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Infant Color Vision: Moving Tritan Stimuli do not Elicit Directionally Appropriate Eye Movements in 2- and 4-month-olds

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The purpose of the present study was to investigate the capacity of infants to code the direction of motion of moving tritan-modulated gratings. Infant and adult subjects were tested with 0.2 c/d sinusoidal gratings moving at a speed of 20 deg/sec. Three conditions were tested: luminance-modulated gratings, tritan-modulated gratings, and luminance- vs tritan-modulated gratings superimposed and moving in opposite directions in a chromatic motion nulling paradigm. Two-month-old infants were tested in all three conditions, while 4-month-olds were tested in only the first two conditions. For infant subjects, an adult observer reported the direction of the slow phase of the infant's eye movements; adult subjects judged the perceived direction of motion of the stimuli. Luminance-modulated gratings produced directionally appropriate eye movements (DEM) in all age groups. Tritan gratings presented alone did not produce DEM in either 2- or 4-month-olds, but did so in adults. Mean equivalent luminance contrasts were near zero in 2-month-olds, and small but reliably above zero in adults. In sum, the present study provides no evidence that infants can code the direction of motion of moving tritan gratings. © 1997 Elsevier Science Ltd. All rights reserved.

Infant vision Color vision S cones Tritan Isoluminance Motion Motion nulling Optokinetic nystagmus (OKN) Eye movements

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INTRODUCTION

In human photopic vision, visual signals are initiated by three types of photoreceptors, the L, M and S (long-wavelength-, mid-wavelength-, and short-wavelength-sensitive) cones. These inputs are thought to be combined in early visual processing to form signals in three postreceptoral channels. In one common model of early visual processing (Boynton, 1979; MacLeod & Boynton, 1979; Krauskopf *et al.*, 1982; Derrington *et al.*, 1984), these three channels are a *luminance* channel that receives summed inputs from L and M cones; and two chromatic channels, a *red/green* channel that receives opponent inputs from L vs M cones, and a *tritan* channel that receives opponent inputs from S cones vs L and M cones. Within this model, it is of interest to explore the maturation of responsiveness to red/green and tritan stimuli in infants.

Infants' responses to red/green stimuli have been explored in a number of studies. Three different response measures have been used: forced-choice preferential looking (FPL) (Hamer *et al.*, 1982; Packer *et al.*, 1984; Clavadetscher *et al.*, 1988), visual evoked potentials (VEP) (Allen *et al.*, 1993; Morrone *et al.*, 1993; Kelly *et al.*, 1997) and directionally appropriate eye movements (DEM) (Teller & Lindsey, 1993; Teller & Palmer, 1996; Brown *et al.*, 1995; Dobkins & Teller, 1996). Most of these studies suggest that most infants first become responsive to red/green stimulus differences within the second postnatal month (but c.f. Allen *et al.*, 1993; Adams *et al.*, 1986, 1991).

In the present study we turn to the onset of responsiveness to tritan-modulated stimuli. We begin with a historical review of prior studies of the functional development of infants' S cones and/or infants' responsiveness to tritan differences.

S cones and tritan discriminations in infants

In an early study of chromatic discrimination, Teller *et al.* (1978) tested 2-month-olds' capacity to discriminate a series of broadband chromatic stimuli from a white surround. The luminances of the chromatic stimuli were varied systematically around the adult brightness match, in order to be sure to confront the infant with isoluminant chromatic differences (Peeples & Teller, 1975). These authors found that 2-month-olds could discriminate reds,

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oranges, greens, blues, bluish purples and reddish purples from white, but failed in a zone in the yellow–green and a second zone in the mid-purples. Although the fit of the failure zone with a tritan confusion line was inexact, it was suggestive; and this study thus provoked the speculation that infants might show a developmental delay in the maturation of S cones or in the processing of S-cone-initiated signals.

In a second early study, Pulos *et al.* (1980) used a chromatic adaptation paradigm and increment thresholds to look for the presence of S cones. Since S cones have a maximum sensitivity at about 440 nm, while rods and M and L cones all have maximum sensitivities at longer wavelengths, a spectral sensitivity curve that declines between 450 and 500 nm constitutes a signature for the presence of functional S cones. Tested with 2.2–2.6 log Td yellow adapting fields, both adults and the majority of 3-month-olds showed the S cone signature, while the majority of 2-month-olds did not. Thus, this study again suggested an immaturity of S cones and/or the post-receptoral processing of S-cone-initiated signals during early postnatal development.

More recently, Volbrecht & Werner (1987) carried out a chromatic adaptation study using VEP methodology. In their study, VEP spectral sensitivity curves measured against a 3 log Td yellow adapting field clearly followed an S-cone template, with a sensitivity maximum at about 440 nm, by 4–6 weeks postnatal. The Volbrecht and Werner study thus established definitively the presence of functional S cones in very young infants. However, compared with adults, infants showed a lower relative sensitivity to 440 as compared with 550 nm light. This result provides a third hint at the possibility of a differential insensitivity of S cones or the tritan channel during infancy.

Two more recent FPL studies of chromatic discrimination, specialized to reveal tritan discriminations, have also been carried out in infant subjects. Varner *et al.* (1985) tested 1- and 2-month-olds with 416 nm test fields embedded in a 547 nm surround. These two wavelengths constitute a close approximation to a tritan pair; in foveally tested adults, discrimination between two members of a luminance-matched tritan pair is diagnostic of the presence of functional S cones (Boynton, 1979). Fewer than half of the 1-month-olds responded to these tritan differences, while more than half of the 2-month-olds did so. This result supported the conclusion that, as with red/green stimuli, responsiveness to tritan differences has its onset in the second postnatal month.

