FPL and sweep VEP to tritan stimuli in young human infants

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Abstract

Young infants can distinguish red from green without brightness cues which shows that neural pathways processing color information (the 'red–green' color-opponent pathway) are functional early in life. There is some doubt over whether the 'blue–yellow' pathway is functional in young infants. Here, we show that infants behave like tritanopic adults until 2–3 months post-term age. By 3–4 months, infants distinguish tritan stimuli, and therefore, the 'blue–yellow' pathway must be functional by that age. Our sweep visual evoked potentials to identical stimuli, however, are not significantly above noise levels, in disagreement with the behavioral responses. We discuss several possible explanations for the discrepancy.
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1. Introduction

Adults with normal color vision are trichromatic: They have three cone types with signature spectral sensitivity functions (Smith & Pokorny, 1972, 1975) and the post-receptoral neural mechanisms required to compare their responses (Derrington, Krauskopf, & Lennie, 1984; Krauskopf, Williams, & Heeley, 1982). Long- (L) and medium- (M) wavelength-sensitive cone signals are compared in the L–M cone (or red–green) post-receptoral pathway. The S cone (blue–yellow) pathway is responsible for comparison between short-wavelength-sensitive (S) cone signals and the sum of L- and M-cone signals.

Researchers dating back to Darwin (1877) have asked whether infants are capable of seeing colors in the same way as adults. Visual evoked potential (VEP) evidence indicates that all three cone types are functional in human infants by at least 4 weeks from birth (Knoblauch, Bieber, & Werner, 1998; Volbrecht & Werner, 1987). VEP, forced-choice preferential looking (FPL) and optokinetic nystagmus (OKN) studies indicate that the L–M pathway is functional by 2 months (Allen, Banks, & Norcia, 1993; Morrone, Burr, & Fiorentini, 1993; Peeples & Teller, 1978; Rudduck & Harding, 1994; Teller & Palmer, 1996). These results indicate that all three cone types and at least one of the color-opponent pathways are functional in human infants by 2 months of age.

Results from some studies investigating the S cone pathway suggest that its development may progress more slowly than that of the L–M pathway while other studies suggest no difference in developmental time course. Among the studies suggesting a developmental lag, Peeples, Teller, and Sekel (1978) reported that 2-month-olds were able to distinguish red from green but could not distinguish yellow–green and purple from white, without luminance cues. The latter colors are similar to those that excite S cones selectively in adults, and are known as tritan stimuli because tritanopic observers are unable to distinguish them. Thus, the finding that 2-month-olds discriminate red from green, but not tritan colors, suggests that development of the S cone pathway may lag behind that of the L–M pathway. Another study provides evidence for a lag in S cone pathway development (Teller, Brooks, & Palmer, 1997): OKN to red–green stimuli is elicited by 2 months, but OKN to tritan stimuli remains absent as late as 4 months.

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Some VEP and FPL studies have not observed a clear developmental lag in the S cone pathway. They demonstrated responses to tritan stimuli by about 2 months of age (VEP: Crognale, Kelly, Weiss, & Teller, 1998; Suttle, Anderson, & Harding, 1997) or slightly later (FPL: Pulos, Teller, & Buck, 1980; Varner, Cook, Schneck, McDonald, & Teller, 1985).

Methodological differences are likely to account for at least part of the disagreement between OKN, FPL and VEP findings. For example, the OKN technique involves moving stimuli, so a lack of OKN response may reflect insensitivity to tritan colors, insensitivity to tritan colors when temporally modulated, or insensitivity to tritan colors when in motion (Teller et al., 1997). Alternatively, perhaps the neural pathway responsible for an eye movement response to tritan stimuli is not fully functional until later than 4 months of age.

In adults, OKN responses elicited by isoluminant chromatic stimuli are diminished in comparison with those elicited by luminance-modulated stimuli, and the effect is greater for tritan than for red–green stimuli (Crognale & Schor, 1996). In addition, thresholds for the discrimination of direction of motion of tritan stimuli are much higher than for the detection of the same stimuli. Thus, in the mature visual system, the S cone pathway is relatively insensitive to moving stimuli, so it is perhaps unsurprising that moving tritan stimuli fail to elicit an OKN response in infants.

The VEP reflects retino-striate visual pathway function. The lack of a significant VEP before about 2 months of age may reflect a weak retino-striate signal, or a relatively high level of EEG noise. Alternatively, the signal may be significantly above noise, but might arise at a position away from the recording site, perhaps deep in the cortex, or laterally displaced from the site. If, however, significant VEPs are elicited, it is reasonable to conclude that signals significantly above noise levels are preserved from photoreceptor to at least the striate cortex.

Consistent FPL responses to tritan stimuli demonstrate that useful S cone signals are available from the photoreceptors through to the visual cortex, and can be used to drive a behavioral response. Before 2–3 months, FPL responses to tritan stimuli are not significantly above chance performance (e.g., Pulos et al., 1980). This response failure could be caused by one or more of the following limitations: First, the signal itself may be noisy (as discussed in Banks & Shannon, 1993). The low signal-to-noise ratio may arise at various points along the visual pathway. Second, the infant may be able to distinguish the stimuli, but may be unmotivated to look toward them. Third, the infant may lack the necessary motor neural connections required to make a behavioral response (although this lack of connection would have to be specific to the S cone pathway).

The present study re-investigates the development of the S cone pathway using behavioral (FPL) and electrophysiological (VEP) techniques. We maximize the comparability of our VEP and FPL results by using very similar, temporally modulated stimuli in both cases.

2. Methods

2.1. Subjects

Six color-normal adults and one mildly deuteranomalous adult participated. The adult data aid the interpretation of the infant data. The adults were 37 years old or younger. Their color vision was assessed using the Farnsworth–Munsell 100-Hue test and the Ishihara pseudoisochromatic plates, each illuminated using a MacBeth easel lamp.

Fifty-three infants participated. They were recruited by mailed invitation from City of Berkeley birth records. A signed declaration of informed consent was obtained from a parent. Infants were 1–4 months of age from their term date, and data were collected at one age from each infant. FPL responses were recorded from 35 infants and VEPs from a separate group of 18 infants. It would have been preferable to obtain both response types from each infant, but this was impractical.

2.2. Stimuli

Stimuli were presented on a Sony Trinitron 17 in. color monitor with a refresh rate of 67 Hz. A Minolta CS-100 photometer was used to measure luminance as a function of gun value and the red, green, and blue color guns were each gamma-corrected to ensure linear luminance output. The radiant power spectra of the phosphors were measured using a spectroradiometer (Photo Research model PR1980BXS). The spectra were used to determine the proportions of red, green, and blue phosphor luminance required to generate colors with known positions in color space.

We generated tritan stimuli to modulate the S cone pathway selectively. As will be explained later (see Experiment 1), stimuli that isolate S cones in adults probably isolate S cones reasonably well in infants. We therefore used the same stimuli for infants and adults. Tritan stimuli along an axis that passes through white appear green at one end of the axis and purple at the other end. We describe the relative luminance of the green and purple elements in terms of elevation out of the adult isoluminant plane in the DKL color space (Derrington et al., 1984).

