

The Effect of Light Adaptation on Scotopic Spatial Summation in 10-Week-old Infants

RONALD M. HANSEN,* RUSSELL D. HAMER,† ANNE B. FULTON*

Received 3 October 1990; in revised form 14 January 1991; received for publication 31 July 1991

Psychophysical area-intensity functions of individual 10-week-old human infants and adults were obtained in the dark adapted state, and in the presence of a steady background that elevated threshold 1 log unit above the dark adapted level. For dark adapted infants, the mean diameter for complete spatial summation (4.42°; SD: 1.67°) was significantly larger than that of adults (2.32°; SD: 0.09°). The background reduced the mean critical diameter to 2.67° for infants (SD: 0.64°) and to 1.16° for adults (SD: 0.08°). Spatial probability summation has similar effects on infant and adult thresholds, and, therefore, does not appear to account for the developmental decrease in critical diameters. Rather, decreases in receptive field size are suspected.

Spatial summation Scotopic sensitivity Human infants Development

INTRODUCTION

Spatial summation functions illustrate the retina's ability to integrate stimulus energy over area (Hood & Finkelstein, 1986). For adults, the area for total spatial summation varies with retinal eccentricity, stimulus duration and spatial configuration (Graham & Bartlett, 1939; Hallett, Marriott & Rodger, 1962; Hallett, 1964; Scholtes & Bouman, 1977; Zuidema, Verschuure, Bouman & Koenderink, 1981). The critical diameter for complete spatial summation in peripheral retina (15° eccentricity) is about 2° in diameter. It has been reported that the critical diameter is about 9 to 17° for 4-week-old infants, 6° at age 11 weeks, and 2.6° for adults tested in the same conditions (Hamer & Schneck, 1984; Schneck, Hamer, Packer & Teller, 1984). These authors concluded that immature neural organization and spatial probability summation, but not optical factors, could account for the large summation areas of infants.

In the present study, complete spatial summation functions were obtained from individual infants to refine the comparison of critical diameters for dark adapted 10-week-old infants and adults. Also, subjects adapted to a dim, steady background were tested to estimate light adapted critical areas. Backgrounds are known to influence receptive field organization (Barlow, Fitzhugh

& Kuffler, 1957). The effect of backgrounds on infants' spatial summation has not, to our knowledge, been studied.

METHODS

Apparatus

The apparatus and procedures were similar to those described previously (Hansen, Fulton & Harris, 1986). Three 500 W tungsten sources were used to project two test stimuli and the background onto a large rear projection screen in a dark room. Test stimuli were 50 msec broadband blue ($\lambda < 510$ nm) flashes presented 20° to the right or left of the center of the screen. The stimulus diameters varied from 0.5° to 10°. Calibrated neutral density filters controlled stimulus intensity. The background was a red (Wratten 29 transmitting $\lambda > 610$ nm), 109° diameter field centered on the rear projection screen.

Calibrations

Calculation of flash intensity was based on radiance measurements of the stimuli with a calibrated photodiode (UDT 11A) placed in the position of the subject's eye. Then the number of quanta $\text{sec}^{-1} \text{cm}^{-2}$ (503 nm) incident at the cornea was determined taking into account the output of the source, the sensitivity of the detector, and the spectral transmittance curve of the blue filter.

General procedure

Thresholds were estimated using a two-alternative forced-choice preferential looking method (Teller, 1979).

*Department of Ophthalmology, Children's Hospital and Harvard Medical School, 300 Longwood Avenue, Boston, MA 02115, U.S.A.

†Smith Kettlewell Institute of Visual Sciences, 2232 Webster Street, San Francisco, CA 94115, U.S.A.