In a follow-up study, Clavadetscher *et al.* (1988) also found that 7-week-olds responded to tritan differences, while 3-week-olds did not. However, the failure points of infants who failed to make chromatic discriminations coincided with null values for rod rather than cone-mediated vision (V'_λ rather than V_λ) in the short- to mid-wavelength spectral region. These authors, therefore, raised the possibility that the tritan discriminations seen by Varner *et al.* (1985) were mediated by rod-initiated rather than S-cone-initiated signals (see also Brown, 1990; Knoblauch *et al.*, 1996). If so, then the participation of S-cone-initiated signals in chromatic discrimination may be delayed even beyond the 1- to 2-month onset times suggested by Varner *et al.* (1985) and Clavadetscher *et al.* (1988).

Uniform vs differential loss

In addition to the question of onset times of responsiveness to chromatic stimuli in infants, a second question has often been posed. Presuming that infants are less sensitive than adults on all three dimensions of color space, do infants manifest a *uniform loss* of sensitivity to stimuli modulated along all three dimensions, or do they show a *differential loss* of sensitivity to one or both chromatic dimensions in comparison to the luminance dimension? (For more detailed discussions of the question of uniform vs differential loss, see Banks & Bennett, 1988; Banks & Shannon, 1993; Teller & Lindsey, 1993; Teller & Palmer, 1996; Brown *et al.*, 1995.)

The question of uniform vs differential sensitivity loss has been most often addressed by examining contrast thresholds or contrast sensitivities for both chromatic and luminance-modulated stimuli (C and L, respectively), and comparing the ratio between them (e.g. the C/L sensitivity ratio) for infants vs adults (Allen *et al.*, 1993; Morrone *et al.*, 1993; Kelly *et al.*, 1997; Brown *et al.*, 1995; Dobkins & Teller, 1996). Although there is some controversy in the literature, most of these studies are consistent with the conclusion that for red/green vs luminance-modulated stimuli, infant and adult C/L ratios are the same to within about a factor of two, in either one or the other direction [but see Morrone *et al.* (1993) for a more complex view]. For tritan stimuli, the question of uniform vs differential loss has not been explicitly examined.

At the theoretical level, Banks and his colleagues (Banks & Bennett, 1988; Banks & Shannon, 1993) have carried out an ideal observer analysis of a wide range of infant chromatic discrimination data from our laboratory. The ideal observer analysis suggested that, in comparison to adults, infants manifest a uniform loss of sensitivity for red/green vs luminance-modulated stimuli. In contrast, the analysis suggested a large and differential loss of sensitivity for tritan stimuli. Therefore, from the perspective of Banks and colleagues' infant ideal observer, either the S cones or the tritan channel manifests a differential immaturity in early development. Moreover, if the tritan discriminations observed by Varner *et al.* (1985) and Clavadetscher *et al.* (1988) were in fact mediated by rod- rather than S-cone-initiated signals, then the differential loss of S-cone-initiated signals could be even larger than is suggested by the ideal observer analysis.

Motion and color

Studies of the onset of responsiveness to red/green chromatic differences have recently been extended to the motion domain. In an initial study, we (Teller & Lindsey, 1993; Teller & Palmer, 1996) tested infant subjects with moving red/green gratings and an eye movement-based response measure. Most 2-month-old infants produced *directionally appropriate eye movements* (DEM) to moving red/green gratings, while most 1-month-olds did not. Other recent DEM studies have confirmed that 3-month-olds also code the direction of motion of moving red/green stimuli (Brown *et al.*, 1995; Dobkins & Teller, 1996). Thus, cross-study comparisons suggest that with DEM as with FPL and VEP response measures, and with moving as with stationary stimuli, the 1- to 2-month age range spans the onset of individual infants' responsiveness to red/green chromatic differences.

In the same study (Teller & Lindsey, 1993; Teller & Palmer, 1996), a DEM-based variant of chromatic motion nulling (Cavanagh & Anstis, 1991) was also used. In chromatic motion nulling, a chromatic grating moving in one direction is superimposed on a luminance-modulated grating moving in the other direction. The contrast of the luminance-modulated grating required to cancel the perceived motion of the chromatic grating, and yield a perceptual motion null, is called the *equivalent luminance contrast* of the chromatic grating. Under spatial and temporal frequency conditions comparable to ours, Cavanagh and Anstis found equivalent luminance contrasts of 6–12% for red/green gratings, and about 3–5% for tritan gratings.

In addition to the use of C/L ratios, it can be argued that the chromatic motion nulling paradigm provides a second approach to the question of uniform vs differential loss (Teller & Lindsey, 1993; Teller & Palmer, 1996). That is, a constant equivalent luminance contrast for infants and adults can be taken to signify a uniform loss of sensitivity to the two stimulus components in infants. A reduced equivalent luminance contrast in infants would indicate a differential loss of sensitivity for chromatic with respect to luminance-modulated stimuli; while an enhanced equivalent luminance contrast in infants would indicate a differential precocity for chromatic with respect to luminance-modulated stimuli.

Under the conditions tested, we (Teller & Lindsey, 1993; Teller & Palmer, 1996) have found that the equivalent luminance contrast of red/green gratings remained constant or nearly constant at about 10% for 1-month-olds, 2-month-olds, and adults. This finding, like many of the studies employing stationary stimuli, is consistent with the notion of a uniform or near-uniform loss of sensitivity to red/green vs luminance-modulated gratings in infants, and extends this result to the case of moving stimuli.

