

THE DEVELOPMENT OF LIGHT ADAPTATION IN HUMAN INFANTS

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(Received 1 June 1982; In revised form 18 October 1982)

Abstract—Increment threshold functions were measured from -4.0 to $1.2 \log \text{cd/m}^2$ in 7-12-week-old infants using a behavioral forced-choice paradigm. The slopes of the infant functions were considerably, shallower than the slopes of adult functions over the same luminance range. The value of the infant slope increased rapidly between 7 and 12 weeks postnatally. A number of explanations for this developmental shift are considered. It is concluded that changes with age in either spatial summation or intensity-response function gain could cause the increase in slope.

Light adaptation Development Infants Psychophysics Increment threshold function

INTRODUCTION

The processes of light and dark adaptation permit the adult human visual system to operate over an enormous range of illumination levels. Little is known about how these processes develop.

Several mechanisms contribute to visual adaptation in adults. First, pupillary changes modulate retinal illumination, but such changes are insignificant given the total dynamic range of the visual system (Barlow, 1972). Salapatek et al. (1977) have demonstrated adult-like pupillary responses in the photopic range by 2 months of age; thus, this mechanism probably contributes to adaptation in a mature, albeit negligible, fashion by this age. Second, the staggering of sensitivity provided by the two different types of photoreceptors which adults possess aids adaptation by dividing the total logarithmic intensity range roughly in half. Anatomical (Abramov et al., 1982), electroretinographic (Barnet et al., 1965), and behavioral data (e.g. Powers et al., 1981; Teller et al., 1978) confirm the existence and functioning of both rods and cones during early postnatal life. Thus, this staggering of sensitivity should also contribute to the total dynamic range of the infant visual system. Pupillary responses and the staggering of sensitivity, however, cannot fully account for light adaptation in the adult; additional neural mechanisms must contribute to visual adaptation (Ripps and Weale, 1969). For this reason, one would expect a significant contribution from these neural mechanisms to the development of adaptation.

Light adaptation in adults has most often been studied using the increment threshold paradigm (Barlow, 1972). The increment

threshold function represents the relation between the just-detectable intensity increment and background intensity. Specifically, the increment threshold function plots log increment intensity as a function of log background intensity. This function is affected by a variety of factors (e.g. target size, duration, eccentricity and spectral characteristics).

The increment threshold function is bounded generally by two asymptotic regions: (1) a region at low background luminances in which threshold is independent of luminance; (2) a region at high luminances in which threshold is directly proportional to luminance (Weber's Law). The slopes of these regions are 0.0 and 1.0, respectively, with a smooth transition between these two regions.

Several lines of evidence suggest that light adaptation may be mature (as evidenced by adult-like slopes on Weber functions) by 3 months of age and perhaps not before. First, Hansen and Fulton (1981) have shown that the slope of the scotopic increment threshold function increases postnatally. (The same sort of postnatal change has been observed in rats; Fulton and Graves, 1980.) By 3 months, the slope of the linear portion of the increment threshold curve was essentially the same as the adult value of 0.96. Hansen and Fulton tested only one infant at each age so their results must be regarded as preliminary.

Second, 3-month-olds are about 1.0 log units less sensitive than adults at absolute dark-adapted threshold (Powers et al., 1981) and also about 1.0-1.5 log units less sensitive than adults in photopic incremental sensitivity tasks (Peeples and Teller, 1978, Pulos et al., 1980). This relatively constant difference in threshold between infants and adults across luminance levels

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suggests that the 3-month-old's increment threshold function is parallel but shifted vertically relative to the adult function. This suggests, in turn, that the visual system may be adapting at 3 months of age like it does in adults. This is not very strong evidence, however, because it is based on comparisons across studies which differed in subjects, procedures and stimuli.

Some indirect evidence concerning the status of early adaptation processes comes from studies of infant temporal processing. Horsten and Winkelman (1962, 1964) and Heck and Zetterstrom (1958) measured flicker electroretinograms in young infants. Regal (1981) used a behavioral technique to measure critical flicker frequency (CFF) in 1-, 2- and 3-month-olds. These three groups of investigators agree that time-average luminance affects CFF qualitatively in the same way at 2 months (and perhaps earlier) as it does in adults. This suggests that adaptation affects temporal processing similarly in young infants and adults.

Fiorentini et al. (1980) have demonstrated adult-like luminance-dependent changes in the spatial contrast sensitivity functions (CSF's) of 2.5-month-olds using the visually-evoked potential. A 2.0 log unit reduction in luminance (from 6.0 to 0.06 cd/m²) led to decreases in the high-frequency cut-off and the bandwidth of the CSF and to a diminution of the low-frequency fall-off. Similarly, Dobson et al. (1981) have demonstrated a decrease of about 1 octave in 2-month-olds' visual acuity with a 4.0 log unit decrease in luminance. The same effects are commonly observed in adults (van Nes and Bouman, 1967; van Meeteren and Vos, 1972; Sloan, 1968). These changes—a decline in acuity, a decrease in bandwidth and a diminution of the low-frequency fall-off—are thought to be indicative of the decreased lateral inhibition and increased spatial summation which accompany dark adaptation. This suggests that adaptation qualitatively affects pattern vision similarly in young infants and adults.

