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Development of contrast sensitivity in normal and amblyopic monkeys

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INTRODUCTION

The aim of this chapter is to discuss the development of spatial vision in primates and explore the possible underlying neural limitations on visual performance in infants. The basic measure of spatial vision for the purposes of this chapter is the spatial contrast sensitivity function. The development of contrast sensitivity is described, both in the central and peripheral visual field, in non-human primates, and parallels are drawn between development in animals and in humans. To explore the neural basis for behaviourally assessed development, parallels between anatomical and physiological development of the retina and lateral geniculate nucleus (LGN) are discussed, together with measured performance in infant monkeys. Finally, the effects of abnormal visual experience on the development of contrast sensitivity and on development of the visual nervous system are described.

Several conclusions are drawn from the data presented. First, the basic form of contrast sensitivity development is quite consistent across individuals and primate species. Second, development follows an essentially normal sequence in animals whose visual experience is abnormal, such as results from strabismus and anisometropia; the primary effect of the abnormal visual experience is to slow development. Finally, behavioural development seems to reflect anatomical and physiological changes in the retina and LGN under normal conditions. However, in amblyopes, performance seems to reflect compromised development at the level of the striate cortex.

NORMAL DEVELOPMENT OF CONTRAST SENSITIVITY

The spatial contrast sensitivity function describes the performance of the visual system in terms of the range of resolvable spatial frequencies and the minimum detectable contrast for patterns within that range. The contrast sensitivity function therefore provides information about the spatial scale and overall sensitivity of the visual system under study. There has been much interest in describing the development of contrast sensitivity. It is well known that spatial resolution in newborn primates is a factor of 30–50 times poorer than in adults

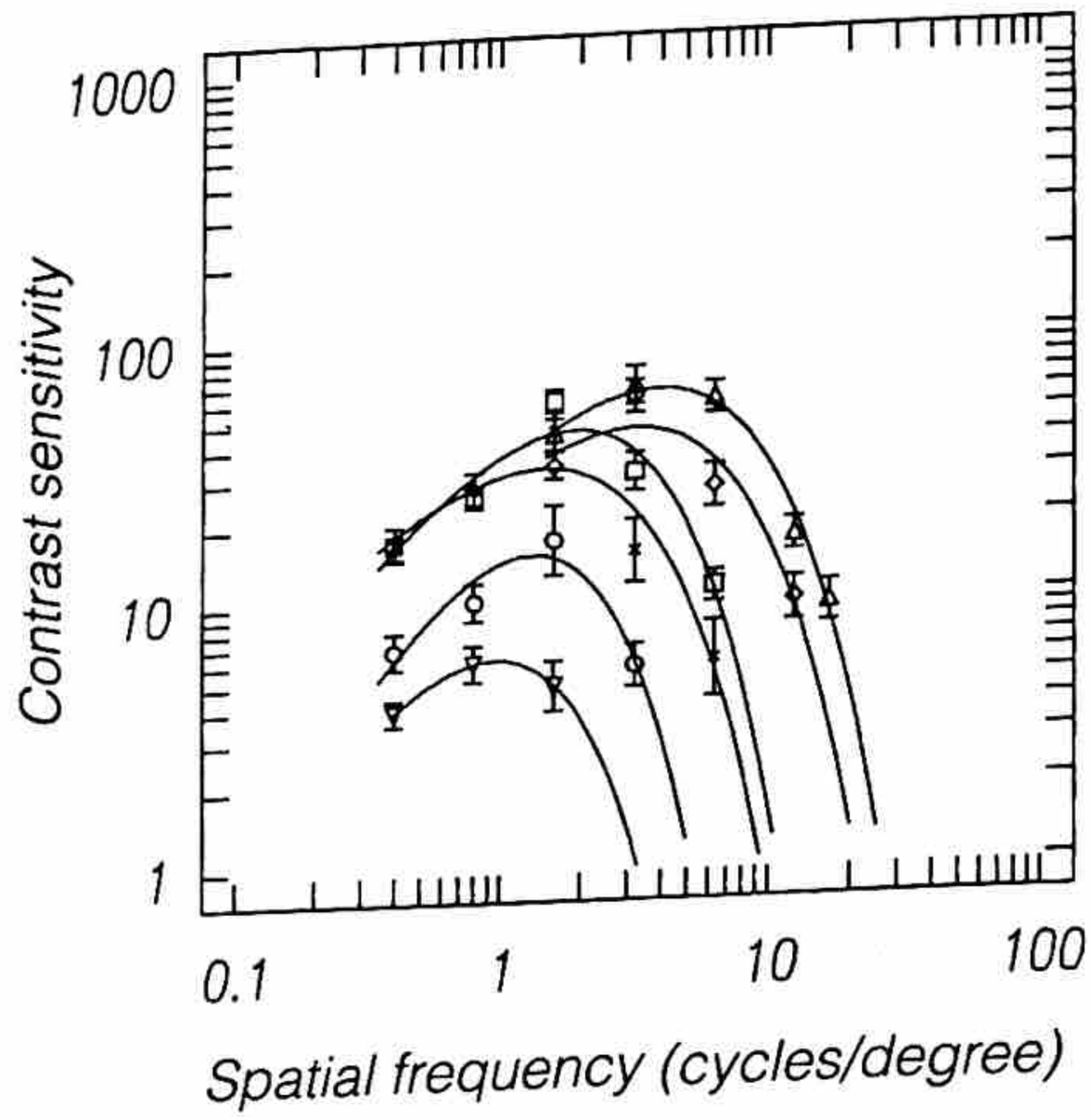

Fig. 1.1 The development of contrast sensitivity in an infant monkey. Different functions show contrast sensitivity at different ages: ▽ = 10 weeks, ○ = 11 weeks, × = 14 weeks, ❑ = 15 weeks, ◊ = 26 weeks, △ = 38 weeks (data from Boothe *et al.* 1988).

and approaches adult levels with a characteristic time course (Boothe *et al.* 1985). Sensitivity to contrast is also immature in newborns, approximately a factor of 10 poorer than in adults. Changes in the form of the contrast sensitivity function during development provide a window into the anatomical and physiological processes that limit performance in infants.