The purpose of the present study was to repeat the Teller & Lindsey (1993); Teller & Palmer (1996) study with tritan stimuli. Two specific goals were addressed. First, we wished to see whether or not 2-month-old infants would produce directionally appropriate eye movements (DEM) in response to moving tritan gratings. When they failed to do so, 4-month-old infants were also tested, and also failed. And second, we wished to use chromatic motion nulling to measure 2-month-olds' and adults' equivalent luminance contrasts for tritan stimuli. The experiment showed that infants' equivalent luminance contrasts were very close to zero. Unfortunately, the equivalent luminance contrasts of adults were also smaller than we had expected, with the result that the question of uniform vs differential loss could not be addressed definitively by the present data. A brief report of this project has been presented previously (Teller *et al.*, 1994).

METHODS

Overview

In the main experimental series, three experiments were carried out on 2-month-old infants. In Experiment 1, contrast thresholds were measured for luminance-modulated gratings presented alone. In Experiment 2, tritan-modulated gratings were presented alone, at a series of relative luminance contrasts of the yellow–green vs violet bars of the tritan grating (the *tritan grating series*), spanning V_λ isoluminance in steps of 5%. These variations of the luminance component of the tritan gratings were used in order to be sure to confront each subject with his or her individual isoluminance point (Peeples & Teller, 1975). In Experiment 3, each of the stimuli in the tritan grating series was nulled against luminance-modulated gratings of either 5 or 10% contrast. The DEM response measure was used in all cases.

Two other age groups were tested with different parts of this experimental design. First, when 2-month-olds did not respond to near-V_λ-isoluminant tritan gratings in Experiment 2, 4-month-olds were also tested in Experiments 1 and 2. No nulling experiments (Experiment 3) were carried out with 4-month-olds. Second, adult subjects were tested in Experiments 2 and 3 (see below for a discussion of response measures). Experiment 1 was not performed on adults because performance approached 100% at a luminance contrast of 1%, and lower contrasts could not be produced due to apparatus limitations.

Apparatus and stimuli

The color video system consisted of an Adage 3006 graphics subsystem and a Barco 6351 high-resolution RGB color monitor. A MicroVax II minicomputer served as host for the graphics hardware. The CIE chromaticity coordinates of the red, green, and blue phosphors were (0.63, 0.35; 0.28, 0.61; and 0.15, 0.07), respectively. All stimuli were gratings spatially modulated through a white with CIE coordinates (0.31, 0.31) (MacLeod–Boynton coordinates $r = 0.65$, $b = 0.02$). Isoluminance values of stimuli of different chromaticities were defined and calibrated to conform to Judd's modified V_λ. For the adult standard observer, V_λ-isoluminant tritan gratings presented alone produced cone contrasts of 0, 0, and 87% for L, M and S cones respectively, and 21% for rods.

The stimuli were 0.2 c/d vertical sinewave gratings, moving across the video screen at a speed of 20 deg/sec

(4 Hz). The space-average luminances of all stimuli were 12cd/m^2. The stimuli subtended 65×52 deg at the test distance of 33 cm. All viewing was binocular.

A mirror suspended at the upper margin of the monitor reflected an image of the infant's right eye to a video camera at the side of the stimulus monitor. The image provided by this camera was displayed on two auxiliary video monitors. One auxiliary monitor was used by the adult *holder* to locate the subject in three dimensions in front of the stimulus screen, and the other was used by the adult *observer* to judge the direction of the subject's eye movements.

Stimulus specification. The stimuli were generated in a fashion similar to that described by Teller & Palmer (1996). The major difference is that in the present experiment we sacrificed maintaining the highest possible chromatic contrast for each individual stimulus, in order to maintain a constant space-average chromaticity and constant chromatic contrast across all stimuli in the tritan series (c.f. Palmer *et al.*, 1993).

For Experiment 1, the luminance-modulated (black/white) gratings were generated in the traditional fashion, and their contrasts are specified as traditional Michelson contrast.

For Experiment 2, the tritan-modulated, or test gratings can be thought of as a sum of two components: a V_λ-defined isoluminant tritan-modulated component and a luminance-modulated component. For the tritan component, chromatic contrast is defined as a percent of the available gamut. Thus, the highest tritan contrast available on the monitor at V_λ-defined isoluminance was defined as 100%. This stimulus modulated the S cones by 87%. In practice, lower chromatic contrasts (70–80% of the gamut) were used. The contrast of the luminance component was defined by Michelson contrast relative to the mean luminance of the combined stimulus.

For Experiment 3, the stimuli were composed of two gratings moving in opposite directions: a black/white *nulling* grating and a tritan *test* grating. The tritan test grating was itself constructed from two components, as in Experiment 2. For both nulling and test gratings, luminance contrast and chromatic contrast were defined relative to the mean luminance and chromaticity of the combined stimulus.

Subjects

Adult subjects were laboratory personnel, including author TEWB. Ages ranged from 22 to 34 yr. Five adult subjects were tested. Infant subjects were recruited from the Infant Studies Subject Pool at the University of Washington. All infant subjects were born within 10 days of their due date, with normal deliveries and no health problems by parents' report. Male infants with family histories of color vision deficiency were excluded from the study. Infants were tested for 1–5 sessions within a 1 week time span. On average, 2-month-olds and 4-month-olds began testing on the 62nd and 115th postnatal day, respectively. Fifty-one infants provided usable data. The number of infants per condition was: Experiment 1, 2-month-olds, $n = 9$; 4-month-olds, $n = 9$; Experiment 2, 2-month-olds, $n = 8$; 4-month-olds, $n = 9$; Experiment 3, 2-month-olds, 5% nulling contrast, $n = 7$; 10% nulling contrast, $n = 9$. Incomplete data sets (< 5 trials per point) from 13 additional infants were discarded.

