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SPATIAL SUMMATION IN DARK-ADAPTED HUMAN INFANTS

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Abstract—Behavioral measures of spatial summation in 4- and 11-week old human infants were obtained using the forced-choice preferential looking technique. Infants exhibit complete spatial summation over large areas (4 weeks: 8.9°; 11 weeks: 5.5°), much larger than those of adults tested in the same apparatus (2.6°). Thus, infants' summation areas are larger than adults' by factors of 12 at 4 weeks and 4 at 11 weeks. It is argued that at most, one-half of this difference between the infant and adult data may be due to optical factors (e.g. defocus and small eye size). The remainder probably reflects differences in the neural organization of the immature and mature visual systems.

Spatial summation Infant vision Visual development Infants' rod vision

INTRODUCTION

Spatial summation, the ability to integrate stimulus energy over an extended sensory surface, is a fundamental property of sensory systems. In vision, the region over which a complete area-intensity trade-off occurs is called a summation area. Formally, this tradeoff, known as Ricco's law, is written as $I \cdot A = k$: a stimulus is maintained at constant detectability by keeping the product of intensity and area (i.e. the total energy per unit time contained in the stimulus) constant. In adult humans, visual summation areas are, at most, 1 to 2 deg in diameter; these occur in the peripheral retina under scotopic conditions (Weinstein and Arnulf, 1946).

In adults, behaviorally measured spatial summation areas correlate well with other behavioral measures of spatial processing (such as spatial contrast sensitivity functions, Westheimer sensitization functions) as well as with some physiological measures of spatial processing in adult primates, such as receptive field profiles (Westheimer, 1972; Ransom-Hogg and Spillman, 1980; Oehler *et al.*, 1982). It is therefore of great interest to investigate spatial summation in the developing human visual system.

In this article we report behavioral measurements of spatial summation in human infants under dark-adapted conditions. The data reveal striking differences between infant and adult spatial summation areas.

METHODS

Procedure

The procedure used was virtually identical to the modification of Teller's forced-choice preferential looking (FPL) technique (Teller *et al.*, 1974; Teller, 1979) used by Powers *et al.* (1981) to measure scotopic spectral sensitivity in 1- and 3-month old infants.

The infant was held in front of a large translucent screen upon which the stimulus was projected from the rear. On each trial the stimulus was presented either to the left or to the right of the center of the infant's field of view by an adult experimenter. Side of presentation (left or right) and intensity of the stimulus were designated by a pre-determined pseudo-random sequence. On each trial an adult observer, who was uninformed as to the position and intensity of the stimulus, viewed the infant's face via an infrared-sensitive television monitor system and judged the position of the stimulus by watching the infant's eye and head movements. The observer received feedback after each trial.

Apparatus, stimulus and calibrations

The apparatus has been described previously (Powers *et al.*, 1981). The stimulus consisted of 502 nm light produced by passing light from a 45 W tungsten-halogen source through an interference filter (half-bandwidth = 10 nm). The stimulus was then reflected by a pair of mirrors onto the rear of a large translucent screen, appearing as a homogeneous disc of light from the front of the screen.

Stimulus intensity was varied using a combination of Oriel and Wratten No. 96 neutral density filters. The four spot sizes, when viewed from the plane of the subject's eyes (43 ± 2 cm in front of the screen), subtended 0.65, 2.65, 10.7 and 17.1 deg of visual angle, respectively. The center of the stimulus was positioned 25 deg to the left or right of the center of the screen (i.e. the center of the stimuli were 20 cm to the right or left of the center of the screen). The actual attenuation (for 502 nm narrow-band light) of each neutral density filters used in this study was measured *in situ* using a calibrated silicon photodiode (United Detector Technology, PIN 10 DFP).

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Infants

All infants began testing either between their 22nd and 33rd postnatal day (4-week olds), or between their 68th and 80th postnatal day (11-week olds).

Testing took 7–10 sessions for the 4-week olds and 4–8 sessions for the 11-week olds, spread over a period of no more than two weeks. Each session took 1–1½ hr. All but one of the infants had been born within ±10 days of their due dates according to report of the parents. Frederik (open circle with slash in Fig. 2) was born 13 days after his due date. Six 4-week olds and five 11-week olds completed the study. Thirteen infants began, but did not complete the study due either to fussiness (six of the 4-week olds and six of the 11-week olds), or due to the parents decision to withdraw from the study (one 4-week old).

