Vision Res. Vol. 22, pp. 575 to 587, 1982
Printed in Great Britain

0042-6989/82/050575-13$03.00/0
Pergamon Press Ltd

RAYLEIGH DISCRIMINATIONS IN YOUNG HUMAN INFANTS

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(*Received* 1 *June* 1981; *in revised form* 12 *November* 1981)

Abstract—The capacity of young infants to discriminate 3 × 3° broadband red or 550 nm green squares from a 589 nm yellow surround was tested by means of the forced-choice preferential looking technique. All 3-month olds, about 3/4 of the 2-month olds, and just under half of the one-month-olds could make at least one of these discriminations. Taken together with other known properties of infant color vision, the failures of discrimination shown by the younger infants are more readily modeled as immaturities of neural processing than as an absence or anomaly of LWS or MWS cones.

INTRODUCTION

The neural substrate of human color vision could develop along many pathways. One possibility is that all of the receptor types and neural elements that subserve color vision are complete at birth. A second possibility is that one or more receptor types lag behind others in development or contain an anomalous photopigment. Finally, it is possible that all receptor types are normal, functional and equally mature at birth, but that elements of post-receptoral neural processing mature postnatally.

Among these options, the second possibility—that one or more of the infant's receptor types may be less than fully functional—has guided most of the current research on infant color vision, including the present project. Receptor-based models for infant color vision are appealing because the most common forms of reduced color vision in adults are usually attributed to an absence of or insensitivity in one or more receptor types, or to the presence of an anomalous photopigment. Furthermore, clear diagnostic tests based on such models are available to establish the presence of these specific deficits in adults. It is likely that with appropriate modifications such diagnostic tests can be applied to infants. A similar approach has proven successful in explorations of color vision in other species (e.g. De Valois *et al.*, 1974).

In a behavioral experiment it is, of course, impossible to demonstrate the *absence* of a receptor type or of a chromatic discrimination capacity, since such conclusions rely on the interpretation of negative results (cf. Teller, 1979). However, questions of the following kind can be addressed empirically. At how early an age can each specific adult receptor type (rods and SWS, MWS and LWS cones) be shown to be functional and be shown to have its characteristic spectral sensitivity? At how early an age can one establish that infants can make at least one wavelength discrimination and thus that at least two receptor types are functional? At how early an age can each of the congenital forms of adult reduced color vision—protanopia, deuteranopia and tritanopia, and the corresponding anomalies—be ruled out as a descriptor of the color vision of infants? And, at how early an age can humans be shown to be normal trichromats? The recent literature provides some partial answers to these questions. (For a more detailed review, see Teller and Bornstein, 1982.)

The dark-adapted spectral sensitivity of 1- and 3-month old infants conforms well to the CIE scotopic luminosity curve from 430 through 650 nm (Powers *et al.*, 1981). Thus, receptors with adult-like, rhodopsin-mediated spectral sensitivity (presumably rods) are clearly functional by 1 month. Infants younger than one month have not yet been tested.

Within the last few years, infants' capacity to make wavelength discriminations have been studied by a variety of paradigms which rule out brightness artifacts (e.g. Peeples and Teller, 1975; Schaller, 1975; Oster, 1975; Bornstein, 1976). These studies show unequivocally that by two and three months postnatal, most infants can make some discriminations solely on the basis of wavelength differences. Thus, 2- and 3-month old infants must be at least dichromats. At the same time, they have sometimes failed to make discriminations that are easy for color-normal adults (e.g. Teller *et al.*, 1978), and their status as normal trichromats is far from established. Wavelength discrimination in infants younger than 2 months has never been demonstrated unequivocally, due to a lack of testing with modern paradigms.

If infants *are* dichromats, are they protanopes, deuteranopes, or tritanopes; or are they dichromats of some non-standard type? Adults affected with either

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of the two most common forms of congenital dichromacy—protanopia and deuteranopia—cannot discriminate among brightness-matched stimuli of wavelengths ≥ 550 nm (Hsia and Graham, 1965). This wavelength region can be called the Rayleigh locus, and discriminations among stimuli from this spectral region can be called *Rayleigh discriminations.* Using a habituation paradigm and group averages, Bornstein (1976) demonstrated that 3-month old infants as a group can discriminate 560 from 570 nm; i.e. they can make at least one Rayleigh discrimination. Further, 2- and 3-month old infants can discriminate white from green and blue-green stimuli that lie close to adult protanopic and deuteranopic neutral points (Bornstein, 1976; Teller *et al.*, 1978). Thus, it seems likely that 2- and 3-month olds are neither protanopes nor deuteranopes, and that they have functional LWS and MWS cone systems.

Studies of spectral sensitivity also suggest that young infants are not protanopes. The luminosity functions of adult protanopes are substantially depressed in the long-wavelength region (Wyszecki and Stiles, 1967; Alpern and Torii, 1968a). However, under conditions of neutral adaptation, the spectral sensitivity of infants between 1 and 4 months of age resembles that of color-normal adults throughout the middle and long wavelength portions of the spectrum (Dobson, 1976; Peeples and Teller, 1978; Moskowitz-Cook, 1979). On the other hand, the luminosity functions of adult deuteranopes differ only slightly from those of normal adults (Wyszecki and Stiles, 1967; Alpern and Torii, 1968b), and the available infant spectral sensitivity data do not have the precision to distinguish between the two. Deuteranopia in 2- and 3-month olds seems unlikely, however, in light of the data cited above on Rayleigh and neutral point discriminations.

A third, less common form of genetic dichromacy is tritanopia. There are two studies consistent with the possibility that infants may have a tritan deficit. Teller *et al.* (1978) reported that 2-month olds failed to discriminate broad-band yellow-greens (dominant wavelengths about 540 and 560 nm) and mid-purples from white. Although this pattern of failure does not fit any of the standard dichromacies well, it is more suggestive of a tritan than a protan or deutan deficit. Further, Pulos *et al.* (1980) failed to isolate the short-wavelength-sensitive (SWS) mechanism in most 2-month old infants under conditions of chromatic adaptation that reveal it in adults and most 3-month olds. Thus, the SWS mechanism may be less than fully functional at 2 months postnatal.

Another possibility is that human infants are dichromats of a non-standard form. Within the context of receptor-level models, current color theory departs from classical views in an increasing emphasis on the role of rods in adult color vision. It is now well established that under many conditions, such as large fields, peripheral viewing, and low luminances, adult red–green dichromats can make discriminations along the Rayleigh locus, and it is likely that under these conditions they are using their rod systems in place of the deficient cone system (Smith and Pokorny, 1977; Breton and Cowan, 1980; Nagy, 1980). Perhaps the wavelength discriminations that infants have made in previous studies have been based on the use of rods plus one of the three cone types.* Smith, Pokorny, and Newell (1978) have calculated the neutral points and other properties of color vision in an organism possessing only rods and a single cone type. They predicted that the rods in combination with SWS, MWS or LWS cones would yield neutral points at 476, 526 and 538 nm, respectively. The fact that 2-month old infants have thus far exhibited a neutral zone in a broad region around 550 nm (Teller *et al.*, 1978) and that infants' rod systems are functional very early (Powers *et al.*, 1981) make the possibility that infants could use rods, plus the MWS or LWS cones to make Rayleigh discriminations an interesting option.

