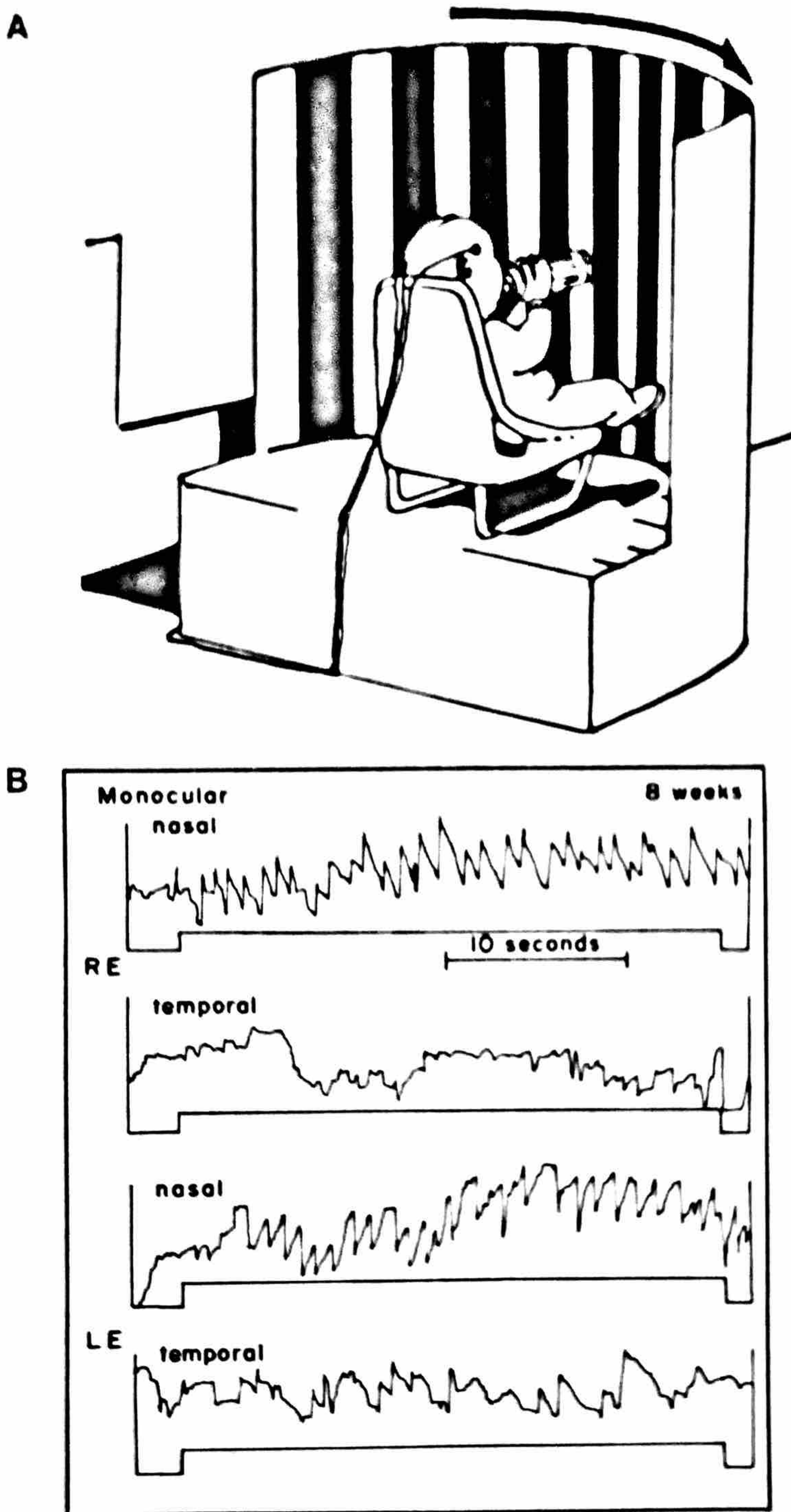


FIGURE 3. (A) A human infant (holding a bottle) positioned in front of an OKN target. The pattern is drifted across the infant's visual field at a constant speed while eye movements are recorded by electrooculography (EOG). (B) Sample EOG records from a single young human infant. The top two traces are records for the right eye; the bottom two traces are records for the left eye. The records show a more vigorous, consistent OKN response for nasalward target direction relative to temporalward target direction for each eye. (From Naegele and Held, 1982.)

IV VISUAL SENSITIVITY AND RESOLUTION

It appears that the developing visual system has adequate optics to form a clear image and adequate oculomotor control to provide for the fixation and stabilization of that image. We now proceed to consider the development of the purely visual processes that determine sensitivity to light and to the spatial and temporal distribution of image contrast.

There are two distinct kinds of developmental change that contribute to changes in visual performance during development, which we can term changes of *scale* and changes of *sensitivity*. By changes of scale we mean changes in the spatial and/or temporal filtering or integration properties of elements of the visual system. The visual system of infants operates on a very much coarser scale than that of adults, at least spatially, and it may be that if allowance is made for this, the infant's visual capacity is otherwise more-or-less adultlike. We use the term "sensitivity" to describe the efficiency or accuracy with which the visual system can process targets adjusted for changes in spatial or temporal scale. Thus the sensitivity of an immature observer cannot be properly estimated if performance is only measured with targets selected for adults; it is often necessary to adapt the spatial or temporal characteristics of the display to the scale of the system under study. Regrettably, it is not always possible to distinguish the contributions of these two types of developmental change because it is often not possible to make the measurements of the spatial and temporal characteristics of vision that are needed to estimate or compensate effects of scale. The result is that some measurement that might appear to represent a development of sensitivity could in fact be the result of changes in the scale of visual processing that unknown to the experimenter, rendered the chosen test target inappropriate for the younger visual system.

A Absolute Sensitivity and Light Adaptation

A good example of the influence of changes of scale on inferences about development arises in the consideration of the absolute sensitivity of infants to light. This is reliably found to be substantially poorer than in adults. Absolute threshold for the detection of light increments upon a dark background is elevated in 1–2 month old human infants by at least 1.2 logarithmic units relative to the adult (Powers et al., 1981; Brown, 1986; Hansen et al. 1986). Absolute sensitivity improves with age, although as late as 18 weeks postnatally sensitivity has not reached adult levels. Similarly, detection thresholds have been reported to be elevated under conditions of photopic illumination in young infants. Photopic sensitivity is reduced in infants aged 2–3 months by about 1.1 logarithmic units relative to the adult (Peeples and Teller, 1978; Pulos et al., 1980).

Initially, a number of studies suggested that the visual mechanisms underlying adaptation to changes in level of illumination are immature in young infants. Increment threshold functions that relate visual detection

thresholds to the intensity of an adapting background light were found to be shallower for 1- and 2-month-old human infants than for older infants and adults for both scotopic and photopic levels of illumination (Hansen and Fulton, 1981; Dannemiller and Banks, 1983). Figure 4A and B show increment threshold functions for 7- and 12-week-old infants compared with average adult performance. The interpretation of this shallow slope is complicated, however, because adult observers have shallow increment threshold functions when small test targets are used (Barlow, 1972; illustrated in Figure 5). Because of the coarser scale of the infant's visual system, it may be that targets that are "large" for adults are functionally "small" for infants. Indeed, recent studies of light adaptation in infants, in which very large test fields were used, show that the slopes of increment threshold functions in infants are similar to those of adults if the larger spatial summation areas of the infant (Hamer and Schneck, 1984) are taken into account. Thus an apparent change in function related to sensitivity can in fact be attributed to the difference in spatial scale between infant and adult.

While adults and infants typically have increment threshold functions of the same shape for large test fields, the functions of infants are elevated by an amount that reflects their poorer sensitivity near absolute threshold. No simple effect of spatial scale can account for this difference between infants and adults. Brown (1986) showed that the lowest background intensity that elevates visual thresholds is similar in infants and adults. Because this measure of infants' sensitivity (the adapting effectiveness of background light) is apparently adultlike, she concludes that their reduced sensitivity for the *detection* of light must be due to incomplete development of mechanisms in the visual pathway that are central to the (probably retinal) mechanisms responsible for light adaptation.

B Spatial Vision

The most useful basic measure of spatial visual function is now generally thought to be the *contrast sensitivity function*, which describes the performance of the visual system in terms of the minimal detectable contrast for sinusoidal grating patterns of varying spatial frequency (Campbell and Green, 1965). The inverse of the threshold at each spatial frequency is the contrast sensitivity, hence the name of the measure. Figure 6 shows typical contrast sensitivity functions for cat, monkey, and human observers obtained with stationary gratings. All these show a characteristic bandpass shape, with a range of intermediate spatial frequencies being detectable at lower contrasts than either lower or higher frequencies. More traditional measures of visual acuity, such as line resolution, are also captured by the contrast sensitivity function: the spatial frequency at which contrast sensitivity falls to 1 corresponds to the resolution limit for grating targets. These limits are about 3–6 cycles per degree for cats, and between 30 and 50 cycles per degree for macaque monkeys and humans.