We used heterochromatic flicker photometry to determine the relative luminances of green and purple that appear isoluminant in five adults (one mildly deuteranomalous). The stimuli were vertical 0.2 cpd sinewave gratings. They were pattern-reversed at 20 Hz and viewed binocularly from a distance of 40 cm. This 20 Hz

reversal rate was used because it is high enough to allow the percept of minimum flicker and low enough to allow an S cone response (Kaiser, 1991; Stockman, MacLeod, & Lebrun, 1993). A low spatial frequency was used in order to avoid luminance artefacts due to chromatic aberration and to increase the probability that we did not exceed the infants' chromatic acuity (Morrone et al., 1993). The relative luminances of the green and purple elements were varied (without changing mean luminance) until perceived flicker was minimal. The mean of several settings across the five adults served as our definition of the isoluminant green/purple mixture and a DKL elevation of zero.

To minimize rod intrusion in the adult and infant measurements, we used the maximum mean luminance possible (46 cd/m^2 when viewed directly; 13 cd/m^2 with blue filter; see below). At this luminance level, the upper limit of our range of elevations was restricted by the blue phosphor to 36°, and the range extended from −90° to 36°.

Infants viewed the stimuli binocularly. Adults viewed the VEP stimuli binocularly, but the psychophysical stimuli monocularly (because binocular viewing was impractical in our S cone adapting set-up, described below). In all infant experiments and in the adult psychophysical experiments, the spatial frequency was 0.2 cpd and viewing distance was 40 cm. At this distance, 3.5 spatial cycles were visible in FPL and 2AFC experiments, and 9.1 cycles in infant VEP experiments (gratings were presented on slightly less than half the monitor in the FPL set-up). In adults, VEPs were recorded in response to 0.2-cpd (viewing distance = 40 cm) and 1-cpd (viewing distance = 1 m; 20 spatial cycles) gratings. At 40 cm, the screen subtended 37° × 29°; at 1 m, it subtended 17° × 12°.

Temporally modulated gratings were presented in onset–offset mode at 4 Hz. For all temporally modulated stimuli, an onset:offset duty cycle of 1:4 was used because it elicits robust VEPs in adults (Rabin, Switkes, Crognale, Schneck, & Adams, 1994) and infants (Crognale et al., 1998; Suttle et al., 1997). A temporal frequency of 4 Hz was used because it elicits maximum amplitude VEPs to tritan stimuli in adults (Rabin et al., 1994), and it is near the peak of the chromatic temporal contrast sensitivity function of 3- and 4-month-old infants, at least for red–green stimuli (Dobkins, Anderson, & Lia, 1998). In addition, 4-month-old infants do not respond to isoluminant tritan stimuli drifting at 4 Hz (Teller et al., 1997). We wanted to determine whether this failure might represent an inability to discriminate the colors when temporally modulated.

2.3. Procedure: psychophysics

With infants we used FPL (Teller, 1979) as the psychophysical technique. The infants were seated on the par-

ent's lap or (rarely) in an infant seat 40 cm from the monitor. An occluder prevented the parent from seeing the monitor (Teller, 1979). The experimenter viewed the infant through a peephole above the center of the monitor. Before displaying the gratings, the monitor displayed a uniform gray field, and the adult observer attracted the infant's attention to the center of the display using a small toy. Once satisfied that the infant was looking toward the screen center, the experimenter removed the toy and initiated a stimulus presentation. The grating stimuli were displayed randomly on either the left or right half of the screen; the experimenter was unaware of the position. The experimenter used any aspect of the infant's behavior to decide whether the pattern appeared on the left or right. The other half had a uniform field of the same average luminance and chromaticity as the grating. The experimenter was given auditory feedback concerning the correctness of their judgement after each trial.

In the adult psychophysical measurements, the stimuli were presented randomly on the left or right of the monitor in a two-alternative, forced-choice paradigm; the other half of the display was uniform, and had the same average luminance and chromaticity. The observer verbally indicated the side containing the grating.

In order to determine whether our green–purple stimuli isolated the S cones, we conducted a control experiment in adults. We rendered color-normal adults temporarily tritanopic by S cone adaptation. This was accomplished by adding a bright blue light (white light presented through a Wratten 47B filter) to the stimulus by use of a half-silvered mirror (Rabin et al., 1994). Observers adapted to the blue light for at least 4 min before beginning the experiment. The average luminance of the grating stimulus was 13 cd/m^2. Under these viewing conditions, isoluminant tritan stimuli at low contrast (10% of the maximum possible for our display) were indiscriminable to our adult observers. The same stimuli viewed directly (that is, without the blue light) were clearly visible. The fact that the grating was not distinguishable under the S cone adaptation condition shows that the tritan stimulus allowed S cone isolation, and that rod intrusion was not a problem, in adults.

2.4. Procedure: visual evoked potentials

Sweep VEPs were recorded using the same procedure in infants and adults. Active electrodes were placed at O1 and O2 of the International 10-20 system, both referred to OZ, and an earth electrode was placed at CZ. A reference position at OZ was preferable for practical reasons, so that the active and reference electrodes could be held in place using an elasticated headband. We compared reference sites at OZ and CZ (findings not presented here, but referred to in Section 6.2) and found that while absolute amplitude of the signal was smaller

using reference OZ, signal to noise ratio was similar in both situations. Electrode positions were abraded using Omniprep before electrode placement. Each VEP trial consisted of a 1 s observation period followed by a 10 s recording period (Norcia, Clarke, & Tyler, 1985).

Infants were observed by an experimenter throughout each trial; if the infant looked away at any point during the 11 s period, the trial was disregarded. After recording, the VEP was digitized and 1 s data windows, overlapping by 0.5 s, were Fourier analyzed to determine response amplitude and phase at a range of frequencies. As expected for onset–offset stimuli (McKeefry, Russell, Murray, & Kulikowski, 1996), the signal was strongest at the fundamental frequency of the stimulus. The mean of response amplitude at adjacent frequencies (3 and 5 Hz for the 4 Hz stimulus) was taken as an estimate of EEG noise (Norcia et al., 1985; Norcia & Tyler, 1985). In all cases, amplitude and phase was averaged from 5 sweep VEP trials.

3. Experiment 1: S cone pathway isolation

Tritan stimuli are specified according to cone spectral sensitivity functions measured in adults. If infant and adult spectral sensitivities differ, stimuli designed to isolate specific mechanisms in the adult visual system will allow less selective excitation in the infant visual system. Thus, if infant spectral sensitivity is different from that of adults, isoluminant tritan stimuli based on adult spectral sensitivity functions might be inappropriate for the infant observer because they may allow modulation of the L–M and L+M neural pathways.

In young infants, lens pigment density is ~10 times lower than in adults (Hansen & Fulton, 1989) and macular pigment density is ~5 times lower (Bone, Landrum, Fernandez, & Tarsis, 1988). Thus, preretinal absorption of short-wavelength light is less in infants than in adults. In addition, the newborn infant fovea has much lower cone optical density than adults caused by a 16-fold difference in cone outer segment length (Youdelis & Hendrickson, 1986). Anatomical factors of this kind may cause spectral sensitivity differences between young infants and adults. To investigate this possibility, we estimated spectral sensitivity of the adult visual system in three conditions: the system lacking macular pigment, the system lacking lens pigment, and the system with cone outer segments 16 times shorter than normal.

