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Does Chromatic Sensitivity Develop More Slowly than Luminance Sensitivity?

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Chromatic sensitivity is very low in humans during the first few months of life. We examined whether low chromatic sensitivity reflects a deficiency among chromatic mechanisms or whether it is simply a manifestation of poor visual sensitivity in general. The sweep VEP was used to measure contrast sensitivity to gratings varying in the mixture of red and green components. For infants from 2 to 8 weeks of age, sensitivity to all mixtures was lower than color-normal adults' sensitivity, but infant and adult ratios of luminance/chromatic sensitivity were similar. This finding is consistent with the hypothesis that infants have functional MWS and LWS cones and the requisite post-receptor chromatic mechanisms to compare their signals.

Color vision Human infants Contrast sensitivity Development

INTRODUCTION

Human neonates' vision is immature in many respects. For example, contrast sensitivity, grating acuity and vernier acuity in the first month of life are all at least an order of magnitude poorer than in adulthood (Atkinson, Braddick & Moar, 1977; Banks & Salapatek, 1978; Norcia & Tyler, 1985; Shimojo, Birch, Gwiazda & Held, 1984).

The ability to discriminate chromatic stimuli is also quite immature in the first few months. In a series of well-controlled experiments, Teller *et al.* showed that 3to 4-week-old infants fail to make a variety of chromatic discriminations (Clavadetscher, Brown, Ankrum & Teller, 1988; Hamer, Alexander & Teller, 1982; Packer, Hartmann & Teller, 1984; Varner, Cook, Schneck, McDonald & Teller, 1985). In addition, 8-week olds fail to discriminate many broadband colors from white (Teller, Peeples & Sekel, 1978). These results have been confirmed by one laboratory (Allen, Banks & Schefrin, 1988), but another has found suggestive evidence that newborns can in fact make some chromatic discriminations (Adams, Maurer & Davis, 1986; Adams, Courage & Mercer, 1991). The consensus is that the ability to make chromatic discriminations is poor during the first few months, if not absent altogether. By 12 weeks of age, nearly all infants demonstrate the ability to discriminate a variety of hues. These include the long-wavelength colors used in Rayleigh discriminations (Allen *et al.,* 1988; Clavadetscher *et al.,* 1988; Hamer *et al.,* 1982; Packer *et al.,* 1984) and the colors used in tritan discriminations (Allen *et al.,* 1988; Varner *et al.,* 1985).

Rayleigh discriminations involve wavelengths above 550 nm which do not stimulate the short-wavelength-sensitive (SWS) cones. Consequently, such discriminations require medium-wavelength-sensitive (MWS) and long-wavelength-sensitive (LWS) cones and the neural machinery to compare their signals. The two most common forms of adult color deficiency – deuteranopia and protanopia – refer to losses of MWS and LWS cones, respectively (Boynton, 1979); thus, people with the most common types of deficiency cannot make Rayleigh discriminations. Because neonates also seem unable to make Rayleigh discriminations, they too may lack adequate numbers of MWS or LWS cones or, alternatively, they may be unable to process differential signals among those cones (see Teller & Bornstein, 1987). We will refer to these explanations of early chromatic discrimination failures as the chromatic deficiency hypothesis.

Recently, Banks and Bennett (1988) put forth another account of the early Rayleigh discrimination failures. They proposed that neonates have a full complement of MWS and LWS cones and the post-receptor machinery to compare their signals, but that their overall visual sensitivity is too low to allow them to demonstrate their chromatic capabilities. This reduced sensitivity is due to the inefficient manner in which the neonate's retina absorbs and transduces incident photons and to a general sensitivity loss due to inefficient post-receptor mechanisms.

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Similarly, they proposed that older infants exhibit reliable chromatic discrimination because of increased visual sensitivity, and not because of some change in chromatic mechanisms *per se.* Banks and Bennett (1988) labeled this the visual efficiency hypothesis and showed that it is consistent with the existing data (see also Banks & Shannon, 1992).

The experiment reported here was designed to differentiate the chromatic deficiency and visual efficiency hypotheses. To do so, stimuli consisting of two spatial sinusoids of equal contrast were presented, one produced by modulating the green gun on the CRT and the other by modulating the red gun. The two sinusoids were added in spatial counterphase. The ratio of $R/(R + G)$ was varied, where R and G are the mean luminances of the red and green sinusoids, respectively. $R/(R + G)$ ratios of 0, 0.5, and I yielded green-black, red-green, and red-black sinusoids, respectively. VEPs were recorded for these stimuli in order to estimate contrast sensitivity for a range of color ratios.

One can predict contrast sensitivities to our stimuli for color-normal and color-defective individuals using the ideal-observer approach introduced by Geisler (1989). This approach uses known optical and photoreceptor characteristics of the human eye to determine the "ideal" or optimal possible performance of an observer, given the physical and physiological constraints built into the system. The properties of such an ideal observer are described in detail elsewhere (Banks & Bennett, 1988; Geisler, 1989), so only a brief description of the most important assumptions is given here. This approach incorporates parts of the visual system up to and including the photoreceptors and uses cone outputs only to determine thresholds. We therefore assumed that post-receptor mechanisms are equally efficient in signaling the presence of luminance- and chromatically-varying gratings. Any difference in sensitivity must be due to loss of information caused by ineffective quantum capture in the cones. In deriving these predictions, we assumed for the color-normal observer that SWS, MWS and LWS cones are arranged in a ratio of 1: 16:32. We used Smith-Pokorny cone fundamentals as an estimate of cone sensitivities (Smith & Pokorny, 1975). Cone contrast, that is contrast defined by the maximum and minimum responses of the cones, was computed for each $R\ I(R + G)$ ratio (Stromeyer, Cole & Kronauer, 1985). Stimulus contrast was then adjusted to achieve a constant cone contrast for each stimulus used. Relative sensitivity was thus predicted as the inverse of the stimulus contrast value necessary to achieve a constant cone contrast for each color ratio. The predictions for the dichromats assume that the deuteranope's MWS cones are replaced by LWS cones, and the protanope's LWS cones are replaced by MWS cones.