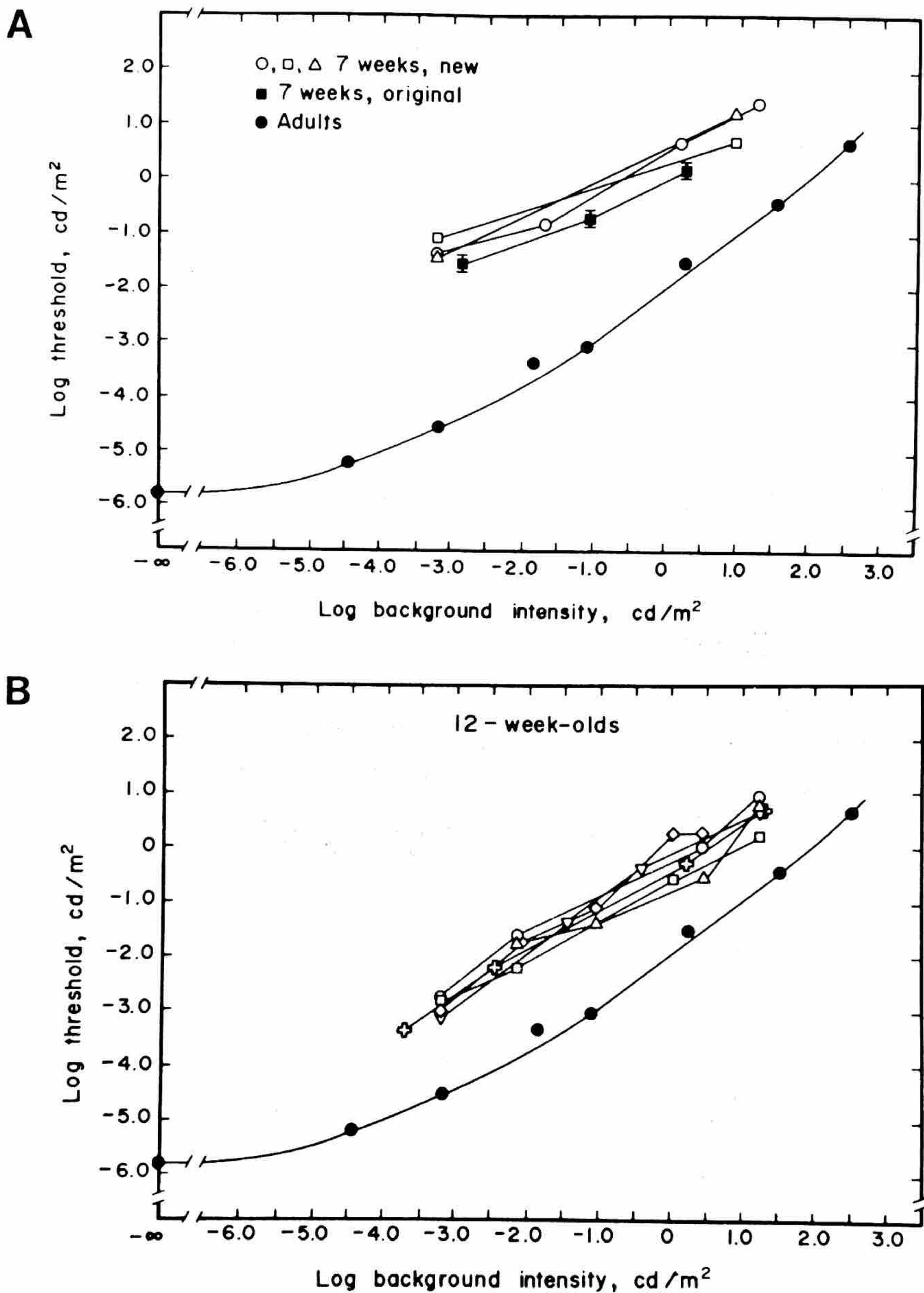


FIGURE 4. (A) Increment threshold functions for 7-week-old human infants (open symbols) compared with data from adults (filled symbols). The slopes of the infant functions are shallower than those for the adults. (B) Increment threshold functions for 12-week-old human infants (open symbols) compared with data from adults (filled symbols). By this age the slopes of the functions were adultlike. (From Dannemiller and Banks, 1983.)

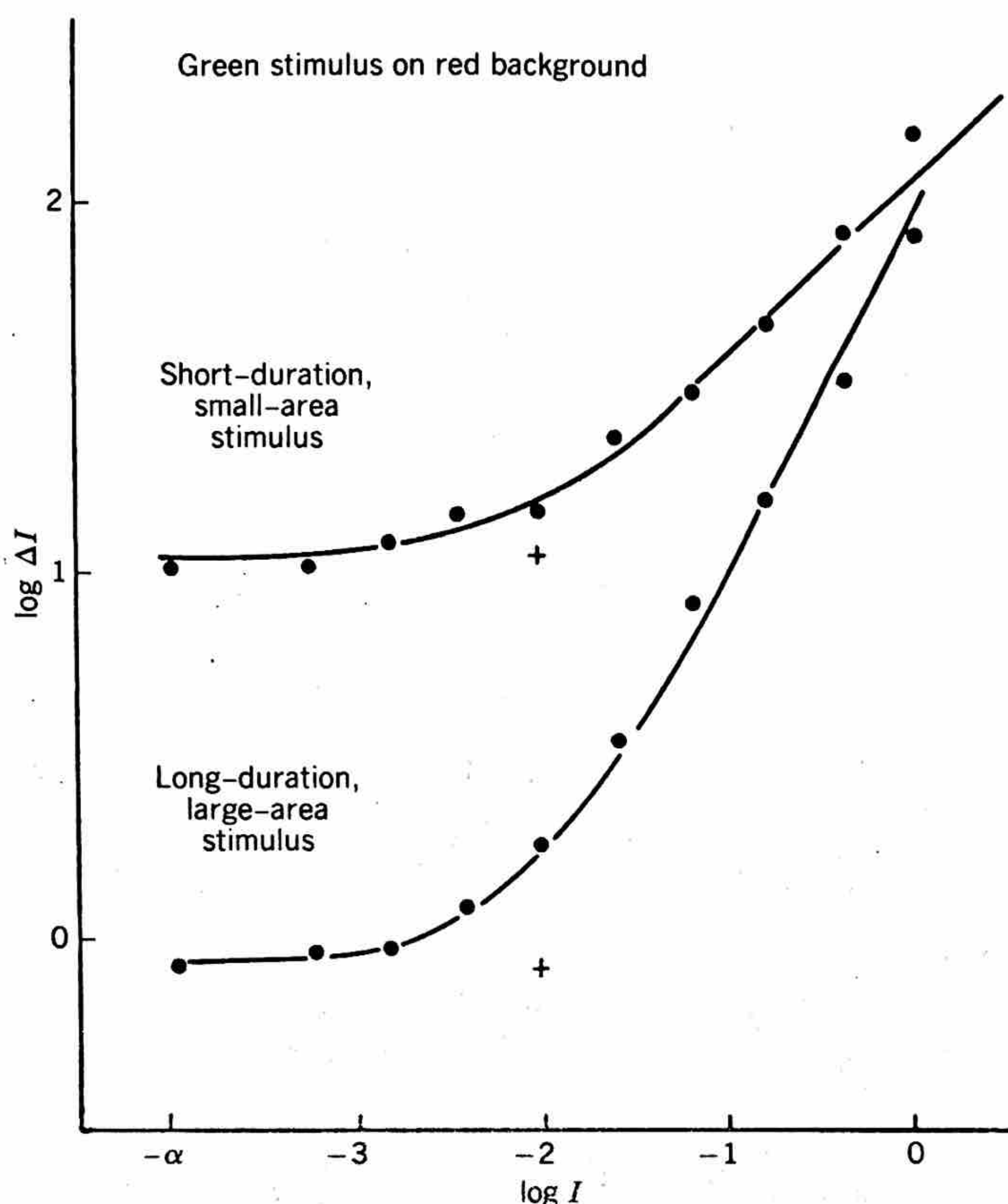


FIGURE 5. Increment threshold functions for adult observers with large, long-duration (bottom curve) and small, short-duration (top curve) test spots. The slope for the top curve is shallower than that for the bottom curve. (From Barlow, 1972.)

The development of sensitivity to spatially varying stimuli has been the subject of a great many studies in a variety of species, including cats as well as primates. The limit of spatial resolution, that is, the finest spatially periodic pattern that can be resolved, shows a similar developmental profile in all species examined. Spatial resolution in newborns is at least a factor of 10 poorer than in adults; it improves rapidly over the early weeks or months of life, then continues to develop at a slower rate to adult levels.

The interpretation of grating resolution measurements in neonatal kittens is hampered by the cloudy optic media that persist for several weeks after eye opening (see Section II and Chapter 2). However, it appears that in kittens, as in monkeys, these optical defects do not limit performance. The earliest behavioral measures of acuity in kittens can be obtained at about 1 month, at which time acuity is about 0.5 cycles per degree (Mitchell et al., 1976; Giffin and Mitchell, 1978; Sireteanu, 1985). During the next 2 months, resolution improves rapidly to near adult levels. By 4 months, resolution development is essentially complete at the level of 5–8 cycles per degree.