For the first two conditions, we took transmission spectra of those pigments (Wyszecki & Stiles, 1982) and discounted adult spectral sensitivity by these values. In this way, we derived spectral sensitivity functions for the adult eye without lens pigment in one case and without macular pigment in the second case, exaggerating the situation in infants. Fig. 1 shows adult spectral sensi-
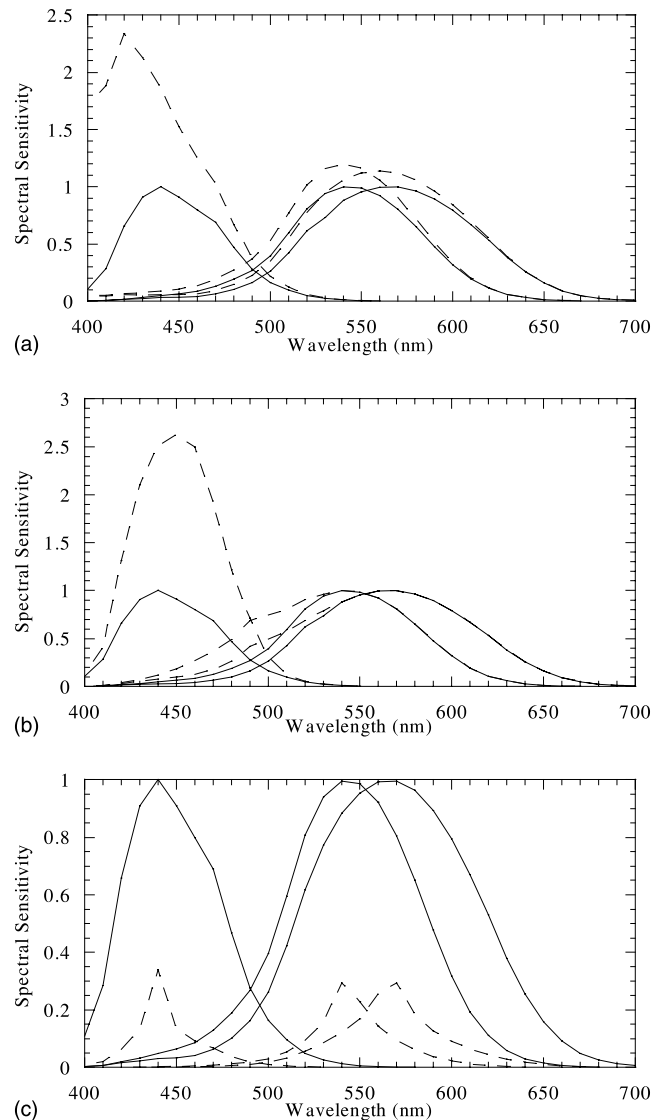

Fig. 1. L, M and S cone adult spectral sensitivity functions (Smith & Pokorny, 1975) are shown, normalized to 1.0 (solid lines). Spectral sensitivity functions for the adult eye with: (a) no macular pigment (dashed lines) are shown relative to the adult values, (b) no lens pigment (dashed lines) are shown relative to the adult values and (c) 16-fold reduction in cone outer segment length are indicated by dashed lines.

tivity functions (Smith & Pokorny, 1972, 1975) normalized to 1.0, and our derived functions adjusted for zero macular pigment (a) and lens pigment (b). Sensitivity is increased 2- to 3-fold at short wavelengths when lens or macular pigment is discounted, but sensitivity to medium and long wavelengths is relatively unaffected.

For the third condition—shorter cone outer segments—we used Lambert's law to calculate cone spectral sensitivity (Wyszecki & Stiles, 1982). Fig. 1c shows adult spectral sensitivity functions normalized to 1.0, and our derived functions adjusted for outer segment length.

We investigated whether standard tritan stimuli, defined according to adult spectral sensitivity, isolated S

Table 1
Positions in DKL space (azimuth and elevation) of stimuli that allow S cone isolation in the normal adult visual system, and in the three hypothetical visual systems discussed here

	Azimuth	Elevation
Adult eye	90	0
Adult eye: no macular pigment	89.1	3.4
Adult eye: no lens pigment	89.7	0.8
Adult eye: shorter outer segment	89.9	2.5

cones in these three hypothetical visual systems. If so, it is likely that the same is true for the young infant visual system because the three hypothetical situations exaggerate the situation in young infants.

We determined the positions in DKL space of stimuli that would isolate S cones in each of the three hypothetical visual systems. To do so, we used the adjusted spectral sensitivity functions shown in Fig. 1, and translated between cone excitation and DKL space using the method described by Brainard (1996).

Table 1 shows the rotation of those stimuli, in azimuth and elevation, with respect to an adult tritan (S cone) axis through a fixed white point. In each case, the stimuli are rotated less than 1° away from the adult S cone axis (azimuth) and less than 4° away from the adult isoluminant plane (elevation), showing a similarity with previous findings on individual variations in adults (Smith & Pokorny, 1995).

In this experiment, we determined whether adults can discriminate these slight rotations, and thus whether such stimuli allow reasonable isolation of the S cone pathway in adults. If so, then standard tritan stimuli probably also allow isolation of the S cone pathway in infants.

In two adults, we adapted S cones using a blue filter, as described above (see Section 2). Stimuli were situated along a tritan axis in DKL space (azimuth of 90°) and at 2.5°–5° intervals up to 25° away from the tritan axis (azimuth of 65°–115°). At all azimuth settings, the stimuli were at the mean isoluminant point determined by heterochromatic flicker photometry in five adults. Cone contrast was constant at 0.085, 10% of the maximum contrast possible for the tritan stimulus using our monitor.[2] At low contrast, the isoluminant tritan stimulus was not distinguishable through the filter, but was clearly distinguishable without S cone adaptation (no blue filter).

Under S cone adaptation, the observers were effectively tritanopic, so we would expect that the low-con-

trast tritan stimuli would be indistinguishable in this situation. L and M cones are not adapted by the filter (Rabin et al., 1994), so if the L–M pathway is effective in distinguishing the stimuli at any of the azimuth settings chosen, the gratings will be visible. Grating visibility was determined using the 2AFC paradigm (see Section 2).

3.1. Results

Fig. 2 shows performance (% correct) as a function of azimuth for the two adult observers rendered tritanopic by S cone adaptation. At azimuth of 90°, the stimuli are along a standard tritan axis, and modulate selectively the S cone, color-opponent pathway in these adults. At all azimuth settings, stimuli are at the mean of our adult observers' isoluminance settings, so the luminance pathway should not be useful in discriminating the colors. Our observers are rendered tritanopic by S cone adaptation, so it is not surprising that performance is around chance when viewing stimuli at 90° azimuth. As the azimuth is changed, away from the tritan axis, it becomes increasingly likely that L and M cones may be used in the discrimination of the stimuli. Performance remains around chance, however, at azimuth settings of 2.5°–10° either side of the tritan axis.