Finally, it is possible that infants, whether they are dichromats or trichromats, have one or more anomalous pigments; i.e. pigments with λ_{max} shifted away from the usual adult values of about 445, 535 and 565 nm. Juvenile pigments are known in other species (Bridges, 1972; Liebman, 1972), and these options probably should not be discarded without evidence.

In summary, infants appear to have at least dichromatic color vision by 2 months of age, but the number of functional photopigment systems and their respective $\lambda_{max,s}$ have not yet been established. There is some evidence against protanopia in 1-month olds (Moscowitz-Cook, 1979), some against deuteranopia in 2-month olds (Teller *et al.*, 1978), and some evidence that is consistent with either a tritan deficit or with color vision based on the use of rods and LWS cones in these young infants (Teller *et al.*, 1978; Powers *et al.*, 1981). By 3 months of age infants, as a group, can make at least one Rayleigh discrimination (Bornstein, 1976), making unlikely both protanopia and deuteranopia as models for the color vision of infants 3 months of age or older. Rayleigh discriminations have not been investigated in infants younger than 2 months of age.

The objectives of the present research were the following. First, we wanted to replicate on individual infants the observation (Bornstein, 1976) that 3-month olds as a group can make Rayleigh discriminations, and to gather enough data on each infant so that the extent of individual differences among infants could be visualized. Second, we wanted to extend these observations to younger infants, to see whether a developmental trend could be found, and to search for the earliest age at which most normal infants can make Rayleigh discriminations. Third, we wished to determine the earliest feasible age for using behavioral

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*A person with only one cone type plus rods is often technically called a monocone monochromat (e.g. Pokorny *et al.*, 1970) rather than a dichromat.

testing to diagnose the presence of red–green congenital color deficiencies. Finally, we sought to explore an important class of alternative models, based on the assumption of neural rather than receptor-level deficits.

METHODS

The forced-choice preferential looking (FPL) technique was used for the present experiments (for details see Teller *et al.*, 1974; Teller, 1979). In FPL testing, an infant is presented with a visual stimulus that appears randomly either on the right or on the left in an otherwise homogenous field (Fig. 1).

In the present version of the method, an adult observer, who is blind to the position of the stimulus, holds the infant in front of the stimulus display and observes the infant's face by means of a TV camera-monitor system (Fig. 2).

The observer is required to judge the position of the stimulus on each trial based on the infant's looking behavior. Feedback is provided on each trial in order to optimize the observer's use of relevant cues from the infant. If the observer performs significantly above chance, we conclude that the infant is capable of discriminating the stimulus from its surroundings, since information regarding the position of the stimulus can reach the observer only via the infant's behavior.

The paradigm used for separating wavelength discrimination from brightness artifacts is identical to that used previously (Peeples and Teller, 1975; Teller *et al.*, 1978). In the present study, a 3° x 3° red or green square was embedded in a yellow surrounding field (Fig. 1). The red or green square was presented at each of a series of different luminances surrounding the adult heterochromatic brightness match. All luminance steps in the series were so small (see *Calibrations* below) that at least one of the luminance levels should have confronted the infant with a brightness match between the stimulus and the screen.

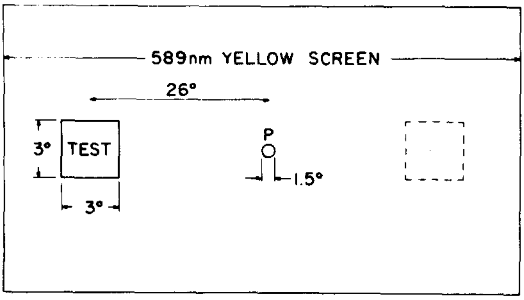

Fig. 1. Infant's view of the stimulus screen (not to scale). The screen is illuminated with 589 nm yellow light from a low-pressure sodium lamp. A 3° x 3° test stimulus, which can vary in both wavelength composition and luminance, is presented randomly in one of two stimulus positions, 26° to the left or right of a 1.5° peephole P. In the case depicted here, the test stimulus is being presented on the left. The yellow screen extends vertically and horizontally over almost the entire visual field.

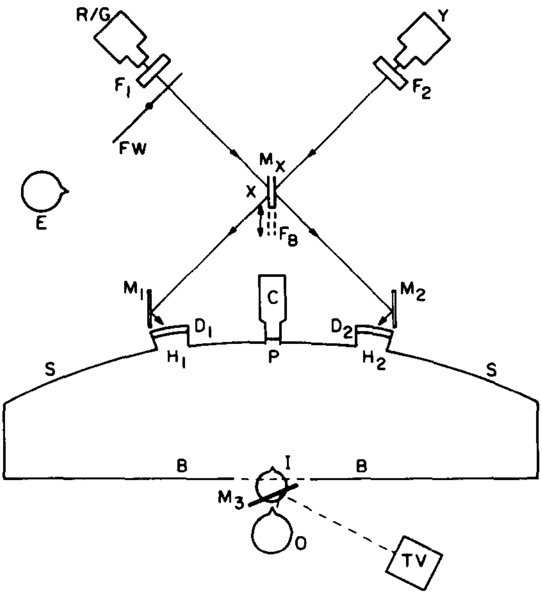

Fig. 2. Schematic top-view of the apparatus (not to scale). Light from two slide projectors, R/G and Y, passed through spectrally selective filters at F1 and F2 and variable neutral density filters at FW, and arrived at a cross-point X. For the test stimulus (generated by projector R/G) to be presented on the left (right), the mirror M_x was rotated into (out of) the projector beams. The light was then reflected from mirrors M_1 and M_2 to diffusers D_1 and D_2, and filled the holes H_1 and H_2 in the screen S. The infant I, held by the Observer O, viewed the display through an opening in a baffle B. The television camera C was situated 32 ± 2 cm directly in front of the infant behind a peephole P in the screen. The observer watched the infant's face and eye movements on a television monitor TV via mirror M_3.

Many levels of performance are possible in an experiment of this kind (cf. Fig. 3). An infant might produce significantly above-chance performance at all luminance levels in the series. Such performance would imply that the infant has made at least one discrimination in the series on the basis of wavelength alone (Peeples and Teller, 1975). On the other hand, an infant's data might dip to chance over a narrow range of luminances (Teller *et al.*, 1978). Such an infant provides no evidence of being able to make the wavelength discrimination being tested, and the dip to chance is taken to indicate the luminance level at which the minimum brightness difference is available to the infant, i.e. the infant's brightness match. For further discussion, see Peeples and Teller (1975), Teller *et al.* (1978) and Teller and Bornstein (1982).