Procedure

DEM response measure. For the directionally appropriate eye movement (DEM) response measure, on each trial the observer made a forced-choice judgment of the *direction of the slow phase of the infant's eye movements*. The Neither-Direction category used by Teller & Lindsey (1993; Teller & Palmer, 1996) was not used in the present experiments.

Infants. Infant subjects were held by an adult *holder* in a vertical position 33 cm in front of the stimulus monitor. The holder used the image of the infant's face on one of the auxiliary monitors to keep the infant's right eye centered on the screen and in good focus. A second adult, the *observer*, used the second auxiliary monitor to observe the infant's face and eye movements. The observer triggered presentation of the moving gratings when the infant was judged to be alert and fixating the screen. The observer and holder were blind to the contrast and direction of motion of the stimulus.

Stimulus duration was unlimited, but in practice was usually about 3–5 sec. Stimuli were terminated and replaced by fixation patterns when the infant was judged not to be attentive and fixating the screen. Trials were terminated by a judgment made by the observer. In the retained data sets, the number of trials per point ranged from 5 to 23 with a mean of 11.

Adults. Adult subjects were seated 33 cm from the video monitor, and instructed to center their gaze on the screen. In preliminary experiments, two subjects were tested with several nulling contrasts between 0 and 10%, and judged the perceived direction of motion of the stimulus. For 5 and 10% nulling contrasts, a second group of runs was performed, in which an observer judged the direction of the subject's eye movements. As has been reported previously (Teller & Lindsey, 1993; Teller & Palmer, 1996), agreement between the two response measures was excellent. The three additional adult subjects were therefore tested only with direction-of-motion judgments, and only these judgments are reported. All data sets for adults are based on 20 trials per point, except that runs with 0% nulling contrast yielded 100% of judgments in the test direction; these runs were terminated at 10 trials per point.

At the end of testing, a control condition was run on the two most extensively tested adult subjects. Each subject was retested with the tritan test grating alone (Experiment 2—0% contrast of the nulling grating), with the luminance component of the test grating set to ±1 and ±2% around his or her individual minimum performance point, as determined in the 5 and 10% nulling contrast conditions (Experiment 3). This control was run in order to test the possibility that a minimum would be found between the stimuli of the original tritan series.

Performance remained near 100% test responses for all stimuli.

Data reduction. Responses were tabulated for agreement with the direction of motion of the stimulus, or, in the nulling experiments, with the direction of motion of the tritan test grating. The term "percent test responses" will be used to denote the coincidence of the subject's responses with the direction of motion of the tritan test grating in the nulling experiments.

Analysis. The theoretical analysis of Teller & Palmer (1996) was applied to the data from the present experiments. Briefly, this analysis fits Weibull functions to the data of Experiment 1 and U-shaped functions derived from Weibull functions to the data of Experiments 2–3. The upper asymptotes of the theoretical functions were set to 0.95 for infants (Teller *et al.*, 1992) and 1.00 for adults. The U-shaped functions have three free parameters: t, the threshold, which describes the steepness of the sides of the U; d, the deviation of the response minimum from V_λ-defined isoluminance; and e_{max}, the equivalent luminance contrast, which is related to the width of the U at the level of 50% test responses. (More technically, we distinguish between e_{max}, the equivalent luminance contrast of a 100% gamut-contrast tritan grating, and e_{test}, the equivalent luminance contrast of a test grating of the particular chromatic contrast used in the experiment. The width of the U is equal to the nulling contrast used minus e_{test} (see Teller & Palmer, 1996 for more detail). Although positive values of equivalent luminance contrast are found in adults, negative values are also possible, and would indicate that the presence of the chromatic component of the tritan grating made the tritan grating *less* rather than more effective.

For Experiment 1, Weibull functions were fit to each individual subject's data, and the value of the threshold parameter, t, was estimated for each infant. The solid lines in Fig. 1(E, F) show Weibull functions with the group mean value of t. Two 4-month-olds [including Julia in Fig. 1(B)] gave unusually flat functions. The Weibull fits indicated thresholds of 21 and 34% for these two infants. Both values are extrapolations beyond the range of contrasts used, and inflate the value of the mean. Thus, for the 4-month-olds in Experiment 1, median values of t are given along with the mean values below. In all other conditions, mean and median values were very similar, and median values are not given.

For Experiments 2 and 3, U-shaped functions were fit to the data from each individual infant, and values of the parameters d, t, and e_{max} were estimated for each infant. As expected from the known variability of photopic luminous efficiency curves across subjects, different individual subjects showed slightly different values of d, the deviation of the response minimum from V_λ-isoluminance. In Figs 2(E, F), 3(E, F) and 4(E, F), each data set from Experiments 2 and 3 has been shifted along the abscissa by the individual value of d, to normalize all data sets to a deviation of zero. Values of the parameters t and e_{max} were averaged across subjects in each age group to arrive at group estimates of these parameters. The solid lines in Figs 2(E, F), 3(E, F) and 4(E, F) show fits of the group mean values of t and e_{max} to the normalized data.

RESULTS

Experiment 1: Contrast thresholds for luminance-modulated gratings

The results for luminance-modulated gratings are shown in Fig. 1. Results from 2-month-olds and 4-month-olds are shown in the left and right columns, respectively. Figure 1(A, B) shows data from three individual infants in each age group, selected to illustrate the range and variability of the data. The frequency of directionally appropriate eye movement responses generally increased with increasing luminance contrast. However, there were marked individual differences in the eye movement patterns of different infants, and in the overall regularity of the psychometric functions. Figure 1(C, D) shows the group mean psychometric functions for 2- and 4-month-olds, respectively.