These findings indicate that the L and M cones are not useful in the discrimination of stimuli 2.5°–10° away from a standard tritan axis. Colors that stimulate selectively the S cone, color-opponent channel in the hypothetical visual systems we considered here are less than 2° from a standard tritan axis in DKL space (Table 1). Our results suggest that stimuli along a standard tritan axis would not elicit a response from the L–M cone, color-opponent channel in an observer with no lens pigment in one case, no macular pigment in another case, or with shorter cone outer segments in the third case. Even if all three conditions are combined, azimuth
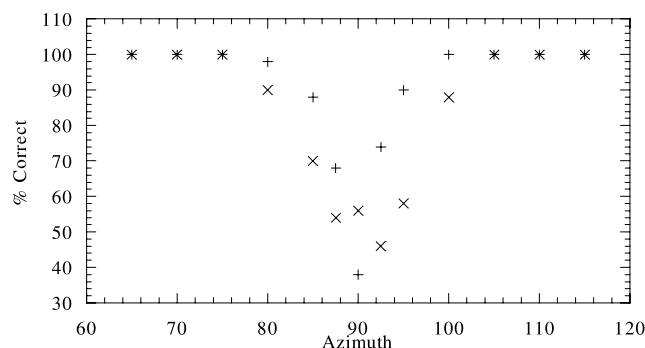

Fig. 2. Performance (% correct) of two adult observers rendered tritanopic by S cone adaptation. The stimulus was varied from a standard tritan color pair, at 90° azimuth to 35° away from this, in steps of 2.5°–5°. Performance is around chance at 2.5°–10° away from the standard tritan axis.

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[2] It should be noted that the stimuli presented to adults in psychophysical experiments were at low contrast to render the gratings indiscriminable at isoluminance through the filter. Infants, however, are likely to require higher contrasts (e.g., Allen et al., 1993; also see results of our Experiment 2). Thus, it was not possible for the contrasts to be equal in psychophysical experiments for the two subject groups.

rotation is less than 2.5° so S cone isolation is very likely in this scenario.

Note that the S cone isolating stimuli for the hypothetical visual systems considered here show a greater rotation in terms of elevation than azimuth. This suggests that the young infant visual system may require slightly different luminances between two presumably tritan stimuli to ensure that they are isoluminant. We explore this possibility in Experiment 2.

4. Experiment 2: Infant and adult psychophysical responses to tritan stimuli

The primary aim of this experiment was to determine whether young infants (1- to 4-month-olds) fail to discriminate tritan stimuli. In addition, we determined isoluminance of nominal tritan stimuli in infants.

Infants' visual sensitivity depends in part on temporal modulation rate. Visual acuity and contrast sensitivity are higher for temporally modulated, as opposed to static, stimuli (Atkinson, Braddick, & Moar, 1977; Sokol, Moskowitz, McCormack, & Augliere, 1988). Conversely, infants may have more difficulty in discriminating drifting as opposed to static tritan stimuli (Teller et al., 1997; Varner et al., 1985). We wanted, therefore, to determine whether young infants behave like tritanopes with temporally modulated and static stimuli. For this reason, one group was tested with static stimuli, and another with on–off flickered stimuli that were otherwise identical.

Adults: S cones were adapted in two adult observers, as described above (Experiment 1). The stimuli were stationary, low color-contrast (10% of maximum) tritan stimuli, at a constant azimuth of 90° (along the S cone axis in DKL space); elevation was varied around the mean adult isoluminant point (elevation 0). Because the observers were rendered effectively tritanopic, we expected chance performance at the elevation closest to the observer's isoluminant point.

Infants: Vertical 0.2-cpd sinewave gratings were presented to 1- to 4-month-old infants. The color contrast was high (S cone contrast = 85%), but the stimuli were otherwise identical to the ones shown to adults. The two colors in the gratings were along the S cone axis, and were presented at elevations of −27° to 27°. Two 1-month-olds (4–6 weeks), ten 2-month-olds (6–10 weeks) and three 3-month-olds (11–13 weeks) were tested with static stimuli. Seven 2-month-olds, seven 3-month-olds and six 4-month-olds were tested with temporally modulated stimuli. If infants were able to distinguish the colors without luminance cues, performance should be significantly above chance at all elevations. If infants are tritanopic, however, they should be unable to distinguish the tritan stimuli without luminance cues. Specif-

ically, lower performance should be observed over a range of elevations including the isoluminant point.

4.1. Results

Adults: As shown by Fig. 3, adults' performance drops to chance at an elevation close to the mean adult isoluminant point (elevation 0), demonstrating that tritanopic observers are unable to distinguish the tritan stimuli when luminance cues are eliminated.

Infants: Fig. 4 shows infants' performance as a function of elevation of standard static and temporally modulated tritan stimuli. Two-month-olds (Fig. 4a and b) performed significantly above chance at one or more elevations away from adult isoluminance (elevation 0) and at chance for elevations at or around 0. Chance performance suggests that these infants are unable to distinguish the tritan stimuli without luminance cues (or that they are relatively unmotivated to look at such stimuli). Thus, our results indicate that infants behave like tritanopes up to at least 2 months. At 3 months (Fig. 4c and d), some infants performed below 70% near the adult isoluminant elevation, while others performed above 75% at all elevations. Five of the six 4-month-olds tested with temporally modulated stimuli performed at 70% or greater across all elevations (Fig. 4e). Taken together, these results suggest that, with the spatial and temporal parameters used in this study, infants behave like tritanopes until at least 2 months, and not at 4 months. In addition, our results indicate that 4-month-olds' lack of response to drifting tritan stimuli (Teller et al., 1997) does not reflect an inability to see the colors, or to see them when temporally modulated.

Of the 15 infants tested with static stimuli, 11 showed performance minima near the adult isoluminant eleva-
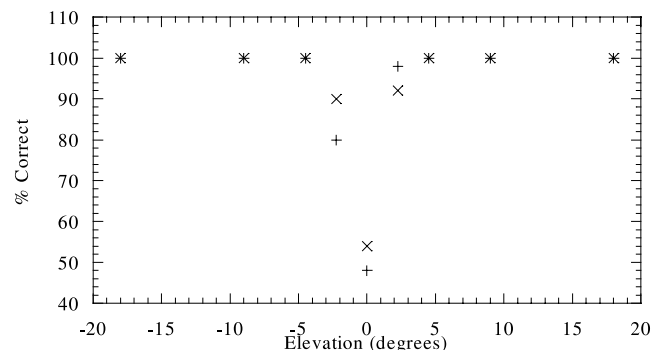