Each experimental session began with a minimum of 15 min of dark-adaptation, during which time the only illumination in the room was a 60 W tungsten source covered by a red filter (−0.7 log cd/m²). After the dark-adaptation period was complete, the red light was turned off and testing proceeded in total darkness.

Breaks were taken whenever necessary to accommodate the infant's various needs, during which time the red light was turned on. Each infant was tested using a sequence of spot sizes ordered in a latin square design so as to counterbalance any order effects that might result from going from small to large spots or vice versa. Four or five stimulus intensities were used for each spot size. The intensities were separated by about 0.5 log unit (l.u.). Testing at one spot size continued until either one hour had elapsed or the infant was no longer in a testable state (too sleepy or too fussy). The stimulus sequence for that spot size was continued in the next session (the following week day); this process continued until a minimum of 20 trials at each of the test intensities was completed. Then testing at a new spot size began. Thus, three or four psychometric functions were generated (one for each spot size) for each infant.

For comparison with the infants' data, and to verify that classical spatial summation data were obtainable under the conditions to which the infants were exposed, three adults were tested.

Adult testing

A two-alternative forced-choice paradigm (with stimuli presented according to the method of constant stimuli) was used to test the adults under three viewing conditions. In the first viewing condition (25 deg eccentricity) the subject fixated a dim red LED located in the center of the screen, and the stimuli were presented randomly either 25 deg to the left or 25 deg to the right of this fixation light. In the second condition (42 deg eccentricity), the fixation light was moved 25 cm upward from the center of the screen. In the final condition (free-viewing), the fixation light was turned off and the subject was instructed to scan the screen freely, utilizing any available cues in order to detect the stimulus. As in the infant testing, the adults viewed the screen binocularly.

Within each viewing condition each subject was tested on 5 spot sizes (the same 4 that were presented to the infants, plus one whose diameter subtended 0.16 deg of visual angle). Three to seven intensities, spaced approximately 0.2 l.u. apart, were tested for each spot size. In order to reproduce the infants' testing conditions as closely as possible, most intensities were presented on 20 trials. However, occasionally 30 or 40 trials were presented, and, on "easy stimuli" (stimuli which the subject reported were easy to localize, and which, indeed, he or she never erred in detecting) as few as 5 or 10 trials were presented.

Each subject took two to three 1 hr sessions to complete one viewing condition. Within each session, spot sizes were presented in blocks of 10 trials each, with the order of presentation of spot size being determined by a sequence (latin square design) similar to that used for the infant testing.

Defocus

One additional control experiment was performed on one of the adults (R.D.H.) using a method of adjustment. (Pilot work had shown adult method of adjustment data to be nearly identical to the data obtained using a forced-choice procedure.) Using the 25 deg eccentricity condition (stimuli presented only on the right side of the screen), the subject viewed the stimuli under 3 conditions of optical defocus: the subject viewed the stimuli through −8 diopter (D) spherical lenses, through −4D spherical lenses, or

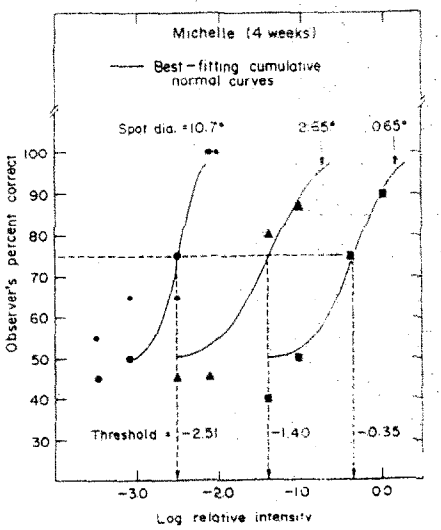

Fig. 1. Psychometric functions for one 4-week old infant (Michelle) tested on 4 spot sizes (0.65′, 2.65′, 10.7′ and 17.1′ dia.). The smooth curves are best-fitting cumulative normal curves fit to each data set using probit analysis (Finney, 1971). Threshold is defined as the intensity corresponding to 75%-correct on the normal curve (median of the probit-fit). For clarity, Michelle's 17.1′ data are represented as small solid circles, and the associated normal curve was omitted. The threshold for this data set was −2.43 l.u.

without lenses (no defocus).* For each defocus condition, five adjustment thresholds were obtained at each of the 5 spot sizes.