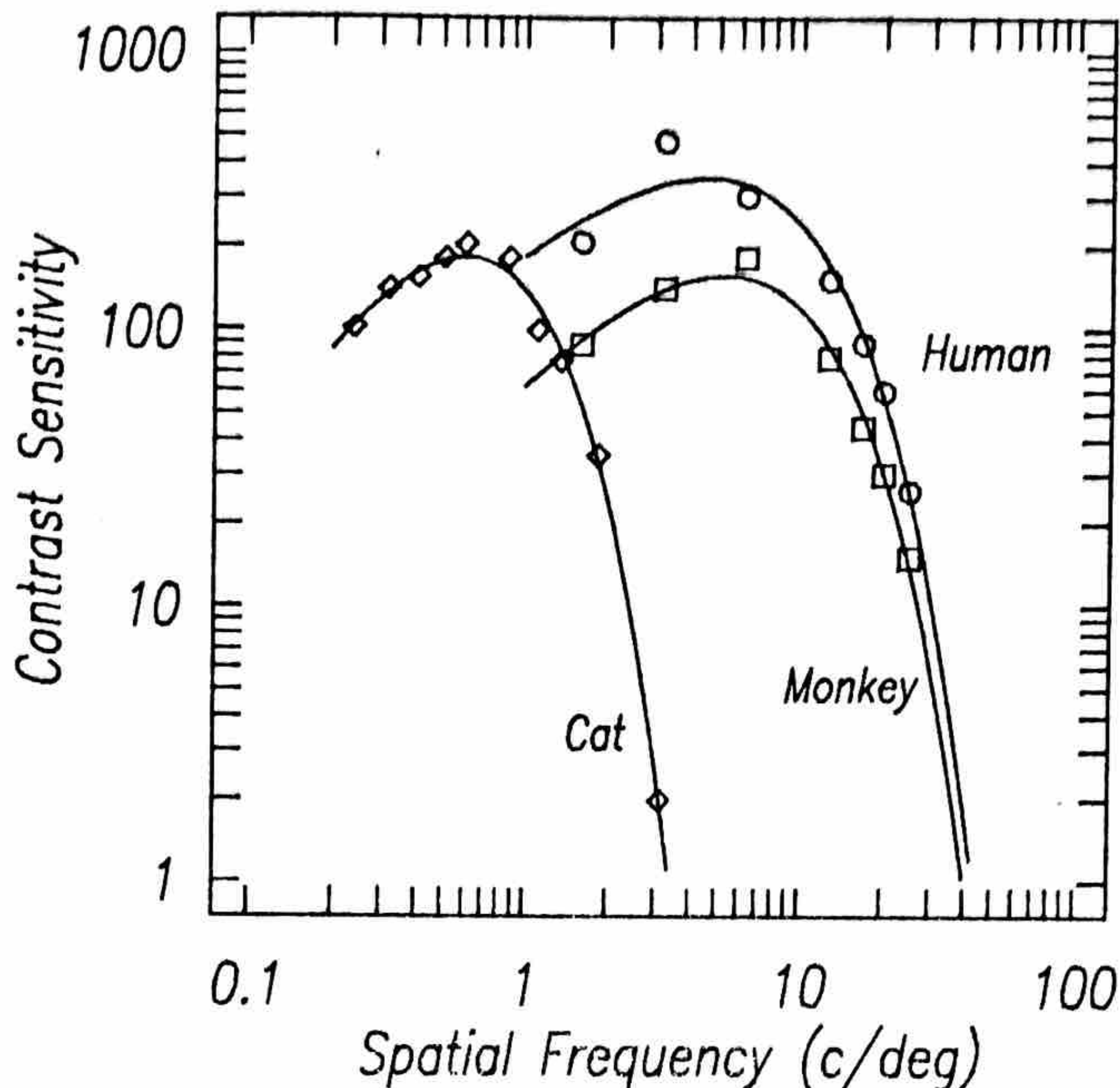


FIGURE 6. Contrast sensitivity functions for individual adult cat, monkey, and human subjects. All data were collected using stationary grating targets, operant two-alternative forced-choice psychophysical methods. Note that the peak sensitivity is similar for cats, monkeys, and humans; however, the range of spatial frequencies resolved is lower for the cat than for primates. [Primate data from Williams et al. (1981); cat data courtesy of T. Pasternak.]

Figure 7 (bottom) shows this developmental time course for the cat based on measurements made using the jumping stand technique.

The development of spatial resolution in primates is much slower than in cats. Whereas spatial resolution is adultlike by about 4 months in the cat, adult levels of resolution are not attained until near the end of the first year in monkeys (Boothe et al., 1988) and between 3 and 5 years in humans (Mayer and Dobson, 1982; Birch et al., 1983). The time courses for the development of resolution in monkeys and humans are shown in Figure 7 (middle and top, respectively). Comparison of the human and monkey data reveals several similarities. Spatial resolution is comparable in newborn human and monkey infants, both measuring between 1.0 and 2.0 cycles per degree. Although obscured by the use of a logarithmic scale for age in Figure 7, resolution improves rapidly for the first 6 postnatal weeks in monkeys (Teller et al., 1978; Lee and Boothe, 1981) and months in humans (reviewed by Dobson and Teller, 1978), followed by subsequent gradual development until adult levels of 30–50 cycles per degree are reached. The time courses for the development of resolution in monkeys and humans actually superimpose fairly well if human age is plotted in postnatal months and monkey age is plotted in postnatal weeks (Teller and Boothe, 1979)—a “four-to-one” rule that we will return to later.

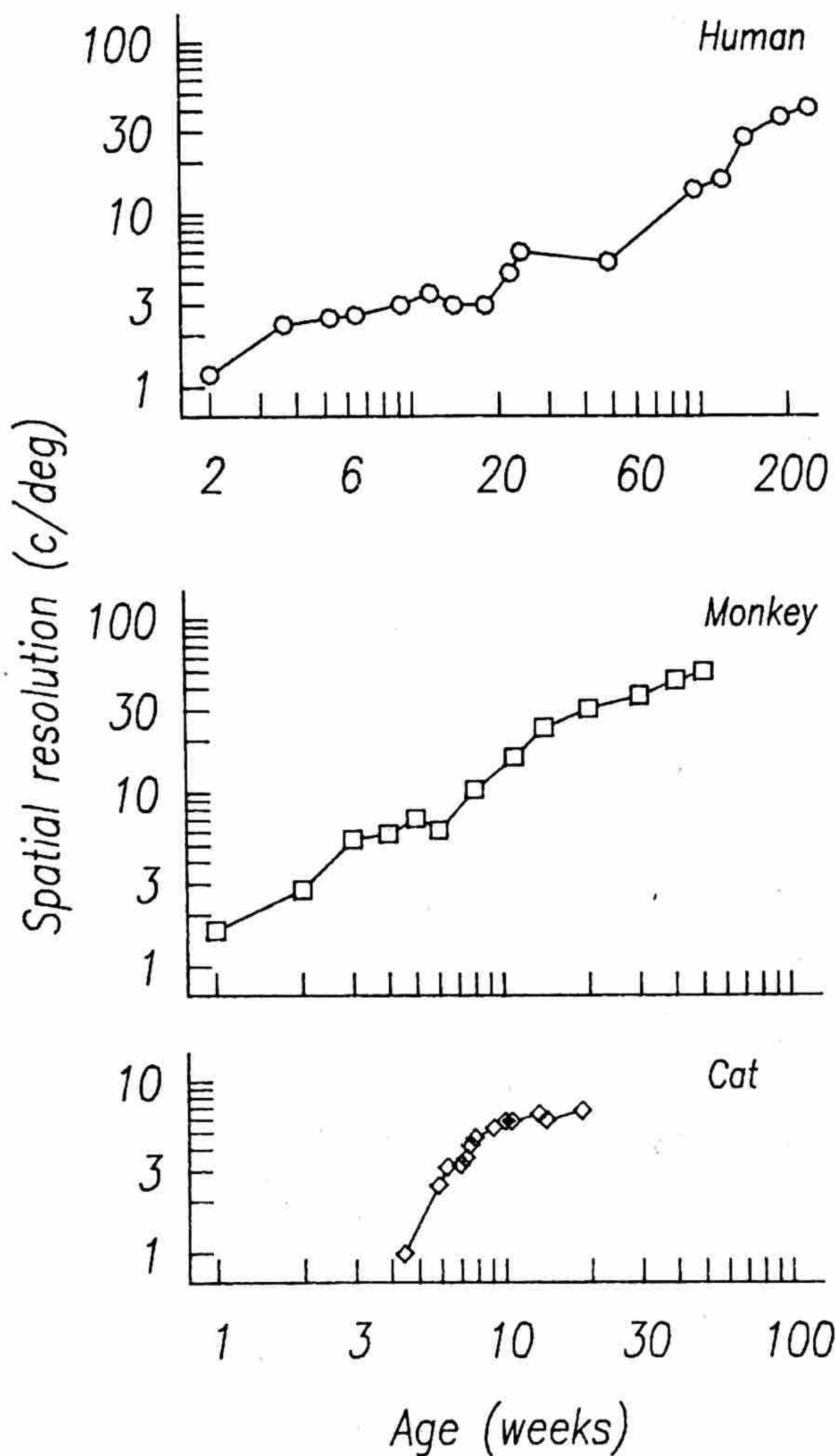


FIGURE 7. Development of spatial resolution for cat (bottom), monkey (middle), and human (top). Cat data were collected using the jumping stand technique (Mitchell et al., 1976; Giffin and Mitchell, 1978). Primate data were collected using a combination of FPL and operant techniques. Note that age is plotted on a logarithmic scale and that the age scale is different for human infants. This format creates the appearance that the developmental time course is roughly linear in primates. [Human infant data are from Mayer and Dobson (1982); monkey data are unpublished normative data of L. Kiorpes.]

The development of the whole contrast sensitivity function has been assessed in primate infants. Contrast sensitivity data are available for human infants and children from two age ranges: 1–3 months (Atkinson et al., 1977a; Banks and Salapatek, 1978) and 2½–8 years (Bradley and Freeman, 1982); one contrast sensitivity function for one 6-month-old infant has also been published (Harris et al., 1976). Macaque monkey data are available for ages ranging from 5 weeks to 1 year.