Finally, light adaptation may show postnatal development because of various structural immaturities of the young infant's retina. This speculation is based on electrophysiological evidence which indicates that the retina is the major site of light adaptation (e.g. Boynton and Whitten, 1970). Dowling (1977) has shown that both photoreceptor adaptation and network mechanisms operate to accomplish light adaptation. Work on non-human species suggests a possible link between the postnatal development of the retina and light adaptation. Tucker et al. (1979) have shown that postnatal morphological changes in kitten photoreceptors are correlated with changes in various aspects of retinal sensitivity measured electrophysiologically. Fulton and Graves (1981) have observed similar results in developing rats. The human retina undergoes structural development and refinement postnatally (Abramov et al., 1982; Mann, 1964). The postnatal maturation of retinal structures in human infants may, therefore, influence the development of light adaptation.

Our understanding of the development of light adaptation mechanisms is, therefore, far from complete. The one direct study (Hansen and Fulton, 1981) covered only the scotopic range and examined a very small number of infants. Previous studies which have included the photopic range have provided only indirect

information concerning adaptation. We have directly investigated the postnatal development of light adaptation from 7 to 12 weeks in a reasonably large number of infants. Increment threshold functions were measured over a range which covered both scotopic and photopic levels using the forced-choice preferential looking technique (Teller, 1979). We used the slopes of these functions to assess the maturity of light adaptation in young infants.

METHODS

Subjects

Infants were recruited by letter and phone from birth announcements in local newspapers. Complete data were obtained on six 12-week-old infants (mean age = 11.5 weeks; SD 1.0 weeks) and six 7-week-old infants (mean age 7.0 weeks; SD = 0.4 weeks). Three other 7-week-olds furnished partial data. One additional infant who was 6 weeks premature was tested at 12 weeks postnatal age. Three 12-week-olds and six 7-week-olds were excluded from the study due to fussiness, sleepiness, or failure to return to complete testing. All sessions for each infant were conducted within a 2-week period. Three adults also served as subjects.

Apparatus

Stimuli. Increment thresholds were measured against a large, 60' horizontal x 40' vertical, white adapting field (tungsten, GE CZX/DAB 500W). The luminance of the adapting field could be varied over a large range using a combination of neutral density filters and a variable aperture. Figure 1 is a schematic of the apparatus.

The increment target was a small, white (tungsten, DEK/DFW 500 W), 6° x 6°, segment of a 1 c/deg squarewave grating. Since this target was added (rear-projected) to the adapting field, the mean luminance of the squarewave segment did not equal the mean luminance of the adapting field. A movable mirror allowed the target to be placed either 20' to the left or 20' to the right of the center of the background field. Neutral density filters (Wratten No. 96) and a crossed polarizer controlled the luminance of the target independent of the adapting field luminance. The increment (AI) in the present experiment was defined as the difference between the luminance of one of the bright bars and the luminance of the uniform background. The inset in Fig. 1 shows a luminance profile of the stimulus field and illustrates this definition.

The target and background luminances, neutral density filters and variable apertures were measured and calibrated periodically in situ using a photometer (Spectra Brightness Spot Miter No. 15025-UB) and a standard source (Spectra Regulated Brightness Source No. BSR-9-B). The background field was nearly homogenous the luminance at the center of the screen was 0.02 log units higher than at either edge. The increment target and background were equal in luminance at both the right and left test positions.

Observation system. Since the lower luminance stimuli generally did not provide enough light to illuminate the infant's face sufficiently, an infrared observation system was employed. The components of this system were an infrared-sensitive camera (Panasonic, WV- 1100A; Vidicon Type 20PE 13A), a video monitor (Panasonic, WV-5400), and two infrared lights (tungsten light bulbs plus Kodak i.r. filter No. S7). The infrared lights were virtually invisible and, thus, did not disturb the state of adaptation. They did provide enough infrared light, however, to produce a clear image of the infant's face on the video monitor.

Conditions

Background luminances covering it 5.2 log unit range (-4.0 to 1.2 log cd/m²) were used for testing infants. Each infant was tested at it minimum of four background luminances. At least two, hour-long sessions were required to complete data collection on each infant. Two backgrounds were usually tested within a session. Infants viewed the screen using natural pupils.

To assign orders of stimulus presentations, the six background luminances available were divided into two sets: the three lowest and the three highest luminances. During the first session a subject was randomly assigned to and tested on one of the backgrounds from the lower luminance set and one of the backgrounds from the higher luminance set. A similar procedure was used for the remaining two backgrounds from each set during subsequent sessions. Within a single session, the lower luminance background wits always tested first. This was necessary in order to avoid the need for two periods of dark adaptation in a session.