Data analysis

A cumulative normal curve was fit to each psychometric function using probit analysis (Finney, 1971). Threshold for each function was defined as the intensity corresponding to the median (75% correct) on the cumulative normal curve.†

A repeated measures, unweighted-means analysis of variance was performed on the threshold data (sections 7.3, 7.8 in Winer, 1971). Two of the six 4-week old infants failed to complete testing at all four spot sizes. Therefore, the analysis of variance was carried out in two ways—(A) analyzing the data with the two missing data cells filled in ("plugged") with conservatively chosen values, and (B) analyzing data only from those subjects having completed all four spot sizes. The values used to "plug" the missing data cells in the 4-week olds' data were the grand means of *all* infant thresholds (including the 11-week olds' thresholds) at that spot size. At a spot diameter of 10.7°, the "plugged" value was −2.939 l.u.; at 17.1°-dia., the "plugged" value was −2.945 l.u. (mean of 10 thresholds in each case).

The statistical significance (or lack of significance) of the main effects and interactions (age × spot size) was the same whether analysis (A) or analysis (B) was performed. Therefore, all F ratios and probability values reported herein are from analysis (A), i.e. with all subjects included and the missing cells "plugged".

RESULTS

Fig. 1 displays some sample psychometric functions for one 4-week old infant (Michelle) who was tested on four different spot sizes. All four data sets are shown. However, for clarity only three of the four corresponding best-fitting cumulative normal curves (solid curves) are shown. Note that as the spot diameter increased from 0.65° to 10.7°, Michelle's threshold decreased from −0.35 to −2.51 l.u.

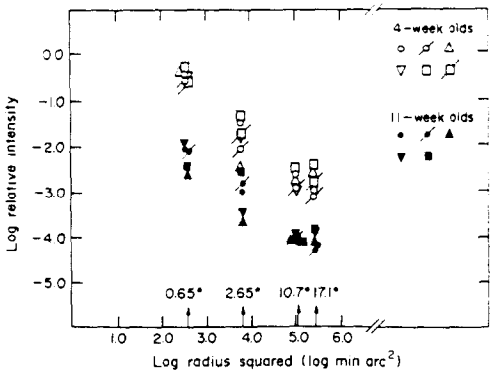

Fig. 2. Thresholds (log relative intensity) as a function of log spot radius squared (proportional to log area), for all infants tested. Different symbols represent data obtained from individual infants. Open symbols: 4-week olds; solid symbols: 11-week olds. For clarity, the 11-week olds' data have been shifted down 1 log unit.

Threshold values for all infants are shown in Fig. 2. The open symbols represent the data obtained from the 4-week olds. The solid symbols represent the 11-week olds' data. For clarity the 11-week olds' data have been arbitrarily shifted down on the ordinate by 1.0 log unit. The largest range of thresholds observed for any spot size at either age is 1.1 l.u., consistent with previous measures of scotopic thresholds in young infants (Powers *et al.*, 1981; Hamer *et al.*, 1983). For both age groups, there is a systematic decrease in the thresholds of individual infants as stimulus area increases.

The group means are shown in Fig. 3, along with comparable mean data obtained from three adult

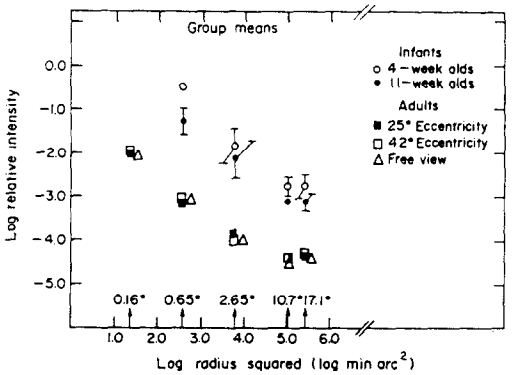

Fig. 3. Group mean data for the 4-week olds (open circles), 11-week olds (solid circles) and a group (3) of adults tested on each of 3 viewing conditions—25° eccentricity (solid squares), 42° eccentricity (open squares) and a free view (open triangles) condition. None of the data have been shifted in this figure. Standard deviation bars less than or equal to the size of a data point are not shown.

*A retinoscopic refraction of R.D.H.'s right eye was performed on-axis and 25° off-axis (from the temporal visual field). At each of these axes, a refraction was measured for each of these defocus conditions. The refractions were: *on-axis:* plano −0.25 × 90° (no defocus), −4.00 − 1.00 × 90° (+4D), −8.00 − 0.50 × 90° (+8D); *25° off-axis:* −0.25 − 1.25 × 90° (no defocus), −5.00 − 2.50 × 90° (+4D), −10.00 − 4.50 × 90° (+8D). Note that off-axis refraction shows that both plus sphere and plus cylinder are induced. Thus, optical defocus was always greater than or equal to that indicated by the nominal values of the plus lenses used.