Figure 1(E, F) shows the data for all individual infants. For each infant, fitting the model to the data from Experiment 1 involves only one parameter—the contrast threshold, t. The quality of the model fit to each data set was measured by a χ^2 statistic with 5 degrees of freedom. For these fits, the mean chi-squares were 4.6 and 3.1 for 2-and 4-month-olds, respectively. Since the expected value of χ^2 is 5 for 5 degrees of freedom, we consider the model fits satisfactory.

The mean values of the threshold parameter, t, across individual infants were 10 ± 2% and 12 ± 4% for 2- and 4-month-olds, respectively. These values are not reliably different from one another. However, as discussed in Methods, the threshold value for 4-month-olds is probably inflated by the presence of two infants with very flat psychometric functions [including Julia in Fig. 1(B)], and medians may be a more appropriate description of central tendency for this group. The median value for the 4-month-olds was 7 ± 3%. The solid lines in Fig. 1(E, F) show the best-fitting Weibull functions derived from the mean value of t across subjects.

Experiment 2: Tritan gratings

The results for tritan test gratings presented alone, with various contrasts of the luminance component of the tritan grating, are shown in Fig. 2. Results from 2- and 4-month-olds are shown in the left and right columns, respectively. Adult subjects gave 100% test responses to all stimulus values, and are not plotted.

Data from selected individual infants are shown in Fig. 2(A, B). Data from 2- and 4-month-olds were quite similar. All individual infants showed a high percentage of appropriately directed eye movements at the extremes of luminance contrast, and a performance minimum in the vicinity of V_λ isoluminance. In each age group, one infant showed directionally appropriate responses on more than 75% of trials at all luminance contrast values

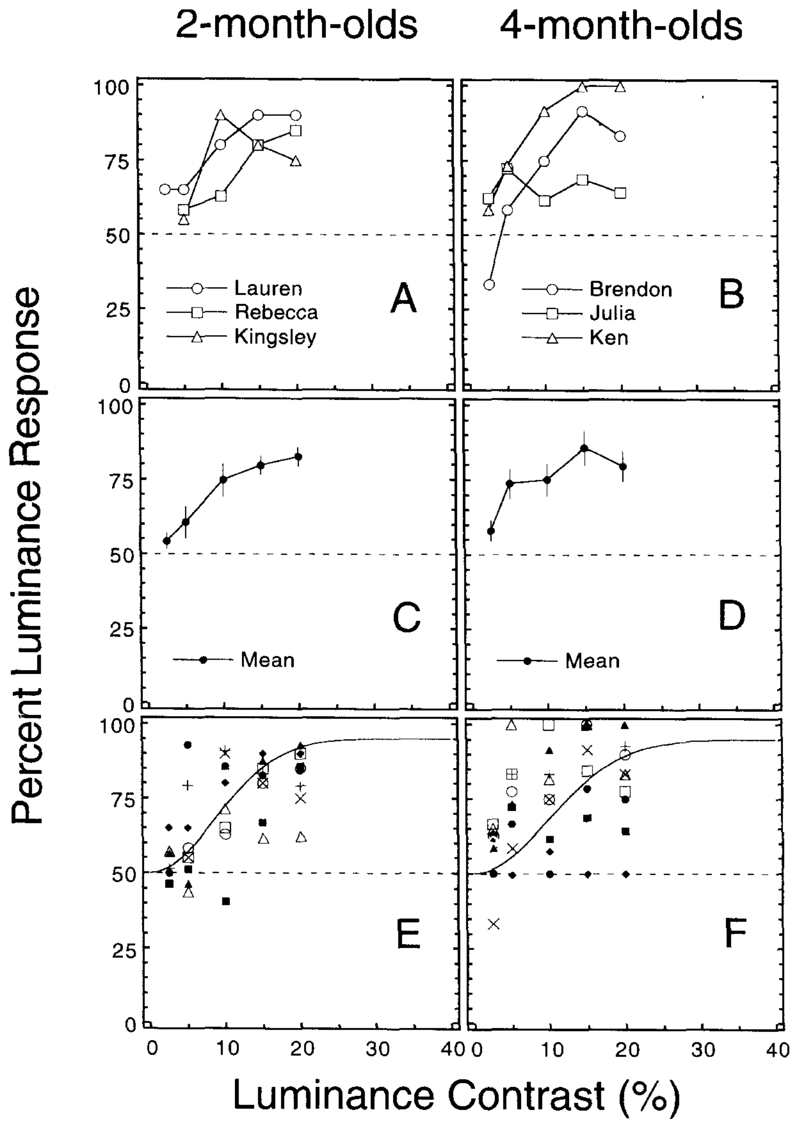

FIGURE 1. Experiment 1: Responses to luminance-modulated gratings. Left and right columns show data from 2- and 4-month-olds, respectively. Abscissae show the contrast of the luminance-modulated grating. Ordinates show the percent "Luminance" responses; that is, the percent of trials on which the direction of the subject's eye movements was judged to coincide with the direction of motion of the luminance-modulated grating. (A, B) Data from three individual infants of each age group. (C, D) Group means for each age group. The error bars in all figures show ± 1 SEM. (E, F) Data from all individual infants. The solid lines show the best fitting theoretical curves derived from group average values of the threshold parameter, *t* (see text).

in the tritan grating series, while the remaining infants had minima below 75% at one or more contrast values. The locations of the minima along the abscissa varied among infants, from zero (V_λ isoluminance) to +15% in 2-month-olds, and from −10% to +10% in 4-month-olds.