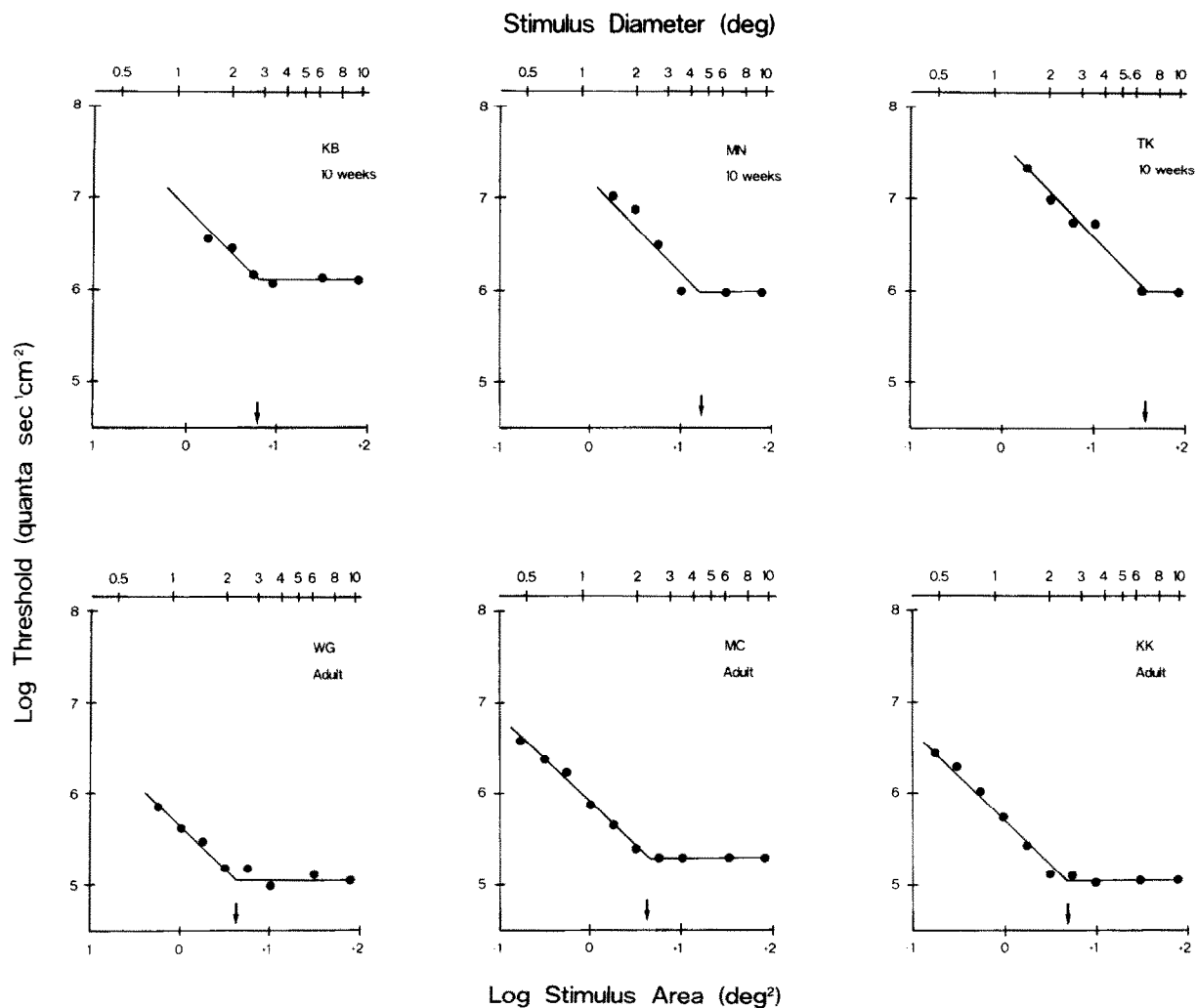


FIGURE 1. Representative spatial summation functions from dark adapted 10-week-old infants and adults. Log threshold in quanta $\text{cm}^{-2} \text{sec}^{-1}$ is plotted as a function of log stimulus area in deg^2 . The second abscissa shows stimulus diameter in deg arc. The critical area for complete spatial summation is indicated by the arrow. The data represent subjects with the smallest (left panel), average (center panel), and largest (right panel) critical areas.