†In two cases, the probit program did not converge to a maximum likelihood estimate of a best-fitting cumulative normal curve within 10 iterations. In these cases, the median of a weighted least squares fit to the data was used to define threshold. In one additional case, the program converged but produced a curve judged by the authors to be a very poor fit to the data. The threshold according to the probit analysis was almost 3 SD different from the mean of the other infants' thresholds. Thus, for this data set, threshold was defined as the intensity corresponding to the intersection of a horizontal line at 75% correct with the line passing through the two lowest data points (at 77 and 100% correct). This threshold is plotted as a solid square in Fig. 2 at 2.58 log min arc² on the abscissa.

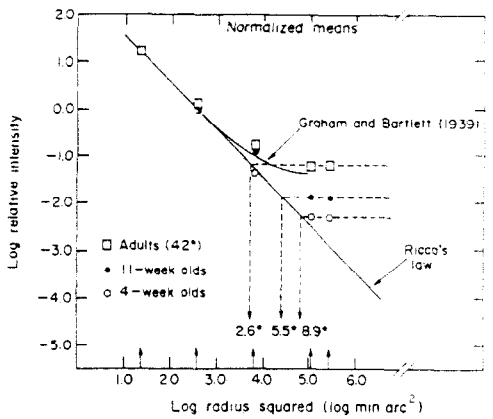

Fig. 4. Normalized group mean data. Infants' data are represented by open (4-week olds) and solid (11-week olds) circles. Data from adults test at 42° eccentricity are represented by open squares. The infants' data have been shifted to match Ricco's law (solid line with slope = −1) at the smallest spot size at which they were tested (2.58 log min arc², or 0.65° dia.). The adults' data were shifted to match Ricco's law at 1.39 log min arc² (0.16° dia.). The smooth curve represents the classical spatial summation data of Graham and Bartlett (1939; see text and footnote [*] on this page). The diameter of the spatial summation area is estimated for each group by determining the abscissa value of a point on the Ricco's-law line intersected by a horizontal line that best fits the two right-most data points in each case. These estimated summation areas have diameters of 2.6°, 5.5° and 8.9° for the adults, 11- and 4-week olds, respectively.

subjects tested under each of the 3 viewing conditions. The adult spatial summation curves did not alter significantly as stimulus eccentricity was increased from 25 to 42 deg. A free-viewing condition also had no effect on the shape of the curve.

None of the data have been shifted in Fig. 3 so that absolute differences in sensitivity among the three groups are preserved in this figure. For example, at 17.1° (5.42 log min arc²) the 4-week olds and 11-week olds are, on the average, 1.6 and 1.2 log units less sensitive than the adults respectively. These values are close to previously measured absolute differences between infant and adult thresholds (Powers *et al.*, 1981; Hansen and Fulton, 1981).

The data in Fig. 3 suggest an orderly decrease in thresholds with increasing age—at each spot size, the younger infants (open circles) are the least sensitive, the adults are the most sensitive, and the 11-week olds' data are intermediate. The 11-week olds' thresholds are, in fact, significantly lower than the 4-week olds' thresholds [$F(1,9) = 17.20$; $P < 0.005$]. The difference between the 4-week olds' and 11-week olds' thresholds tends to diminish as stimulus area increases (cf. Fig. 4); however, this trend (age × size interaction) is not statistically significant [$F(3,25) = 2.29$; $0.10 < P < 0.25$].

The adults are significantly more sensitive than the infants [$F(2,11) = 192.59$; $P < 0.001$]. Furthermore, the difference between the infant and adult data diminishes as the spot area increases. For example, the difference between the mean adult threshold (at 42° eccentricity) and the mean 4-week old threshold at 0.65 deg spot diameter (2.58 log min arc²) is 2.57 l.u.; at 17.1 deg (5.42 log min arc²), this difference is 1.57 l.u. Comparable differences between the 11-week olds' and adults' thresholds at these same 2 spot sizes are 1.80 l.u. and 1.22 l.u., respectively. Thus, the shape of the adults' and infants' spatial summation curves differ significantly [$F(6,31) = 5.22$, $P < 0.005$].