A series of contrast sensitivity functions measured in an individual infant monkey at several ages during development (Boothe *et al.* 1988) is shown in Fig. 1.1. The youngest data set was collected at the age of 10 weeks (inverted triangles, lower left function); the oldest data set was collected at 38 weeks (triangles, upper right function). Between the youngest and oldest test ages, the function shifted systematically to both higher spatial frequencies and higher contrast sensitivity. These changes can be characterized as changes in *spatial scale* and *sensitivity*. Spatial scale is the horizontal position of the curve that captures the spatial frequency range of the system; sensitivity is the vertical position of the curve which captures the range of contrasts to which the system is sensitive. As the function shifts with age toward higher spatial frequency and sensitivity it is shifting from coarse to fine spatial scale and from low to high sensitivity to contrast.

Some models of contrast sensitivity development suggest that different spatial frequency components develop at different rates (Wilson 1988). If this were the case, the function would change shape over the course of development. An analysis by Movshon and Kiorpes (1988) confirmed the observation, apparent from inspection of the functions in Fig. 1.1, that the contrast sensitivity function does not change shape during development. Therefore, it is not

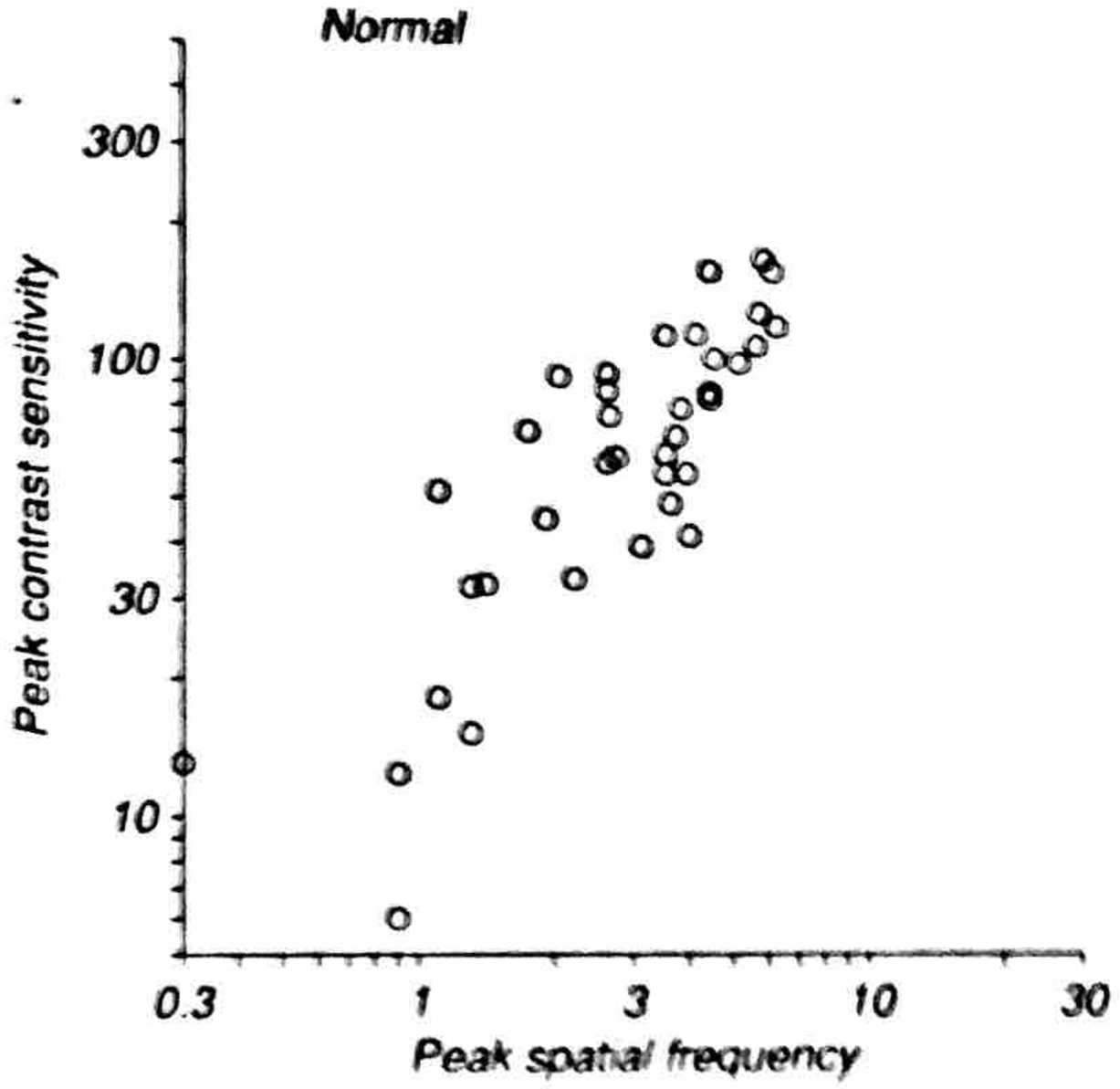

Fig. 1.2 The relationship between peak spatial frequency and peak contrast sensitivity for 13 infant monkeys ranging in age from 5–57 weeks. Data derived from the analysis presented in Movshon and Kiorpes (1988).

likely to be the case that the underlying frequency components of the function develop independently. Given that the function does not change shape but instead shifts rigidly horizontally and vertically, the developmental relationship between shifts in spatial scale and sensitivity can be determined. This relationship is illustrated in Fig. 1.2, where peak contrast sensitivity is plotted as a function of peak spatial frequency; the data are derived from contrast sensitivity functions of monkeys ranging in age from 5–57 weeks (Movshon and Kiorpes 1988). Fig. 1.2 shows that the changes in spatial scale and sensitivity occur simultaneously.