Procedure

Infants. At the beginning of each session the infant and parent were taken to it dark room for 20 min of dark adaptation. A dim red light provided the only illumination in the room.

Following dark adaptation the infant was seated on the parent's lap facing the adapting field at a distance of approx. 40 cm. The parent and infant were enclosed on all sides by opaque curtains which eliminated any stray light from the apparatus. The observer stood outside the curtains and watched the infant on the video monitor. Before testing began, the infant was encouraged to look at the background field for at least 2 min to allow adaptation to that level.

Prior to the determination of the first threshold the observer was given a number of practice trials (approx. 8 on average) in which it highly visible target was presented to the infant. The purpose of this practice phase was twofold: (1) to familiarize the observer with each infant's unique preferential looking cues (Teller, 1979); (2) to acclimate the infant to the experimental conditions.

The forced-choice preferential looking technique (FPL, Teller, 1979) wits used to measure threshold. The FPL technique employs an adult who judges the most probable position of the target on each trial based on observation of the infant's eye and head movements. This technique has three important features.

First, the observer is unaware of the location of the stimulus on each trial. Second, the observer is free to use any cue from the infant to make a right or left judgment on each trial. Third, once the observer responds, she is given feedback. This technique has been very effective in infant psychophysical experiments. The same well-trained observer was used for all the infants in this experiment.

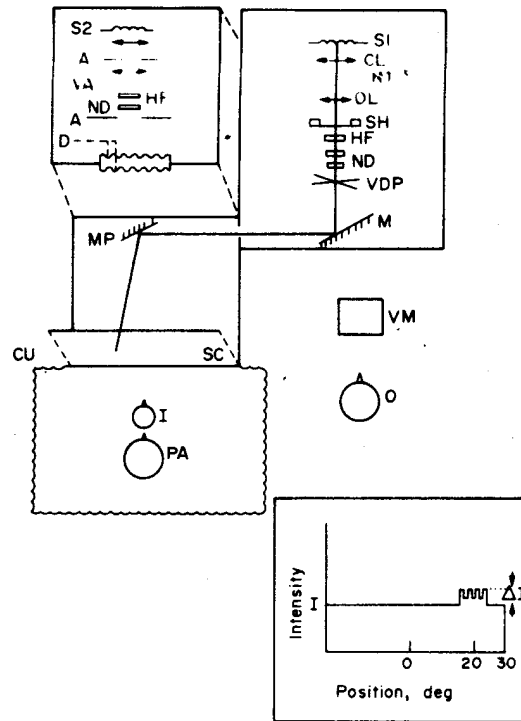


Fig. 1. Schematic of the apparatus used to test infants and adults. Abbreviations are its follows: (S1 and S2) sources; (CL) collimating lens; (RT) ronchi transparency; (OL) objective lens; (HF) heat filter; (Sh) shutter; (ND) neutral density filters; (VDP) variable density polarizer; (M) mirror; (MP) positioning mirror; (A) aperture; (VA) variable aperture; (D) diffusers; (SC) screen, (I) infant; (PA) parent; (CU) curtains; (O) observer; (VM) video monitor. The components of the background channel (S2) were elevated slightly relative to those of the test channel (S1). The mirror presenting the test field (MP) was then angled slightly to place the increment vertically in the center of the screen. The infrared camera and illumination lights were located directly above the screen. *Inset:* intensity profile of the stimulus field showing the background with the increment target in position on the right side of the screen.

A trial consisted of the following sequence of events. The observer attracted the infant's attention to the center of the screen by using her hand or a noisemaking toy before the trial began. Once she judged that fixation "as central, she removed the centering stimulus and initiated a trial by depressing a button on a response box. The increment target then appeared 20" to either the left or the right of the center. The increment target remained on until the observer responded or until 20sec had elapsed, at which time the observer was required to make a response. The observer could also disregard the trial prior to responding if the infant did not attend at all. Feedback was provided automatically to the observer after each trial by

electronic circuitry which activated a green (correct) or a red (incorrect) LED on the response box.

The luminance of the increment target was varied over trials according to a 2-down, 1-up staircase rule (Wetherill and Levitt, 1965). This rule estimates the luminance of the target for which the observer is 71% correct. Step size was set at 0.3 log unit. Infants were run for 10 or 12 reversals.* The first two reversals were ignored for each threshold calculation to minimize bias due to the starting position of the staircase. The remaining reversal points were averaged to compute threshold.