After the infant had dark adapted for 30 min, an adult *holder* positioned the infant 50 cm in front of the rear projection screen. Two small, red LEDs flickering at 0.5 Hz provided a central fixation target. An adult *observer* watched the infant with an infrared viewer and reported when the infant was alert and looking at the fixation target. Control experiments with adults showed that observers could reliably detect horizontal eye movements to positions $>3^\circ$ from the central fixation target. The fixation target was then extinguished and a stimulus presented. On every trial, the observer reported stimulus location (right or left). A third adult, the *experimenter*, presented stimuli, recorded responses, and gave the observer feedback on every trial. Thresholds were determined using a transformed up-down staircase (Wetherill & Levitt, 1965). Each infant was tested using six stimuli (1.5–10° diameter) in two or three sessions. The order of presentation of stimulus sizes was randomized.

In the second experiment, after 30 min of dark adaptation, the infant's dark adapted threshold for detecting 10° diameter, 50 msec flashes was determined. Next, a background that was expected to elevate the threshold 1 log unit above the dark adapted value (retinal illumi-

nance about $-1.3 \log$ scot td for both infants and adults) was introduced and the infant was shown the background for 3 or 4 min. Then, the threshold for detecting a 10° diameter, 50 msec stimulus was measured. For each subject this background reduced sensitivity by about 1 log unit. Thresholds for the remaining five stimulus diameters (1.5–5.5°), presented in random order, were determined in two or three sessions. Pilot observations in the light adapted condition indicated that infants could not be reliably tested with stimuli $<1.5^\circ$ diameter. No similar problem was observed in the dark adapted testing.

Subjects

A total of 26 infants participated. 10 infants completed testing in the dark adapted condition, and 10 others in the light adapted condition. 6 infants failed to complete testing because of fussiness or sleepiness (5 infants), or failure to return for additional sessions (1 infant). No data from infants who did not complete testing are included in this report.

All infants were born within 10 days of their due date. At the first session their ages were 68 to 75 (median: 72)

days. Each infant completed testing within 7 days of the first session. Thorough ophthalmic examination demonstrated no ocular abnormalities. Informed consent was obtained from parents before testing began.

Five young adults, ages 20–23 (median: 22) years, were tested using the same apparatus and procedure except they reported verbally stimulus location, and were tested with 10 stimulus sizes (0.5–10° diameter) in both the dark adapted condition and in the presence of a steady background that elevated threshold about 1 log unit above the dark adapted value. Testing was done in two sessions on separate days.

RESULTS

For all stimulus sizes, infants' thresholds are higher than those of adults. In the dark adapted condition, the mean infant threshold for detecting 10° diameter stimuli is 6.00 (SD: 0.07) log quanta cm⁻² sec⁻¹ and is 0.95 log units above the comparable adult threshold. These values correspond to a mean retinal illuminance of -3.9 (SD: 0.12) log scot td sec for adults, and -2.8 (SD: 0.06) log scot td sec for infants. These thresholds are similar to other estimates from infants (Hansen & Fulton, 1981; Powers, Schneck & Teller, 1981; Brown, 1986, 1988; Hansen *et al.*, 1986).

Both dark adapted infant and adult spatial summation functions (log threshold vs log stimulus area; Fig. 1) are similar in shape to those reported previously for adults (Graham & Bartlett, 1939; Scholtes &

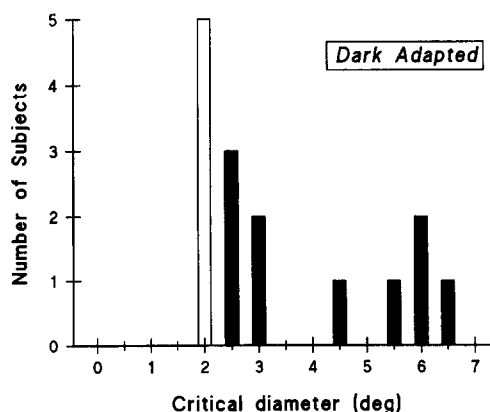


FIGURE 2. Summary of critical diameters for dark adapted infants (solid bars) and adults (open bar). The number of subjects with critical diameters falling within a 0.5 deg range, beginning with the value on the ordinate, is shown.