Group means are shown in Fig. 2(C, D). Both groups show response minima between 50 and 75% test responses in the group means. However, the group mean curves are probably artificially broadened, and the minima made somewhat shallow, by the uncompensated variations in the deviation parameter *d* among individual subjects.

Fitting of the model to each individual data set involves three parameters—the contrast threshold, *t*, the deviation, *d*, and the equivalent luminance contrast, e_{max}. Mean values of model parameters for 2- and 4-month-old infants, respectively were: for the threshold, *t*, 8 ± 2 and 9 ± 2%; for the deviation, *d*, 6 ± 2% and 5 ± 1%; and for the equivalent luminance contrast, e_{max}, −1.3 ± 1.9% and −0.7 ± 0.9%. Model fits were reasonable; the mean chi-squares for 6 degrees of freedom were 6.1 and 4.7 for the 2-and 4-month-olds, respectively. The negative equivalent luminance contrast values found in infants were not reliably below zero.

Figure 4(E, F) shows the data from all individual infants. The individual data sets are shifted by the best-fitting individual values of *d* to be centered at zero on the normalized luminance contrast axis. In each case, the solid line shows the prediction from the model, derived from the mean values of *t* and e_{max} across subjects.

In summary, the main results of Experiment 2 are as follows. First, tested with the tritan grating series, both 2- and 4-month-old infants failed to show directionally appropriate eye movements for one or more stimuli near

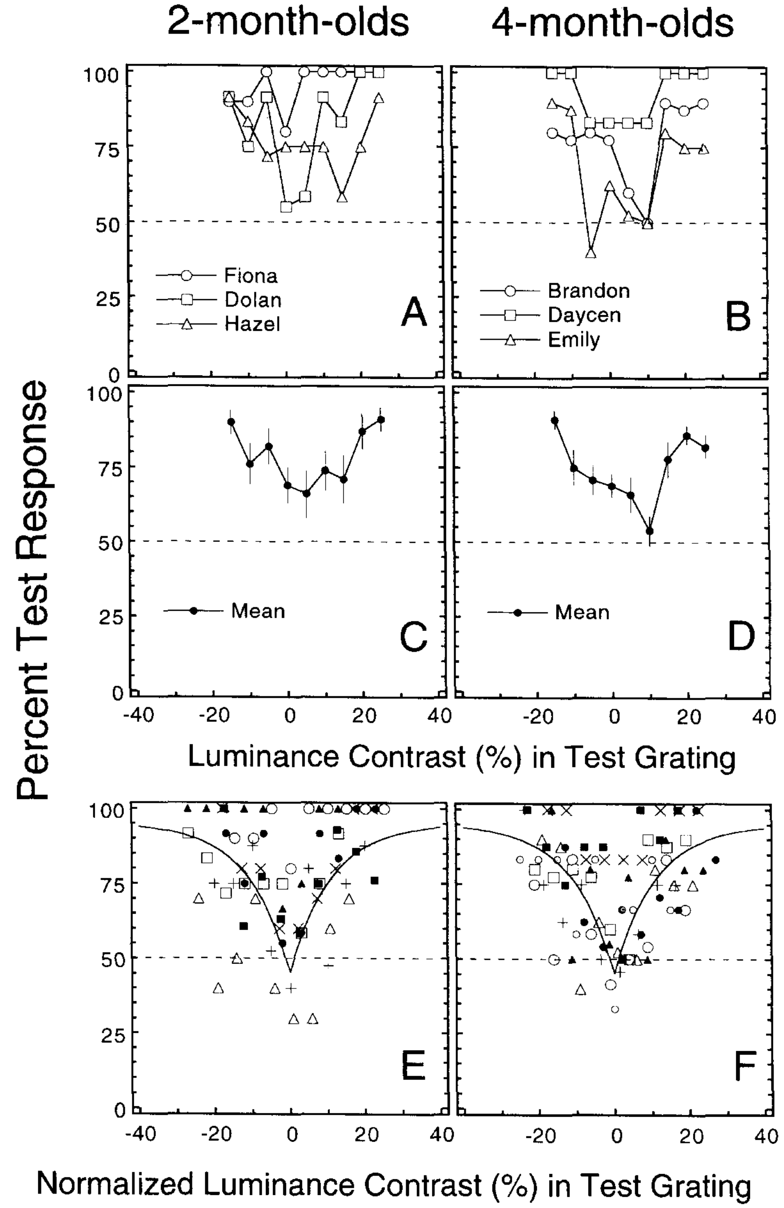

FIGURE 2. Experiment 2: Responses to tritan test gratings. Left and right columns show data from 2- and 4-month-olds, respectively. Abscissae show the percent luminance contrast of the luminance component of the tritan test gratings, where 0 is defined as V_λ-based isoluminance. Positive values indicate that the yellow–green bars of the tritan test grating were of higher luminance than the violet bars. Ordinates show the percent "test" responses; that is, the percent of trials on which the direction of the subject's eye movements was judged to coincide with the direction of motion of the tritan test grating. (A, B) Data from three individual infants of each age group. (C, D) Group means for each age group. (E, F) Data from all individual infants, shifted so that each infant's response minimum coincides with zero on the normalized abscissa. The solid lines show the best fitting theoretical curves derived from group average values of threshold, t, and equivalent contrast ($e_{\max}$) parameters (see text).