The contrast sensitivity function in human infants during the early postnatal months is strikingly different from that of the adult. Figure 8A shows data from young human infants, revealing a number of differences from the adult data shown in Figure 6. Most obvious is the restricted range of spatial frequencies resolved by the infant. Recall that the highest spatial frequency included by the envelope of the contrast sensitivity function represents the resolution limit. The poor spatial resolution of infants described above is directly reflected in the restricted range of resolvable spatial frequencies. Also obvious is the lower amplitude of the contrast sensitivity function in infants. Clearly, infants' sensitivity to contrast across the entire range of resolvable frequencies is reduced by at least a factor of 10 relative to the adult. Notice also that the reduced sensitivity is not uniform across spatial frequencies, meaning that the function must move not only upward but also to the right during development. This, of course, reflects a change in spatial scale as well as a change in sensitivity during development. The practical consequences for the infant is that its visual system can process only large, high-contrast stimuli.

Another important difference between the infant and adult contrast sensitivity function is the absence of a low-frequency falloff in the function obtained from an individual 1-month-old infant (open circles, Figure 8A). The drop-off of sensitivity at low frequencies in the adult contrast sensitivity function is usually attributed to lateral spatial antagonism in the visual system. Its absence in young infants suggests that the inhibitory mechanisms responsible may be immature at birth and develop sometime be-

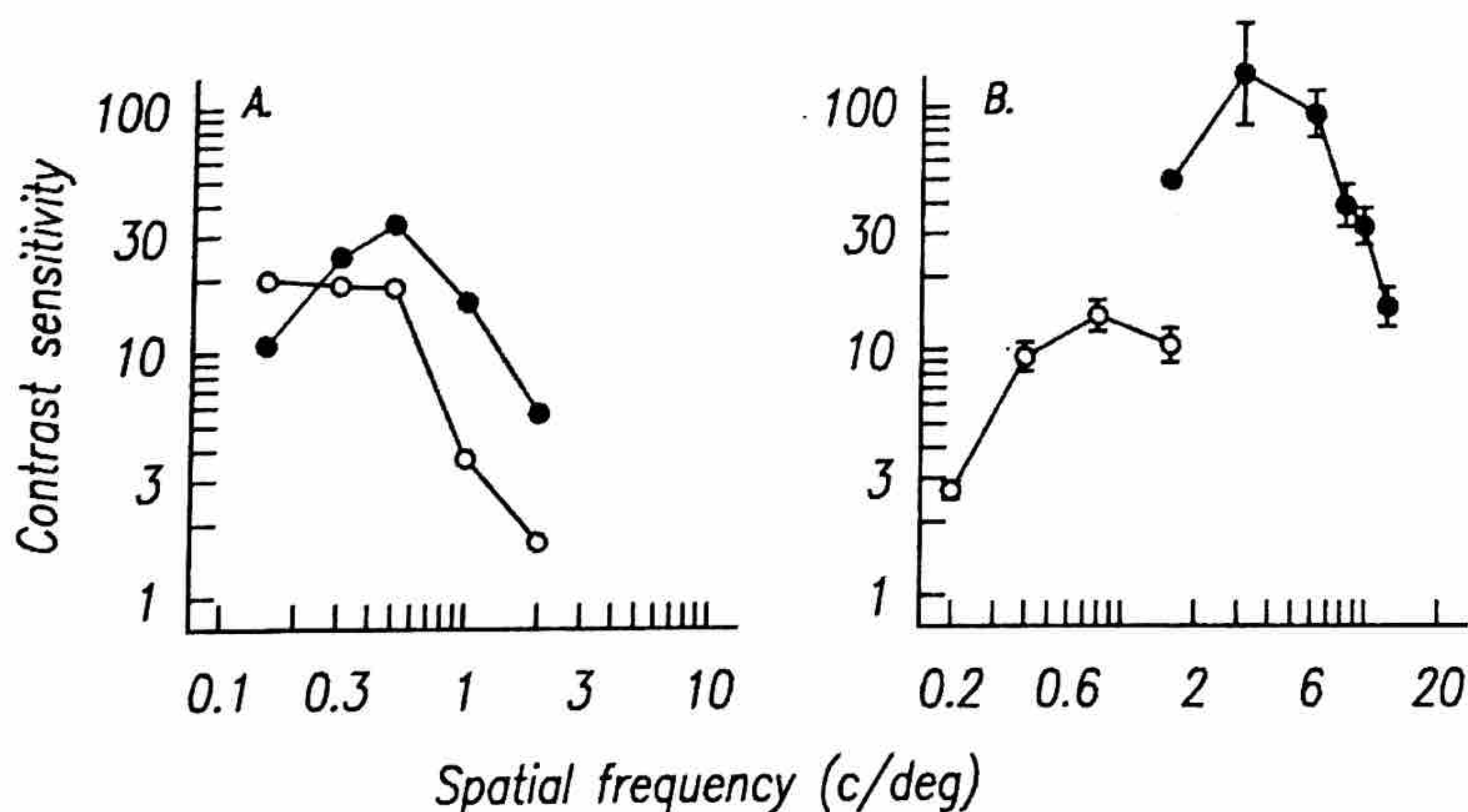


FIGURE 8. (A) Contrast sensitivity data from two young human infants (open symbols, 1-month-old; filled symbols, 3-month-old). Most 1-month human infants do not show attenuation of contrast sensitivity at low spatial frequencies, whereas older infants show the low-frequency falloff in sensitivity. (Data from Banks and Salapatek, 1981.) (B) Contrast sensitivity at two ages from one infant monkey (open symbols, 5 weeks; filled symbols, 9 weeks). Note the presence of the low-frequency falloff in the 5-week data and the combined upward and rightward shift of the function with age. (Data from Boothe et al., 1988.)

tween 1 and 3 months (filled circles, Figure 8A). However, a recent analysis suggests that at least some of this difference may be due to averaging of infant data (see Movshon and Kiorpes, 1988). Thereafter, it appears that the general form of the contrast sensitivity function is similar to that of the adult. Contrast sensitivity data from children reveal that development continues over the early childhood years. Bradley and Freeman (1982) found that the shape of the contrast sensitivity function in 2½-year-old children was similar to that of adults but that sensitivity to contrast over most of the spatial frequency range continued to improve up to at least 5 years. Beyond 5 years, small residual differences in sensitivity between children and adults are generally ascribed to differences in response criterion rather than to immaturity of visual system function (Bradley and Freeman, 1982; Abramov et al., 1984).

The progression of contrast sensitivity development between the ages of 3 months and 2½ years is not well-documented in human infants, largely because of methodological limitations. This gap can, however, be bridged by data from monkey infants if we use the four-to-one rule for relating monkey to human developmental time courses. Boothe et al. (1980, 1988) have studied the development of the contrast sensitivity function in individual monkey infants at ages ranging from 5 to 50 weeks. Similar to human infants, contrast sensitivity functions from monkeys at the earliest test ages were considerably reduced in overall amplitude as well as range of resolvable spatial frequencies (Figure 8B). Unlike data from human infants, though, the low-frequency falloff of sensitivity was present at the earliest tested ages in the monkey. However, based on the age correspondence of monkey weeks and human months established for the development of spatial resolution, the low-frequency falloff should be observable by 3 weeks in the monkey. Since the earliest age studied by Boothe et al. (1988) was 5 weeks, their data may not be relevant to this issue. If the four-to-one rule about developmental time course holds, it would be necessary to study contrast sensitivity in monkeys younger than 5 weeks to establish the absence of a low-frequency falloff in newborn monkeys.

Examination of the longitudinal development of contrast sensitivity in infant monkeys reveals that the observed changes in contrast sensitivity are the result of the function shifting upward in sensitivity and rightward toward higher spatial frequencies concurrently (compare open and filled symbols, Figure 8B). This process is evident from the plot of improvement in contrast sensitivity at the peak, peak spatial frequency, and cutoff frequency as a function of age for an individual infant monkey shown in Figure 9. In terms of the issues of scale and sensitivity we raised at the start of this section, the top panel in Figure 9, showing the development of peak contrast sensitivity, is a pure measure of sensitivity. The middle panel, showing the development of the spatial frequency at which peak sensitivity is observed, gives a good measure of the changes of scale. The bottom panel, showing the development of spatial resolution, shows a composite measure