Absolute sensitivity predictions of the ideal observer are of course much higher than those expected of human observers. This is due to the fact that the ideal observer summates information infinitely across space, while human observers summate information across relatively small areas. Thus, the predictions are slid down the vertical axis to levels of sensitivity expected for human observers while maintaining the relative difference in sensitivity to luminance and chromatic gratings.

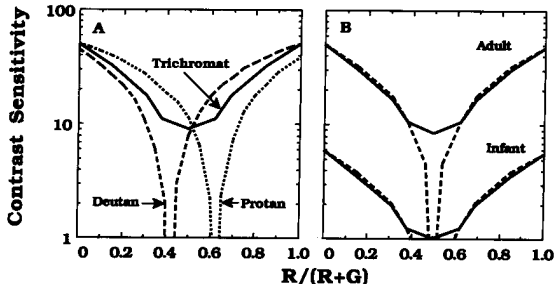

FIGURE 1. Predicted contrast sensitivities as a function of the amount of red in a red/green grating. The abscissa is $R\ JR + G)$, where R and G represent the mean luminances of the red and green component gratings, respectively. The ordinate is contrast sensitivity, the reciprocal of contrast at threshold. (A) Predicted sensitivities for a color-normal observer, deuteranope, and protanope. See text for a description of the method for generating these predicted functions. (B) Predicted sensitivity functions for the visual efficiency (solid line) and chromatic deficiency (dashed line) hypotheses. The chromatic deficiency prediction is for a system with MWS and LWS cones whose outputs are mixed in post-receptor channels so that the system responds only to luminance contrast. The infant curves have been shifted downward from the adult curves. The visual efficiency hypothesis claims that the solid lines are the best descriptions of these sensitivity functions at both ages. The chromatic deficiency hypothesis claims that the solid line is the best description for adults and the dashed line is the best description for infants.

The predicted sensitivities are shown in Fig. 1(A). Color-normal adults (trichromats) should be able to detect the grating at all $R/(R + G)$ ratios, but sensitivity should be lowest at or near the isoluminant value of 0.5 (Mullen, 1985). Protanopes should be unable to detect the grating at a ratio of 0.62 because the red and the green components provide equal stimulation to the MWS cones at that value. Similarly, deuteranopes should fail at a ratio of 0.42.

The predicted contrast sensitivities for the visual efficiency hypothesis and the chromatic deficiency hypothesis are shown in Fig. 1(B). The chromatic deficiency prediction is for a system with MWS and LWS cones whose outputs are mixed in post-receptor channels so that the system responds only to luminance contrast. According to the chromatic deficiency hypothesis, neonates should have very low sensitivity at some $R/(R + G)$ ratio near isoluminance; indeed, if they are lacking MWS or LWS cones, they should not be able to detect the isoluminant grating at all. Therefore, according to this hypothesis, the predicted curve has a larger trough (perhaps an infinite one) than the curve for color-normal adults. Stated another way, the ratio of luminance contrast sensitivity divided by contrast sensitivity at isoluminance should be higher in neonates than in adults. According to the visual efficiency hypothesis, neonates' sensitivity functions should be similar to adults' except for a general sensitivity loss at all red/green mixtures. Stated another way, the ratio of luminance contrast sensitivity divided by contrast sensitivity at isoluminance should be constant across age.

It has been difficult to distinguish these two hypotheses for the following reasons. First, peak luminance contrast sensitivities measured behaviorally in 4- to 8-week olds is very

low (Atkinson et al., 1977; Banks & Salapatek, 1978). Second, in adults, the ratio of luminance/chromatic sensitivity for most spatial frequencies is about 5 for red/green gratings (Mullen, 1985). Therefore, even if the ratio of luminance/chromatic sensitivity were constant with age, neonates would require very high-contrast chromatic gratings to demonstrate their ability to detect them. This point is depicted in Fig. I (B); notice that the predictions for the chromatic deficiency and visual efficiency hypotheses are similar if overall sensitivity is low.

One could distinguish the hypotheses more clearly by elevating these curves. We have accomplished this by presenting saturated colors, at optimal temporal and spatial frequencies for each age, and by using the sweep VEP. Because neonates' luminance contrast sensitivity is 10-20 when estimated with the sweep VEP (Norcia, Tyler & Hamer, 1990), one should be able to measure a reliable threshold at isoluminance if the visual efficiency hypothesis is correct. More specifically, the ratio of luminance/chromatic contrast sensitivity should be similar to values in color-normal adults. On the other hand, if the chromatic deficiency hypothesis is correct, thresholds should be quite high, perhaps unmeasurable, at isoluminance; the ratio of luminance/chromatic contrast sensitivity should be higher in infants than in color-normal adults.