Equipment

A schematic view of the apparatus is shown in Fig. 2. An infant was held 32 ± 2 cm in front of a large screen S which was uniformly illuminated by narrow-band yellow light. The infant viewed the screen through a 14 x 25 cm window in a baffle B. An 8.5 mm peephole P was cut in the center of the screen, behind which was placed a television camera C. Two 22 mm squares H_1 and H_2 were cut in the screen

15.5 cm (measured center-to-center) to the left and right of the peephole and were diffusely illuminated from the rear. The distance from the infant to the center of the peephole, and from the infant to the centers of each of the stimulus squares were 32 ± 2 cm and 35.6 ± 2 cm, respectively. Thus, the peephole subtended 1.5°; and each of the squares H_1 and H_2 subtended 3° × 3°, with their respective centers positioned 26° to the left and right of the center of the peephole.

Two slide projectors (Kodak carousel No. AF-2) with tungsten-halogen lamps (General Electric Quartzline ELH, 300 W) were run from regulated line current. The lamp current could be continuously varied by means of a rheostat. One projector, R/G, was used to generate test stimuli of various wavelengths and luminances. The other projector, Y, was used to generate a stimulus that was always matched to the screen in both dominant wavelength and luminance. The light from the projectors passed through fixed, spectrally selective filters at F_1 and F_2 and through variable neutral density filters at FW, and arrived at the cross-point X. An opaque, double-sided mirror M_x was rotated into or out of the light beams to present the test stimulus on the left or right, respectively. When M_x was rotated out of the light beams, a balancing filter FB was rotated into the beams to compensate for the small intensity loss caused by reflection of the light from M_x. After leaving X, the light was reflected from mirrors M_1 and M_2, passed through diffusers D_1 and D_2, and emerged through the holes in the screen.

Spectrally selective filters were either interference filters (Corion or appropriately blocked Bausch and Lomb) with half-band widths of 10 nm and nominal peak transmissions at 550 ("green"), 580, 589.6 and 600 nm, or a Kodak No. 29 ("red"), a broad-band filter with a cut-off of 620 nm and dominant wavelength of 633 nm. Neutral density filtering was provided by combinations of Kodak No. 96 filters, glass cover slips, and specially constructed cover slips containing small opacities, as needed to generate the exact luminance variations called for by the experimental design. The balancing filter FB was similarly constructed. Front illumination of the screen at 589.6 nm was provided by a low-pressure sodium lamp (Quality Outdoor Lighting, Model No. 2001), run from a voltage-regulated power supply (Sola Electric, 750 W).

An adult observer O held the infant I in front of the screen and watched the infant's face in a television monitor TV via a mirror M_3. The observer could not see the stimuli due to the presence of the baffle. Between trials the observer turned the infant away from the screen while an experimenter E set up the next trial by means of variations of filters at FW and the mirror at X. The experimenter also recorded the responses of the observer (correct or incorrect) and gave the observer trial-by-trial feedback about the correctness or incorrectness of his or her judgements.

Calibrations

The screen luminance was kept constant at 0.7 ± 0.08 log ft-L (1.2 ± 0.08 log cd/m^2) as measured by an SEI exposure meter. The relative luminances used in the R/G channel were selected and calibrated *in situ* with an International Light Photometer. Adjacent luminances in the luminance series were adjusted so that they differed by a target value of 0.08 log units (l.u.) and upon recalibration differed by no more than 0.09 l.u. Previous studies (Peeples and Teller, 1975; Teller *et al.*, 1978) have established that these luminance steps are small enough to confront 2-month olds (and presumably 1-month olds as well) with at least one luminance that falls within the infant's Weber fraction of a brightness match to the screen. Justification of this luminance spacing for 3-month olds is given below.

The luminance match of the Y channel to the screen was made by an adult observer at the beginning of each test session by means of adjustment of the current supplied to the projector bulb, and was rechecked during and after the session. The luminance of the R/G channel with respect to the screen was monitored before each session by replacing the chromatic filter at F_1 with a 589.6 nm filter identical to that used in the Y channel, and setting the wheel FW to a specific location. The adult observer then matched the brightness of this channel to the screen by means of a variation of bulb current, and replaced the appropriate chromatic filter in the R/G channel.

Infants

Healthy, full-term infants whose births were listed in the local newspapers were solicited by mail. All infants but one were born within 10 days of their due date by parents' report. All parents reported that there was no known history of color blindness on either side of their family. Approximately equal numbers of male and female infants were tested.

Infants were tested in two to ten 1-hr experimental sessions between their 18th and 36th postnatal day (4-week olds), or between their 46th and 64th postnatal day (8-week olds), or between their 74th and 92nd postnatal day (12-week olds). Infants were dropped from the study if they failed to produce an average of 20 trials per day over the first three days of the experiment. Out of 92 infants who began the experiment, 10 did not complete testing because of equipment failure and/or experimenter error, and 4 withdrew mid-experiment by the decision of the parents. Of the remaining infants, 10 were excluded because of undue fussiness or sleepiness, and 2 did not produce enough trials to complete a data set. An average of 36, 28 and 41 trials per session were obtained from the 4-, 8- and 12-weeks old infants, respectively, who completed the study.

Experimental design

The study consisted of two phases. In phase 1, twenty seven 2-month old infants were tested. Of these, 12 were re-tested at 3 months of age, along with 13 previously untested 3-month olds. The data from longitudinally and cross-sectionally tested three-month-olds were highly similar and have been combined. In phase 2, the study was extended to include fourteen 1-month olds.

We attempted to test all infants at each age in both the red/yellow and the green/yellow discrimination tasks; most infants were tested on both red and green. Data sets from infants who completed only one discrimination task were retained. Three particularly cooperative 3-month old infants were also tested with 580 and/or 600 nm stimuli. The luminance series for each of the chromatic stimuli consisted of 10 to 18 luminance values presented in a pseudorandom order that was weighted against the repetition of luminance values and stimulus positions. The stimulus ranges were chosen to encompass the heterochromatic brightness match points of both normal and dichromatic adult observers (cf. Table 1).

Testing at each luminance continued until the infant reached one of three criteria—six out of six, nine out of ten, or 13 out of 15 correct—or until 20 trials at that luminance had been presented (cf. Dobson *et al.*, 1978). If $P = 0.5$, the cumulative sequential probability of the scores 6/6, 9/10, 13/15 or 15/20 is 0.034. Infants were said to pass if they achieved any of these scores on all intensities. If infants achieved a score of less than 15/20 (75%) on any single intensity, they were considered to have failed to demonstrate the Rayleigh discrimination being tested.

A few cooperative 1-month olds were tested more extensively. These more extensive data sets were collected because chromatic discriminations have not previously been demonstrated in 1-month olds, and we wished to increase our certainty that the present data could not be explained by statistical or luminance artifacts. The luminance range of the red or green stimulus was extended downward in 0.08 l.u. steps toward decreasing luminances for 0.3–0.5 l.u. beyond the usual range. For three infants this was done with both red and green, for one infant with green alone, and for one infant with red alone. In addition, one 1-month old infant was tested with green with a minimum of 20 trials at all luminance values tested.