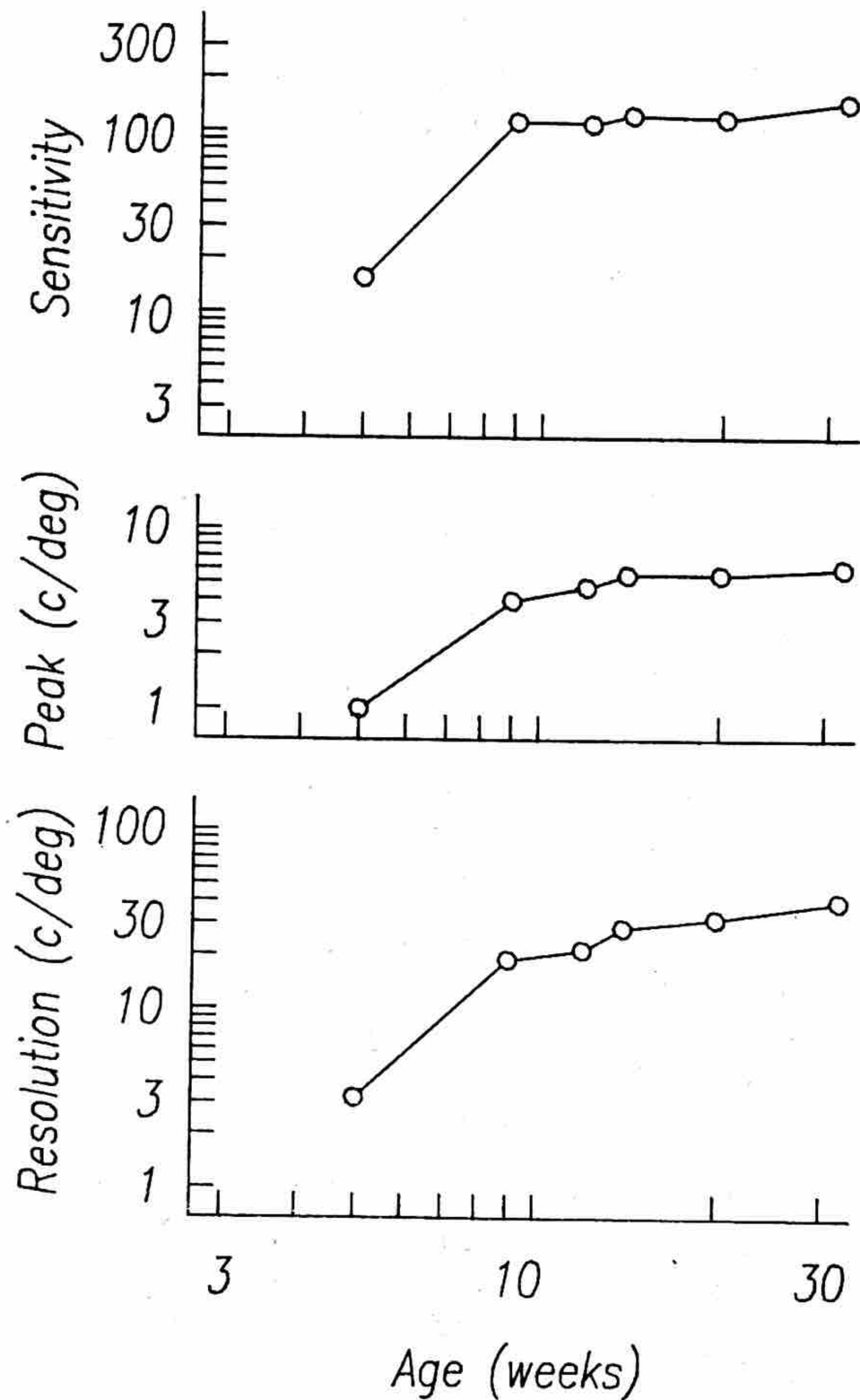


FIGURE 9. Development of the parameters of the contrast sensitivity curve for an individual monkey (the same monkey whose data appear in Figure 8B). The top graph shows development of sensitivity, that is, the height of the peak of the curve; the middle graph shows the development of the spatial frequency at which sensitivity is the highest; the bottom graph shows the development of spatial resolution, that is, the frequency at which the curve falls to a sensitivity of 1. Note that these features develop simultaneously, at similar rates within an individual. Development of contrast sensitivity for this monkey was essentially complete by 30 weeks (Data from Boothe et al., 1988.)

that is probably dominated by the change in the position of the peak but also depends on the contrast sensitivity. We have performed an analysis of the longitudinal data collected by Boothe et al. (1988), which reveals that the shape of the contrast sensitivity function does not change systematically during development, at least after the age of 1–2 months. This means that the changes plotted in Figure 9 adequately capture the phenomenon of contrast sensitivity development over the age range studied.

This pattern suggests that the development of contrast sensitivity cannot

depend solely on one mechanism improving in sensitivity with age. Rather, it may be that an array of functional elements that vary in their spatial characteristics are simultaneously developing both higher sensitivity and finer spatial resolution. These data are consistent with the widely accepted notion that many different size-selective mechanisms ("spatial frequency channels") support spatial visual performance rather than simply one large filter through which visual information is processed (see, e.g., Graham, 1980).

More direct evidence for the existence of a range of size-selective mechanisms in the human infant visual system has been provided in a study by Banks et al. (1985), who used a masking paradigm to measure the bandwidths of spatial frequency selective mechanisms in 1.5- and 3-month-old infants. Using a narrow-band masking noise, they measured threshold elevation as a function of the center frequency of the masking noise. The results showed that threshold elevation occurs when the frequency content of the masking noise differs from the test frequency by less than two octaves (a factor of 4) in 3-month-olds, which is similar to the pattern seen in adult subjects. No masking effects were noted in the 1.5-month-olds. These data support the hypothesis that there are a number of different size-selective mechanisms operating in the visual system of infants as young as 3 months postnatal and that the bandwidth of these spatial frequency channels is at least roughly similar to those of adults.

It is likely that the time course for the development of spatial vision is limited by the development of neural elements at relatively peripheral stages of the visual system. Banks and Bennett (1988) suggest that spatial visual development during the early postnatal months in human infants can be accounted for by the maturation of foveal cone position and morphology. Thereafter, the maturation of response properties of visual neurons at the level of the ganglion cells or lateral geniculate nucleus may limit the developmental process (Blakemore and Vital-Durand, 1986). The notion that peripheral factors limit spatial contrast sensitivity is also generally accepted for adult observers. More central neural structures are, however, thought to limit performance on tasks such as vernier acuity that involve some kind of pattern discrimination (e.g., Levi et al., 1985). It is therefore of interest to study the development of pattern discrimination ability in infants as a possible behavioral method for analyzing cortical maturation.

Discrimination performance in infants has been measured to assess sensitivity to stimulus configuration. Braddick et al. (1986) used an habituation method to study the ability of young human infants to discriminate two patterns that were identical in spatial frequency content and contrast but differed in the phase relationship of the component spatial frequencies. As a group, infants in the 2–3-month age range were able to discriminate the patterns on the basis of the phase information, whereas younger infants failed to demonstrate this ability. A few studies in human infants (Shimojo et al., 1984; Shimojo and Held, 1987; Manny and Klein, 1984) and one study

of macaque monkey infants (Kiorpes and Movshon, 1987, and in press) demonstrate that vernier acuity, as measured by discrimination of a grating stimulus from a grating with a vernier offset (see Figure 10), develops over a time course that is different from that of spatial resolution development. Figure 11 shows the relative rates of development of vernier acuity and grating acuity over the first 11 postnatal months in monkey infants. Grating acuity is relatively better than vernier acuity in newborns; however, vernier acuity develops faster than grating acuity so that in adults vernier performance is considerably better than grating resolution. It is generally believed