This difference is more clearly visualized if the data are all normalized to match Ricco's law at the smallest spot size tested in each age group. Such a normalization is shown in Fig. 4. The average infant data (4 weeks: open circles; 11 weeks: solid circles) have been normalized to match each other and Ricco's law (solid line with slope = −1) at 2.58 log min arc² (0.65 deg spot dia.). The average adult data (open squares, 42 deg eccentricity) have been shifted to match Ricco's law at 1.39 log min arc² (0.16 deg spot dia.). In addition, the classical spatial summation data of Graham and Bartlett (1939)* are represented by the solid curve, which has been shifted to match Ricco's law at spots < 2.58 log min arc² (< 0.65 deg spot dia.). This figure illustrates three main points. First, in spite of the different methods and stimulus conditions used in the two studies (cf. footnote [*] on this page), the present adult data correspond closely to Graham and Bartlett's (1939) classical spatial summation data. Second, the infant's data obey Ricco's law (i.e. adhere closely to the line with slope = −1) out to larger spot sizes than do the adults' data. Third, the older infants' data are more adult-like than the younger infants' data. A more quantitative estimate of Ricco's area (summation area) for each of the three groups of data is also illustrated in Fig. 4. For each of the three sets of data, a line with slope = 0 was plotted half way between the two data points at 5.02 log min arc² (10.7 deg dia.) and 5.42 log min arc² (17.1 deg dia.). Empirically, in each case, these two points fell very close to a horizontal line (the slopes of the lines drawn between them were 0.12, 0.0, and 0.0 for the adults, 11-week olds, and 4-week olds, respectively). The abscissa values at which these horizontal lines intersect the Ricco's-law line give the estimates of the summation areas. The diameters of these estimated summation areas are 2.6 deg for the adults, 5.5 deg for the 11-week olds, and 8.9 deg for the 4-week olds.

Young infants could be substantially out of focus

*The smooth curve representing Graham and Bartlett's classical spatial summation data was fit by eye to the average of the two subjects' data, each tested at two wavelengths ("red" and "violet"), as reported in Graham and Bartlett's Table 2. In accordance with the suggestion of the authors (p. 579) the "violet" data were made to coincide with the "red" data by adding 3.4 l.u. to subject M's "violet" data, and 3.2 l.u. to subject G's "violet" data. Graham and Bartlett tested at 22 different stimulus sizes ranging from radii of 1.127 log min arc² (0.12 deg dia.) to 4.956 log min arc² (10.02 deg dia.). Stimulus duration was 12.8 msec. Stimuli were presented 15 deg in the nasal visual field of the left eye

with respect to the stimulus plane. Therefore, in order to determine whether or not the infants' large summation areas could be an artifact of defocus, one additional experiment was performed on one adult (R.D.H.). Large magnitudes of defocus were introduced by having R.D.H. view the stimulus through either −4D or −8D lenses. The question was whether or not an adult's summation data could be made to look like the infants' data. The results of this experiment are shown in Fig. 5.

As in Fig. 4, the data were normalized to match each other and Ricco's law at 1.39 log min arc^2. Summation areas for each of the defocus conditions were estimated in the same way as in Fig. 4. It is apparent that under conditions of peripheral viewing, this subject's spatial summation curve was relatively insensitive to large magnitudes of blur—the estimated summation area increased from ~2.1′ dia. (no lenses) to 2.7′ and 2.9′ in the +4D and +8D conditions, respectively.

DISCUSSION

It is clear from the data presented in Fig. 4, and from the estimated summation areas derived from those data, that under the present testing conditions the immature visual system exhibits complete spatial summation over much larger stimulus areas than does the adult visual system. The ratio of the average 11-week old estimated summation area to the average adult estimated summation area is 4.4. For the 4-week olds this ratio is 11.9.

There are two general explanations for the difference between the adult and infant spatial summation data—optical and non-optical (neural) factors.