Preliminary results from this experiment were reported by Allen, Banks, Norcia and Shannon (1990). Morrone, Burr and Fiorentini (1990, 1993) also measured neonates' VEPs to luminance-varying and chromatic stimuli and report that the ratio of luminance/chromatic sensitivity decreased from 8 to 20 weeks of age.

METHODS

We tested 14 infants ranging from 2 to 8 weeks in age. Parents provided informed consent. All infants were born within 2 weeks of their due date as reported by the parent and did not suffer birth trauma. None had a relative known to have a color deficiency. All had 1-min APGAR scores of 8 or higher, were free of obvious neurological deficits or pathological signs and had yoked, aligned eye movements with no signs of strabismus or ocular pathology.

Infants were usually tested on three separate occasions. No more than 7 days passed between the first and last session. Some infants were tested on as many as five occasions; one was tested only once. We also tested four adults who were emmetropic or wore their normal correction. Two were trichromatic as indicated by their performance with the Ishihara pseudo-isochromatic test plates, D-15 color cap test, Farnsworth-Munsell 100 Hue test and the Nagel anomaloscope. One adult was mildly protanomalous as classified by the AO-HRR pseudo-isochromatic test plates; she had a narrow (2-3) matching range on the Nagel anomaloscope and passed the desaturated D-15 color cap test with no errors. One adult was classified as a protanope on the Ishihara pseudo-isochromatic test plates, the Nagel anomaloscope, and the D-15 color cap test.

Each infant was seated at a 45-deg angle in a padded infant seat, except for short break periods. Viewing distance was 50 cm. The infant's attention was attracted to the flickering stimulus by a small bell or toy that was dangled in front of the screen throughout the presentation. Trials in which the infant did not appear to fixate the stimulus for the entire 10 sec were discarded. Viewing was binocular.

Viewing distance for the adults was 2m. The adults fixated and accommodated to a small mark in the center of the display during each self-initiated trial. They were instructed to relax, hold still, and not blink. Viewing was binocular.

The stimuli were displayed on a Conrac 7300 color monitor controlled by a Rastertech One/80 color graphics processor. The component gratings were generated by modulating the red and green guns to create vertical spatial sinusoids and then adding the two in spatial counterphase. We wished to isolate the MWS and LWS cones, so an amber filter (PLEXIGLAS, amber No. 2422 that transmitted wavelengths above 550 nm only) was placed in front of the monitor. The CIE chromaticity coordinates of the filtered red and green phosphors were (0.65, 0.34) and (0.42, 0.57), respectively; this places them in the Rayleigh region of the spectrum. The luminance-voltage relationship for the red and green guns was measured with the amber filter in place using a Pritchard photometer (1980BX/SS, Photo Research) and a software look-up table was used to linearize the display. The calibration was checked periodically and corrections were made in the table if necessary.

The contrasts of the red and green components were always equal to one another and $R/(R + G)$ was varied from 0.0 to 1.0. The space-average luminance, $R + G$, was constant at 8 cd/m^2. The spatial frequency of the gratings was set to the peak of the luminance CSF for the appropriate age; this corresponded to 0.8 and 3.2 c/deg for infants and adults, respectively. The gratings were counterphase-flickered at 3 Hz. Each stimulus presentation lasted 10 sec during which time the stimulus contrast increased in equal logarithmic steps every 0.5 sec. To insure that the stimuli ranged from sub- to supra-threshold values, contrast was increased from 0.01 to 0.80 during each presentation. Lower values and a smaller range were used for adults.

For VEP recording, the active electrodes were placed 3 cm above the inion and 1 cm above and 3 cm to the right of the inion. The reference electrode was placed on the central forehead and a ground electrode was placed on the left side of the head just above the ear. All electrodes were held in place with surgical tape. A similar configuration was used with adults with the exception that the ground was attached to the ear. The electrodes were connected via Grass IG3/P511 isolation cables to Grass P511 EEG amplifiers. The amplifier bandwidth was I-10011z at -6dB and the gain was set to 10,000. An 8-bit A/D converter with a self-ranging gain adjustment digitized the EEG waveform at 180 Hz.

Contrast thresholds were estimated by the technique developed by Norcia and colleagues (Norcia & Tyler, 1985; Allen, Norcia & Tyler, 1986; Norcia, Tyler, Hamer & Wesemann, 1989). The amplitude of the EEG at 6 Hz (the second harmonic of the counterphase flicker rate) was estimated using a discrete Fourier transform. The transform was performed using a sliding 2-sec window that was incremented every 0.5 sec, yielding 17 amplitude and phase estimates per contrast sweep. The EEG

noise level was estimated as the average amplitude at 4 and 8 Hz, frequencies just above and below the second harmonic.

The microcomputer that controlled the apparatus estimated contrast thresholds by fitting regression lines to plots of second harmonic amplitude as a function of the logarithm of stimulus contrast. A set of signal-to-noise ratio and phase consistency criteria were employed to insure that the regression line was fit to stimulus-driven activity rather than to noise. The two most important criteria were: (1) the amplitude of the second harmonic had to exceed the amplitude of the noise by 0.5 log units and (2) the phase of the response had to be either constant or gradually leading the stimulus as contrast increased. See Norcia *et al.* (1989) for more detail.