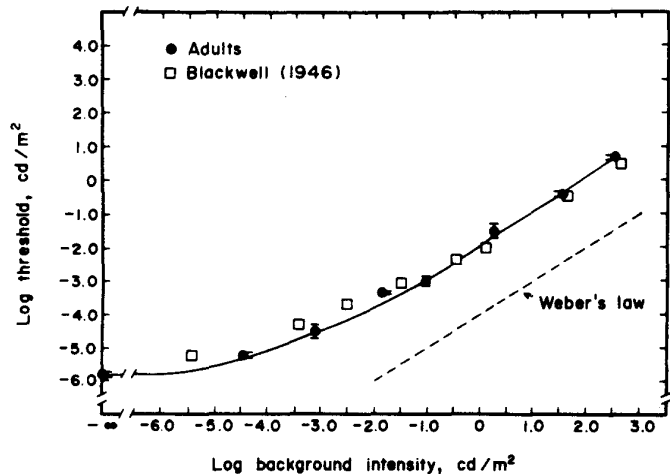


Fig. 2. Solid symbols: average increment threshold function from three adult observers. Open symbols: data from Blackwell (1946). Both studies used large test targets, long duration presentations and allowed free scanning of the stimulus field. Data from the two studies have not been shifted relative to one another. Error bars represent ± 1 SEM.

Adults. We also tested three adults, a female (age 30 yr) and two males (ages 20 and 33 yr) in order to replicate previous work with similar stimulus conditions (i.e. large area increment targets and long duration test trials). The apparatus, procedure and stimulus conditions were the same as those used to test the infants with a few minor exceptions. First, no observer was used with the adult subjects. Instead, the adult subjects themselves responded right or left on each trial using a response box. Second, adults were presented a larger number of backgrounds more closely spaced in luminance. Third, the step size for adult staircases was set at 0.1 log unit.

RESULTS

The averaged results from three adult subjects are shown in Fig. 2. The log luminance of the increment threshold (All has been plotted on the ordinate and the log luminance of the background (1) has been plotted on the abscissa. Note that as

* Step size was set at 0.3 log units under the assumption that the slopes of infant psychometric functions are shallower than the slopes of adult psychometric functions. Pilot testing revealed that 0.1 log unit steps increased the testing time beyond most infants' tolerance limits. An attempt was made to collect 12 reversals for each threshold estimate. For fussy or sleepy infants, however, a minimum of 10 reversals were collected before terminating a staircase and accepting the data.

the intensity of the background increases, the threshold also generally increases. The adult increment threshold function is linear with a slope of 0.95 above approx. $I = -2.0 \log \text{cd/m}^2$. The value of $-5.9 \log \text{cd/m}^2$ for dark-adapted absolute threshold agrees well with the value of $-6.1 \log \text{cd/m}^2$ found by Pirenne (1962) using similar stimulus conditions. Data from Blackwell (1946) – a classic study of the adult increment threshold function – are also shown in Fig. 2. These data points from Blackwell have not been shifted relative to our data. The excellent agreement between these data validates our procedures and calibrations.

Staircase data from a single 12-week-old infant at two background intensities are shown in Fig. 3. The lower curve on the left side of Fig. 3 shows a staircase collected at $I = -3.17 \log \text{cd/m}^2$. The upper curve shows a staircase collected at $+0.50 \log \text{cd/m}^2$. The right side of this figure shows the computed thresholds from both of these staircases plotted against the corresponding background intensities. We analyzed the raw data to determine if the behavior of the staircase procedure varied with age or experimental condition. The 7-week-olds required slightly, but significantly, more trials per reversal in their staircases than did the 12-week-olds ($t = 2.30, df = 42, P < 0.025$). The correlations between log background intensity and both the number of trials per reversal and the maximum range of stimulus values presented during a staircase ranged from -0.04 to -0.12 (all nonsignificant) for both age groups. Thus, background luminance had no systematic effect for either age group on either of these staircase characteristics.

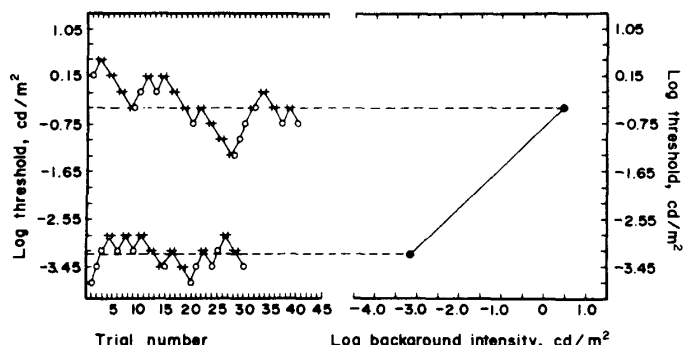


Fig. 3. Staircases collected from the same 12-week-old infant at $-3.17 \log \text{cd/m}^2$ (bottom curve) and $+0.50 \log \text{cd/m}^2$ (top curve). The dashed horizontal line through each staircase represents the computed threshold ignoring the first two reversals. The right side of the figure shows these increment thresholds plotted against the corresponding background intensities.

The results from each of the six 7-week-olds are shown in Fig. 4. The average adult curve is also shown for reference. These increment threshold functions, like adult functions, exhibited an increase in threshold as the intensity of the background increased. There were substantial individual differences in sensitivity within this age group. The 7-week-olds were less sensitive, i.e. they had higher increment thresholds, than the adults. Finally, a least squares linear regression was used to obtain a slope for each infant's data individually. The 7-week-old slopes (mean slope = 0.56) were shallower than the average adult

slope (mean slope = 0.86) over the same luminance range ($t = 3.31, df = 7, P < 0.01$).