Fig. 3. Performance (% correct) of two adult observers under conditions of S cone adaptation. The stimulus was a standard tritan pair (90° azimuth), and the relative luminance of its constituent colors was varied, while mean luminance remained constant. Elevation zero indicates adult isoluminance determined by heterochromatic flicker photometry. With S cone adaptation, performance is around chance at isoluminance, because the observers are rendered tritanopic; without S cone adaptation performance was 100% correct at all color luminance ratios.
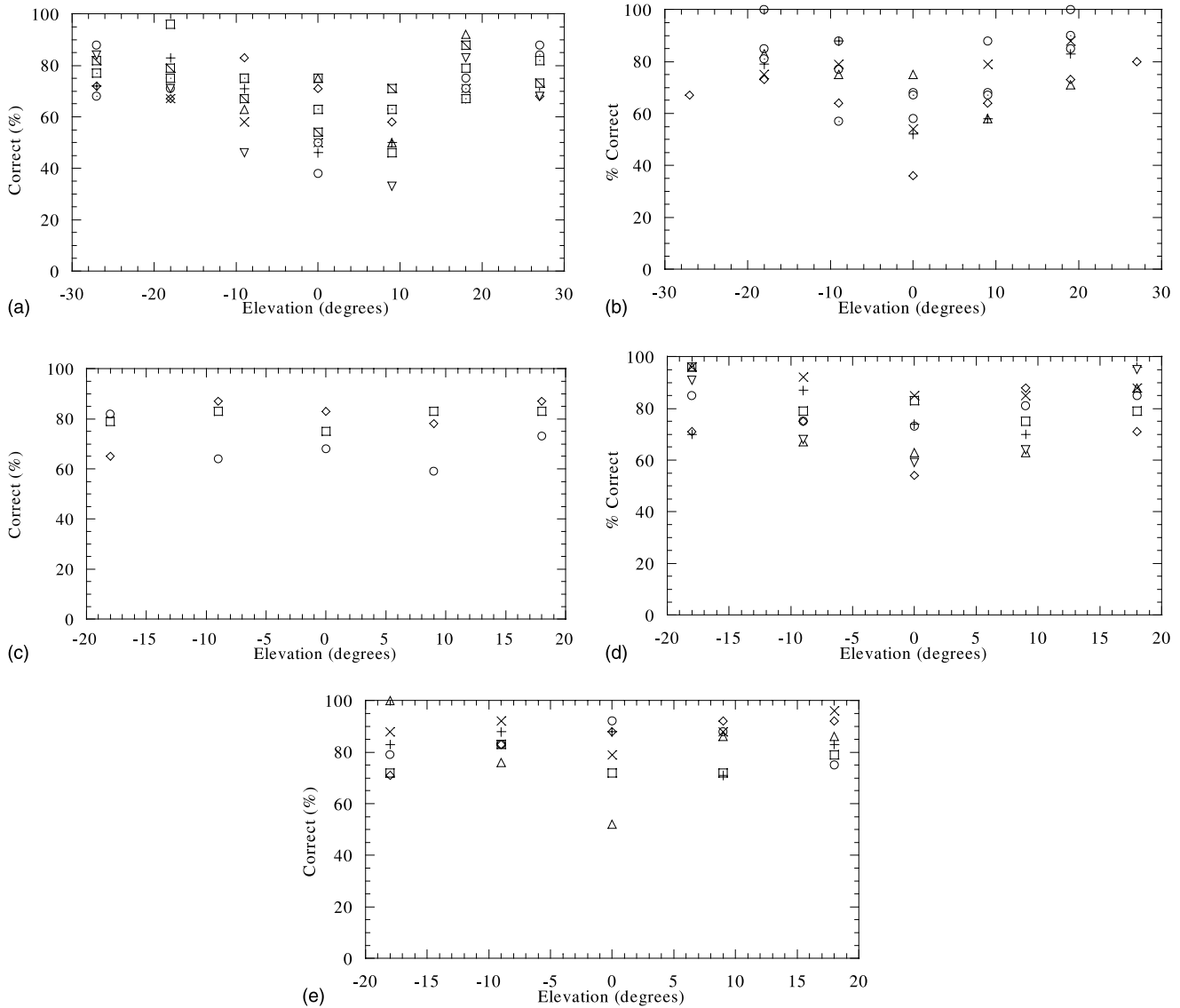
Fig. 4. FPL performance (% correct) of 2-month-olds in response to static (a) and temporally modulated (b) tritan stimuli at and around adult isoluminance. Performance at one or more elevations close to adult isoluminance is around chance, suggesting that these infants are tritanopic. At 3 months, some infants are able to discriminate tritan stimuli (static (c) and temporally modulated (d)) at all elevations. Most of the 4-month-olds (e, tested only with temporally modulated gratings) demonstrated above 75% correct preferential looking responses to tritan stimuli at and around isoluminance, indicating that most infants are no longer tritanopic by this age.

tion and maxima in response to luminance-modulated stimuli. In each case, a Gaussian fit the data reasonably well. From the best-fitting Gaussian, we determined the elevation of minimum performance, and took this as an estimate of isoluminant elevation for each infant. Fig. 5 shows those elevations for each of the 11 infants. The range of estimated isoluminant elevations is $-5.4°$ to $7.2°$, with a mean of $1.8°$. The adult range determined from heterochromatic flicker photometry at the same spatial frequency was $-3.6°$ to $7.2°$ (mean $= 0$), similar to that of infants. Thus, anatomical differences between infants and adults apparently do not cause significant shifts in isoluminance, so adult luminance matches provide reasonable approximations for infants.

5. Experiment 3: Sweep visual evoked potential

Sweep VEPs were recorded from adults and infants. High contrast tritan stimuli were swept in elevation from $36°$ to $-90°$ during the 10-s recording period. In adults, the response was recorded at two spatial frequencies: 0.2 cpd in one case and 1.0 cpd in the second case. The lower spatial frequency was used for comparison with infant VEPs, recorded at 0.2 cpd only; the higher frequency was used to allow optimal signal to noise ratio of the response to chromatic stimuli in adults (Rabin et al., 1994). Temporal frequency was at 4 Hz, and responses were recorded from O1 and O2, referred to OZ. All other aspects of the stimuli and

Fig. 5. Isoluminance for each of eleven 1- to 3-month-old infants was estimated by fitting a Gaussian function to the data from individual infants. Mean isoluminance for infants was at an elevation of 1.8, only 2% of mean luminance away from adult isoluminance.

recording procedure were as described earlier (see Section 2).

5.1. Results

Fig. 6 shows the averaged VEP recorded from one color-normal adult in response to vertical sinewave
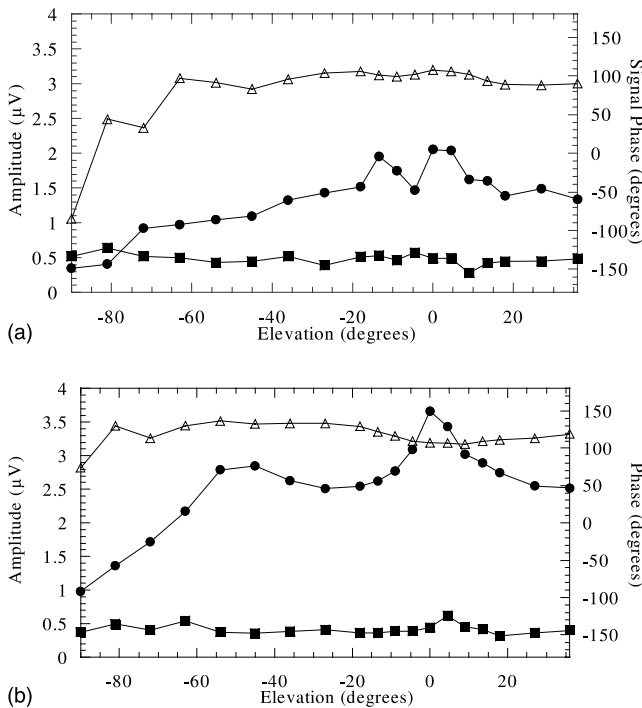