Adults were also tested psychophysically. We used an ascending and descending method of limits to estimate contrast thresholds. The same stimuli used to record VEPs were presented except that descending contrast series were intermixed with ascending series. The contrast sweep range was set to 1.0 log unit. The endpoint values were adjusted so that the stimulus became just-detectable or just-undetectable 37 sec after the beginning of the 10-sec trial. The subject was instructed to indicate the point at which perceived counterphase flicker just appeared or just disappeared by a button press. After a series of practice trials, five responses were recorded for each sweep direction. Threshold was the geometric mean of the 10 responses for each condition.

RESULTS

Color-normal and color-deficient adults

The use of the sweep VEP to measure luminance and chromatic contrast sensitivity in human infants is novel, so we wished first to determine whether the technique worked properly. We did so by measuring VEP sensitivities in color-normal and color-deficient adults and then comparing those results to psychophysically-determined sensitivities. Sensitivities were measured in two trichromatic adults for 11 values of $R/(R + G)$ ranging from 0.0 to 1.0.

Figure 2 displays the VEP and psychophysical thresholds for the color-normal, trichromatic adults. The prediction for such observers is also shown. The shapes of the functions obtained by VEP and psychophysics were quite similar; in both cases, sensitivity was highest for isochromatic, luminance-varying gratings and lowest for heterochromatic, isoluminant gratings. The absolute sensitivities were also reasonably similar, although psychophysical sensitivities were generally slightly higher than VEP sensitivities. The magnitude of the sensitivity trough can be represented by the ratio of sensitivity for isochromatic gratings $[R\ I(R + G) = 0.0$ and 1.0] divided by sensitivity at the lowest point. For DA, this ratio is 5.1 psychophysically and 2.8 with VEPs. For ESS, the ratio is 7.0 psychophysically and 5.8 with VEPs. These functions are similar in shape to the predicted functions for a trichromatic adult.

It is important to show that a color-deficient observer who either has difficulty making or cannot make a Rayleigh discrimination reveals such deficiencies with our VEP technique. To pursue this, we measured VEP contrast sensitivities in two color-deficient adults at a variety of $R/(R + G)$ values. Figure 3(A) displays the protanope's contrast sensitivities along with the predictions for a trichromat and protanope. Reliable VEPs were obtained at six of the seven red-green mixtures tested. No signal was obtained for an $R/(R + G)$ value of 0.6; the amplitude of the VEP at this value never exceeded the amplitude of the noise estimate by more than 0.3 log units and the phase of the response varied randomly within and across trials. Although the protanope's sensitivity to luminance-varying gratings was similar to the trichromats' sensitivities, the region of lowest sensitivity is much deeper and shifted toward red, as expected for someone with no LWS cones. Figure 3(B) displays the results for the protanomalous observer. As expected for someone with a deficit among LWS cones, the point of lowest sensitivity is shifted toward red. The ratio of luminance sensitivity divided by chromatic sensitivity at 0,6 was 9.6, so a larger sensitivity dip was observed, as one would expect for a color-defective observer. The predicted function for a protanopic observer is also shown.

These results show that the VEP technique yields data much like those predicted by a simple model and, more importantly, much like those obtained psychophysically; color-normal adults revealed a relatively small sensitivity dip centered at an $R/(R + G)$ value of about 0.5 and protanomalous and protanopic adults exhibited a larger sensitivity dip displaced toward larger $R/(R + G)$ values.

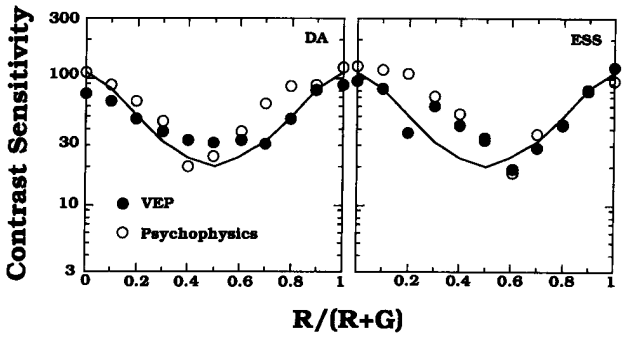

FIGURE 2. Contrast sensitivity as a function of the amount of red in a red/green grating for two color-normal adults. Solid circles are sensitivity estimates from VEP recordings and open circles are sensitivities measured psychophysically. The lines represent the predictions for a color-normal adult; they have been shifted vertically to fit the data.

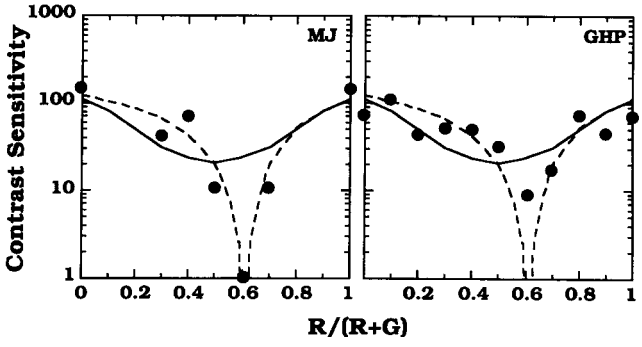

FIGURE 3. Contrast sensitivity as a function of the amount of red in a red/green grating for a protanopic (MJ) and a protanomalous observer (GHP). The data points are sensitivity estimates obtained by VEP. Solid lines are the predictions for a color-normal adult and dashed lines the predictions for a protanope; they have been shifted vertically to fit the data. No detectable signal was obtained at $R/(R + G) = 0.6$ for observer MJ; his sensitivity is plotted as 1.0.