Bouman, 1977; Zuidema *et al.*, 1981). The critical area, A_c , for complete spatial summation was taken as the intersection of a line with slope -1 fit by eye through the thresholds for small stimuli and a horizontal line through the 10° point. The distribution of dark adapted critical diameters is summarized in Fig. 2. For dark adapted infants, the mean critical diameter is 4.42° (SD: 1.67°). The mean critical diameter for adults (2.32°; SD: 0.09) is significantly smaller ($t = 2.77$; d.f. = 13; $P < 0.01$). The adult critical diameters are tightly clustered (range: 2.17–2.41°) compared to the infants' (range: 2.83–6.72°). The infants appear to have a

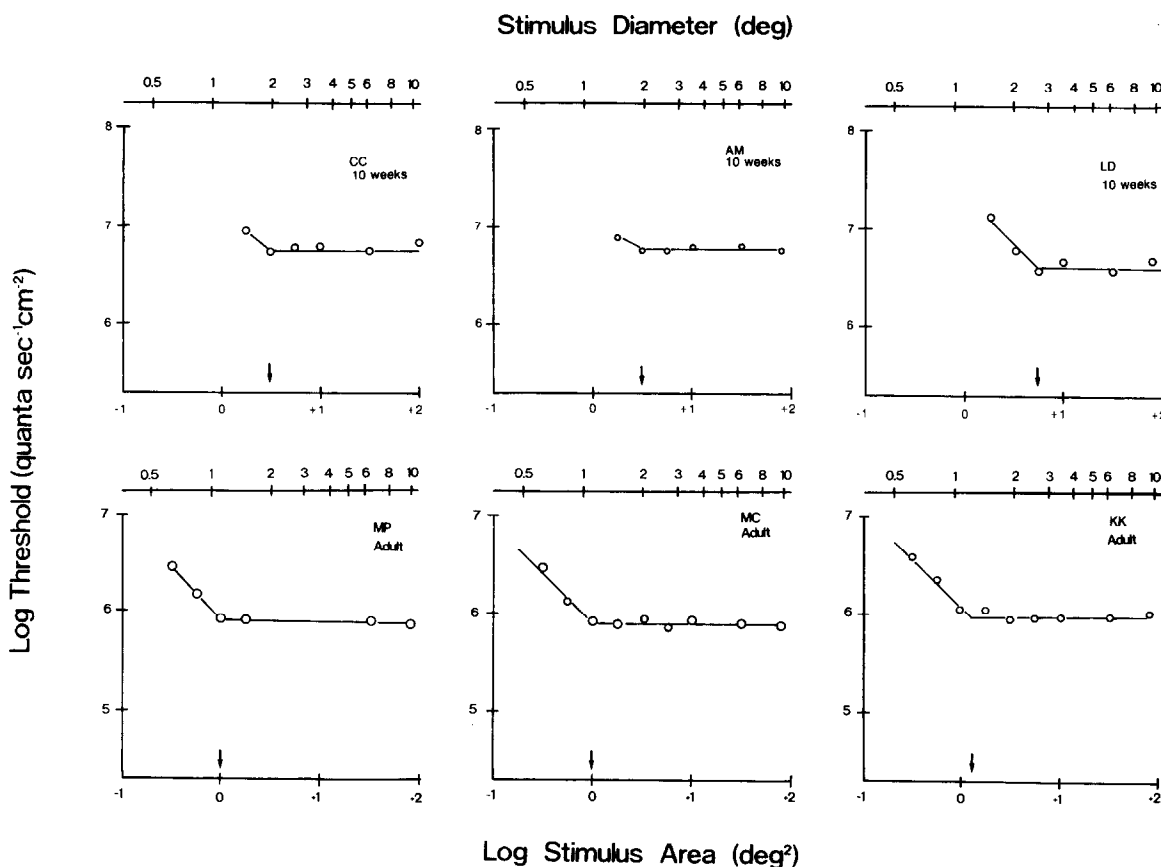


FIGURE 3. Representative spatial summation from infants and adults measured during adaptation to a steady background that elevated threshold about 1 log unit above the dark adapted value. All features of this graph are similar to those of Fig. 1.

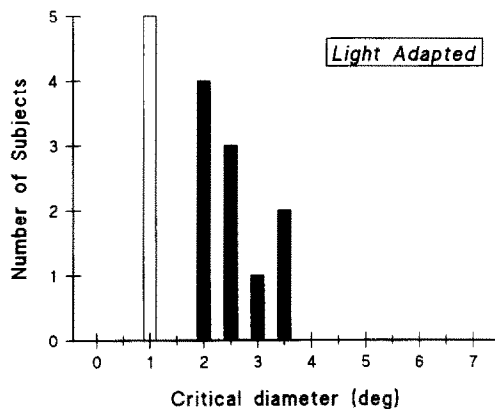


FIGURE 4. Summary of critical diameters from light adapted subjects. The number of subjects with critical diameters within the 0.5 deg range beginning with the value on the ordinate is shown for infants (solid bars) and adults (open bar).