We were unable originally to obtain thresholds at the highest background intensities ($I > 1.0 \log \text{cd/m}^2$) on any of the 7-week-olds. This was due to apparatus limitations. We modified the apparatus to permit the presentation of higher luminance test targets and tested three more 7-week-olds at the highest background level and at least one lower luminance level ($I = -3.0 \log \text{cd/m}^2$). The results are shown in Fig. 5. The average function from the first group of 7-week-olds is also shown. The results from the three additional 7-week-olds were indistinguishable from the first group's results in terms of both overall sensitivity and slope. The average slope of the original group of 7-week-olds was 0.56 and that of the three additional 7-week-olds was 0.56. Thus, shallow slopes were observed in 7-week-olds even when the calculation of these slopes included the highest background level which 12-week-olds were presented.

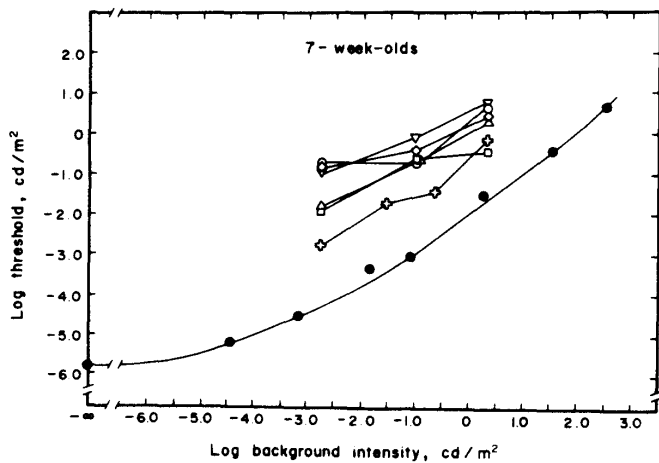


Fig. 4. Increment threshold functions from six 7-week-old infants (open symbols) and the average adult increment threshold function (solid symbols).

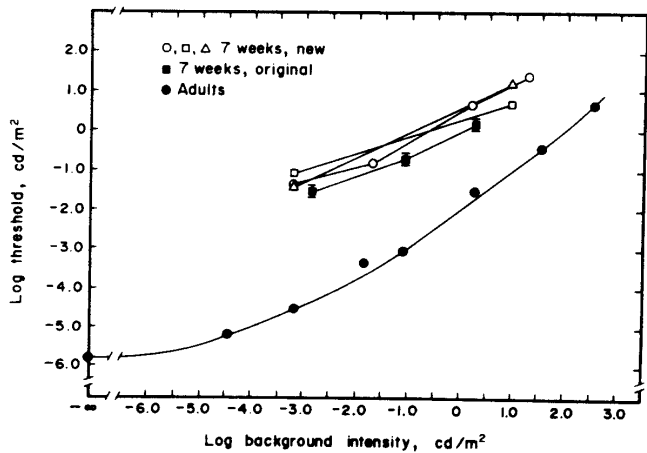


Fig. 5. Increment threshold functions from three additional 7-week-old infants including thresholds above $1.0 \log \text{cd/m}^2$ (open symbols). The solid squares show the average increment threshold function from the original sample of 7-week-olds. The average adult function is also shown for reference.

The results from each of the 12-week-olds are shown in Fig. 6. Thresholds for this age group also rose with increases in background intensity. Individual differences in sensitivity were considerably less at this age than they were at 6 weeks. The average of the 12-week-old slopes (0.79) was significantly different ($t = 2.80, df = 10, P < 0.01$) than the average of the 7-week-old slopes (0.56). The difference between the 12-week-old average slope and the average adult slope over the same luminance range approached significance ($t = 1.74, df = 7, P = 0.06$). Thus, increment threshold function slopes appear more adult-like at 12 weeks than at 6 weeks.

One premature infant was tested at 12 weeks postnatal age. Pediatric examination at birth yielded an estimate of 6 weeks prematurity. Therefore, this postnatal 12-week-old was gestationally equivalent to a postnatal 6-week-old. Data from this infant are shown in Fig. 7. The slope of her function was 0.60, a value close to the average 7-week-old slope of 0.56 and outside the 95% confidence limits on the average 12-week-old slope (0.79 ± 0.08). This suggests that gestational age is a better predictor of increment threshold function slope than postnatal age.