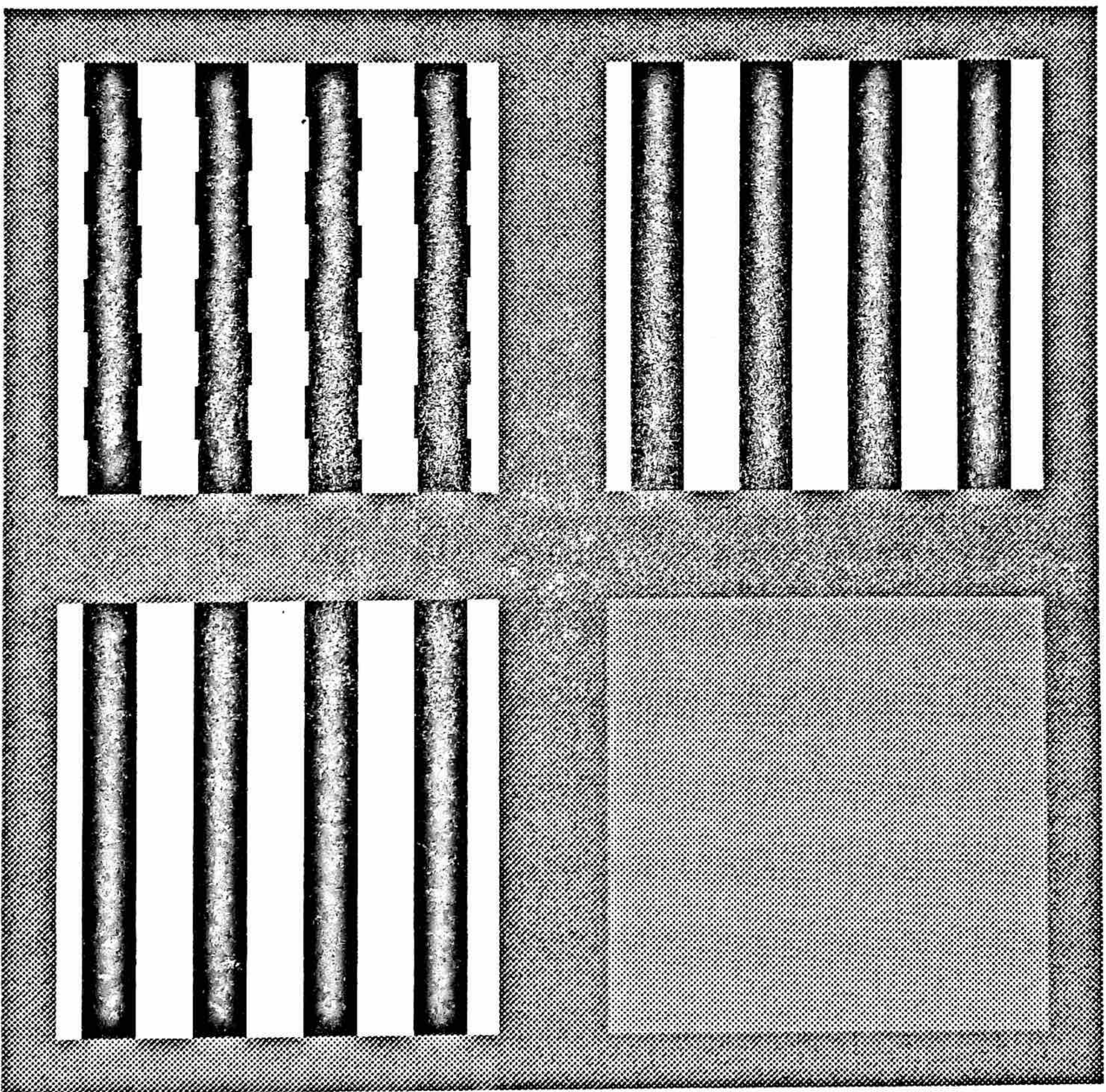


FIGURE 10. The stimulus pairs used by Kiorpes and Movshon (1987) to assess the developmental time courses for vernier acuity (top pair) and grating acuity (bottom pair) in infant monkeys. For grating acuity the grating target (bottom left), which is varied in spatial frequency, is paired with a homogeneous field of equal space average luminance (bottom right). For vernier acuity a grating target of low spatial frequency (top right) is paired with a grating containing offset regions (top left).

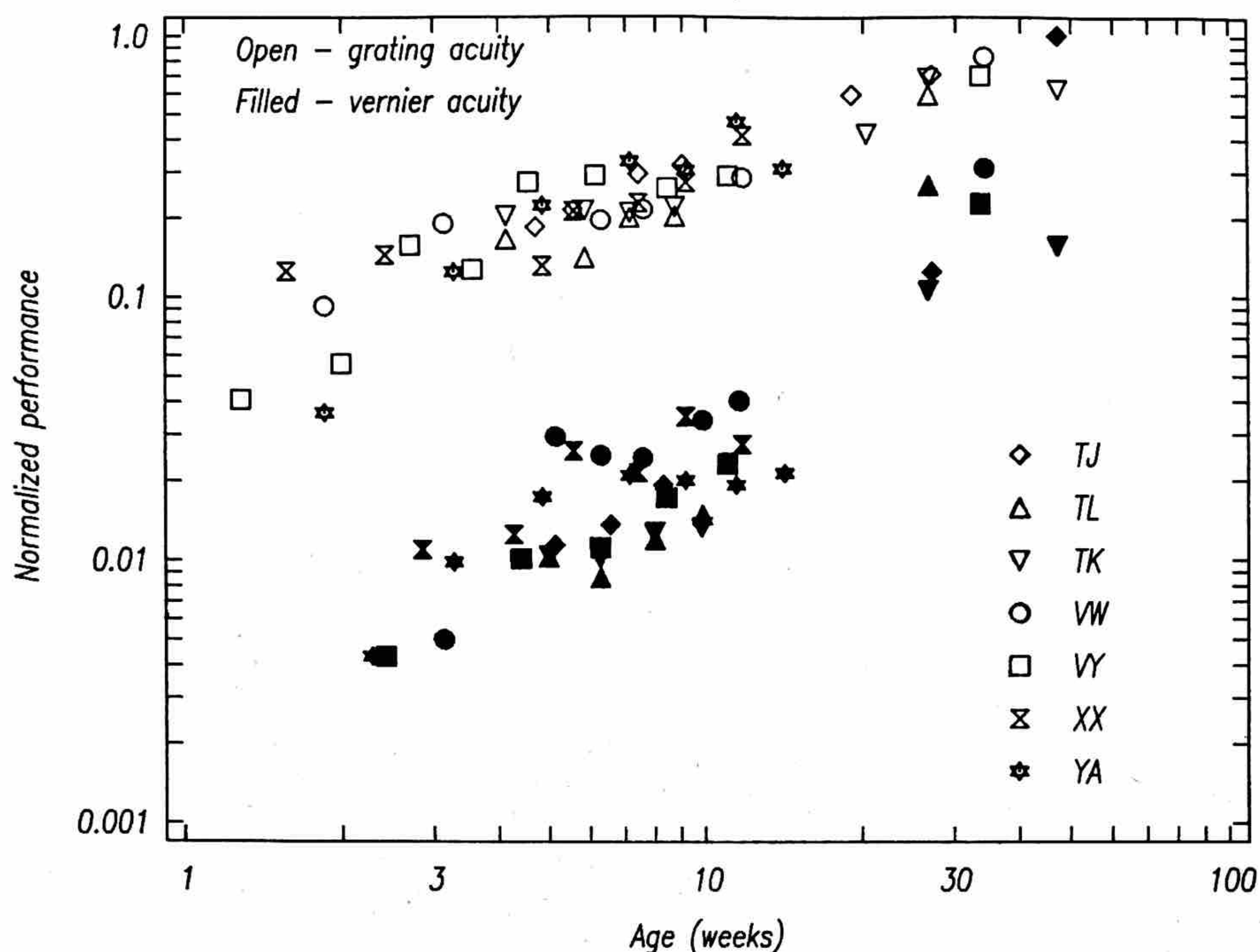


FIGURE 11. Relative rates of development for grating (open symbols) and vernier (filled symbols) acuity in individual infant monkeys. The data are normalized to the best performance obtained from the best animal at the oldest age tested (47 weeks). The values used are 0.14 min arc for vernier and 26.7 cycles per degree for grating acuity. Note that the scale for vernier acuity is the inverse of the usual one, so the normalization may be best considered to be $7.14 \text{ min arc}^{-1}$.

that vernier performance is dependent upon cortical function (Geisler, 1984; Levi et al., 1985; Wilson, 1986). Thus comparison of these two types of acuity may provide a means of relating the development of peripheral and central visual function.

C Temporal Aspects of Vision

The visual system's performance is limited in time as well as in space. One of the classically measured visual functions is the highest frequency at which the flicker of an unpatterned field can be detected, the *critical flicker frequency*. This bears the same relationship to temporal contrast sensitivity that spatial resolution bears to spatial contrast sensitivity; it describes the sensitivity of the visual system to flickering fields at frequencies lower than the resolution limit. The temporal contrast sensitivity function, like its spatial counterpart, is a powerful measure of basic visual performance (see, e.g., Kelly, 1972, for a review). In addition, the adult visual system's sensitivity to spatial patterns is not independent of their temporal characteristics:

the spatial contrast sensitivity function varies in shape and position according to the temporal pattern of presentation (Robson, 1966).

The postnatal development of sensitivity to temporally varying stimuli has been less intensively studied than spatial vision. A number of studies have been conducted to assess the upper limit of temporal resolution, the critical flicker frequency, for young infants. One systematic behavioral study of flicker perception in 1-, 2-, and 3-month-old infants using the FPL technique showed that an adultlike critical flicker frequency of about 50 Hz was present by about 2 months; a further slight improvement was found between 2 and 3 months (Regal, 1981). Similar results were found for longitudinal as well as cross-sectional data.

The development of sensitivity to temporal modulation at rates below the resolution limit, that is, the form of the temporal contrast sensitivity function, is virtually unexplored. However, there is some suggestion that there is further development of temporal contrast sensitivity beyond the age of 3 months. Electrophysiological studies of infant temporal vision (Hartmann et al., 1987) and spatiotemporal interactions (Moskowitz and Sokol, 1980) suggest that 3-month-olds are less sensitive relative to adults at flicker rates below the resolution limit, as measured by the amplitude of the visual-evoked potential. We are not aware of any behavioral measurements of the temporal contrast sensitivity function in infants of any species.

As would be expected from the shape of the spatial contrast sensitivity function, sensitivity to temporal modulation at low spatial frequencies appears to mature before sensitivity at middle and higher spatial frequencies. It is also the case that spatiotemporal interactions of the same character as those seen in adults are also apparent in 3-month-old infants. Atkinson et al. (1977b) showed that spatial contrast sensitivity is enhanced by temporal modulation of the contrast of grating stimuli, but only for relatively low spatial frequencies (cf. Robson, 1966). In adults, this pattern is thought to be due to the independent actions of two sets of visual channels. One set is optimally sensitive to flickering patterns of low spatial frequency, while the other responds best to stationary targets of higher spatial frequency (Graham, 1972). Because infants show a similar pattern of results, it seems reasonable to suppose that they possess both sets of functional channels, at least at the age of 3 months.

D Binocular Vision

Because the two eyes have slightly different views of the world, the two retinal images are slightly disparate when an object is not in the plane of fixation. The adult visual system is exquisitely sensitive to this binocular disparity, which it analyzes to provide the sense of stereoscopic depth, or *stereopsis* (see Kaufman, 1975, for a review). The development of binocular vision has been studied in cats and human infants and has been shown to develop postnatally.

Only in kittens have studies of binocular function unambiguously tested stereopsis. Using the jumping stand technique, Mitchell and his colleagues (1979; Timney, 1981) have shown that kittens have superior performance on a depth discrimination task when tested binocularly relative to performance under monocular test conditions. This superiority of binocular performance develops rather abruptly between 4 to 6 postnatal weeks. By 6 weeks binocular thresholds are about a factor of 5 lower than monocular thresholds.