Adult brightness matches and color vision assessment

We wished to establish foveal heterochromatic brightness matches for color-normal and red-green color-deficient adults, and for color-normal adults viewing the stimulus extrafoveally, in order to establish norms and to provide a wider variety of interpretative contexts for the infant data, as discussed below. Since infant and adult photopic spectral sensitivities are quite similar at λ's ≥ 550 nm, we assume that the adult heterochromatic brightness match was a good first approximation to the infant match. In order to establish the appropriate range of test luminances for infants, we measured foveal red/yellow and green/yellow heterochromatic brightness matches in 15 and 17 color-normal adults, respectively. In addition, since we do not know *a priori* which part of the retina infants might use to make the Rayleigh discriminations, we measured red/yellow and green/yellow brightness matches in 8 color-normal adults at 26° in the periphery (temporal visual field). Furthermore, under the hypothesis that infants' color vision might mimic some or all of the properties of color-deficient adults, we measured these heterochromatic brightness matches foveally in 3 protanopes, 2 deuteranopes, 4 simple protanomalous and 2 extreme deuteranomalous adults.

Color deficiencies of the adult subjects were classified by using a battery of standard tests that included Ishihara Plates (1974 edition), Hardy-Rand-Rittler Pseudoisochromatic Plates (1957 edition), and Farnsworth Panel D-15 test, and diagnosis on the Nagel Anomaloscope (Schmidt–Haensch) by using a method that combined procedures used by both Linksz (1964) and Schmidt (1955).

Each adult subject made brightness matches between the yellow screen and the other chromatic stimuli, first by the method of adjustment and then by the method of constant stimuli. Matches obtained by the two procedures were always quite close (within 0.08 l.u. of each other).

Table 1. Adult heterochromatic brightness matches

	R vs Y			G vs Y		
	n	$\bar{x}$	SD	*n*	$\bar{x}$	SD
N	15	0	0.140	17	0	0.191
Pa	4	0.33	0.200	4	−0.03	0.147
P	4	0.58	0.172	3	0.06	0.115
DA	2	0.17	0.028	2	0.27	0.099
D	3	0.14	0.055	2	0.29	0.057
N	8	0.10	0.093	8	−0.03	0.065

Numbers under $\bar{x}$ are the mean luminances (in l.u.) of the brightness matches for each of the groups of subjects, relative to the mean normal adult foveal match (N). Positive numbers indicate that a group of subjects required, on average, more R (or G) light to achieve a brightness match than color-normal adults viewing the stimulus foveally. Standard deviation (SD) and number of subjects tested (*n*) are also listed for each group. Pa—foveal matches made by simple protanomalous adults; P—foveal matches made by protanopes; DA—foveal matches made by extreme deuteranomalous adults; D—foveal matches made by deuteranopes; N—matches made by color-normal adults, with the test stimulus presented 26° in the temporal visual field of the right eye. The values reported here (and plotted in Figs 7 and 8) for the N group are mean peripheral brightness matches in l.u. relative to their own average foveal matches. Their average red/yellow foveal match was at a luminance 0.05 lm dimmer than the mean red/yellow, foveal match made by the larger group of color-normal adults; their average green/yellow foveal match was 0.06 lm dimmer than the larger group's green/yellow foveal match.

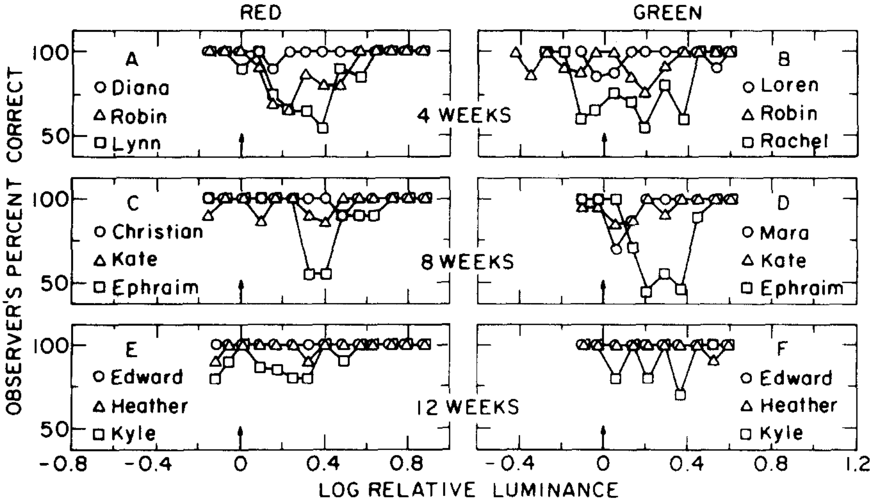

Fig. 3. Representative data sets for red (broad-band) and green (550 nm) stimuli. In each graph, the observer's percent correct (on the ordinate) is plotted against the log relative luminance of the red or green test stimulus (on the abscissa). The arrow at zero on the abscissa indicates the average adult heterochromatic brightness matches of the red or green stimulus to the yellow screen. For each age group—4 weeks (A and B), 8 weeks (C and D) and 12 weeks (E and F)—and for each of the two colors tested, the infants with the best (○) and worst (□) overall performance are shown, along with one judged to be illustrative of typical behavior for its group (△). Performance is about equal for red and green. As groups, older infants do better than younger ones.

RESULTS

Adult brightness matches

The heterochromatic brightness matches made by adults varied somewhat among individuals and conditions, as shown in Table 1.

As expected, protanopes and protanomals required considerably more red light for the red/yellow matches than did color-normals, the difference being about 0.6 and 0.3 l.u. respectively. Deuteranopes, deuteranomals, and color-normal individuals viewing peripherally also required slightly more red light than did color normals.

Variations in the amount of 550 nm light needed for the heterochromatic brightness matches were smaller. Deuteranopes and deuteranomals required about 0.3 l.u. more 550 nm light than did color normals; the other groups were not meaningfully different from normals. Some of these results are indicated on the abscissae of Figs 7 and 8 and will be discussed more fully below.

Data from individual infants

Illustrative individual data sets are shown in Fig. 3 for 1-month olds (A and B), 2-month olds (C and D) and 3-month olds (E and F).

In each case, three data sets are plotted, showing infants with the best (unfilled circles), worst (unfilled squares), and typical (unfilled triangles) performances, where "typical" is chosen by eye to be illustrative of the central tendency for that age group. Within each age there are marked individual differences, with some data sets remaining clearly above chance for all stimulus luminances and others dropping toward chance performance over a limited range of luminances. As groups , the 3-month olds showed the highest overall performance and the 1-month olds the lowest.

These developmental trends also hold for individual infants tested longitudinally. Of the 12 infants tested at both 8 and 12 weeks of age, 6 yielded data sets that dipped below 75% correct when first tested at 8 weeks. None of these infants yielded data sets that dipped below 75% correct when they were retested at 12 weeks.