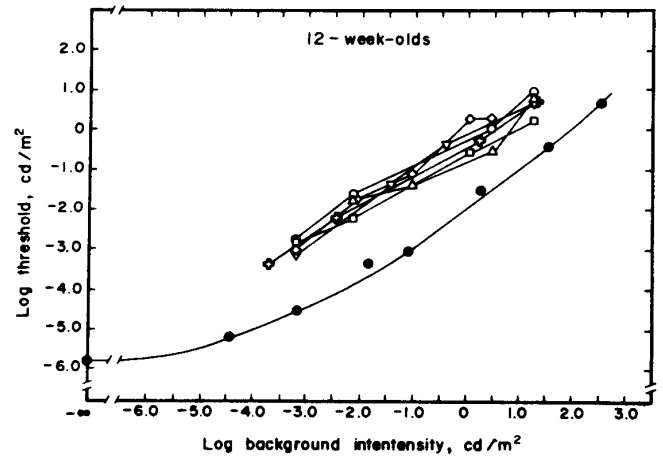


Fig. 6. Increment threshold functions from six 12-week-old infants (open symbols) and the average adult increment threshold function (solid symbols).

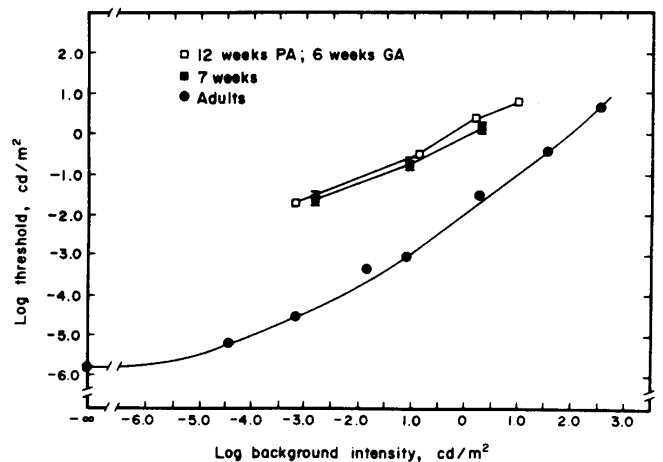


Fig. 7. Increment threshold function from a 12-week-old infant (postnatal age) who was 6 weeks premature. The open symbols represent this infant's data. The solid squares show the average 7-week-old increment threshold function. The average adult function is also shown for reference.

To compare infant and adult slopes graphically, we plotted the average increment threshold function for each infant age group along with a vertically-shifted average adult function. The logic of this procedure is simple: if infants were simply less sensitive than adults with no differences in slope, then a vertical shift of the adult curve should make it coincide with the infant curve except for measurement error. The results of this procedure are shown in Fig. 8. Inspection of Fig. 8 shows that the 7-week slope is considerably shallower than the adult slope over the same luminance range. Thus, light adaptation appears to be immature 7 weeks postnatally. By 12 weeks the slope has become more adult-like.

Figure 9 summarizes these developmental data. The average infant slopes at 7 and 12 weeks are plotted as a percentage of the average adult slope over the same luminance range. A rapid increase in slope is evident between 7 and 12 weeks. The infant slope at 12 weeks is approx. 90% of the value of the adult slope over the same luminance range. The open symbol in Fig. 9 represents the 6-week premature infant who was tested at 12 weeks postnatal age. Her vertical location on this graph clearly places her near the 7-week-olds. Thus, the slope of the increment threshold function is probably under maturational control.

DISCUSSION

The most important result of this study is that the slope of the increment threshold function increases postnatally. This extends Hansen and Fulton's ~ 1981 finding of postnatal slope changes into the photopic range. There are two classes of possible explanations for the shallower infant slopes we observed: (1) nonsensory factors, which change with age, could affect increment threshold slopes; (2) sensory factors, changing with age, could also affect increment threshold slopes.

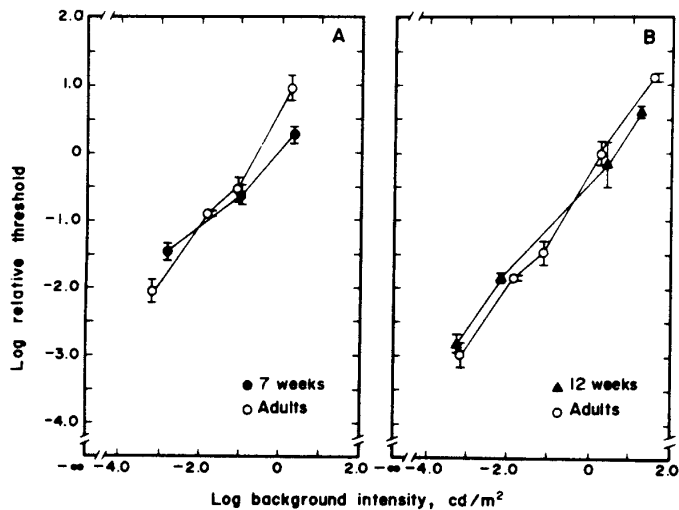


Fig. 8. (A) Average 7-week-old increment threshold function (open symbols) and its vertically translated version of the average adult function over the same luminance range. (B) Average 12-week-old increment threshold function and its vertically translated adult function. Error bars were calculated after overall individual differences in sensitivity were partialled out within each age group. The adult curve was translated

vertically so that the adult mean sensitivity equaled the mean sensitivity of each age group. Error bars represent ± 1 SEM.