bimodal distribution of critical areas (Fig. 2). Half of the infants have critical areas only slightly larger than those of adults.

The background elevates thresholds of infants by an average of 0.98 log units (range: 0.79–1.25 log units). For adults the mean threshold elevation produced by the background is 1.1 log units (range: 0.89–1.2 log units). The shapes of the light adapted spatial summation functions are similar to the dark adapted functions. For both infants and adults the background reduces the area for total summation. For infants, only one or two points (1.5° and 2.0° diameter) lie above the horizontal line through the 10° point (Fig. 3). No infant's data are described by a horizontal line. It was not possible to test infants with diameters smaller than 1.5°. For the five

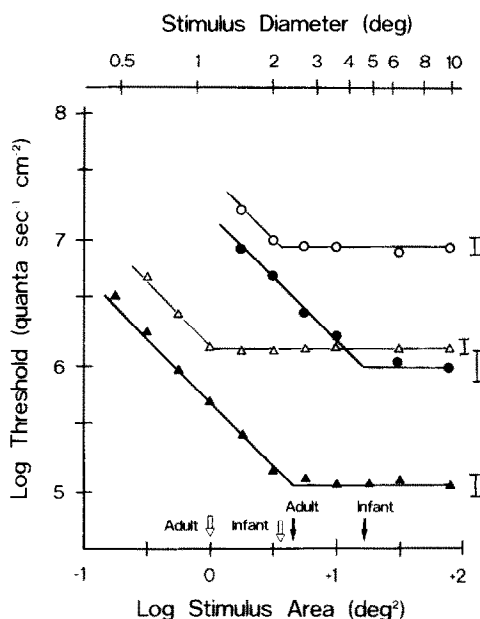


FIGURE 5. Mean log threshold as a function of log stimulus area for infants (circles) and adults (triangles). Arrows point to the critical area determined from the intersection of lines with slope -1 and 0 . Solid symbols refer to dark adapted results; open symbols refer to results obtained during adaptation to a steady background that elevated threshold about 1 log unit above the dark adapted level. The solid arrows mark critical areas for dark adapted results and the open arrows indicate light adapted A_c .