A Pearson correlation (*r*) was calculated between minimum percents correct on red and on green within individual infants. The correlation was 0.25 for the 1-month olds, 0.78 for the 2-month olds, 0.66 for the 3-month olds and 0.73 for all ages combined. Thus, at least in the older age groups, infants who succeeded on one discrimination tended rather strongly to succeed on both. This suggests that variations in performance reflect real individual differences among infants.

The color vision of infants as young as 4 weeks of age has not previously been tested. In the present study, about half of the 4-week olds failed to make one or both discriminations, but the other half succeeded in discriminating at least one of the two stimuli from the yellow screen. Data from two of the more extensively tested 1-month olds are shown in Fig. 4, one (Michael) tested on green, and one (Diana) tested on red.

It is clear from these data that these two young infants made Rayleigh discriminations since they discriminated each of the test stimuli over the entire extended range of luminances tested. To our knowl-

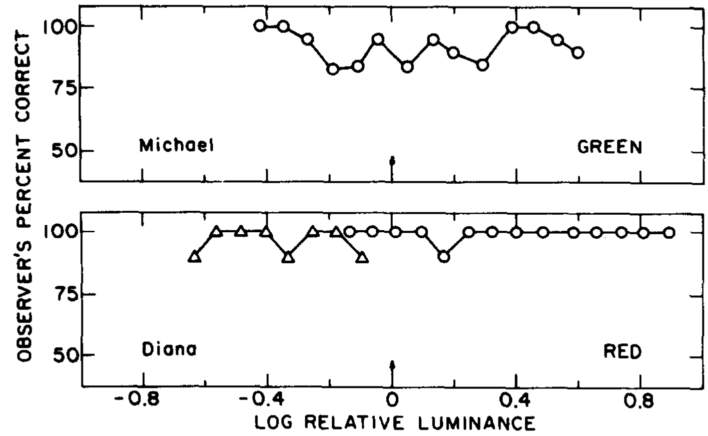

Fig. 4. Individual data sets from two of the more extensively tested 4-week olds, Diana (tested on red over an extended luminance range) and Michael (tested on green with a minimum of 20 trials per point). Axes are as in Fig. 3. Both infants discriminated the test stimuli from the yellow screen.

edge these data and the related data of Fig. 3A and 3B represent the first demonstration of chromatic discrimination in infants less than 8 weeks of age.

Finally, Fig. 5 shows data from three particularly cooperative 3-month old infants who, in addition to being tested with red and green, were also tested with 580 and/or 600 nm stimuli.

All three infants showed discrimination of red and green from the yellow screen. But when the 580 or 600 nm stimuli were used, the data from two out of the three infants dipped toward chance near the adult brightness matches.

These data help to rule out an alternative interpretation of why the average performance of the 12-week olds is improved relative to the two younger age groups (see Fig. 3). That is, perhaps their brightness discrimination capacity is so well developed that their performance in this Rayleigh discrimination task simply results from being consistently presented with discriminable brightness mismatches. Our luminance step size (maximum of 0.09 l.u.) was chosen on the basis of luminance discrimination data taken from 2-month olds (Peeples and Teller, 1975; Teller *et al.*, 1978) using a slightly different stimulus paradigm, and it might not have been small enough to present every 3-month old with a brightness match. However, as shown in Fig. 5, two of the 3-month olds who succeeded on red and green discriminations failed when the 580 and 600 nm stimuli were used. Their data do not support the contention that the infants' luminance discrimination functions are less than 0.08 l.u. in width. Hence, it seems unlikely that these infants' successes with the red and green stimuli could be caused by our missing a very narrow dip to chance. The third infant, Jennifer, discriminated the 600 nm stimulus from the 589 nm screen, and hence failed to provide any evidence concerning the width of her luminance discrimination function.

Group data

The trends with age are more easily visualized when the data are combined across infants. In Fig. 6A we have summarized all infants' minimum percents correct for each age and each color tested. In this plot, minimum points from the red/yellow discriminations are accumulated in bar graph form to the left

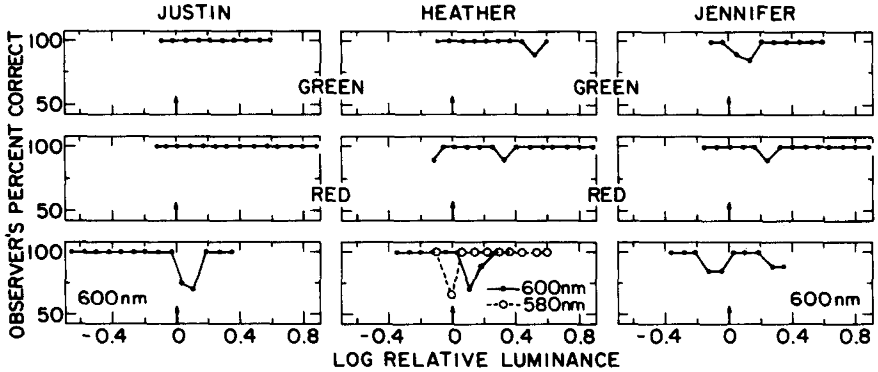

Fig. 5. Individual data sets from three 12-week old infants tested with 580 and/or 600 nm as well as the standard red and green test stimuli. Axes are as in Fig. 3. All three infants clearly discriminated red and green from the yellow screen. Two of the three infants failed to discriminate the 600 nm and/or 580 nm stimulus from the yellow screen.