Binocular function in human infants has been measured by a variety of methods in a number of different laboratories (see Braddick and Atkinson, 1983). However, because none of these studies explicitly measured the discrimination of depth, none can be claimed to have studied stereoscopic vision. It is perfectly possible that an infant could detect the difference between the images in the two eyes and to use this difference to make perceptual judgments without having made any stereoscopic analysis of the pattern of differences. An example is provided by the study of Fox et al. (1980), who investigated the development of binocular function by studying fixational tracking behavior elicited by a disparate target created out of a dynamic random-dot display that lacked monocular cues to depth or form. In most infants, this tracking behavior emerged rather abruptly at an age between 3 and 6 months. Fox and his colleagues argue that their results reflect the development of stereopsis because the infants did not track all disparities equally well. But it seems equally likely that the infants detected the difference between the two retinal images and simply tracked this "zone of difference." There is no reason to imagine that the detectability of such a zone would be independent of disparity.

Another study that employed geometric bar stereograms and a preferential looking method also suggested that stereopsis in human infants develops around the age of 3–6-months (Birch, et al., 1982). Unfortunately, the use of geometric stereograms in this study makes it difficult to rule out some contribution of monocular cues to the results. And again, the study does not demonstrate that stereopsis, rather than the mere analysis of interocular image differences, is responsible. Shimojo et al. (1986) have also presented data that suggest that the nature of binocular vision in infants undergoes a fundamental change at around this same age. Their results appear to show that until the age of 3 months or so, the infant visual system combines the images from the two eyes but does not preserve information about the eye of origin of each feature. Neither stereopsis nor such other binocular process as rivalry can be evident until this "eye-of-origin" information is preserved by the visual system. Their results suggest that beyond about 3 months of age, binocular rivalry is present. Shimojo and his colleagues offer the intriguing speculation that the change in binocular function is related to the segregation of afferents from the two eyes into separate eye dominance columns in the visual cortex (see Chapter 4). This is broadly

in agreement with the expected timing of this process in humans under the now-familiar four-to-one rule relating monkey to human development. It would be interesting to know more about the development of binocularity in monkeys, but we are aware of no studies on this topic.

V SUMMARY AND CONCLUSIONS

In the past two decades, stimulated in part by new testing methods and in part by the renewed interest in the development of the nervous system, there has been a great deal of work on the development of visual performance in animals and humans. As we have seen in this chapter, the course of visual development is very dramatic, especially for most kinds of spatial visual performance. Moreover, most of this development appears to be limited by the development of the visual nervous system itself. Although such factors as the optical quality of the eye and the precision of accommodative and oculomotor control improve during early postnatal life, quantitative examination of these factors reveals that they cannot account for most of the changes in visual performance seen over the same period. There is, of course, a great deal of neural territory between the photoreceptors that register an image and the motoneurons that control the organism's behavioral response, and it is not immediately obvious where the most critical limiting stages lie. From the data that are presently available, however, it seems that in normal development most of the limits to the kinds of performance we have discussed are imposed relatively early in the visual pathway. For simple visual detection and resolution, the limits may be in the retina and are probably before the level of the visual cortex (Blakemore and Vital-Durand, 1986; Friedlander and Tootle, Chapter 2, this volume). Performance on more demanding visual discrimination tasks such as stereopsis or positional resolution may tap more central, cortical mechanisms. Interestingly, as we will see in the next chapter, most of the alterations in visual performance that can be produced by visual experience do not appear to result from changes in development in the peripheral visual nervous system but instead result from functional changes in the cortical structures involved in the higher processing of visual information.

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REFERENCES

- Abramov, I., J. Gordon, A. Hendrickson, L. Hainline, V. Dobson, and E. LaBosiere (1982) The retina of the newborn human infant. *Science* 217:265–267.
- Abramov, I., L. Hainline, J. Turkel, E. Lemerise, H. Smith, J. Gordon, and S. Petry (1984) Rocket-ship psychophysics: Assessing visual functioning in young children. *Invest. Ophthalmol. Vis. Sci.* 25:1307–1315.
- Aslin, R. N. (1981) Development of smooth pursuit in human infants. In D. F. Fisher, R. A. Monty, and J. W. Senders (eds.): *Eye Movements: Cognition and Visual Perception*. Hillsdale, NJ: Erlbaum.
- Aslin, R. N. (1987) Motor aspects of visual development in infancy. In P. Salapatek and L. Cohen (eds.): *Handbook of Infant Perception*, Vol. 1, From Sensation to Perception. Orlando, FL: Academic Press.
- Aslin, R. N., and P. Salapatek (1975) Saccadic localization of visual targets by the very young human infant. *Percept. Psychophys.* 17:293–302.
- Atkinson, J. (1979) Development of optokinetic nystagmus in the human infant and monkey infant: An analogue to development in kittens. *Developmental Neurobiology of Vision: NATO Advanced Study Institute, Series A 27A*:277–287.
- Atkinson, J., and O. Braddick (1976) Stereoscopic discrimination in infants. *Perception* 5:29–38.
- Atkinson, J., O. Braddick, and K. Moar (1977a) Development of contrast sensitivity over the first 3 months of life in the human infant. *Vision Res.* 17:1037–1044.
- Atkinson, J., O. Braddick, and K. Moar (1977b) Contrast sensitivity of the human infant for moving and static patterns. *Vision Res.* 17:1045–1047.
- Banks, M. S. and P. J. Bennett (1988) Optical and photoreceptor immaturities limit the spatial and chromatic vision of human neonates. *J. Opt. Soc. Amer. A.* 5: 2059–2079.
- Banks, M. S., and P. Salapatek (1978) Acuity and contrast sensitivity in 1-, 2-, 3-month-old human infants. *Invest. Ophthalmol. Vis. Sci.* 17:361–365.
- Banks, M. S., and P. Salapatek (1981) Infant pattern vision: A new approach based on the contrast sensitivity function. *J. Exp. Child Psych.* 31:1–45.
- Banks, M. S., B. R. Stephens, and E. E. Hartmann (1985) The development of basic mechanisms of pattern vision. Spatial frequency channels. *J. Exp. Child Psych.* 40:501–527.
- Barlow, H. B. (1972) Dark and light adaptation: Psychophysics. In D. Jameson and L. M. Hurvich (eds.): *Handbook of Sensory Physiology*, Vol. VII/4, Visual Psychophysics. New York: Springer-Verlag.
- Birch, E. E., J. Gwiazda, and R. Held (1982) Stereoacuity development for crossed and uncrossed disparities in human infants. *Vision Res.* 22:507–513.
- Birch, E. E., J. Gwiazda, J. A. Bauer, Jr., J. Naegle, and R. Held (1983) Visual acuity and its meridional variations in children aged 7–60 months. *Vision Res.* 23:1019–1024.
- Blakemore, C., and F. Vital-Durand (1986) Organization and postnatal development of the monkey's lateral geniculate nucleus. *J. Physiol., Lond.* 380:453–491.
- Bonds, A. B., and R. D. Freeman (1978) Development of optical quality in the kitten eye. *Vision Res.* 18:391–398.

- Boothe, R. G., R. A. Williams, L. Kiorpes, and D. Y. Teller (1980) Development of contrast sensitivity in infant *Macaca nemestrina* monkeys. *Science* 208:1290–1292.
- Boothe, R. G., L. Kiorpes, R. A. Williams, and D. Y. Teller (1988) Operant measurements of spatial contrast sensitivity in infant macaque monkeys during normal development. *Vision Res.* 28: 387–396.
- Braddick, O. J. and J. Atkinson (1983) Some recent findings on the development of human binocularity. *Behav. Brain Res.* 10:141–150.
- Braddick, O., J. Atkinson, and J. R. Wattam-Bell (1986) Development of the discrimination of spatial phase in infancy. *Vision Res.* 26:1223–1239.
- Bradley, A., and R. D. Freeman (1982) Contrast sensitivity in children. *Vision Res.* 22:953–959.
- Brown, A. M. (1986) Scotopic sensitivity of the two-month-old human infant. *Vision Res.* 26:707–710.
- Campbell, F. W., and D. G. Green (1965) Optical and retinal factors affecting visual resolution. *J. Physiol., Lond.* 181:576–593.
- Cynader, M., and L. Harris (1980) Eye movement in strabismic cats. *Nature* 286: 64–65.
- Cynader, M., and K. P. Hoffmann (1981) Strabismus disrupts convergence in the cat nucleus of the optic tract. *Dev. Brain Res.* 1:132–136.
- Dannemiller, J. L. (1985) The early phase of dark adaptation in human infants. *Vision Res.* 25:207–212.
- Dannemiller, J. L., and M. S. Banks (1983) The development of light adaptation in human infants. *Vision Res.* 23:599–609.
- Dobson, M. V., and D. Y. Teller (1978) Visual acuity in human infants: A review and comparison of behavioral and electrophysiological studies. *Vision Res.* 18:1469–1483.
- Fantz, R. (1964) Visual experience in infants: Decreased attention to familiar patterns relative to novel ones. *Science* 146:668–670.
- Fantz, R. (1965) Visual perception from birth as shown by pattern selectivity. *Ann. N. Y. Acad. Sci.* 118:793–814.
- Fox, R., R. N. Aslin, S. L. Shea, and S. T. Dumais (1980) Stereopsis in human infants. *Science* 207:323–324.
- Geisler, W. S. (1984) Physical limits of acuity and hyperacuity. *J. Opt. Soc. Am. A.* 1:775–782.
- Giffin, F., and D. E. Mitchell (1978) The rate of recovery of vision after monocular deprivation in kittens. *J. Physiol., Lond.* 274:511–537.
- Graham, N. (1972) Spatial frequency channels in the human visual system: Effects of luminance and pattern drift rate. *Vision Res.* 12:53–68.
- Graham, N. (1980) Spatial-frequency channels in human vision: Detecting edges without edge-detectors. In C. S. Harris (ed.): *Visual Coding and Adaptability*. Hillsdale, NJ: Erlbaum.
- Green, D. G., M. K., Powers, and M. S. Banks (1980) Depth of focus, eye size, and visual acuity. *Vision Res.* 20:827–835.
- Hainline, L., J. Turkel, I. Abramov, E. Lemerise, and C. M. Harris (1984) Characteristics of saccades in human infants. *Vision Res.* 24:1771–1780.