TABLE 1. Mean (SD) critical diameters for infants and adults

	Infants	Adults
Dark adapted	4.42° (1.67°)	2.32° (0.09°)
Light adapted	2.67° (0.64°)	1.16° (0.08°)

infants who had only one point above the horizontal, the area for complete spatial summation was taken as the smallest stimulus diameter on the horizontal line. In all five cases, the threshold above the horizontal line differed significantly ($P < 0.01$) from those on the horizontal branch of the curve. This procedure overestimates the area of complete summation because it assumes the Ricco area ends exactly at that point. Thus, the mean light adapted infant critical diameter of 2.67° (SD: 0.64°) may be a high estimate of summation area (Fig. 4). It is possible to test adults with several stimulus diameters smaller than the critical area. The mean light adapted adult critical diameter is 1.16° (SD: 0.08°).

The mean light and dark adapted spatial summation functions of infants and adults are shown in Fig. 5. Infants are less sensitive than adults in both adaptation conditions, and the steady background decreases the critical diameter of both infants and adults. This scotopic light adaptation reduces the critical diameter to about half the dark adapted value for both infants and adults (Table 1).

DISCUSSION

The area of complete rod-mediated spatial summation is significantly larger for 10-week-old infants not only in the dark adapted condition (Hamer & Schneck, 1984; Schneck *et al.*, 1984; Figs 1 and 2), but also in the light adapted condition (Figs 3 and 4). Furthermore, light adaptation decreases critical areas of both infants and adults (Fig. 5). This decrease in critical area, at least for adults, is attributed to the activation of center-surround inhibitory mechanisms by the background (Barlow *et al.*, 1957; Hood & Finkelstein, 1986). The ratio of mean dark and light adapted critical areas is 2.7 for infants and 4.0 for adults. However, the variances of the infants' critical diameters (Figs 2 and 4) are large, and the light adapted infant critical diameters (Fig. 3) may be overestimates. Therefore, the conclusion that light adaptation has the same effect on critical area for infants and adults cannot be rejected.

The mean critical diameter for the dark adapted 10-week-old infants (4.42°) is smaller than the critical diameter of 5.5° derived from mean threshold data of 11-week-old infants tested by Hamer and Schneck (1984). However, the range of critical diameters for 11-week-old infants (3.5–11.7°) reported by Hamer and Schneck (1984) overlaps broadly the range for 10-week-old infants (2.8–6.7°) found in the present study. On the other hand, the range of critical diameters of 10- and 11-week-old infants overlaps little the range (5.4–14.2°) reported for 4-week-olds (Hamer & Schneck, 1984). In both studies the mean critical diameters of adults (2.6°, 2.3°) were smaller than those of infants. On average,

critical areas of 10-week-old infants are about four times larger than those of adults. There is, however, a large range of critical areas for 10-week-old infants. Some infants have critical areas only slightly larger than adults', while others have critical areas up to nine times larger than the mean adult value (Fig. 2).

Taken as a whole, these psychophysical results parallel in general the developmental decreases in cat, rabbit and monkey receptive field size demonstrated by electrophysiological techniques (e.g. Hamasaki & Flynn, 1977; Masland, 1977; Rusoff & Dubin, 1977; Blakemore & Vital-Durand, 1979, 1981). Optical factors, such as eye size or image defocus, cannot fully account for the large critical areas of infants (Hamer & Schneck, 1984; Schneck *et al.*, 1984). However, because of the shallow psychometric functions of infants (Hamer & Schneck, 1984; Schneck *et al.*, 1984; Hansen *et al.*, 1986; Brown, 1988; Fulton, Hansen, Yeh & Tyler, 1991), the effect of spatial probability summation (Watson, 1979; Hamer & Schneck, 1984; Schneck *et al.*, 1984; Gorea & Tyler, 1986) must be considered to obtain an accurate estimate of infant critical areas.