(a)

(b)

Fig. 6. Sweep VEPs to high contrast tritan stimuli at a range of elevations (zero = adult isoluminance) recorded from a color-normal adult observer. Stimuli were vertical sinewave gratings, on–off modulated at 4 Hz: (a) spatial frequency 0.2 cpd and (b) spatial frequency 1 cpd. Filled circles show signal amplitude; filled squares show noise amplitude, the mean amplitude at two frequencies adjacent to the fundamental (3 and 5 Hz); open triangles show signal phase. At these stimulus parameters, the signal-to-noise ratio is highest around isoluminance, and decreases as luminance differences are introduced.

gratings at 0.2 cpd (a) and 1 cpd (b) swept in elevation from −90° to 36°. Filled circles show the response amplitude at the fundamental frequency of the stimulus (4 Hz) and filled squares show the mean response amplitude at 3 and 5 Hz, an estimate of EEG noise. Open diamonds show the phase of the response at 4 Hz; if the response were time-locked to the stimulus, we would expect phase to be fairly constant. Phase variations of less than 90° are taken to be consistent with a response that is time-locked to the stimulus (Norcia et al., 1985).

Fig. 6 shows that, at both spatial frequencies, the response near isoluminance is significantly above noise, and at constant phase, while the response to luminance-modulated stimuli is at a lower signal to noise ratio. Thus, under these stimulus conditions, signal-to-noise ratio is highest at isoluminance in adults, decreasing as luminance differences are added to the stimulus. Note that amplitude decreases only when large luminance differences exist in the stimulus; at color ratios around isoluminance, there is little variation in amplitude, in agreement with previous findings in adults (Porciatti & Sartucci, 1999; Rabin et al., 1994). At 1cpd amplitude of the response to isoluminant tritan stimuli is higher than at 0.2 cpd, in agreement with previous findings (Rabin et al., 1994).

Fig. 7a shows one sweep VEP in response to tritan stimuli at a range of elevations from −90° to 36° recorded from a 2-month-old infant. Responses from all seven infants in this age group showed a similar trend. The signal is significantly above noise at elevations away from isoluminance, but drops to noise levels around isoluminance. In addition, signal phase is constant when the stimulus is luminance-modulated, but is more variable around isoluminance. Thus, response amplitude and phase characteristics suggest that isoluminant tritan stimuli, at the stimulus and recording parameters used here, do not elicit a significant VEP in 2-month-old infants. When tritan stimuli are sufficiently luminance-modulated, however, the VEP is significantly above noise at this age.

Fig. 7b shows a sweep VEP recorded in response to tritan stimuli at various elevations from one 3-month-old infant. Responses recorded from all seven infants in this age group showed a similar trend. Again, the signal is significantly above noise only when the stimuli are luminance-modulated. At and around isoluminance, the response is slightly above noise, but does not meet our criterion for significance (signal to noise ratio of 3:1). In addition, around isoluminance signal phase is inconsistent, and becomes more consistent as luminance differences are introduced to the stimulus. These response characteristics show that, for the stimulus parameters and recording technique we used, isoluminant tritan stimuli do not elicit a significant VEP in 3-month-old infants.
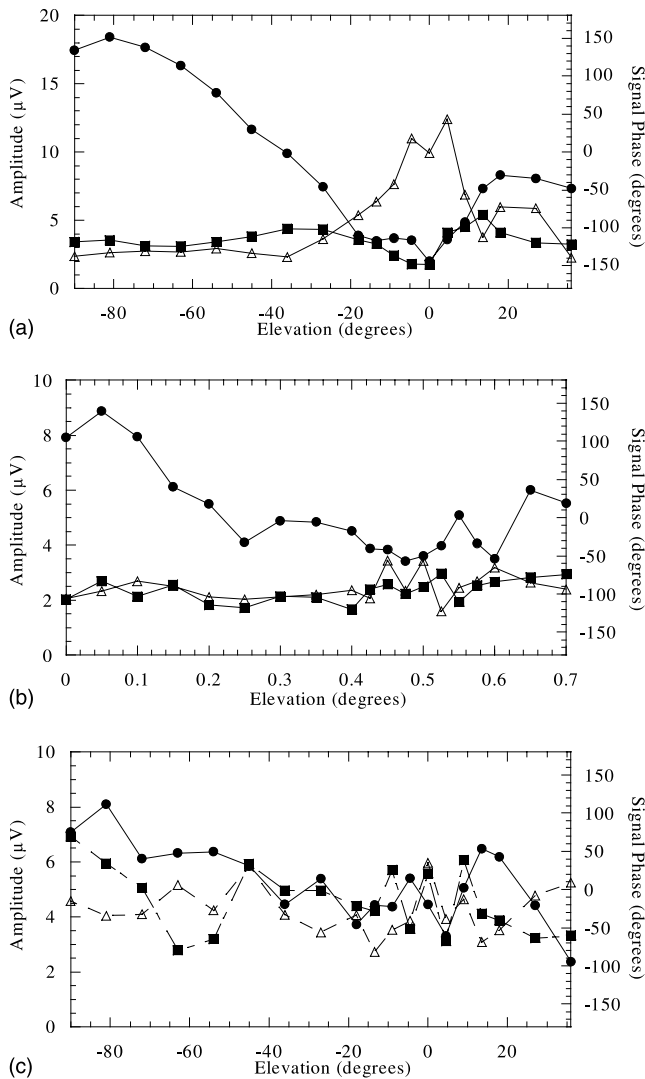
Fig. 7. Sweep VEPs recorded from infants to tritan stimuli at a range of elevations (zero = adult isoluminance). Filled circles show signal amplitude at the fundamental frequency (4 Hz); filled squares show noise amplitude, the mean amplitude at two frequencies adjacent to the fundamental (3 and 5 Hz); open triangles show signal phase. (a) Recorded from a 2-month-old infant. The signal is around noise levels near adult isoluminance, and signal-to-noise ratio increases, and signal phase becomes more consistent, as luminance differences are introduced. (b) Recorded from a 3-month-old infant. As for the 2-month-old, the signal is not significantly above noise levels near isoluminance, and signal-to-noise ratio and phase consistency increase with luminance difference. (c) Recorded from a 4-month-old infant. Signal-to-noise ratio is not significant at any elevation, and phase is variable throughout the sweep.

As explained above, in 2- and 3-month-old infants, sweep VEPs recorded from O1 and O2 were insignificant near isoluminance when the stimuli were temporally modulated at 4 Hz. This finding prompted us to record responses to the same stimuli from a different recording site (OZ in addition to O1 and O2) and different temporal frequency (2 Hz in addition to 4 Hz) in ten of the 2- to 3-month-olds. Our results (not shown) indicated

that these alternative recording conditions did not improve the signal to noise ratio of the response to tritan stimuli around isoluminance.