- Hamer, R. D., and M. E. Schneck (1984) Spatial summation in dark-adapted infants. *Vision Res.* 24:77–85.
- Hansen, R. M., and A. B. Fulton (1981) Behavioral measurement of background adaptation in human infants. *Invest. Ophthalmol. Vis. Sci.* 21:625–629.
- Hansen, R. M., A. B. Fulton, and S. J. Harris (1986) Background adaptation in human infants. *Vision Res.* 26:771–779.
- Harris L., J. Atkinson, and O. Braddick (1976) Visual contrast sensitivity of a 6-month-old infant measured by the evoked potential. *Nature* 264:570–571.
- Harris, L. R., F. Lepore, J-P. Guillemot, and M. Cynader (1980) Abolition of optokinetic nystagmus in the cat. *Science* 210:91–92.
- Hartmann, E. E., J. G. May, G. S. Ellis, Jr., and A. Love (1987) Infant temporal vision: A visual evoked potential (VEP) measure. *Invest. Ophthalmol. Vis. Sci.* 28:303.
- Hendrickson, A. E., and C. Kupfer (1976) The histogenesis of the fovea in the macaque monkey. *Invest. Ophthalmol.* 15:746–756.
- Hendrickson, A. E., and C. Yuodelis (1984) The morphological development of the human fovea. *Ophthalmology* 91:603–612.
- Howland, H. C., R. G. Boothe, and L. Kiorpes (1982) Accommodative defocus does not limit development of acuity in infant *Macaca nemestrina* monkeys. *Science* 215:1409–1411.
- Kaufman, L. (1975) *Sight and Mind*. New York: Oxford University Press.
- Kelly, D. H. (1972) Flicker. In D. Jameson and L. M. Hurvich (eds.): *Handbook of Sensory Physiology*, Vol. VII/4, *Visual Psychophysics*. New York: Springer-Verlag.
- Kiorpes L., and J. A. Movshon (1987) Vernier acuity and spatial resolution in infant monkeys. *Invest. Ophthalmol. Vis. Sci.* 28:359.
- Kiorpes, L., and J. A. Movshon (1989) Differential development of two visual functions in primates. *Proc. Natl. Acad. Sci. USA* 86: in press.
- LeVay, S., T. N. Wiesel, and D. H. Hubel (1980) The development of ocular dominance columns in normal and visually deprived monkeys. *J. Comp. Neurol.* 191:1–51.
- Lee, C. P., and R. G. Boothe (1981) Visual acuity development in infant monkeys (*Macaca nemestrina*) having known gestational ages. *Vision Res.* 21:805–809.
- Levi, D. M., S. A. Klein, and A. P. Aitsebaomo (1985) Vernier acuity, crowding and cortical magnification. *Vision Res.* 25:963–977.
- Lewis, T. L., D. Maurer, and K. Blackburn (1985) The development of the young infants' ability to detect stimuli in the nasal visual field. *Vision Res.* 25:943–950.
- Manny, R. E., and S. A. Klein (1984a) The development of vernier acuity in infants. *Curr. Eye Res.* 3:453–462.
- Manny, R. E., and S. A. Klein (1984b) A three alternative tracking paradigm to measure vernier acuity of older infants. *Vision Res.* 25:1245–1252.
- Mayer, D. L., and M. V. Dobson (1982) Visual acuity development in infants and young children, as assessed by operant preferential looking. *Vision Res.* 22:1141–1151.
- Mitchell, D. E., F. Giffin, F. Wilkinson, P. Anderson, and M. L. Smith (1976) Visual resolution in young kittens. *Vision Res.* 16:363–366.

- Mitchell, D. E., M. Kaye, and B. Timney (1979) Assessment of depth perception in cats. *Perception* 8:389-396.
- Mohn, G., R. Sireteanu, and J. van Hof-van Duin (1986) The relation of monocular optokinetic nystagmus to peripheral binocular interactions. *Invest. Ophthalmol. Vis. Sci.* 27:565-573.
- Moskowitz, A., and S. Sokol (1980) Spatial and temporal interaction of pattern-evoked cortical potentials in human infants. *Vision Res.* 20:699-707.
- Movshon, J. A., and L. Kiorpes (1988) Analysis of the development of spatial contrast sensitivity in monkey and human infants. *J. Opt. Soc. Amer. A.* 5: 2166-2172.
- Naegle, J. R., and R. Held (1982) The postnatal development of monocular optokinetic nystagmus in infants. *Vision Res.* 22:341-346.
- Peeples, D. R., and D. Y. Teller (1975) Color vision and brightness discrimination in two-month-old human infants. *Science* 189:1102-1103.
- Peeples, D. R., and D. Y. Teller (1978) White-adapted photopic spectral sensitivity in human infants. *Vision Res.* 18:49-53.
- Powers, M. K., M. E. Schneck, and D. Y. Teller (1981) Spectral sensitivity of human infants at absolute visual threshold. *Vision Res.* 21:1005-1016.
- Pulos, E., D. Y. Teller, and S. L. Buck (1980) Infant color vision: A search for short-wavelength-sensitive mechanisms by means of chromatic adaptation. *Vision Res.* 20:485-493.
- Regal, D. M. (1981) Development of critical flicker frequency in human infants. *Vision Res.* 21:549-555.
- Robson, J. G. (1966) Spatial and temporal contrast sensitivity functions of the visual system. *J. Opt. Soc. Am.* 56:1141-1142.
- Salapatek, P., R. N. Aslin, J. Simonson, and E. Pulos (1980) Infant saccadic eye movements to visible and previously visible targets. *Child Develop.* 51:1090-1094.
- Shimojo, S., and R. Held (1987) Vernier acuity is less than grating acuity in 2- and 3-month-olds. *Vision Res.* 27:77-86.
- Shimojo, S., E. E. Birch, J. Gwiazda, and R. Held (1984) Development of vernier acuity in human infants. *Vision Res.* 24:721-728.
- Shimojo, S., J. Bauer, Jr., K. M. O'Connell, and R. Held (1986) Pre-stereoptic binocular vision in infants. *Vision Res.* 26:501-510.
- Sireteanu, R. (1985) The development of visual acuity in very young kittens. A study with forced-choice preferential looking. *Vision Res.* 25:781-788.
- Sireteanu, R., and D. Maurer (1982) The development of the kitten's visual field. *Vision Res.* 22:1105-1111.
- Sokol, S., and A. Moskowitz (1985) Comparison of pattern VEP's are preferential-looking behavior in 3-month-old infants. *Invest. Ophthalmol. Vis. Sci.* 26: 359-365.
- Teller, D. Y. (1979) The forced-choice preferential looking procedure: A psychophysical technique for use with human infants. *Infant Behav. Devel.* 2:135-153.
- Teller, D. Y., and R. G. Boothe (1979) The development of vision in infant primates. *Trans. Ophthal. Soc. U.K.* 99:333-337.
- Teller, D. Y., and M. H. Bornstein (1987) Infant color vision and color perception. In

- P. Salapatek and L. Cohen (eds.): Handbook of Infant Perception. Vol. 1, From Sensation to Perception. Orlando, FL: Academic Press.
- Teller, D. Y., R. Morse, R. Borton, and D. Regal (1974) Visual acuity for vertical and diagonal gratings in human infants. *Vision Res.* 14:1433–1439.
- Teller, D. Y., D. Regal, T. Videen, and E. Pulos (1978) Development of visual acuity in infant monkeys (*Macaca nemestrina*) during the early postnatal weeks. *Vision Res.* 18:561–566.
- Timney, B. (1981) Development of binocular depth perception in kittens. *Invest. Ophthalmol. Vis. Sci.* 21:493–496.
- van Hof-van Duin, J. (1978) Direction preference of optokinetic responses in monocularly tested normal kittens and light deprived cats. *Arch Ital. Biol.* 116:471–477.
- van Hof-van Duin, J., and G. Mohn (1986) Monocular and binocular optokinetic nystagmus in humans with defective stereopsis. *Invest. Ophthalmol. Vis. Sci.* 27:574–583.
- Williams, R. A., and R. G. Boothe (1981) Development of optical quality in the infant monkey (*Macaca nemestrina*) eye. *Invest. Ophthalmol. Vis. Sci.* 21:728–736.
- Williams, R. A., R. G. Boothe, L. Kiorpes, and D. Y. Teller (1981) Oblique effects in normally reared monkeys (*Macaca nemestrina*): meridional variations in contrast sensitivity measured with operant techniques. *Vision Res.* 21: 1253–1266.
- Wilson, H. (1986) Responses of spatial mechanisms can explain hyperacuity. *Vision Res.* 26:453–469.
- Yuodelis, C., and A. E. Hendrickson (1986) A qualitative and quantitative analysis of the human fovea during development. *Vision Res.* 26:847–855.