The pattern of development found for the monkeys, a concurrent shift to finer spatial scale and higher contrast sensitivity, is also apparent in contrast sensitivity data from human infants, when measured using behavioural techniques (Banks and Dannemiller 1987). It is worth noting, though, that contrast sensitivity development charted using electrophysiological techniques (sweep VEP measurement) shows an early predominant increase in sensitivity followed by a later increase in spatial scale (Norcia *et al.* 1990).

The primary difference between spatial vision development in monkeys and humans is that macaque monkeys develop about four times faster than humans (Teller and Boothe 1979). Direct comparison of the time courses for the development of spatial resolution in monkeys and humans reveals that the functions roughly compare if human age is plotted in months and monkey age is plotted in weeks. In both cases, newborn resolution is near 1 cycle/degree and adult resolution is between 30 and 50 cycles/degree. The many similarities in visual function between monkeys and humans support the study of the macaque monkey as a model system for humans. More direct questions can

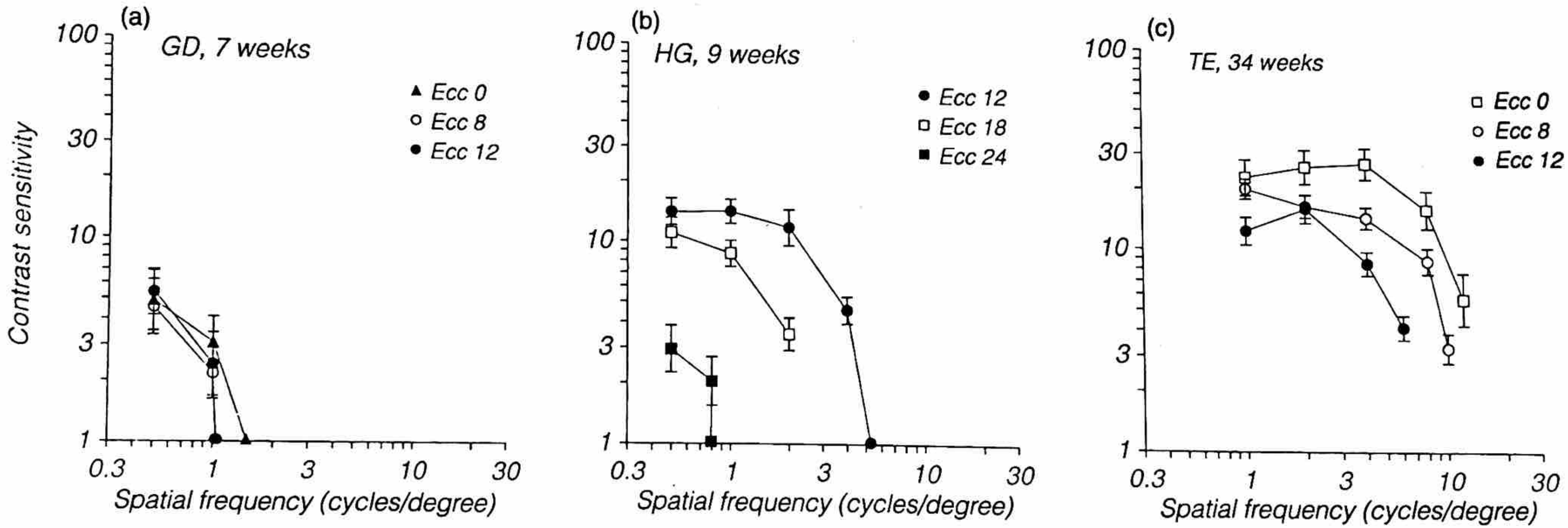

Fig. 1.3 Contrast sensitivity in the peripheral visual field is shown for three monkeys at 3 ages: (a) contrast sensitivity at 0, 8, and 12° eccentric for a 7-week-old; (b) contrast sensitivity at 12, 18, and 24° eccentric for a 9-week-old; (c) contrast sensitivity at 0, 8, and 12° eccentric for a 34-week-old.

then be asked, in the monkey, about the limitations placed on visual performance by the developing visual system.

To understand the limitations on vision in infants it is important to establish what locus (or loci) in the visual system is setting important limits on the measured performance. In adults the fovea is the area of highest sensitivity. Thus contrast sensitivity measurements typically reflect the capability of the central visual field. It is natural to assume that contrast sensitivity data collected from infants also reflect the function of the central visual field. However, recent data from humans and macaque monkeys show that the infant primate fovea is under-developed (Abramov *et al.* 1982; Yuodelis and Hendrickson 1986; Hendrickson and Kupfer 1976; Packer *et al.* 1990). The density of cones in the central retina is low in newborns and increases dramatically during the early post-natal months. Yuodelis and Hendrickson (1986) also reported morphological immaturities in the foveal cones that are likely to reduce the efficiency of light capture (Banks and Bennett 1988; Brown *et al.* 1987). It was suspected, based on these data, that the contrast sensitivity of the central visual field in young monkeys might not be superior to that of the near periphery.