V_λ isoluminance. Second, application of the model provides estimates of the equivalent luminance contrast that are very close to zero. In contrast, adult subjects perform near 100% for all relative luminances of the tritan gratings, and show an equivalent luminance contrast too large to be estimated under the conditions of Experiment 2. (See Teller & Palmer, 1996 for a discussion of the range of conditions that yield good estimates of equivalent contrast.)

Experiment 3: Nulling

The nulling experiment was carried out only on 2-month-olds and adult subjects. The results for 2-month-olds, for 5 and 10% nulling contrast, are shown in the left and right columns of Fig. 3, respectively.

Figure 3(A, B) shows the results for selected individual infants. Most infants gave well-behaved U-shaped functions in the nulling experiment. For 10% nulling contrast, the stimulus range used was not optimal, in the sense that most functions did not return to high response rates at the largest negative contrast used (−5%). A slightly shifted contrast range was used for 5% nulling contrasts, and this problem is ameliorated in these data. Across infants, response minima ranged from 5 to 50%

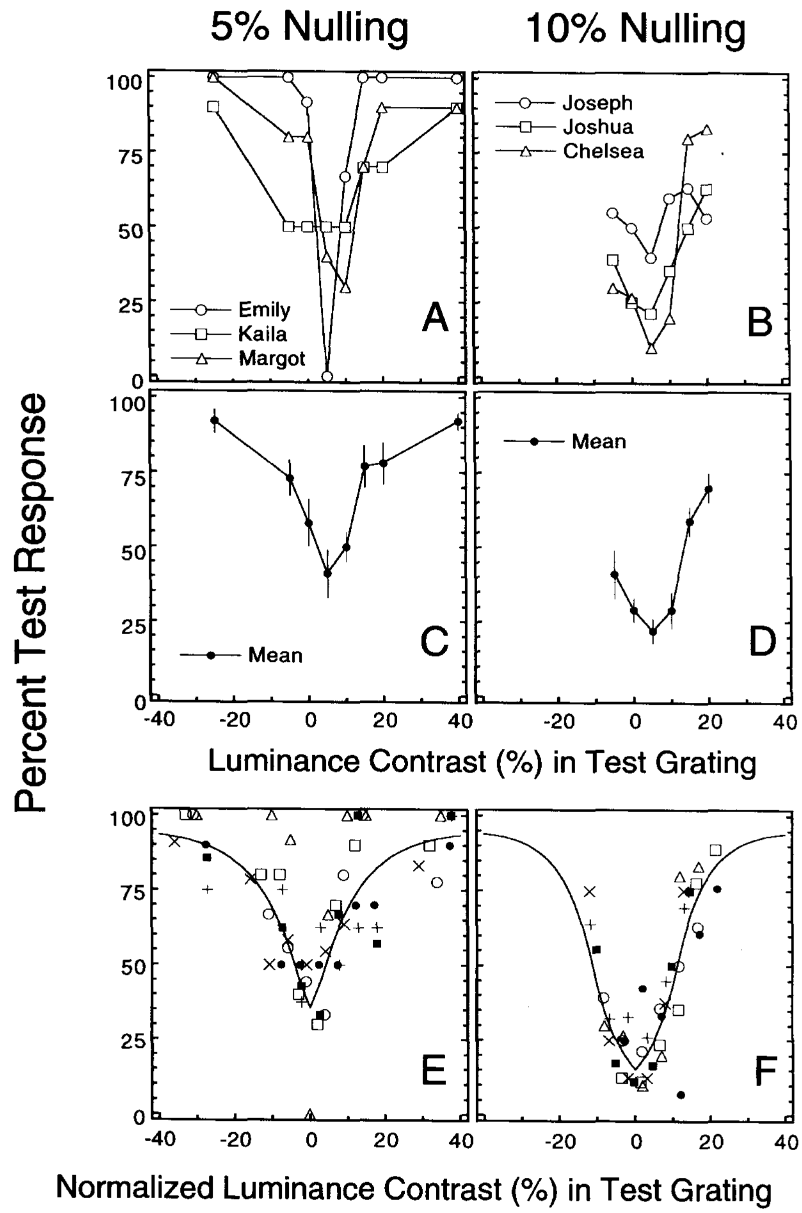

FIGURE 3. Experiment 3: Results of the nulling experiment for 2-month-olds. Left and right columns show the results for nulling contrasts of 5 and 10%, respectively. Abscissae as in Fig. 2. Ordinates show the percent of trials on which the direction of the subject's eye movements were judged to coincide with the direction of motion of the tritan test grating in the nulling paradigm. (A, B) Data from three individual infants for each nulling contrast. (C, D) Group means for each nulling contrast. (E, F) Data from all individual infants, shifted so that each infant's response minimum coincides with zero on the normalized abscissa. The solid lines show the best fitting theoretical curves derived from group average values of threshold and equivalent luminance contrast parameters (see text).

test responses. The locations of the minima along the abscissa spanned the range from −1 to 8% around V_λ isoluminance.

The group means for 2-month-olds are shown in Fig. 3(C, D). The functions are again well-behaved. With 5% nulling contrast, the percentage of test responses falls to a minimum of 40% at a contrast of 5% on the abscissa; with 10% nulling contrast, the percentage of test responses falls to a minimum of 20% at a contrast of 5% on the abscissa.