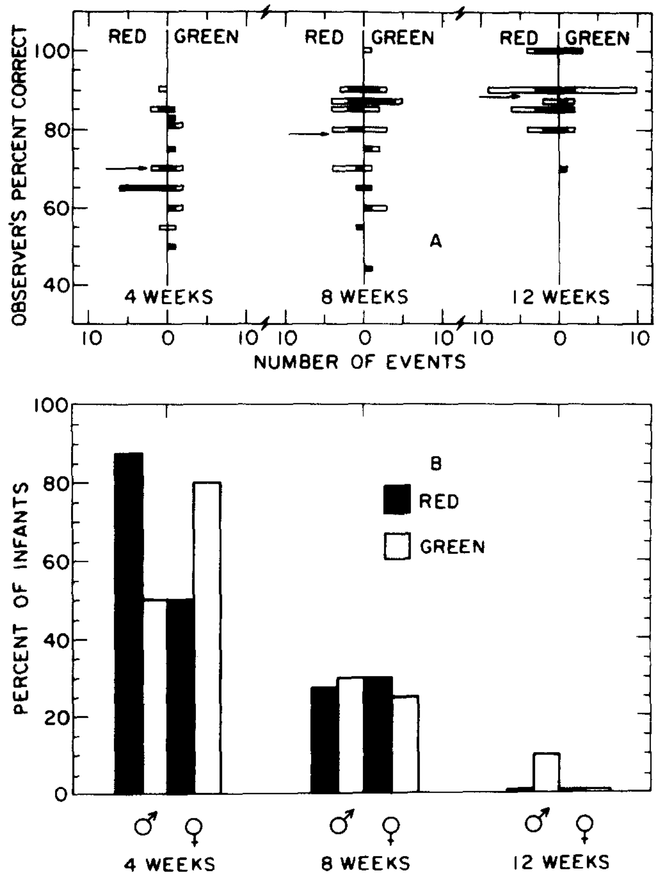

Fig. 6. Frequency distributions of individual infants' performances, classified by age, sex and color (red or green) of the test stimulus. (A) Observer's minimum percent correct. Minima for red stimuli are accumulated leftward, in bar graph form, for each age group; minima for green stimuli are accumulated rightward. Filled portions of bars: male infants; unfilled portions: female infants. The horizontal arrows mark the mean minimum percent correct at each age when all the data, male and female, red and green, were combined. (B) Percentages of infants who "failed," i.e. percentage of data sets that dipped below 75% correct. Dark bars: red. Light bars: green. For each age group the two left-most bars are for male infants; the two right-most are for female infants. The infants' performance increases dramatically between 4 and 12 weeks of age. There were no significant differences between red and green, nor between males and females.

of the vertical line; data from the green/yellow discriminations are accumulated to the right. Filled portions of the bars represent the data from male infants; unfilled portions represent data from female infants.

The horizontal arrows in Fig. 6A mark the mean minimum percent correct at each age when the data from red and green, male and female were combined. This figure shows that the infants' minimum points are distributed continuously over the range of percents correct. The improved performance with age is evidenced clearly in the shift of the distribution of minimum points toward 100% correct and in the group averages.

Figure 6B shows the percentage of infants at each age whose data dipped below 75% correct. The data have been separated for each age group according to sex and according to the color that was tested. It is clear from this representation that, according to this 75% criterion, the performance of the infants improved dramatically with age. After combining all the data within each age group (red, green, male and female), the percentage of data sets that dipped below 75% correct was found to decrease from 68% (17 out of 25 data sets) at 4 weeks of age, to 28% (12 out of 43 data sets) at 8 weeks of age, to 2% (1 out of 45 data sets) at 12 weeks of age. According to a χ^2 test, overall performance of the infants in the red/yellow discrimination improved significantly between 4 weeks and 8 weeks of age ($P < 0.05$), and between 8 and 12 weeks of age ($P < 0.02$). For the green/yellow discrimination performance changed in the direction of improvement between 4 and 8 weeks and between 8 and 12 weeks, but these changes were not statistically significant ($P < 0.10$ and $P < 0.20$, respectively). Between 4 and 12 weeks of age, performance improved dramatically in both Rayleigh discriminations ($P < 0.01$).

The above presentation of group data does not give any indication of where on the luminance axis infants' data tend to dip, i.e. where the infants' region of difficulty is. This region is apparent in Figs 7 and 8. The

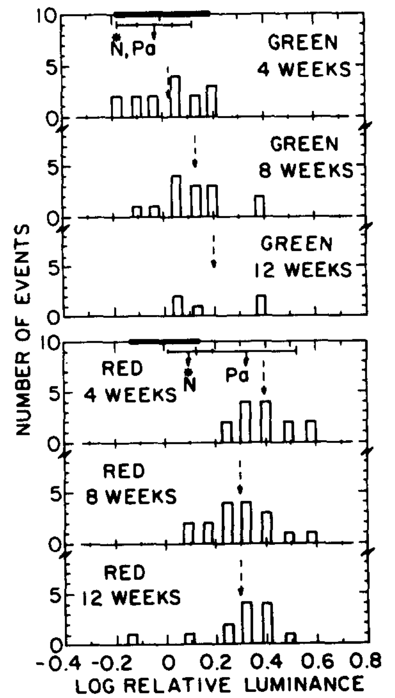

Fig. 7. Frequency distribution of the test stimulus luminances at which infants' minimum performances occurred. Only minima falling to ≤85% correct were included. When a data set had two or more points falling to the same level, all such points were included. The top three distributions are for green, for the 4-, 8- and 12-week olds. The bottom three distributions are for red for each of the age groups. The abscissae are the luminances of the test stimuli in l.u. relative to the mean color-normal adult foveal brightness match. The arrows marked N and Pa indicate, respectively, the mean heterochromatic brightness match for color-normal adults viewing the stimulus at 26° in the temporal visual field, and simple protanomalous adults viewing the stimulus foveally (Table 1). Horizontal bars are ± 1 SD. Thickenings of the axes mark ± 1 SD for the normal adult foveal matches. A single arrow (top) represents both the N and Pa green/yellow matches (since they were identical); the inner pair of bars is ± 1 SD for the N group. The dashed vertical arrows mark the means of the distributions of the infants' data.

top and bottom halves of each of these figures present data from green/yellow and red/yellow discriminations, respectively. The abscissa in each figure is log of the luminance of the red or green test square relative to the average color-normal adult heterochromatic brightness match. The thickened portions of the abscissae mark ± 1 SD for these adult matches. Arrows marked Pa and N indicate, respectively, the mean brightness matches of 4 protanomalous adults viewing the stimulus foveally, and 8 color-normal adults viewing the stimulus 26° in the temporal visual field. Figure 7 presents histograms of all minima falling to 85% correct or less. Data from the 4-, 8- and 12-weeks olds are presented in order of age, top to bottom. Vertical dashed arrows mark the mean minimum luminance for the infants' data.

Figure 8 presents the group means of all the data at each age. The data presented in Figs 7 and 8 clearly demonstrate the tendency for minima in the infants' green/yellow discriminations to occur near the range of normal adult brightness matches.[*] However, in the red/yellow discrimination data there is a systematic disparity between the minima in the infants' data and the normal adult brightness matches; the minima tend to occur 0.3 to 0.4 l.u. above the normal adult matches. As was seen in previous figures (e.g. Fig. 6), Fig. 8 also shows that the infants' performance (measured in terms of the level to which the averaged data dip) improves with age.

Finally, we would like to have a template curve for each age group that depicts the variations over luminance that we expect to obtain from a typical infant. Such a template curve cannot be deduced from the group means presented in Fig. 8. We must first factor out the effect of individual differences in the position of minima on the luminance axis. Toward this goal, the individual data from each age group were normalized so that all minima coincided at zero on the luminance axis and then were averaged.[†] Data from the red/yellow and green/yellow discriminations were combined. This normalization yielded the desired template curves which are shown in Fig. 9.

It is evident that the average infant's data in each age group manifests a distinct region of difficulty (dip) which is considerably narrower and deeper than the comparable group data depicted in Fig. 8. In addition, the data in Fig. 9 demonstrate how the performance of the typical infant in these particular Rayleigh discriminations improves with age—the dips in the data become progressively shallower and perhaps narrower over the course of the first 3 months of life.