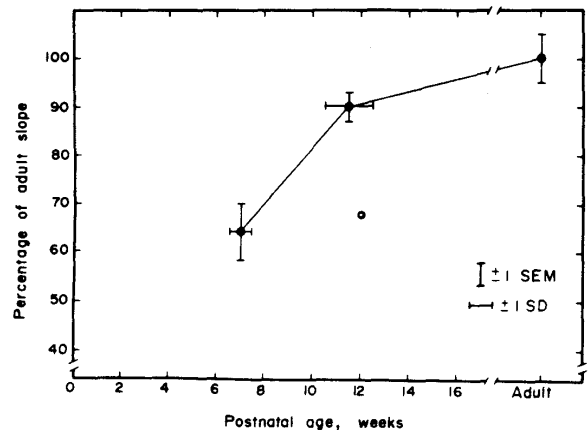


Fig. 9. The average slope of the increment threshold function at 7 and 12 weeks plotted as a percentage of the average adult slope over the same luminance range. The open symbol shows the slope for a postnatal 12-week-old infant who was 6 weeks premature.

Nonsensory explanations

We will discuss the nonsensory explanations first. The primary nonsensory explanation can be stated as follows. Perhaps infants are less attentive in dimmer illumination than they are in brighter illumination. Consequently, their thresholds are relatively higher at dimmer levels because they are less inclined to look at the target, even though they can detect it. To evaluate this hypothesis, we reasoned that the less attentive states at dimmer levels would produce more variability or "noise" in the staircase characteristics. No such systematic effect was found (see Results). We therefore tentatively rule out this potential nonsensory explanation of our data.

Sensory explanations

Let us now examine sensory factors, which could have affected our results. Before considering specific sensory factors, it is useful to consider the obvious hypothesis that shallower infant slopes are due to immature light adaptation processes *per se*. This hypothesis may be weakened by some recent adult psychophysical work which examined increment threshold functions under conditions in which light adaptation could not operate fully. Geisler (1981) and Hood *et al.* (1978) measured increment thresholds under flashed background conditions. They found that the resulting increment threshold functions saturate much more rapidly than functions obtained under conditions which allow complete adaptation. In other words, conditions which lead to incomplete adaptation cause an increase rather than a decrease in adults' increment threshold slopes. Since infant slopes were shallower than adult, we can conclude that if early adaptation processes are immature, the effect of the immaturity is quite different than the effect of minimizing light adaptation in adults.

A number of reasonably specific sensory explanations are worth considering. These explanations involve various pre-retinal and retinal differences between infant and adult eyes. We will discuss these differences and their possible effects on the slope of the increment threshold function in turn.

Pre-retinal factors

One possible explanation involves various pre-retinal factors. The hypothesis might be stated simply as follows: infant light adaptation is similar to adult adaptation; it just appears different due to pre-retinal factors. We consider two pre-retinal factors here: pupil size and retinal image size. Pupil diameter is less in infants than in adults (Banks, 1980; Salapatek *et al.* 1977). Since retinal illuminance is directly proportional to pupil area, young infants should have lower retinal illuminances than adults for the same external luminance. Consequently, infants in our experiment were exposed to a lower range of retinal illuminances than the adults were. The slope of the adult increment threshold function decreases at low retinal illuminance levels (see Fig. 2), so it is possible that infant slopes are similar to adult slopes once differences in pupil size are partialled out. One way to consider this hypothesis is to plot increment threshold functions for all ages in units of retinal illuminance rather than external luminance. To do so, however, also requires that differences in retinal image size (the second pre-retinal factor) be taken into account. Retinal image size is proportional to the posterior nodal distance of the eye. The axial length of the young eye is much shorter than that of the adult eye (Larsen, 1971), so the posterior nodal distance and retinal image size must also be considerably smaller (Lotmar, 1976). Because of the inverse square law of illumination, the smaller image size of the infant eye works to increase retinal illuminance relative to adults. Thus, the two pre-retinal factors we have considered – smaller pupil size and shorter axial length – have opposing effects on retinal illumination. We used Salapatek *et al.*'s (1977) pupil data and Larsen's (1971) eye size data to estimate the combined effects of these two factors on retinal illumination in infants relative to adults. Our calculations showed a negligible difference in actual retinal illumination between 7-week-olds and adults for the same external luminance.* Twelve-week-olds and adults showed even less difference. Thus, we reject the hypothesis that light adaptation is mature in young infants but appears different due to pre-retinal factors alone.

Spatial and temporal integration

* Pupil area would lead to an average difference in 7-week-old retinal illumination relative to adults) of -0.23 log units. Assuming nodal distance is correlated with posterior segment distance, the 7-week-old's shorter eye would actually lead to an increase in retinal illumination relative to adults of +0.34 log units. Thus, the combined effect is +0.11 log units, a negligible effect given the magnitude of the slope differences we observed.