Sweep VEPs from four 4-month-olds showed no significant response to tritan stimuli at any elevation (see Fig. 7c). Our study was not longitudinal, so we had no VEP recordings from these infants at an earlier age. Note, however, that in experiment 4, most 3- to 4-month-old infants demonstrated an ability to discriminate stimuli identical to those used for our VEP recordings, so it seems that the sweep VEP is not necessarily a reliable indicator of infants' ability to discriminate chromatic stimuli. This issue will be discussed later.

6. Discussion

Immaturities of the infant eye include relatively low lens and macular pigment density, and low cone optical density due to short cone outer segments. Each of these factors may contribute to spectral sensitivity functions that are quite different from those of adults. For this reason, we wanted to verify whether stimuli that selectively modulate S cones (tritan stimuli) in infants are different from those in adults. We found (Experiment 1) that S cone isolating stimuli in an adult visual system without macular or lens pigment (exaggerating the situation in infants) or with 16 times shorter cone outer segments, are similar to standard tritan stimuli. Further, we determined that such stimuli are not distinguished by an effectively tritanopic adult observer. Thus, it seems unlikely that standard tritan stimuli would elicit a response from the luminance pathway or the L–M color-opponent pathway in infants.

The results of Experiment 2 indicate that isoluminance of tritan stimuli in infants is very close to that of adults, in agreement with earlier findings that spectral sensitivity is similar in infants and adults (Bieber, Volbrecht, & Werner, 1995; Volbrecht & Werner, 1987). We found that individual 2-month-old infants show chance performance not only at zero elevation (mean adult isoluminance) but in some cases at elevations away from this point (elevation range −5.4° to 7.2°). In these infants, luminance cues may be provided by a stimulus at adult isoluminance. It seems important, therefore, to present stimuli at and around adult isoluminance when the focus of a study is the age of functional onset of color vision (e.g., Peeples & Teller, 1978).

None of the 2-month-old infants in our study demonstrated FPL or VEP responses to low-spatial-frequency, high-contrast tritan stimuli without luminance cues. There are at least four possible explanations for this finding. First, perhaps S cones are not functional at this age, so that neither VEP nor FPL responses to S cone isolating stimuli are significant. Previous work demonstrating functional S cones by at least 4 weeks of age,

however, make this explanation unlikely (Volbrecht & Werner, 1987). Second, S cones may be functional, but the post-receptoral S cone pathway may not be providing useful signals. Transient VEPs to tritan stimuli without luminance cues are evident by, on average, 2 months of age (Crognale et al., 1998; Suttle et al., 1997). Thus, previous findings suggest that S cones and retino-striate processing are functional in most 2-month-olds. A behavioral response, however, requires function of the visual pathway beyond the striate cortex, in addition to functional connections for a motor response. Thus, the third possibility is that immaturity of post-striate S cone visual pathway and/or neural connections required for a behavioral response, might explain the lack of FPL response from the youngest infants in our study. Finally, the FPL response may be limited by factors unrelated to visual function, such as a lack of motivation to look toward the stimulus. The apparent insensitivity to tritan stimuli demonstrated by young infants in the present study, and others using behavioral techniques, may partly reflect non-sensory factors of this kind (Clava-detscher, Brown, Corlene, & Teller, 1988; Pulos et al., 1980; Teller, Peeples, & Sekel, 1978, 1997; but see also Varner et al., 1985).

When the same stimuli were temporally modulated, about half of the group of seven 3-month-olds responded significantly above chance to tritan stimuli at and around adult isoluminance, and about half of them failed to respond at one or more elevations. Five out of six 4-month-olds demonstrated discrimination of these stimuli at all elevations. Taken together, these results indicate that the S cone pathway and connections with the motor cortex required for a behavioral response are functional by 3–4 months of age. In all infants tested in all age groups, however, sweep VEPs were not significantly above noise around adult isoluminance, but, at least in younger infants were significant when large luminance differences were present in the stimulus.

We found lower signal to noise ratio in older infants, and this is consistent with some previous reports of diminished VEP amplitude during development (Suttle et al., 1997; Zemon, Hartmann, Gordon, & Prunte-Glowazki, 1997). However, it is contrary to reports of an increase in amplitude during development, peaking at preadolescence, then steadily decreasing with age (Crognale et al., 1998; Madrid & Crognale, 2000). The apparent disagreement between studies reflects at least three factors. First, the latter studies used transient VEPs, while the present study used sweep VEPs (the significance of VEP technique will be discussed later (Section 6.2.6)). Second, our finding of lower signal to noise ratio in older infants applies to luminance modulated stimuli only, since we had not elicited a significant signal to noise ratio in response to isoluminant stimuli from infants at any age in our study. Third, in the present study responses were recorded from young in-

fants, while others included older infants, children and in some cases adults. Thus, our finding applies to a particular technique, stimulus, and developmental time window.

6.1. FPL vs VEP

In general, studies of infant visual function using VEPs reveal higher sensitivity than those using behavioral techniques, such as FPL. In other words, we might expect a significant VEP to be present, in the absence of an FPL response. Contrary to this, in our study, most 3- to 4-month-olds demonstrated FPL responses, but no significant VEP, to tritan stimuli around isoluminance.

Our discrepant behavioral and electrophysiological findings may reflect methodological differences. The VEP is a pooled neural response recorded from an area of the scalp over the primary visual cortex. FPL responses rely on an infant's preference for a pattern over a uniform stimulus. If the infant looks reliably towards a pattern, we assume that the infant can discriminate the elements of the pattern. If not, we assume that the infant is unable to see the pattern, although non-sensory factors such as poor motivation may also explain this behavior. FPL responses presumably require neural signals generated in the primary visual cortex, and beyond here to the motor cortex. In infants, as well as in adults, the super-threshold stimulus will not necessarily give rise to a significant VEP. For example, in adults, the VEP to high contrast luminance-modulated gratings (elevation $-90°$) was not significantly above noise, but the stimulus was always clearly visible (see Fig. 6). This finding is in agreement with previous work (Crognale, Switkes, & Adams, 1997) and may be due to a combination of factors including non-linearity of the VEP to chromatic stimuli, and interactions between groups of neurons involved in the gross potential (discussed by Crognale et al., 1997).

These findings bring to the surface a number of questions regarding the VEP and FPL techniques as methods of assessing visual function in infants. What does the VEP tell us about visual function? By what age do VEP thresholds correlate with psychophysical thresholds? When using the VEP to assess infant vision, what is the most appropriate way to assess noise, in order to optimise comparability with psychophysical findings? Some of these questions have been addressed with regard to assessment of visual acuity (e.g., Riddell et al., 1997), but further research is required to investigate the correlation of electrophysiological and psychophysical assessment of color vision in infants.

6.2. Comparison with previous studies

In the present study, we presented tritan stimuli at a temporal frequency of 4 Hz, to make our findings

comparable with those of a previous study using OKN (Teller et al., 1997). In that study, tritan stimuli were *drifting* at a frequency of 4 Hz, and infants failed to demonstrate eye movement responses to the stimuli, even at 4 months of age. In the present study, 4 Hz on–off tritan stimuli without luminance cues were discriminated by some 3-month-olds and most 4-month-olds tested. Our results demonstrate that infants are able to distinguish temporally modulated tritan stimuli at 3–4 months of age. It remains possible, however, that infants are unable to distinguish such stimuli when drifting, or that tritan stimuli do not elicit an eye movement response at this age (Teller et al., 1997).