DISCUSSION

Using the FPL technique, we have tested the capacity of 1- 2- and 3-month old human infants to make Rayleigh discriminations, i.e. to discriminate among stimuli of wavelengths ≥550 nm. At 4 weeks of age, about half of the infants discriminated a 3° × 3° broad-band red or 550 nm green square, or both, from a 589 nm yellow surround. The proportion of infants that can make these discriminations increases with age, so that by 2 months of age the majority of the infants are making Rayleigh discriminations, and by 3 months of age virtually all infants

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[*] The apparent reverse age trend in the green-yellow discrimination data (infants' mean minima progress away from the mean adult brightness match with increasing age) is probably not meaningful trend, reflecting, more than anything else, the small number of minima falling below 85% correct in the 12-week olds' data.

[†] Occasionally a data set had no minimum (e.g. all points at 100% correct). In this case the data point closest to the center of the luminance range tested was aligned with zero on the abscissa. A few other data sets had two or more relative minima dipping to the same level of percent correct. In this case the minimum lying closest to the center of the luminance range was used to normalize the data on the abscissa.

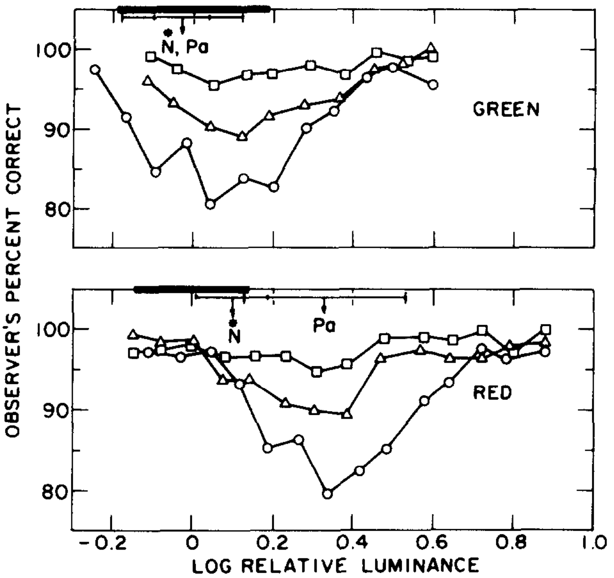

Fig. 8. Means of data from all infants at each age for green (top) and red (bottom). ○: 4-week olds (Green: $n = 13$; Red: $n = 12$). △: 8-week olds (Green: $n = 23$; Red: $n = 21$). □: 12-week olds (Green: $n = 20$; Red: $n = 25$). Arrows, SD bars and axis thickenings as in Fig. 7. The average performance improves with age.

are doing so. The latter observations thus confirm the previous report (Bornstein, 1976) that 3-month old infants discriminate among some pairs of stimuli of wavelengths greater than 550 nm, and show, under the present stimulus and testing conditions, a clear developmental trend in the proportion of infants who do so.

Interpretation of successful Rayleigh discriminations

The successful Rayleigh discriminations made by some infants at each age strongly imply that these infants have at least two receptor types sensitive to middle- and long-wavelength stimuli. Such infants must also have the neural substrate necessary for the comparison of outputs from the two receptor types, and the necessary neural substrate to preserve wavelength information all the way through the nervous system to the motor outputs which control the infant's looking behavior. According to classical color theory these two receptor types would contain the LWS and MWS cone photopigments. However, as discussed in the introduction, the possibility of the combination of either LWS or MWS cones with rods, and the possibility of one or more anomalous pigments, cannot be ruled out.

Interpretations of failures to make Rayleigh discrimination and changes with age

As outlined in the introduction, the failure of some infants to make Rayleigh discriminations are open to

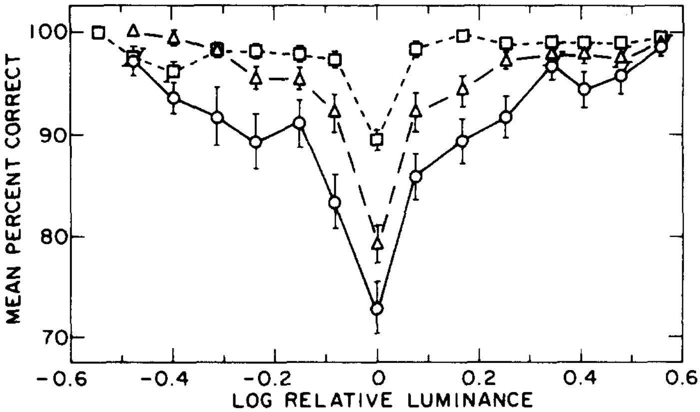

Fig. 9. Normalized data, depicting the performance of the average infant at each age, after factoring out individual differences in the luminance at which discrimination is most difficult. All data sets were shifted laterally so that their minima coincided at zero on the abscissa. Means of data from all infants were then calculated. Each point represents the average of 10 to 45 data points. Vertical bars (not shown if less than or equal to the size of a data point) are ± 1 SEM. ○: 4-week olds. △: 8-week olds. □: 12-week olds.

two main, nonexclusive lines of interpretation within color vision theory. The first is that the color vision of these infants differs from that of color-normal adults because of the properties of their photopigments or photoreceptor types. The second is that their color vision may be limited by immaturities of neural processing.

In the context of receptor-level theory, difficulty in making Rayleigh discriminations is attributed to an absence, anomaly, or extreme insensitivity of either LWS or MWS cones (or both). Within this context, one would interpret the developmental trends observed here as reflecting the maturation of one or both of these cone types. Such maturation could occur along more than one dimension—either changes in sensitivity, reflected as parallel vertical shifts in the spectral sensitivity curves of one or more cone types, or changes in the wavelength of peak sensitivity.

The improvement in Rayleigh discrimination capacity over age could result from a major increase in the sensitivity of the MWS and/or LWS cones. However, if in addition, the shape or $\lambda_{\max}$ of one or more of these spectral mechanisms differed from that of normal adults, we would expect infants' heterochromatic brightness matches to differ from adults'. This possibility is particularly appealing because it provides a possible explanation for the finding (Figs 7 and 8) that infants' regions of minimal discrimination of red from 589 nm yellow is closer to the brightness matches of protanomalous adults than to the matches of normal adults. However, the possibility that infants are protanomalous appears to be contradicted by the results of the infant spectral sensitivity studies discussed earlier.

The second major interpretation of discrimination failures is that the LWS and MWS receptors are both functional in young infants, but that the infants who fail lack elements of the neural processing needed to analyze the information coming from the receptors. There is substantial evidence to suggest that the neural processing in the infant photopic visual system is immature. For example, young infants' grating acuity is four to five octaves poorer than adult acuity (Dobson and Teller, 1978), and their contrast sensitivity functions are depressed in the high frequency range and lack a low frequency falloff (Banks and Salapatek, 1981). These data suggest that the overall spatial resolution capacities of infants may be relatively poor, and it is reasonable to speculate that infants' spatial summation areas may be large. One consequence of large summation areas would be a functional mixing of small stimuli with their surrounds, with a consequent degrading of wavelength discrimination (cf. Gordon and Abramov,, 1977; Loop *et al.*, 1979). Thus, the improvement in Rayleigh discrimination capacities of infants could be the result of maturational decreases in the size of summation areas within a system in which the LWS and MWS cones are relatively well developed from the start.