The influence of spatial probability summation (SPS) on thresholds depends both on the slope of the psychometric function and on the response properties of the underlying neural substrate (Watson, 1979; Gorea & Tyler, 1985). If there were no center-surround antagonism, that is, if the response profile of the visual neurons were monophasic (Gorea & Tyler, 1986), and the psychometric function very shallow, SPS alone would lead to decreases in threshold with stimulus area that mimic Ricco's law. Specifically, for areas larger than A_c , SPS is predicted to cause threshold to decrease linearly with slope $1/\beta$; where β is the slope parameter (exponent) of the Weibull function (Weibull, 1951; Quick, 1974; Gorea & Tyler, 1986; Mayer & Tyler, 1986). Pooled data obtained from dark adapted subjects using a 10° diameter, 50 msec stimuli (Fulton *et al.*, 1991) yield $\beta = 2.77 (\pm 0.2; n = 4)$ for 10-week-olds and $4.8 (\pm 0.3; n = 5)$ for adults. Using these values, SPS predicts the slope of the spatial summation function, for stimuli larger than A_c , to be -0.36 for infants and -0.21 for adults for the dark adapted condition. Despite some steepening, light adapted infants' psychometric functions remain shallower than adults' (Brown, 1988) and so predict that SPS would have a similar effect on thresholds for stimuli larger than A_c . However, in both the dark and light adapted condition, we find the slope of the second branch of the spatial summation function is indistinguishable from zero for both adults and infants (Figs 1, 3 and 5). No dark adapted infant had a slope greater than -0.08 for the branch of the spatial summation function beyond A_c . The mean slope for dark adapted adults is $0.012 (\pm 0.06)$. Light adapted infants had horizontal branch slopes of -0.07 or less; adults had a mean slope of $0.01 (\pm 0.03)$. Thus, the form of the spatial summation function is consistent with the presence of center-surround antagonism (excitatory/inhibitory) in the scotopic visual system of 10-week-old infants (Banks & Salapatek, 1978; Fiorentini, Pirchio &

Spinelli, 1980; Gorea & Tyler, 1986) in both dark and light adapted conditions. Furthermore, the absence of threshold decreases with stimuli larger than A_c , especially prominent in the light adapted functions, indicates that the underlying excitation and inhibition are balanced (Gorea & Tyler, 1986).

In summary, light adaptation decreases critical areas in rod-mediated spatial summation of 10-week-old infants. Critical areas for complete spatial summation of infants are significantly larger than those of adults in both the dark and light adapted conditions. Spatial probability summation cannot account for the age-dependent decreases in critical area. Developmental decreases in receptive field size provide a more plausible explanation for the decrease in critical area.

REFERENCES

Banks, M. S. & Salapatek, P. (1978). Acuity and contrast sensitivity of 1-, 2- and 3-month-old human infants. *Investigative Ophthalmology and Visual Science*, *17*, 361-365.

Barlow, H. B., Fitzhugh, R. & Kuffler, S. W. (1957). Changes of organization in the receptive fields of the cat's retina during dark adaptation. *Journal of Physiology*, *137*, 338-354.

Blakemore, C. & Vital-Durand, F. (1979). Development of the neural basis of visual acuity in monkeys: Speculation on the origins of deprivation amblyopia. *Transactions of the Ophthalmological Society of the United Kingdom*, *99*, 363-368.

Brown, A. M. (1986). Scotopic sensitivity of the two-month-old human infant. *Vision Research*, *26*, 707-711.

Brown, A. M. (1988). Saturation of rod initiated signals in 2-month-old human infants. *Journal of the Optical Society of America*, *A*, *5*, 2145-2158.

Fiorentini, A., Pirchio, M. & Spinelli, D. (1980). Scotopic contrast sensitivity in infants evaluated by evoked potentials. *Investigative Ophthalmology and Visual Science*, *19*, 950-955.

Fulton, A. B., Hansen, R. M., Tyler, C. W. & Yeh, Y.-L. (1991). Temporal summation of dark adapted 10-week-old infants. *Vision Research*, *31*, 1259-1269.