In contrast with our findings, previous studies have demonstrated VEPs to tritan stimuli by about 2 months of age (Crognale et al., 1998; Suttle et al., 1997). We now consider several plausible explanations for the discrepancy between the present and previous VEP studies.

6.2.1. Temporal frequency

Earlier VEP studies have used temporal frequencies of 1 Hz (Crognale et al., 1998) and 2 Hz (Suttle et al., 1997), slower than the frequency of 4 Hz used in the present study. We investigated the possibility that the response to isoluminant tritan stimuli at this temporal frequency is poor at the electrode sites from which we recorded, by recording at 4 and 2 Hz in some infants (data not shown). We found that the slower frequency did not allow a clearer signal, indicating that temporal frequency does not account for the difference between this and previous VEP studies.

6.2.2. Electrode montage

In previous work, an active electrode has been positioned at OZ, with reference electrode at CZ (Suttle et al., 1997) or between OZ and CZ (Crognale et al., 1998). In the present study, most recordings were made with active electrodes at O1 and O2 and a common reference at OZ. The same electrode montage was used in infants and adults. The response to isoluminant tritan stimuli using this montage was reliable and significantly above noise in all adults tested, but not in any of the infants. Responses to luminance-modulated stimuli only were significantly above noise in the younger infants. To determine whether our electrode montage may account for the low signal-to-noise ratio in response to chromatic stimuli in our study, we recorded responses from some infants with the active electrode at OZ and reference at CZ, as in previous studies. The amplitude of both signal and noise were increased with the OZ vs CZ montage, but signal-to-noise ratio was not increased, suggesting that electrode montage does not account for the difference between our findings and those of transient VEP studies.

6.2.3. EEG noise estimation

We estimated noise from the mean amplitude of the response at non-harmonic frequencies, adjacent to the fundamental frequency. Perhaps evoked responses from the immature visual system are dominated by low temporal frequency components. Indeed, evidence of this is provided from the power spectrum of the human infant visual evoked response to visual noise (Moskowitz & Sokol, 1980). Response amplitude depends upon the type of visual stimulus used, and will vary across a range of temporal frequencies. In the present study, noise amplitude was estimated as the mean of the response amplitude at two frequencies adjacent to the fundamental frequency. Perhaps this method may have provided an overestimate of EEG noise, and thus an underestimate of signal to noise ratio.

6.2.4. Lack of S cone pathway function

Perhaps our lack of significant VEP to tritan stimuli in infants reflects a lack of function of the retino-striate pathway processing S cone signals. We cannot exclude this possibility for 2-month-olds. However, 3- to 4-month-olds in our study demonstrated behavioral responses to tritan stimuli, indicating that the S cone pathway, from retina to striate cortex and beyond, is functional by this age. Thus, S cone pathway dysfunction appears unlikely, at least in 3- to 4-month-old infants.

6.2.5. Criteria for significance

Criteria for responses significantly above noise levels differ between studies. In the present study, the criterion for significance was a signal-to-noise ratio of 3.0, tougher than in some previous studies. For example, Suttle et al. (1997) used a signal-to-noise ratio of 1.5 as the criterion for a significant response, and noise was determined from the response to a uniform, unmodulated, screen. Crognale et al. (1998) determined whether an evoked potential was present in the response by direct observation of the response to the grating stimulus, rather than by comparison to a 'noise' response.

6.2.6. Sweep vs transient VEP techniques

To our knowledge, the present study is the first to use the sweep VEP to investigate development of the S cone pathway. Previous studies have used either the transient VEP (Crognale et al., 1998; Suttle et al., 1997) or the steady-state VEP (Volbrecht & Werner, 1987). The transient VEP differs from the sweep VEP in a number of ways. First, in the transient VEP technique, numerous (30–50) evoked potentials are averaged, while the sweep VEP averages the amplitude and phase at specific frequencies in a small number of response sweeps (5–10). Previous studies using the transient VEP in infants have found that the response to chromatic stimuli is of more complex morphology than the response to luminance

modulated stimuli. This finding might reflect relatively complicated changes in the chromatic pathways during maturation (Crognale et al., 1998). In the present study, the fundamental frequency (4 Hz) was taken to indicate signal amplitude. Perhaps signal to noise ratio might have been higher if harmonic frequencies had been chosen to represent signal amplitude. We found, however, that amplitude was higher at the fundamental frequency than at higher harmonic frequencies. Thus, it is unlikely that a harmonic frequency would have allowed a higher signal to noise ratio (but see also our discussion of noise estimation above, and mentioned below).

Second, in the present study, sweep VEP noise was estimated from the response to the pattern stimulus at non-harmonic frequencies, while in the transient VEP noise is estimated in a different way, such as from the response to a uniform screen. Third, all temporal frequencies within the bandwidth of the amplifier are included in the transient VEP, and response components which are not time-locked to the stimulus are reduced by averaging, while in the sweep VEP technique, response amplitude and phase at specific temporal frequencies are noted. It is likely that differences in technique, as described above, explain the discrepancy between our findings and those of transient VEP studies.

6.3. Development of S cone vs luminance pathway

Can our results tell us anything about the relative patterns of development of the S cone and luminance pathways? To address this question, we turn to sweep VEPs recorded from adults and infants (Figs. 4 and 5), in response to comparable stimuli. Note that 2- and 3-month-old infants demonstrate a dip in response amplitude around isoluminance. By contrast with results from young infants, the adult sweep VEP is maximal around isoluminance, and is diminished in amplitude when luminance difference is introduced.

There are at least two possible explanations for this difference between infant and adult sweep VEPs. First, it appears from these responses that infants are more sensitive to luminance than to chromatic stimuli, while adults show the opposite trend. It is tempting to conclude that these results provide evidence for different patterns of development of the S cone and luminance pathways. However, adult and infant recordings are both in response to a low spatial frequency stimulus, which is likely to have different relative effects on the luminance and chromatic pathways in infants and adults (Allen et al., 1993). Second, the difference between adult and infant sweep VEPs could reflect different orientations of VEP sources with respect to electrode positions. For example, the response to isoluminant tritan stimuli might arise at a position deeper in the cortex of the infant brain than the adult brain, while the luminance response may arise at similar positions in infants and adults. If this were the case, detection of VEPs to isoluminant tritan stimuli would be relatively difficult in infants.

In summary, our behavioral findings indicate that infants behave as tritanopes until 3–4 months of age, when most infants demonstrate an ability to discriminate tritan stimuli. This age of onset did not depend on temporal modulation: A similar trend was observed for stationary and onset–offset tritan stimuli. Contrary to our behavioral results from infants, the sweep VEP in response to isoluminant tritan stimuli was absent in all of the infants we tested. In addition, the signal to noise ratio of responses to luminance-modulated stimuli was lower in older (4-month-old) than younger (2-month-old) infants, suggesting that the VEP may become masked by noise during infancy. Thus, our results show that the absence of a sweep VEP to isoluminant tritan stimuli in infants does not necessarily indicate that the neural pathway of interest is not functional, and raises questions regarding the correlation of electrophysiological and psychophysical methods of visual function in infants.

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