Another sensory explanation we considered involves differences in spatial and temporal integration between infants and adults. In adults, spatial summation areas and temporal integration times become larger and longer, respectively, as luminance decreases (Barlow, 1958). These changes in summation with adaptation level reflect a trading-off between sensitivity to light and temporal and spatial resolution (van Meeteren and Vos, 1972). Young infants show larger spatial summation areas (Hamer, 1982) and longer temporal integration times (Fulton and Hansen, 1982) than adults at dark-adapted, absolute threshold. Assume that these differences persist across illumination levels. Since summation and integration parameters affect the response to quanta from both the background and the test target equally, these differences in spatial and temporal integration can be modeled by a diagonal shift of the adult increment threshold function. Larger values for these integration parameters would result in a shift of the adult function along a vector oriented at 225° with respect to the origin (a shift to the left and down). Such a shift would bring a steeper portion of the adult function into coincidence with the infant function, a shift in the wrong direction to account for our findings. We conclude that the differences observed between infant and adult spatial and temporal integration are unlikely to account in any simple way for the developmental shift in increment threshold slope.

There is, however, one specific version of the spatial and temporal integration hypothesis which might account for our slope data. This hypothesis is suggested by the observation that shallow increment threshold slopes like those we observed in infants are also observed in adults when the duration and/or test target size is small relative to some critical value (e.g. Barlow, 1957; Glezer, 1965). These critical values are thought to reflect temporal integration and spatial summation. As mentioned above, critical duration and area become longer and larger, respectively, as luminance decreases (Barlow, 1958). Thus, small and/or brief test targets begin to fall completely within the critical area or duration as luminance decreases causing an elevation of threshold at lower intensities relative to higher ones. The net effect is a shallower slope on the increment threshold function for small and/or brief targets.

The test target durations in this study were controlled by the observer and were about 5 sec on average. These long durations must have been well beyond the critical duration of the infant visual system since temporal resolution in infants is not greatly different from adult temporal resolution at mesopic and photopic levels (Regal, 1981). Consequently, it is unlikely that threshold was elevated at lower background intensities due to target duration being short relative to critical duration. The target size we used – 6° x 6°, outside dimensions – was certainly large relative to adult summation areas (Wilson, 1970; Inui *et al.*, 1981), but may have fallen below the critical area of the infant's visual system at low illumination levels. Hamer (1982) provides some support for part of this hypothesis. He found that Ricco's Area (i.e. largest diameter target showing complete summation) at dark-adapted absolute threshold may be as large as 9° and 5° in

4- and 12-week-olds respectively. Consequently, this version of the spatial-temporal integration hypothesis remains viable.[§]

Intensity-response function gain

Any factor which tended to prolong the horizontal, linear portion of the increment threshold function at low background luminance levels could produce the type of results we observed in infants. One plausible factor of this sort would be a lower gain on the function which relates intensity to response in retinal neurons (e.g. Naka and Rushton, 1966). A lower gain on such a function would tend to elevate absolute threshold and to prolong the portion of the increment threshold function where sensitivity is unaffected by background luminance. Both of these effects are compatible with known infant visual psychophysics (Powers *et al.*, 1981; Hansen and Fulton, 1981). Such a lower gain could arise in a number of ways. First, summation across a population of neurons with a wide range of sensitivities would lower the gain of the second-order neuron on which the variable first-order neurons converge. Some support for this hypothesis exists in studies on retinal development in cats. Rusoff and Dubin (1977) found that ganglion cells in the kitten showed a great deal of variability in their center sizes early in life. This variability decreased with development. Second, retinal neurons in immature organisms may simply show less gain in their intensity-response functions.

CONCLUSION

We have shown that the slope of the increment threshold function increases postnatally. We considered a number of possible explanations for this finding. Three simple explanations were ruled out: a nonsensory explanation, a sensory explanation based on pre-retinal factors and a sensory explanation based on spatial and temporal integration. Two other sensory explanations seem feasible: one which assumes that our target size was small relative to Ricco's Area for infants but not for adults and another which assumes that the effective gain of the intensity-response function is lower in infants than in adults. Either of these mechanisms may be manifestations of the marked postnatal development of the human retina reported by Abramov *et al.* (1982) and Mann (1964).

Acknowledgements—We thank Alice B. Andrews for observing all the infants, Dr Ruth Manny and Tony Galardo for serving as adult subjects, and Dr Wilson S. Geisler for discussions on the project and for his criticisms of the manuscript. This research was supported by NIH Research Grant HD 12572 and NIMH Research Scientist Development Award MH 00318 to MSB.

[§] It is possible that some other aspect of the test stimulus besides its outside dimension determined threshold for infants. The target consisted of six evenly spaced light bars each 0.5° wide. Thresholds for infants may have been determined by the visibility of this striation in the target. Slopes may have been shallower for infants due to their relatively poorer spatial resolution at lower light levels. This suggests that adult-like slopes might still be found during early infancy by using a large test target which eliminates these resolution problems.

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