The development of contrast sensitivity across the visual field was then investigated in monkeys to confirm the suspicion that, initially, central field sensitivity is similar to that of the near periphery (Kiorpes and Kiper 1995). In Fig. 1.3(a) contrast sensitivity data from a young infant monkey are shown. The sensitivity under free-viewing conditions (eccentricity of 0) was similar to that measured at locations in the peripheral visual field (eccentricities of 8 and 12°). At more peripheral locations, there was a progressive decrease in contrast sensitivity with increasing eccentricity. This result is illustrated in Fig. 1.3(b) where data from a second slightly older infant monkey are shown. Over the next 4–6 post-natal months, there was differential development of contrast sensitivity as a function of location in the visual field. In Fig. 1.3(c) contrast sensitivity data from an 8-month-old monkey are shown for eccentricities between 0 and 12°. There was a shift to lower sensitivity and reduced spatial scale with increasing eccentricity for this older animal; this pattern is consistent with that found in fully mature animals and adult humans tested under the same conditions.

It is clear that the post-natal development of contrast sensitivity reflects predominantly the development of the central visual field. An analysis of the pattern of development across the visual field showed that the central field undergoes substantially greater improvement in spatial scale and sensitivity than is seen at more peripheral locations. However, the same developmental pattern shown in Fig. 1.1 was also apparent at peripheral locations. At each location within at least the central 12°, there was a concurrent improvement in both spatial scale and sensitivity with increasing age. At 24° eccentricity there was little change in either spatial scale or sensitivity over the age ranges tested. The improvements in foveal sensitivity and spatial scale were greater and continued over a longer period of time than at more peripheral locations; moreover, the extent of post-natal development declined with increasing eccentricity.

The pattern found for contrast sensitivity development across the visual field is consistent with that expected based on concurrent changes in cone density already mentioned. In accord with the anatomical immaturity of the fovea in newborns, contrast sensitivity is similar for the central visual field and near periphery. Superiority of foveal contrast sensitivity becomes significant between about 12 and 24 weeks, which is the time during which foveal cone density increases dramatically in monkeys (Packer *et al.* 1990). Given that visual performance in the monkey develops about four times faster than in the human, one might expect to find superiority of foveal contrast sensitivity in the second post-natal year in humans.

The apparent concordance between retinal development and the pattern of behavioural changes in contrast sensitivity suggests that the retina may be providing a crucial limit on visual function in infants. Banks and Bennett (1988) modelled quantitatively the extent to which the immaturities in photoreceptor density and cone morphology could account for measured post-natal changes in contrast sensitivity in human infants. They concluded that, while these factors may contribute to the relatively poor acuity and contrast sensitivity of the infant, a significant proportion of the developmental changes cannot be accounted for at the level of the photoreceptors. A similar conclusion was reached by Brown (1990). Therefore, it is likely that neural factors central to the photoreceptors impose a second important limitation on visual behaviour.

The earliest post-receptoral level at which the development of neural processing has been studied is the lateral geniculate nucleus. Blakemore and Vital-Durand (1986*a*) studied the development of spatial resolving power and overall responsiveness in macaque monkey LGN neurones. They reported three features of LGN development that are of interest for the analysis of behavioural development. First, there is an overall increase in responsiveness and spatial resolution during the first post-natal year that is reminiscent of the improvement in contrast sensitivity and spatial scale seen behaviourally. Second, the progressive improvement in spatial resolving power is similar in time course and extent to that measured behaviourally in macaques (Jacobs and Blakemore 1988; Kiorpes 1992*a*; Movshon and Kiorpes 1993). The time course for development of grating acuity measured behaviourally is shown in Fig. 1.4 (open circles; from Kiorpes 1992*a*) along with spatial resolution for the LGN cell with the highest resolution at each age (filled triangles; from Blakemore and Vital-Durand 1986*a*). The performance of the best LGN cells is slightly better than the monkey behaviour at each age and parallels the behavioural data well. It is important to note that, particularly at the youngest ages, neither behaviour nor geniculate physiological measures achieve the resolution permitted by the photoreceptor mosaic (Movshon and Kiorpes 1993).

Finally, Blakemore and Vital-Durand (1986*a*) reported differential development of resolution depending on receptive field position. Neurones with receptive field positions within the central 10° showed a considerably greater post-natal increase in spatial resolution than those at more peripheral locations. This result is consistent with behavioural data described above on the