Infants

The same sensitivity functions were measured in 14 infants from 2 to 8 weeks of age. At least six sensitivity estimates were obtained for each infant, 11 for most infants, and 14 for one. Figure 4 plots the VEP sensitivities for four infants spanning the age range we tested; each point is the average sensitivity from five contrast sweeps. The predicted function for a color-normal observer is also plotted; it has been shifted vertically in each panel to fit the data. As expected, infants' contrast sensitivity is uniformly lower than adults'. However, the shapes of the sensitivity functions are similar to the ones we observed in color-normal adults: sensitivity is highest for isochromatic, luminance-varying gratings at *R JR* + G) values of 0.0 and 1.0 and lowest for values of about 0.5, the presumed isoluminant value. Significantly, each infant yielded a reliable VEP at all red-green mixtures, including the presumed isoluminant mixture.

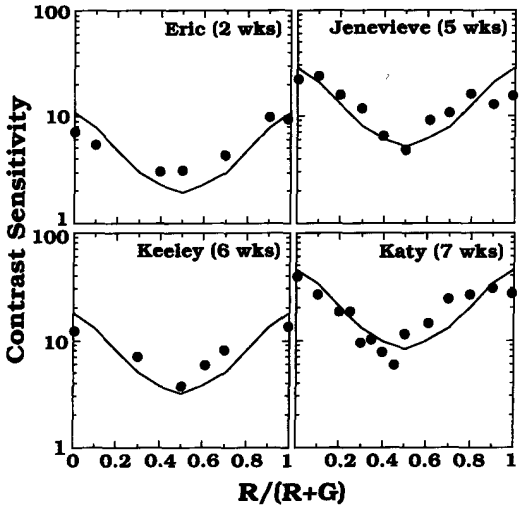

FIGURE 4. Contrast sensitivity as a function of the amount of red in a red/green grating for four infants from 2 to 7 weeks of age. The solid lines represent the visual efficiency prediction each shifted vertically to fit the data.

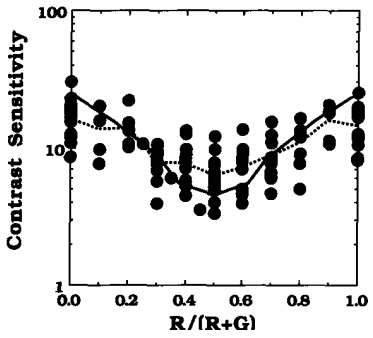

FIGURE 5. Contrast sensitivity as a function of the amount of red in a red/green grating for all 14 infants tested. The data are normalized by shifting each infant's data vertically so that the mean sensitivity for each infant equals 10. The solid line represents the visual efficiency prediction while the dashed line connects the group mean sensitivities at each color ratio tested.

Figure 5 displays the data from all 14 infants. The data are normalized such that the mean sensitivity for all stimuli equals 10 for each infant. The solid line is the predicted sensitivity while the dashed line connects the mean sensitivities for all infants at each color ratio. The figure shows that none of the infants in our sample exhibited large sensitivity dips as predicted by a chromatic deficiency hypothesis; rather their sensitivity functions were similar in shape to those of color-normal adults. Indeed, the difference between luminance and chromatic sensitivity for the group mean values was less than predicted by the visual efficiency hypothesis. This issue is addressed below.

The critical data from this experiment can be summarized by calculating the ratio of luminance/chromatic sensitivity for each infant and adult. Figure 6 displays these ratios. The values for luminance contrast sensitivity represent the averages of each individual's sensitivity at *R I(R* + G) values of 0.0 and 1.0; the values for chromatic contrast sensitivity represent the lowest sensitivity from each individual. These ratios are 2.8-5.8 in the color-normal adults and 9.6-oc in the protanomalous and protanopic adults. In infants, the ratios range from 1.3 to 6.6, values closer to those of the color-normal adults.

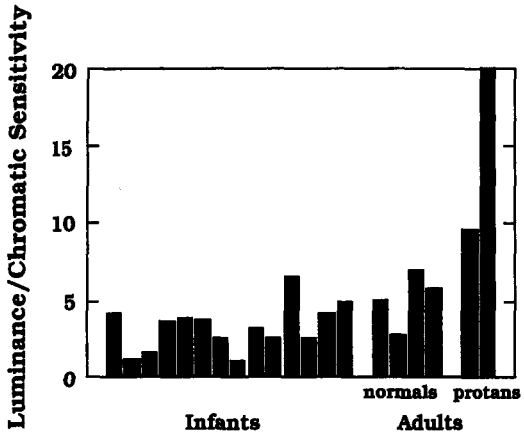

FIGURE 6. Ratios of luminance/chromatic sensitivity for each infant, both color-normal adults, and both color-deficient adults. The luminance contrast sensitivity for each individual was estimated from the average of their contrast sensitivities at $R/(R + G)$ of 0.0 and 1.0; occasionally, we included a. sensitivity from a value of 0.9. The chromatic contrast sensitivity for each individual was simply the lowest sensitivity observed. This always occurred between *R I(R + G)* values of 0.3 and 0.7 and nearly always between values of 0.4 and 0.6. Ratios for the 14 infants are represented by the bars on the left. Ratios for the four adults are represented by the bars on the right; the two bars farthest to the right represent the protan observers' ratios.

DISCUSSION

We have shown that adult contrast sensitivity measured with the sweep VEP agrees closely with sensitivity measured psychophysically for both luminance and isoluminant chromatic stimuli. For color-defective individuals, the specific type of color vision defect can be classified using the sweep VEP.