Optical factors

(1) The effect of optical blur. Although estimates of adult spatial summation areas in foveal vision seem to be quite sensitive to relatively small amounts of defocus of the retinal image (<2D of defocus can cause a 19-fold increase in estimated summation area; Ogle, 1961), −4 and −8D defocus caused relatively small changes in the estimated summation area for one adult subject (R.D.H.) viewing the stimulus 25° in the periphery. His estimated summation area increased from about 2.1′ dia. to 2.7′ dia. when −4D blurring lenses was used, and to 2.9′ dia. with −8D lenses. These represent increases in area by factors of 1.6 and 1.9, respectively. Thus, if the infants were, on average, 4–8 D out of focus relative to the plane of the stimulus screen, and if their scotopic acuity were as fine as adults', this might account for *at most* factor of 2 difference between the adult and infant spatial summation data. Without any salient stimuli to attend to other than the target spots, it is reasonable to assume that if an infant were not accommodating to the stimulus he or she would revert to the dark-focus. Recent measurements of dark-focus in infants 3–12 months of age (using the method of isotropic photorefraction described in Atkinson *et al.*, 1982) range between 50 and 100 cm (Aslin and Dobson, personal communication). Thus, it seems unlikely that the older infants tested in the present study would be more than 1D out of focus relative to the plane of the stimulus screen (situated at 2.4D). The effect of accommodative defocus is therefore likely to be negligible for the 11-week olds; and unless the 4-week olds have a dark-focus substantially different from the older infants, accommodative defocus should be an unimportant factor for them also.

(2) Effect of eye size. Part of the difference between infant and adult behaviorally measured summation areas must be due to the difference in size of the optical components of the infant and adult eye. Therefore, it may be more fruitful to compare infant and adult summation areas in terms of *retinal area* rather than in terms of the angular subtense of the stimuli. Young infants' eyes (<6 months of age) are smaller than adults' by a factor of ~1.4 (Larsen, 1971d; Blomdahl, 1979; Harayama *et al.*, 1981; Hirano *et al.*, 1979; Abe, 1979). From the available A-scan ultrasound data on the dimensions and properties of the optical elements of the infant eye, Enoch and Hamer (1983) have proposed a new schematic eye for infants. Using this schematic eye, we have computed estimates of the diameter of the retinal image corresponding to a spot subtending 1° of visual angle.* For the adult eye (using values from the Gullstrand schematic eye, Gullstrand, 1924) the value is 0.291 mm per degree of visual angle. For the young infant (1–3 months of age) the computed value is likely to fall between 0.180 and 0.210 (depending on the assumed position of the lens of the eye*). Thus, for a given stimulus, the area of the retinal image is approximately 1.9–2.6 times smaller in the average young infant's eye than in the average adult's eye. The average of these two numbers is 2.25; this number represents our current best estimate of the ratio of adult retinal image size to the young infants' retinal image size. Thus, in terms of *retinal*

*In order to estimate the size of the retinal image corresponding to 1° of visual angle, a chief ray trace was performed on a schematic infant eye (Enoch and Hamer, 1983). The cornea and lens of the eye were assumed to be thin lenses. A single reasonable value for the corneal power, −45.5D, was used (Enoch, personal communication) for both age groups. The position of the pupil (2.42 mm and 2.52 mm behind the corneal apex for the 4- and 11-week olds, respectively) and the axial length of the eye (16.85 and 17.30 mm for the 4- and 11-week olds, respectively) for each age group were estimated by linear interpolation from Larsen's (1971a, b,c,d) data. Once these values are chosen, the retinal image size depends only on the position of the lens of the eye. The appropriate position for this thin lens is not known; so it was varied parametrically within the confines of the measured boundaries (Larsen, 1971b) of the lens in infants. Before 6 months of age, Larsen's (1971b) data indicate that the lens is about 4 mm thick. The indices of refraction used were 1.0 for air and 1.336 for all the intraocular media (Gullstrand, 1924). Lotmar's (1976) schematic eye for newborns was not used primarily because he assumes a corneal curvature that is too steep (Enoch, 1979).

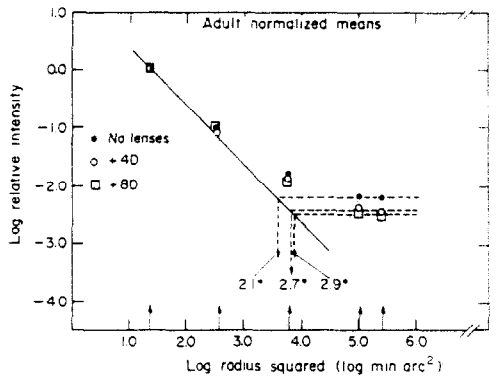

Fig. 5. *Defocus control experiment.* Normalized means (matching Ricco's law at 1.39 log min arc², or 0.16° dia.) for one adult (R.D.H.) viewing the stimuli at 25° eccentricity under 3 conditions of optical focus—with +8D optometric trial lenses in front of the eyes (open squares), with +4D lenses (open circles) or without lenses (solid circles). R.D.H. has normal vision without any optical correction. Spatial summation areas (estimated as in Fig. 4) changed relatively little with these large magnitudes of defocus (from diameters of 2.1° without lenses, to 2.7° and 2.9° in the +4 and +8D conditions, respectively).

area, the estimated spatial summation areas are 1.9 times (for the 11-week olds) to 5.2 times (for the 4-week olds) larger than the average adult estimated summation area. Therefore, part but not all of the difference between the adult and infant spatial summation data can be ascribed to the difference in eye size between the two groups.