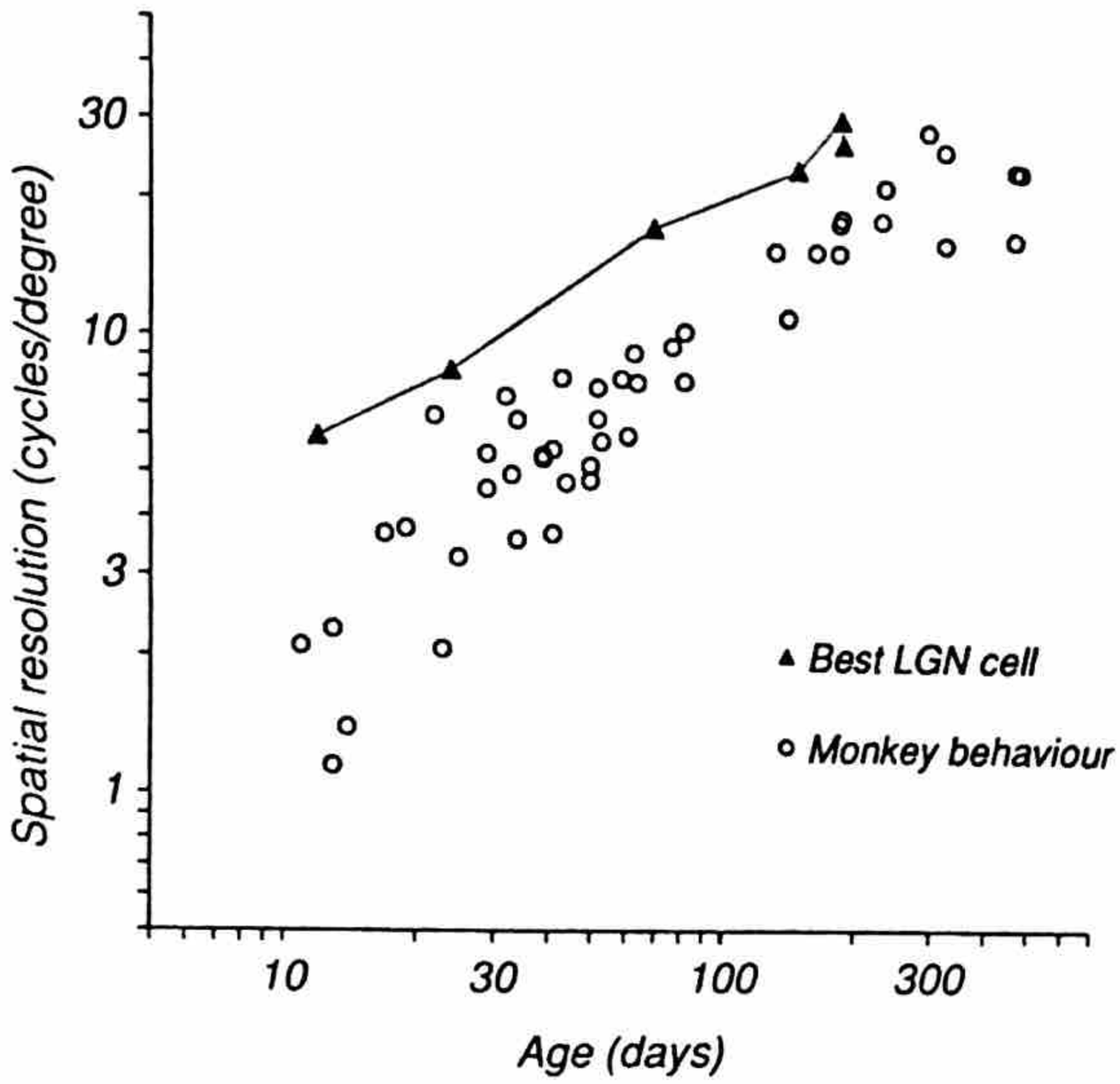

Fig. 1.4 The development of spatial resolution in monkeys as measured behaviourally is compared with the development of spatial resolving power of neurones in the LGN. The behavioural data (circles) are from Kiorpes (1992*a*). The physiological data (triangles) represent the highest resolution shown by an LGN neurone at each age; the data are from Blakemore and Vital-Durand (1986*a*).

development of contrast sensitivity across the visual field. Taken together, the remarkable consistency between the development of spatial contrast sensitivity and the development of receptive field properties of LGN neurones suggests that neural processing between the photoreceptors and the LGN may provide a crucial limit for visual development.

Additional data on the development of LGN cell contrast sensitivity lend further weight to the suggestion that a critical limitation on the development of visual performance is set at or before this level of the system. Blakemore and Hawken (1985; and unpublished observations) measured contrast sensitivity over a range of spatial frequencies for individual LGN neurones. Composite contrast sensitivity 'functions' for newborn, 2-month-old, and 8-month-old macaque LGN show the same bandpass character that behavioural functions show. Importantly, the shift in the composite contrast sensitivity functions with age is consistent with the pattern measured behaviourally. That is, the composite neural functions show a simultaneous shift to both higher contrast sensitivity and spatial frequency as do the behavioural functions for individual monkeys (see Figure 1.1).

The preceding discussion documented the post-natal changes in macaque monkey spatial vision that are consistent with what is known about spatial vision development in humans. These changes seem to unfold according to a prescribed maturational plan, since there is considerable consistency across individual monkeys, across locations in the visual field, and across primate

species. Comparisons of quantitative behavioural and physiological data from the macaque reveal remarkable similarities in the pattern of development reflected at the level of the LGN and that measured behaviourally, suggesting that maturation of neural processing at or before the LGN may be underlying behavioural contrast sensitivity in infants. While under normal conditions the development of spatial vision appears to proceed according to a prescribed maturational plan, it is clear that this plan can be disrupted.

DEVELOPMENT OF CONTRAST SENSITIVITY IN AMBLYOPIA

Numerous visual disorders in infancy and early childhood are associated with a condition called amblyopia. Amblyopia is generally defined as a deficit in visual function that cannot be corrected optically and appears in the absence of obvious ocular pathology. Conditions such as cataracts, strabismus (misalignment of the visual axes), and anisometropia (unequal refractive errors for the two eyes) are associated with the development of amblyopia when they occur during the early childhood years; the same conditions are not associated with amblyopia when they occur in adults. Thus abnormal visual imput during an early *sensitive period*, when the visual system is susceptible to influence by the visual environment, leads to relatively permanent deficits in visual performance (Harwerth *et al.* 1986; Movshon and Kiorpes 1990; Kiorpes 1992*b*).