Our data show quite clearly that the information for discriminating long-wavelength lights is preserved up to the infants' visual cortex, the site at which the VEP is generated. This finding implies that all 14 of the infants tested have functional MWS and LWS cones and the necessary post-receptor chromatic neural mechanisms to process and transmit the color content of the stimuli. It also supports the visual efficiency hypothesis that neonates' inability to make chromatic discriminations in behavioral experiments is a consequence of their generally poor visual sensitivity rather than a deficiency among chromatic mechanisms *per se*.

Possible artifacts

The ratio of luminance/chromatic sensitivity appears to be similar in 2- to 8-week-old infants and color-normal adults. That is to say, the ability to signal chromatic variations via the MWS and LWS cones and the appropriate post-receptor circuits develops at about the same rate as the ability to signal luminance variations. Our data are, therefore, consistent with the visual efficiency hypothesis and not the chromatic deficiency hypothesis outlined earlier. Before accepting these conclusions, however, a number of possible experimental artifacts should be evaluated.

First, the $R/(R + G)$ value corresponding to isoluminance can vary from one color-defective individual to another because of differences in their pre-retinal media and in the cone type they are missing. It was impossible with our procedure to identify the isoluminant value for each child and then measure contrast sensitivity at precisely that value. Perhaps many of the infants were color defective and unable to preserve chromatic information at a particular red-green mixture, but we simply missed this value. This criticism is rather implausible because the $R/(R + G)$ values we tested were generally closely spaced and, as shown by Fig. 3, color-defective adults exhibit sensitivity losses relative to normals over a range of red-green combinations. Our procedure was adequate for distinguishing the two possibilities.

Second, perhaps the infants' VEPs reflect the responses of rods and one cone type rather than the responses of MWS and LWS cones (see Brown, 1990; Clavadetscher *et al.*, 1988). For an observer using rods and MWS cones, the sensitivity dip should fall at an $R JR + G)$ value of 0.61, and for one using rods and LWS cones, it should fall at 0.40. The infant data do not dip consistently at those values, so the VEPs of these infants probably do not reflect the contribution of rods and one cone type. Of course, it is possible that a few of the infants used rods and one cone type.

Third, there is evidence in adults that the response latencies of MWS and LWS cones differ (Lindsey, Pokorny & Smith, 1986; Cushman & Levinson, 1983). Perhaps the differing latencies of the two cone types produce a time-varying luminance artifact that masks a post-receptor color defect. If this explanation is correct, the magnitude of the artifact should depend on the alternation rate of the stimulus. To test this, we measured sensitivity in a few observers with both a 3 and 5 Hz stimulus. The ratio of the sensitivity values did not depend on alternation rate; therefore, the response at intermediate red-green ratios does not reflect a cone response latency artifact.

Fourth, Morrone *et al.* (1990) suggest that the presence of a reliable VEP at the presumed isoluminant point in our study was caused by luminance artifacts due to the eye's chromatic aberration. This suggestion seems rather unlikely because luminance artifacts at low spatial frequencies are negligible in most eyes (Flitcroft, 1989) and the frequency presented to infants was very low at 0.8 c/deg. In addition, our color-deficient adults, who were tested at 3.2 c/deg, exhibited significantly larger sensitivity dips at the presumed isoluminant point than the infants did. Therefore, luminance artifacts due to chromatic aberration had very little if any effect on our adult data and presumably had less effect on the infant data collected at much lower spatial frequencies.

One can estimate the effect that chromatic aberrations would have on the contrast of the stimuli in our experiment. The stimuli were viewed through an amber filter, unlike the stimuli of Morrone et al. (1990, 1993). This of course reduces the effects of chromatic aberration because the dominant wavelengths of the component gratings are closer together. The dominant wavelength of the stimuli in our experiment were about 568 nm for the green grating and 632 nm for the red grating. The chromatic difference of focus for these wavelengths is 0.25 D at the very most for the adult eye (Wald & Griffin, 1947). One can use the equations of Green, Powers and Banks (1980) to estimate the contrast reduction due to 0.25 D at 0.8 c/deg with a 3 mm. pupil, a reasonable estimate for the infants in this study. A grating of 100% contrast will be reduced to 99.85% contrast by 0.25 D of defocus. If one considers that the least amount of contrast for which an evoked potential was recorded from any infant in this study was 2.6%, then the chromatic aberration of the infant eye would have to be at least 17 times greater than that of the adult eye (2.6/0.15) in order to produce an evoked potential in the most sensitive infant tested. As this seems unlikely, we believe that our results are not affected by chromatic aberrations.

Comparison with other studies

Other support for a visual efficiency hypothesis of development comes from studies using a very different technique to test infant vision. Teller and Lindsey (1993) used optokinetic nystagmus (OKN) in response to moving gratings to measure contrast thresholds in infants. They tested infants with both luminance and chromatic gratings. In addition, they measured relative sensitivities to luminance and chromatic gratings by determining the contrast of a drifting chromatic grating required to null the OKN driven by a fixed contrast luminance grating drifting in the opposite direction. Infants as young as 4-weeks-old demonstrated OKN when viewing iso-

luminant red-green gratings. Thus, infants must have some form of functional color vision at this age. Also, infants had comparative null values to adults. Equal null values across age groups provide evidence of uniform losses of sensitivity to luminance and chromatic stimuli in the infant compared to the adult and thus provide converging evidence in support of the visual efficiency hypothesis.