Non-optical factors

Since the difference between infant and adult spatial summation areas cannot be entirely accounted for in terms of the differences between the optics of infant and adult eyes, the present data suggest that the neural organization of the infants' visual system differs from adults' and that this organization is changing measureably over the first few months of life. More specifically, the infants' larger summation areas are indicative of quite coarse spatial processing, even coarser than the adult peripheral visual system (Weinstein and Arnulf, 1946; Ransom-Hogg and Spillmann, 1980). This is consistent with the one previous scotopic measure of spatial processing in human infants (Fiorentini *et al.*, 1980). These authors found, using VEP to measure spatial contrast sensitivity in infants that their contrast sensitivity was less than adults' and that their scotopic acuity (estimated by extrapolating the high-frequency limb of the contrast sensitivity function to 100% contrast) was about a factor of 3 poorer than adults. Photopic measures of spatial processing in infants also show that, both in terms of acuity (Allen, 1979; Dobson and Teller, 1978; Mayer and Dobson, 1982) and contrast sensitivity (Atkinson, Braddick and Moar, 1977; Banks and Salapatek, 1976, 1978), human infants have quite coarse spatial processing that improves systematically with age over the first few years of life. Analogous development of photopic acuity and contrast sensitivity has been found to occur in monkeys (Teller *et al.*, 1978; Boothe *et al.*, 1980). It is reasonable to suppose that these behavioral manifestations of coarse spatial processing, as well as any developmental changes in these behaviors, reflect (more or less directly) the properties of receptive fields in the developing visual system. There are electrophysiological data consistent with this supposition. Recordings from the retina, lateral geniculate nucleus (LGN) and striate cortex in kittens indicate that receptive fields are much larger in the immature visual system than in the adult visual system, and that they decrease in size with age (see Norton, 1981 for a review). In infant primates, although receptive fields appear to have adult-like dimensions in the periphery, foveal receptive fields measured in LGN and striate cortex are relatively large at birth and decrease in size with age (Blakemore and Vital-Durand, 1979, 1981). However, it should be kept in mind that the visual system in non-human primates may be further developed at birth than the visual system in newborn humans (Abramov *et al.*, 1982; Hendrickson and Kupfer, 1976; Mann, 1964). In particular, the newborn Macaque's retina appears to be less homogeneous than the newborn human's retina—the fovea is more mature in the Macaque at birth, with more adult-like cones than are observed in a neonatal human retina (Abramov *et al.*, 1982; Hendrickson and Kupfer, 1976; Mann, 1964). In addition, we know that there is good agreement between psychophysical measures of receptive-field-like properties in adult humans and monkeys (sometimes referred to as perceptive fields, e.g. Ransom-Hogg and Spillman, 1980; Oehler *et al.*, 1982; also cf. Westheimer, 1972) and physiological measures of receptive fields in the visual system of adult monkeys (Hubel and Wiesel, 1960; Demonasterio and Gouras, 1975; for explicit comparison of the physiology and psychophysics see Ransom-Hogg and Spillmann, 1980 and Oehler *et al.*, 1982). Thus, the present data suggest that receptive fields are larger in the infant visual system than in the adult visual system, and that they decrease in size with age.