While amblyopia is typically measured as a deficit in acuity, the character of the amblyopic deficit can be specified by examination of the contrast sensitivity function. Human amblyopes typically show deficits in contrast sensitivity throughout the middle-to-high spatial frequency range (Hess *et al.* 1980). Monkeys raised with visual conditions that simulate those associated with amblyopia in humans also show deficits in contrast sensitivity (Harwerth *et al.* 1983; Smith *et al.* 1985; Kiorpes 1989; Kiorpes *et al.* 1993). Contrast sensitivity functions for each eye of four amblyopic monkeys are shown in Fig. 1.5; two monkeys were raised with esotropic strabismus (Fig. 1.5(a,b)) and two were raised with anisometropia induced by an extended-wear contact lens (Fig. 1.5(c,d)). Two of the amblyopic animals show modest deficits with the amblyopic eye (filled circles; Fig. 1.5(a,c)); while two show severe deficits (Fig. 1.5(b,d)). In all cases, the animals show the same pattern of contrast sensitivity loss in the amblyopic eye as typically shown by human amblyopes; the largest deficits are in the mid-to-high spatial frequency range.

Given that amblyopia is a disorder of visual development, it is important to understand how it arises. Our studies have followed the development of spatial resolution and contrast sensitivity, as well as other visual functions such as vernier acuity, in monkeys raised with either esotropic strabismus oranisometropia. The development of vision in these amblyopic animals appears to be slowed compared with development in normal animals (Kiorpes *et al.* 1989;

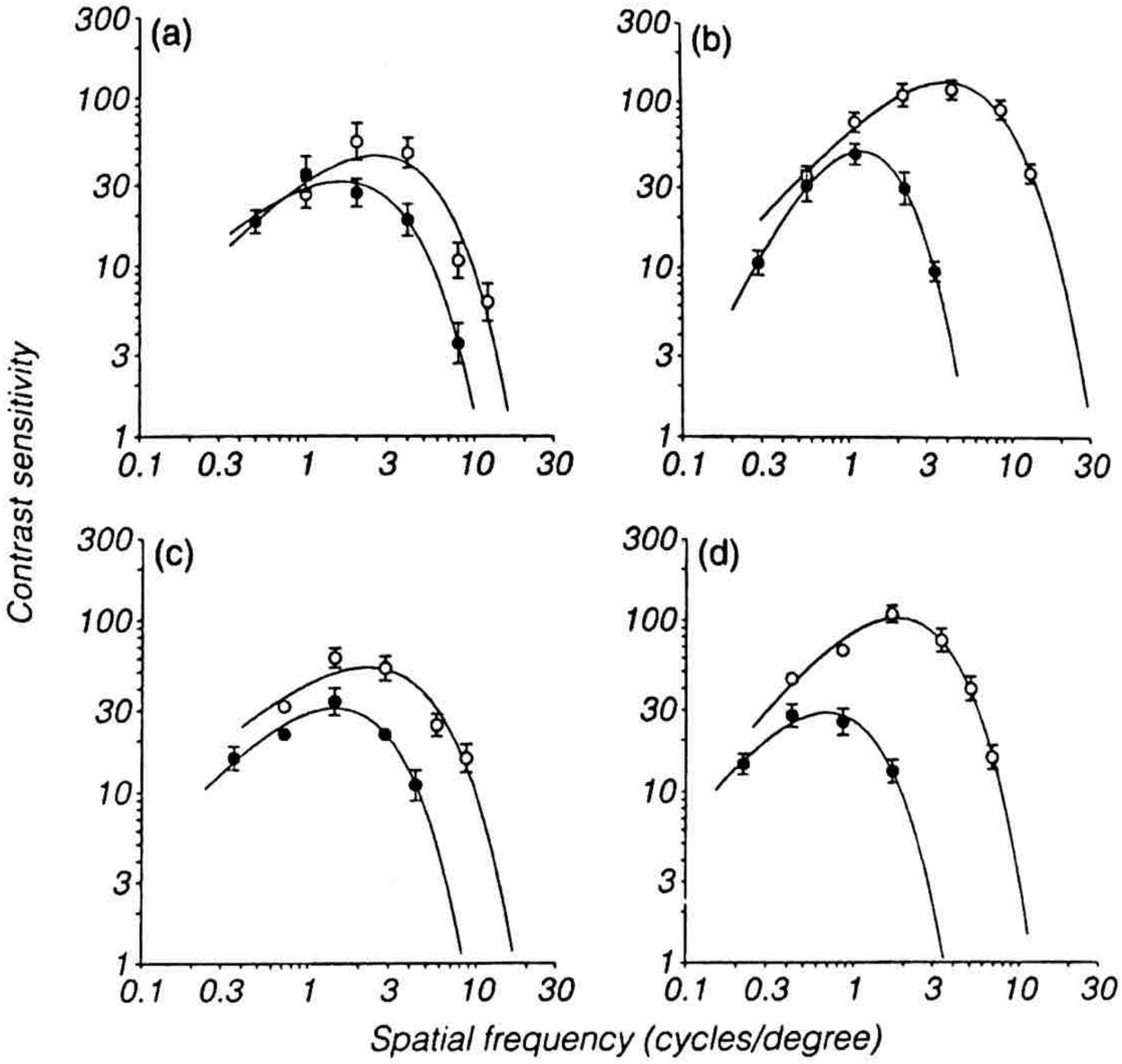

Fig. 1.5 Contrast sensitivity functions are shown for each eye of four monkeys with experimentally produced amblyopia. Filled and open symbols represent data from the amblyopic and fellow eyes, respectively. Panels (a) and (b) show data from two strabismic amblyopes; panels (c) and (d) show data from two lens-reared anisometropic amblyopes (induced with a –10 dioptre extended-wear contact lens). See Kiorpes *et al.* (1993) for details.