Gorea, A. & Tyler, C. W. (1986). A new look at Bloch's law for contrast. *Journal of the Optical Society of America*, *A*, *3*, 52-61.

Graham, C. H. & Bartlett, N. R. (1939). The relation of stimulus and intensity in the human eye: II. Intensity thresholds for red and violet light. *Journal of Experimental Psychology*, *24*, 574-587.

Hallett, P. E. (1963). Spatial summation. *Vision Research*, *3*, 9-24.

Hallett, P. E., Marriott, F. H. C. & Rodger, F. C. (1962). The relationship of visual threshold to retinal position and area. *Journal of Physiology*, *160*, 364-373.

Hamasaki, D. L. & Flynn, J. T. (1977). Physiological properties of retinal ganglion cells of 3-week-old kittens. *Vision Research*, *17*, 275-284.

Hamer, R. D. and Schneck, M. E. (1984). Spatial summation in dark adapted human infants. *Vision Research*, *24*, 77-85.

Hansen, R. M. and Fulton, A. B. (1981). Behavioral measurement of background adaptation in human infants. *Investigative Ophthalmology and Visual Science*, *24*, 893-897.

Hansen, R. M., Fulton, A. B. & Harris, S. J. (1986). Background adaptation in human infants. *Vision Research*, *26*, 771-779.

Hood, D. C. & Finkelstein, M. A. (1986). Sensitivity to light. In Boff, K. R., Kaufman, L. & Thomas, J. (Eds), *Handbook of perception, vol. 1, sensory processes and perception* (pp. 5-59 & 5-62). New York: Wiley.

Masland, R. H. (1977). Maturation of function in the developing rabbit retina. *Journal of Comparative Neurology*, *175*, 275-286.

Mayer, M. J. & Tyler, C. W. (1986). Invariance of the slope of the psychometric function with spatial summation. *Journal of the Optical Society of America*, *A*, *3*, 1166-1172.

Powers, M. K., Schneck, M. & Teller, D. Y. (1981). Spectral sensitivity of human infants tested at absolute threshold. *Vision Research*, *21*, 1005-1016.

- Rusoff, A. & Dubin, M. W. (1977). Development of receptive field properties of retinal ganglion cells in kittens. *Journal of Neurophysiology*, *40*, 1188–1198.
- Schneck, M. E., Hamer, R. D., Packer, O. S. & Teller, D. Y. (1984). Area threshold relations at controlled retinal locations in 1-month-old human infants. *Vision Research*, *24*, 1753–1763.
- Scholtes, A. M. W. & Bouman, M. A. (1977). Psychophysical experiments on spatial summation at threshold level of the human peripheral retina. *Vision Research*, *17*, 867–873.
- Teller, D. Y. (1979). The forced choice preferential looking method: A technique for use with human infants. *Infant Behavior and Development*, *2*, 135–153.
- Quick, R. F. (1974). A vector-magnitude model of contrast detection. *Kybernetik*, *16*, 65–67.
- Watson, A. B. (1979). Probability summation over time. *Vision Research*, *19*, 515–522.
- Weibull, W. (1951). A statistical distribution function of wide applicability. *Journal of Applied Mechanics*, *18*, 292–297.
- Wetherill, G. B. & Levitt, H. (1965). Sequential estimation of points on a psychometric function. *British Journal of Mathematical Statistics, Psychology*, *18*, 1–10.
- Zuidema, P., Verschuure, H., Bouman, M. A. & Koenderink, J. J. (1981). Spatial and temporal summation in the human dark adapted retina. *Journal of the Optical Society of America*, *71*, 1472–1480.

Acknowledgements—We thank Christopher Tyler for valuable discussions of probability summation and Linda Medwar, Maura Padula and Catherine Trowbridge for their technical assistance. This project was supported by NIH Grant EY 05325. A preliminary report of this study was presented on 3 May 1989 at the ARVO meeting, Sarasota, Florida.