Morrone *et al.* (1990, 1993) report that chromatic contrast sensitivity and acuity develop more rapidly than luminance sensitivity and acuity. This conclusion obviously differs from ours. Their methodology was both similar and dissimilar to ours. Morrone *et al.* used the steady-state VEP as their response measure, although they did not use the sweep version. They varied the mixture of red and green sinusoidal components in a plaid stimulus to estimate luminance and chromatic contrast sensitivity and acuity; however, their red and green lights were the phosphor outputs of their CRT, so their green did not fall in the Rayleigh region. For their contrast sensitivity estimates, they used 0. 1 c/deg gratings rather than the 0.8 c/deg we used. Finally, they varied the temporal frequency of the stimulus within subjects. While these factors may account for some differences between the outcomes of the different experiments, the disagreement between their conclusion and ours can be best understood by consideration of the following three points.

(1) Close inspection of their contrast sensitivity data, which we have reproduced in Fig. 7(A) reveals that the ratio of luminance/chromatic sensitivity was actually fairly constant with age. Figure 7(B) plots those ratios which varied from an average value of about 3.5 at 6 weeks to about 3 at 30-34 weeks. The contrast sensitivity data of Morrone *et al.* (1990, 1993) are in fact reasonably consistent with the visual efficiency hypothesis.

Figure 7 also plots the luminance and chromatic sensitivities and the luminance/chromatic sensitivity ratios we obtained; they are similar to those obtained by Morrone *et al.* However, one should note that the sensitivity estimates of Morrone *et al.* (1990) are 2-3 times lower for both luminance and chromatic sensitivity for infants of the same age. Their VEP technique appears to be less sensitive than the sweep technique. This may explain their inability to record VEP responses to an isoluminant grating for infants between the ages of 4 and 7 weeks.

In addition, they report that chromatic acuity does not develop to a level which would allow infants to see our 0.8 c/deg chromatic grating until about 15 weeks of age. This discrepancy can be accounted for by the same reason. Figure 11 of Morrone *et al.* (1993) shows that when infant Patrick has a chromatic contrast sensitivity comparable to what we measure for younger infants, his chromatic acuity is well above 0.8 c/deg and thus would easily detect our chromatic grating.

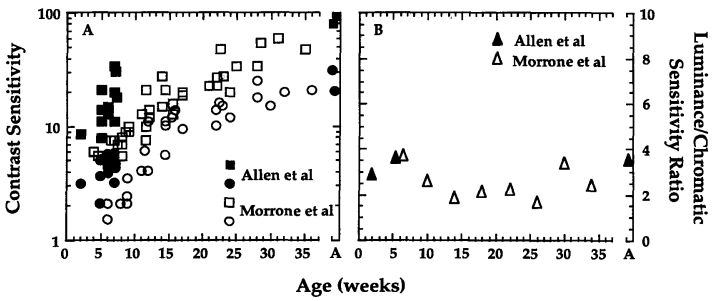

FIGURE 7. Summary of data from present experiment and from Morrone *et al.* (1990). (A) Luminance and chromatic contrast sensitivity as a function of age. The open symbols are from Morrone *et al.* and the solid symbols are from the present study. The squares represent luminance sensitivities; for our data, they are the averages of contrast sensitivities for $R/(R + G)$ values of 0.0 and 1.0 and for the data of Morrone *et al. (1990),* they are taken from their Fig. 3(A). The circles represent chromatic sensitivities; for our studies, they represent the lowest sensitivity observed for each infant while for the data of Morrone *et al.* they represent sensitivity at some predetermined ratio of R *I(R + G). (B)* Luminance/chromatic sensitivity ratios as a function of age. The open symbols represent ratios from Morrone *et al.;* the solid symbols represent the ratios from the present study.

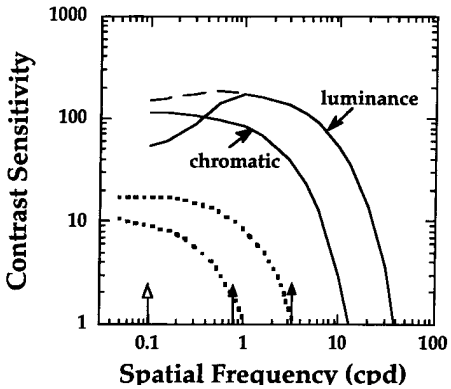

FIGURE 8. Luminance and chromatic CSFs at different ages. The solid lines represent adult functions obtained by Mullen (1985); the dashed extension to the adult luminance CSF represents the higher sensitivity one expects for a counterphase flickering grating. The dashed lines represent hypothetical functions for neonates under the assumption that adult and neonatal luminance and chromatic CSFs are the same except for a diagonal shift (I log unit down the sensitivity axis and 0.5 log units to the left on the spatial frequency axis). The open arrow shows the spatial frequency at which Morrone et al. (1990) measured contrast sensitivities for all ages. The solid arrows represent the spatial frequencies at which sensitivities were measured in infants and adults in the present study.