Kiorpes 1989; Kiorpes 1992*b*). In Fig. 1.6 the development of grating acuity for normally-raised monkeys (open circles) and amblyopic eyes of monkeys raised with esotropic strabismus (filled circles) is shown. The amblyopic eyes lag behind normal eyes during development. Kiorpes (1992*b*) found this pattern of development for vernier acuity in amblyopes as well as for grating acuity.

This slowed progress of visual development is also apparent in the contrast sensitivity data. As shown in Fig. 1.5, the contrast sensitivity functions for the amblyopic eyes are shifted to lower spatial frequencies and contrast sensitivities compared with the non-amblyopic eyes. This pattern is consistent with that of younger normal animals. Recall that the progress of contrast sensitivity development in normal animals, already described, is one of progressive shifting up toward both higher sensitivity and spatial scale so that functions from younger animals show both lower contrast sensitivity and a lower range of spatial frequencies than older animals. It is important to note that the amblyopic contrast sensitivity function does not differ in shape from non-amblyopic

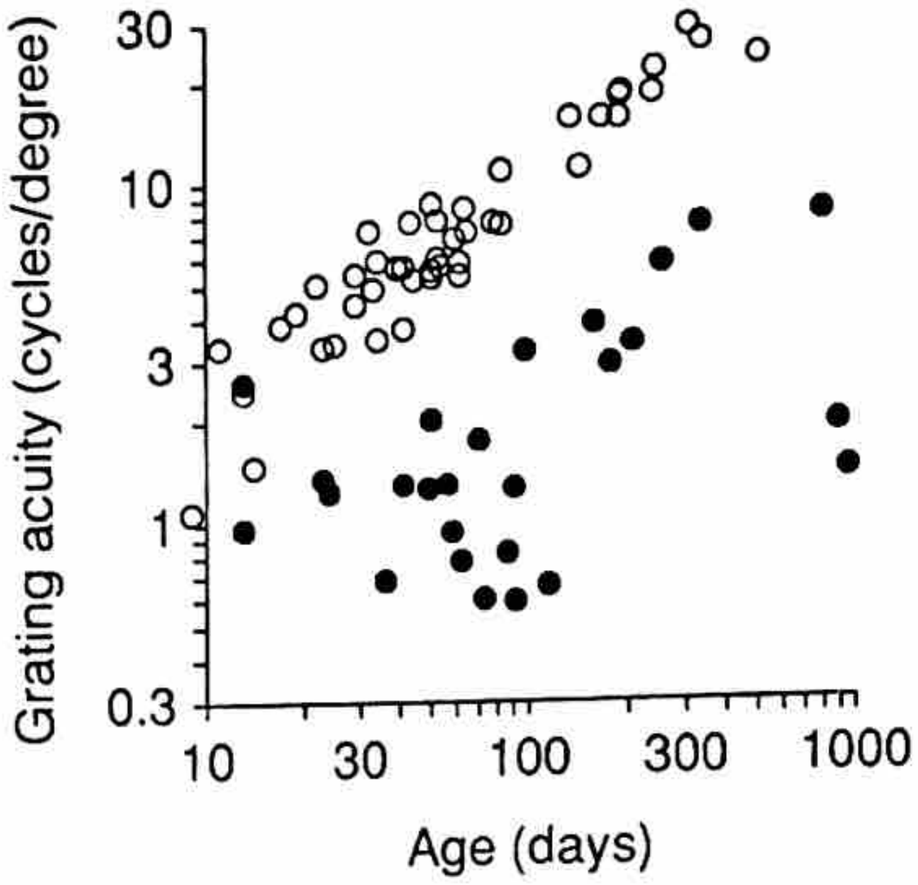

Fig. 1.6 The developmental time course for amblyopic eyes is compared with that for normal monkeys. The open circles represent development for normal eyes; the filled symbols represent development for the amblyopic eyes of strabismic amblyopes. Data from Kiorpes (1992*b*).