Another example of a neural loss hypothesis, and one which we would like to discuss in some detail, is that infant color vision is more comparable to adult peripheral color vision than to adult foveal color vision. This possibility could come about either if infants are using their peripheral retinas to make chromatic discriminations, *or* if the area that will be fovea has not yet developed its foveal properties and in its immature states bears a functional resemblance to adult peripheral retina.

Adult peripheral color vision has a number of properties in common with the results of the present experiment and earlier experiments on infant color vision. First, small chromatic stimuli in the periphery appear desaturated compared to the same stimuli viewed foveally (Moreland, 1972; Gordon and Abramov, 1977); and the apparent hues of chromatic stimuli from the middle-and long-wavelength regions of the spectrum can change in the direction of yellow when they are viewed peripherally (Stabell and Stabell, 1979a, b). The poorer performance of the younger infants in the present study could possibly be due, in part, to such a yellowing and desaturation of the red and green stimuli, making them less discriminable from the yellow screen. The previous observation (Teller *et al.*, 1978) that infants fail to discriminate yellow-greens from white is also consistent with this characteristic of adult peripheral retina.

Second, as noted above, there are good reasons to speculate that infant's spatial summation areas are large. The same is true of adult peripheral vision. The causes of the coarser spatial-resolution properties of the adult peripheral retina are likely to be related to those responsible for the well known color deficits often found beyond 25°–30° eccentricity (cf. Wooten and Wald, 1973). Since all three cone mechanisms appear to be present out to at least 70°–80° eccentricity (Weale, 1953; Wooten and Wald, 1973; Wooten *et al.*, 1975), such losses in peripheral color vision are thought to reflect neural convergence and a consequent fusion of chromatic channels (Wooten and Wald, 1973). Consistent with this view of adult peripheral color vision is the observation by Gordon and Abramov (1977) that peripheral color vision can be dramatically improved by increasing the size of the stimuli used—a 1.5°, monochromatic stimulus viewed 45° in the periphery appears desaturated and of uncertain hue, but when increased in size to 6.5°, it appears colored and saturated, similar to a 5′ spot viewed foveally.

Third, in the present experiment, color-normal adults required more red light for a brightness match to 589 nm yellow at 26° peripheral than they did with foveal fixation, while matches between 550 nm green and 589 nm yellow did not differ for foveal vs peripheral viewing (Table 1). Although the adult peripheral matches do not account quantitatively for the infants' data, the qualitative similarity between infants' regions of minimal discrimination and the adult peripheral matches is consistent with the hypothesis that whatever part of the retina the infants are using under these conditions is functionally similar to adult peripheral retina.

Finally, chromatic adaptation studies reveal a fourth similarity between adult peripheral color vision and infant color vision. In adult peripheral color vision the SWS mechanism is relatively depressed in sensitivity and/or difficult to isolate by means of standard chromatic adaptation techniques (Wooten and Wald, 1973). Analogously, chromatic adaptation sufficient to reveal the foveal SWS mechanism in adults does not appear to do so consistently in young infants (Pulos *et al.*, 1980).

The suggestion that infant vision is similar to adult peripheral vision has been made before in other contexts. The fovea is poorly developed anatomically at birth (Mann, 1964; Abramov *et al.*, 1982), and Bronson (1974) has suggested that infants are essentially without a functional foveal before three months of age. Many of the known characteristics of infant vision—low acuity (Dobson and Teller, 1978), relatively flat contrast sensitivity functions (Banks and Salapatek, 1981), high critical flicker frequency (Regal, 1981) and well-developed scotopic vision (Powers *et al.*, 1981) are in accord with the properties of adult peripheral vision.

Finally, the possibility that infants' discrimination failures should be attributed to non-sensory factors such as motivation, cognition, or attention, and that the age trends observed in the present study represent maturation on these dimensions, cannot be discarded *a priori*. However, motivational and cognitive approaches are typically lacking in specificity and explanatory power when applied to questions of sensory development. For example, we know of no motivational nor cognitive theory that would offer an explanation of why infants' red-yellow discrimination failures would be displaced from the adult brightness match, nor why the spectral sensitivities of 2-month olds should differ from those of adults under yellow adaptation (Pulos *et al.*, 1980), but resemble those of adults under neutral adaptation conditions (Peeples and Teller, 1978).

Tests for red-green dichromacies in infants

Part of the motivation for the present study was to collect data on presumptively genetically color-normal infants, upon which a test for classical red-green dichromacies and severe anomalies could be built (Teller *et al.*, 1979). It is now clear that, by use of the present paradigm and stimulus parameters, the success rates of infants less than 3 months of age are too low to allow an unambiguous differentiation of color-deficient from color-normal infants. Detection of the red-green dichromacies at 3 months would appear to be a feasible undertaking in the laboratory, although the inefficiency of the technique still precludes any extensive color vision screening in clinical settings.

SUMMARY

In summary, we have shown that many 1-, 2- and 3-month old infants can discriminate broad-band red and 550 nm green from 589 nm yellow, and thus must have at least two functional photopigment systems operating in the middle- and long-wavelength regions of the spectrum. On the other hand, about half of the 1-month olds and ⅛ of the 2-month olds who were tested on both red and green failed to make either of these discriminations. The improved group performance with age suggests that the percentage of infants that have the necessary physiological substrate to make these discriminations increases rapidly with age, and the continuous range of performances of the infants suggests that at each age we have sampled a population containing infants at various stages of a continuous developmental process.

Two major interpretations of infants' failures to make Rayleigh discriminations—absence or immaturity of one or more receptor types and immaturities of neural processing—were discussed briefly. A specific version of the second hypothesis, namely, that the immature infant retina shares many of the functional properties of adult peripheral retina, was developed in greater detail. Although the present data do not distinguish unequivocally between this and many alternative interpretations, the idea that infant vision resembles adult peripheral vision has both the breadth of explanatory power to unite current data and the specificity to make it an attractive and testable working hypothesis for the immediate future.

Acknowledgements—This research was supported in part by grants BNS 78-23053 and 5T32 EY07031 to DYT. We thank Laurie Alvord, Leslie A. Morris, Marilyn E. Schneck, E. Eugenie Hartmann, Orin Packer, Elsie Vassdal, Corinne Mar, Randy Nielsen and Steven Scott for their invaluable assistance in the laboratory and in data analysis, Ralphe Tigre for technical support, Marjorie Zachow for secretarial assistance, and Drs Israel Abramov, Marc Bornstein, Thomas Piantanida, Joel Pokorny, and Allen Nagy for their helpful comments on the manuscript.

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