(2) As shown in Fig. 8, adult chromatic contrast sensitivity approaches or even exceeds luminance sensitivity at very low spatial frequencies (Mullen, 1985). With counterphase-flickering stimuli like those used in the current experiment and that of Morrone *et al.,* the low-frequency fall-off of the luminance CSF is less pronounced; this is illustrated by the dashed line in Fig. 8. Let us assume for the moment that infant luminance and chromatic CSFs are the same as adults, but simply shifted to lower sensitivities and spatial frequencies. If that were so, one

would expect neonatal CSFs like those shown by the dotted lines. Morrone *et al.* measured luminance and chromatic sensitivities at 0.1 c/deg, which is indicated by the unfilled arrow. We measured sensitivities at the peaks of the age-appropriate luminance CSF: 0.8c/deg in infants, and 3.2c/deg in adults. These values are indicated by the solid arrows. You can see that by measuring sensitivity at 0.1 c/deg, Morrone *et al.* were in a sense measuring sensitivity at different places on the CSF at different ages; in the younger infants, they were making measurements just below the peak of the CSF and in older infants (assuming that 35-week olds have nearly adult-like CSFs), they were measuring far below the peak. Thus, if the relationship between luminance and chromatic sensitivity did not change with age, except for the well-known shift in peak frequency and overall sensitivity, one would expect the luminance/chromatic sensitivity ratio at 0. 1 c/deg to decrease as a function of age just as Morrone *et al.* reported. We avoided this problem by making our measurements at the peak of the luminance CSF for the appropriate age and observed no such decrease in the sensitivity ratio.

(3) Morrone *et al.* estimated grating acuity for luminance-varying and isoluminant stimuli as a function of age. They observed a larger increase in chromatic acuity and took this as further evidence that chromatic sensitivity develops more rapidly than luminance sensitivity. Because the slope of the high-frequency limb of the CSF increases monotonically with increasing frequency (Banks, Geisler & Bennett, 1987), a change in contrast sensitivity (i.e. a vertical shift of the CSF along the log sensitivity axis) produces a smaller change in the high frequency cut-off if the observer's absolute sensitivity is high (as in older infants) than if the observer's sensitivity is low (as in neonates). Thus, a given reduction in contrast sensitivity leads to a larger difference in the high-frequency cutoff if sensitivity is low than if it is high. Therefore, the fact that chromatic acuity changes more with age than luminance acuity does not imply more rapid development among chromatic mechanisms. Thus, the findings of Morrone *et al.* (1990, 1993) are not necessarily in conflict with a visual efficiency hypothesis of color vision development and may be interpreted as providing support for this hypothesis.

Comparison of infant and adult color vision

As pointed out in the discussion of Figs 4 and 5, the depth of the infants' sensitivity trough around the isoluminant point appears to be slightly smaller than the one observed in color-normal adults. Before drawing the conclusion that chromatic information is actually conveyed *more* efficiently than luminance information by post-receptor circuits in the immature visual system, it is important to consider the consequences of differences in optical and receptoral properties. There are two factors relevant to this issue. First, the ocular media and macular pigmentation of the young eye are clearer than in the mature eye (Bone, Landrum, Fernandez & Tsraris, 1988; Hansen & Fulton, 1989). Thus, the spectral distribution of lights at the photoreceptors differs in neonates and adults. Could such differences have led to the shallower sensitivity troughs we observed in neonates? We think not because age differences in the lenticular and macular pigments have little effect at the long wavelengths we tested and their primary effect in neonates is to shift the expected isoluminant point to slightly higher values of $R/(R + G)$ rather than to lessen the depth of the trough in the sensitivity functions. Second, the outer segments of neonatal cones, at least in the fovea, are much shorter than their adult counterparts (Yuodelis & Hendrickson, 1986). Assuming that the concentration and extinction coefficient of the photo-pigment are the same in infants and adults (Banks & Bennett, 1988), this means that neonatal cones should exhibit less self-screening than adult cones (Wyszecki & Stiles, 1982). Less self-screening is associated with narrower action spectra (Brindley, 1970), which in turn implies less overlap in the spectra of MWS and LWS cones. As a consequence, the "cone contrast"(Stromeyer et al., 1985) should be somewhat greater at isoluminance in neonates than in adults. Thus, the reduced self-screening one expects in neonatal cones should allow greater sensitivity at isoluminance than one might otherwise predict, so our data do not necessarily imply greater efficiency among post-receptor chromatic channels than among luminance channels.

Our results clearly imply that infants as young as 2 weeks of age have functional MWS and LWS cones and the post-receptor circuits needed to transmit this information to the visual cortex. They do not imply, however, that neonates have mature color vision. We have only demonstrated that the chromatic information required to make a Rayleigh discrimination can drive the VEP, which presumably means that the information is transmitted to the visual cortex. We do not know whether such information can be used behaviorally, although there are suggestions in the literature that it can be (Adams *et al.*, 1986, 1991). Also, our procedure was designed to isolate the MWS and LWS cones and, consequently, provided no information about SWS cones and associated post-receptor channels. There is electrophysiological evidence (Volbrecht & Werner, 1987; Shannon, Banks & Allen, 1991) that infants as young as 5 weeks have functional SWS cones, but behavioral studies (Varner *et al.*, 1985; Allen *et al.*, 1988) have been unable to demonstrate the ability to make tritan discriminations (those requiring SWS cones) before 8 weeks. The visual efficiency hypothesis, which predicts Rayleigh and neutral-point discrimination failures quite accurately (Banks & Bennett, 1988; Banks & Shannon, 1992), cannot explain why infants fail to demonstrate tritan discriminations behaviorally. The Rayleigh and tritan discrimination findings to date leave open the possibility that chromatic signals from all three cone types are preserved up to the visual cortex but lost at higher stages involved in behavioral responses.

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