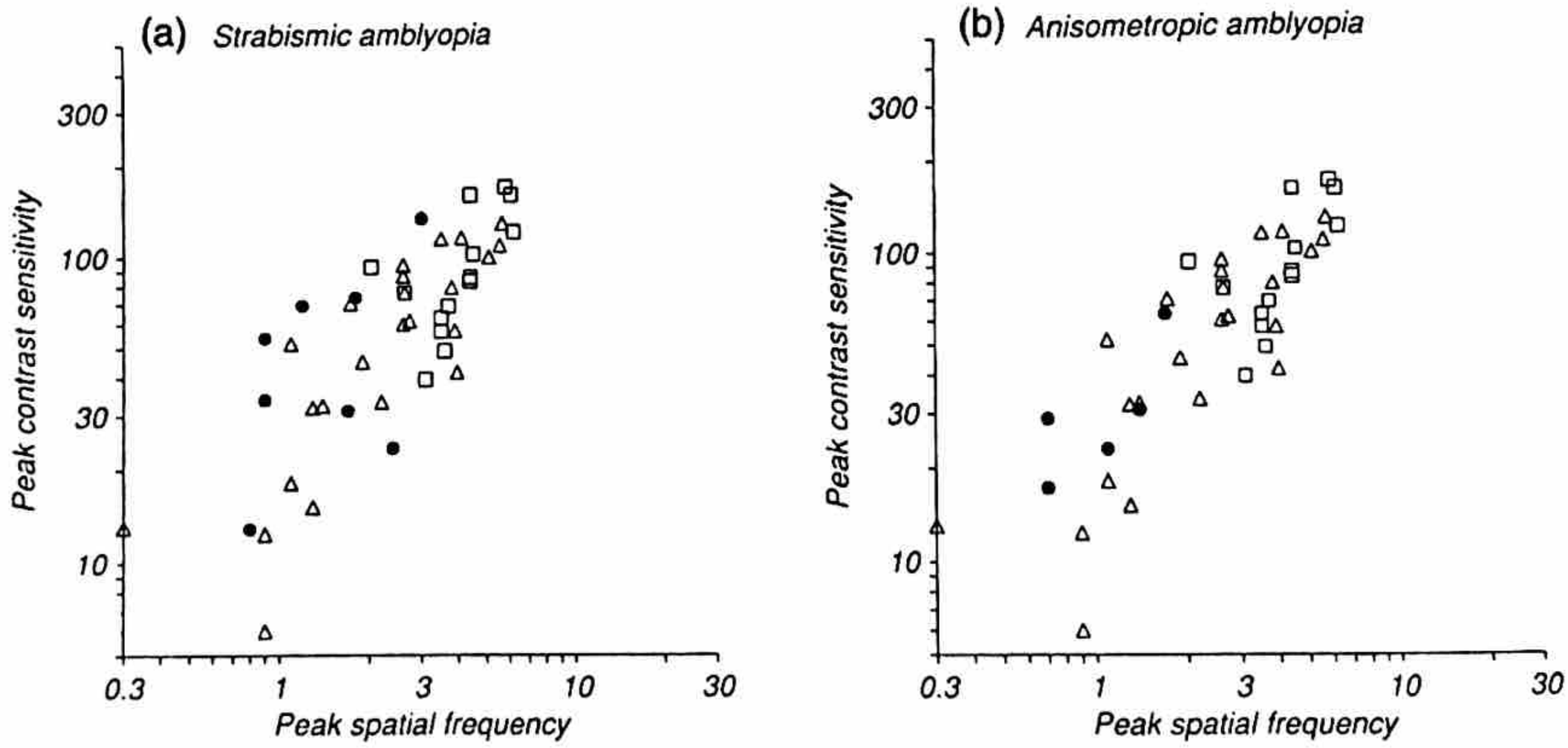

Fig. 1.7 The relationship between peak spatial frequency and peak contrast sensitivity is shown for amblyopic eyes. The filled circles in (a) and (b) show data from strabismic and anisometropic amblyopes, respectively. The open symbols reproduce subsets of the normal data in Fig. 1.2: triangles show the relationship for monkeys younger than 20 weeks; squares show the relationship for monkeys older than 26 weeks. The relationship for the amblyopic eyes is similar to that of the young normal animals.

functions (Kiorpes 1989; Kiorpes and Movshon 1989). Consistent with this result, the relationship between overall contrast sensitivity and spatial scale for amblyopic eyes is similar to that of normal contrast sensitivity development. This point is illustrated in Fig. 1.7 where the relationship between peak contrast sensitivity and peak spatial frequency is shown for strabismic amblyopic (Fig. 1.7(a)) and anisometropic amblyopic (Fig. 1.7(b)) eyes. The relationship for normal animals (see Fig. 1.2) is reproduced in Fig. 1.7 but here data from animals

younger than 20 weeks are shown as open triangles and data from more mature animals are shown as open squares. It is clear that the amblyopic eyes (represented with filled circles in each panel) perform similarly to young normal animals rather than visually mature animals.

As the studies described above show, under normal visual conditions development proceeds according to a particular maturational plan. However, when visual imput is abnormal during the early sensitive period, the maturational plan is disrupted. In amblyopia, the disruption appears to be a slowing of development. Slowed development will have the effect of leaving the visual system in an immature state at the end of the sensitive period. Therefore, the performance of amblyopes is like that of young normals. It is worth noting that this process describes well the development of amblyopia as results from strabismus and anisometropia. However, given more severe forms of deprivation, for example, lid suture, the developmental process can be halted or even reversed. In such cases, the performance of the visual system can be compromised to levels poorer than would be expected in a newborn (Harwerth *et al.* 1983; Blakemore 1990; Movshon and Kiorpes 1993).

While there is good evidence for placing the critical limitations on visual development in normal individuals at or before the level of the LGN, there is no evidence to suggest that the same limitations apply in the case of amblyopes. Monkeys raised with monocular deprivation show extremely severe deficits in visual performance (Harwerth *et al.* 1983); however, spatial resolution of LGN cells in monocularly deprived monkeys is normal (Blakemore and Vital-Durand 1986*b*; Levitt *et al.* 1989). Similarly, there is no evident abnormality of retinal anatomy in amblyopic animals (Hendrickson *et al.* 1987). The effects of abnormal visual experience must therefore appear more centrally in the visual pathways than the LGN. Indeed, several studies have reported deficits in spatial resolution and/or contrast sensitivity of striate cortical neurones from amblyopic monkeys (Movshon *et al.* 1987; Eggers *et al.* 1984).

To conclude, it appears that, in normal development, limitations set early in the visual pathways are relayed faithfully through the striate cortex and subsequent processing regions. However, when visual experience is abnormal, the striate cortex appears to develop abnormally and loses information available at the LGN. Additional studies comparing behavioural, physiological, and anatomical development in monkeys will be needed to determine precisely how it is that experience exerts its effects on visual processing.

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