Another non-optical factor that must be mentioned is the possible effect of probability summation. If an organism can detect a stimulus via any of n independent mechanisms, the probability, P, that it will detect a given stimulus is related to the probability, p, of detecting the stimulus via any single summation area alone by the following expression (Peyrou and Piatier, 1946)

$$P = 1 - \prod_{i=1}^{n}(1 - p_i),\ 0 \leq p_i \leq 1.$$

It is easy to show that recruiting new summation areas (by increasing spot size, for example) will increase the organism's chances of detecting the stimulus much more if the slope of the organism's psychometric function (as measured via a *single* summation area) is shallow

than if it is steep. Due to probability summation, an increase in stimulus area will increase the detectability of the stimulus (above "threshold"). To maintain constant detectability the stimulus intensity must be decreased; and the amount by which it must be decreased is greater for a shallow psychometric function than for a steep psychometric function. Thus, *probability summation* across many small but independent (spatial) summation areas could conceivably mimic *spatial summation* within a single, large summation area if the organism has a shallow enough psychometric function. Unfortunately, in order to assess the effect of probability summation we need certain information that is not yet available, especially for the developing visual system. For example, it is necessary to make some assumptions about the spatial configuration of and overlap among summation areas, about the degree of correlation of neural activity among summation areas, and about the magnitude of and spatial dependence of the slope of the underlying psychometric function.* Therefore, a useful quantitative model of the relative contributions of probability summation and linear spatial summation is not yet feasible for infant vision. What can be said is, no matter what the relative contribution of these two fundamental mechanisms is to the visual detection process in infants, the present data still demonstrate a clear (non-optical) difference from adult vision.

Retinal Locus

It is well known that in adult vision, the diameter of spatial summation areas are minimal in the fovea (5–7 min arc) and increase in diameter monotonically, up to a maximum of ~2° in diameter, as more peripheral loci on the retina are tested (e.g. Weinstein and Arnulf, 1946; Scholtes and Bouman, 1977; Ransom-Hogg and Spillman, 1980; Zuidema *et al.*, 1981). The current version of the forced-choice preferential looking technique does not allow one to specify the retinal locus that is being stimulated. The infant views the stimulus screen freely; the stimulus is kept on continuously throughout each trial; and the holder-observer can translate or rotate the infant a few centimeters in any direction in order to try to direct its gaze in the approximate direction of the two possible stimulus positions. Thus, one does not know what retinal locus was used by the infants to detect the stimuli, if indeed any *single* locus was used for all the conditions tested. Recently, Schneck *et al.* (in preparation) achieved some control of retinal eccentricity in infant vision testing by incorporating a "fixation-flash" method of stimulus presentation into the FPL technique. Using this modified version of FPL, these authors measured dark-adapted thresholds in 1-month old infants, using two spot sizes (~3° and ~17° dia.) presented at each of two eccentricities (9°, 18°, 27° and 36°). Their results were consistent with the present results, in that the infants appeared to have very large summation areas. In addition, little or no dependence on retinal eccentricity was found. If it turns out that the properties of the young infant's visual system are relatively homogeneous as a function of retinal eccentricity, this would increase the generality of previous data obtained using the free-viewing version of FPL. In any case, the present data show that, whatever part (or parts) of the retina are being used to detect the stimuli, the infants' data differ markedly from the adults' (even when the adults were viewing the screen freely), but are comparable to data obtained under the more controlled viewing condition of "fixation-flash" FPL (Schneck *et al.*, in preparation).

In conclusion, dark-adapted 4- and 11-week old human infants appear to have very coarse spatial processing as assessed by a behavioral measure (FPL) of spatial summation. Infants' estimated summation areas are quite large in diameter (~8.9° at 4 weeks and ~5.5° at 11 weeks). In terms of stimulus area, these summation areas are much larger (by factors of 11.9 and 4.4, respectively) than those estimated in adults (~2.6° dia.) tested under nearly identical conditions.

Recent estimates of infant dark-focus (Aslin and Dobson, personal communication) and the results of an adult control experiment involving substantial defocus of the stimuli support the conclusion that the differences between the infant and adult data are not likely to be due to out-of-focus images in the infants' eyes. In addition, even when the difference in eye size is accounted for (so that summation areas are specified in terms of *retinal* area rather than *stimulus* area) infant summation areas are approximately 2 (11-week olds) to 5 (4-week olds) times larger than those of adults. We conclude, then, that the present data reflect a neural organization in the infant visual system that is quite different from the mature visual system. Furthermore, maturational changes in spatial processing by the infant visual system under scotopic conditions may be behaviorally demonstrable within the first few months of life.

*In our experience, infant's psychometric functions tend to be shallower than those of adults tested under similar conditions. In the present study, the ratio of the adult mean slope of the psychometric function (at 75% correct) to the mean slope for infants (4- and 11-week olds' data combined) was 5.6. Recently, Mayer and Dobson (1982) have presented an analysis of the slopes of infant's psychometric functions in the context of detection of black and white square wave gratings at photopic levels. They too find the infants tend to have shallower psychometric functions than adults.

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