Mean values of model parameters for 2-month-olds, for 5 and 10% nulling contrasts, respectively, were: for the threshold, t, 8 ± 2 and 5 ± 1%; for the deviation, d, 5 ± 1 and 3 ± 1%; and for the equivalent luminance contrast, $e_{\max}$, 1.2 ± 0.5 and −1.1 ± 1.3%. [For the 10% nulling contrast condition, data sets from two infants could not be analyzed by the full three-parameter model, because they had insufficient data at negative contrast values to define the U-shaped curve. By fixing the threshold to the value found in Experiment 1 ($t = 10$), and the deviation to the mean found in Experiment 2 ($d = +5$), we were able to estimate $e_{\max}$ values of −5.1 and +5.5 for these two infants. These values are included in the mean values given above. Without these two subjects, the mean equivalent luminance contrast for the remaining seven infants was −1.5 ± 1.1%.]

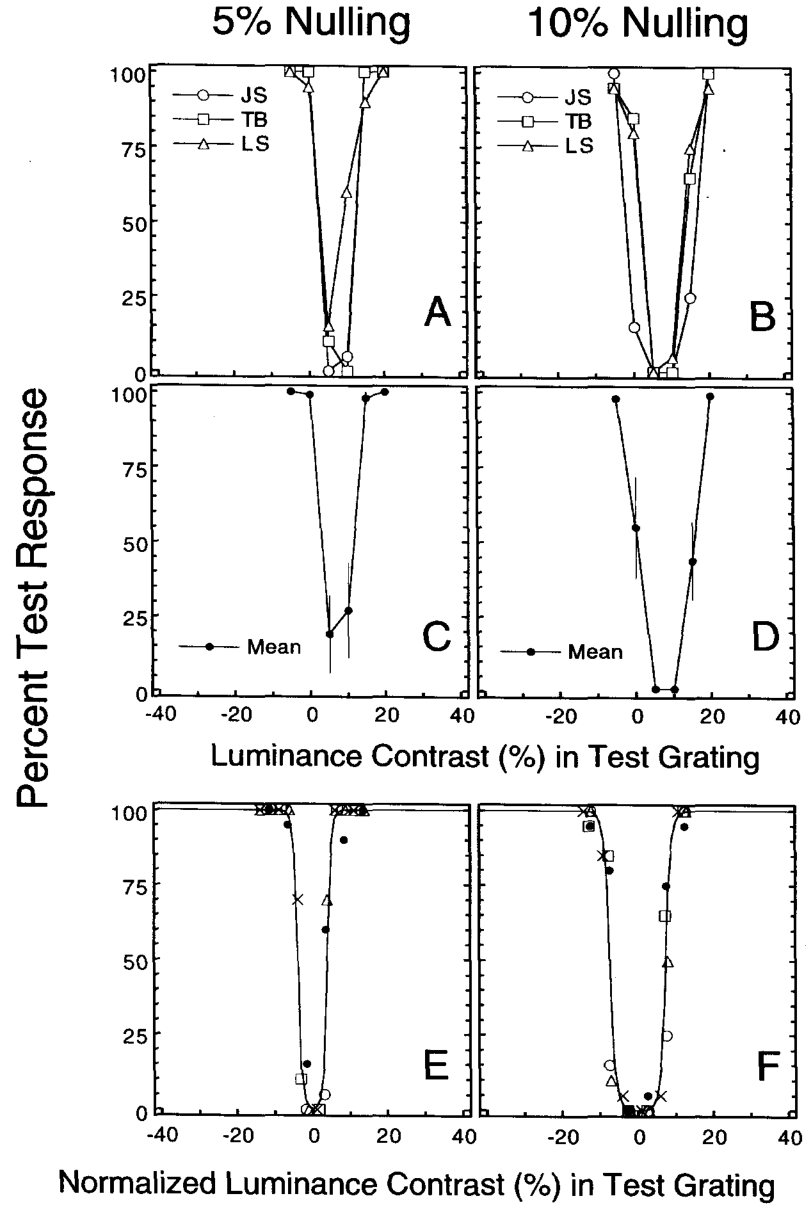

FIGURE 4. Experiment 3: Results of the nulling experiment for adult subjects. The ordinates show the percent of trials in which the perceived direction of motion coincided with the direction of motion of the tritan test grating in the nulling paradigm. All other conventions as in Fig. 3.

Figure 3(E, F) shows the data from all individual infants. As in Fig. 2(E, F), the individual data sets are shifted by the best-fitting individual values of d to be centered at zero on the normalized luminance contrast axis. In each case, the solid line shows the prediction from the model, derived from the mean values of t and $e_{\max}$ across subjects.

As in Experiment 2, the negative value of $e_{\max}$ for the 10% nulling condition was not statistically reliably below zero. $e_{\max}$ For the 5% nulling contrast was reliably greater then zero if this estimate is considered alone [$t(6) = 2.3$, $P < 0.051$. However, this is the only one of four estimates of $e_{\max}$ in infants; the other three estimates were all negative. If one takes into account the fact that four tests were conducted, then by the Bonferroni method, the t-statistic would have to be greater than 3.5 to be significant at the $P < 0.05$ level, and greater then 3 to be marginally significant at the $P < 0.10$ level. Thus, the set of four measurements does not differ reliably from zero.

Adult subjects. The results for the adult subjects are shown in Fig. 4. The results for 5 and 10% nulling contrasts are shown in the left and right columns, respectively. As discussed in Methods, the adult subjects' judgments of the perceived direction of motion of the stimuli are shown. Results from DEM measures were highly similar and are not plotted.

Results from three individual adult subjects are shown in Fig. 4(A, B). As in the case of the infants, the three adult subjects are selected to illustrate the extremes of the data. For both the 5 and 10% nulling conditions, all data sets showed minima of 0% test responses. For the 5% nulling condition, the locations of the minima occurred at deviations of 5–10% on the abscissa; for the 10% nulling

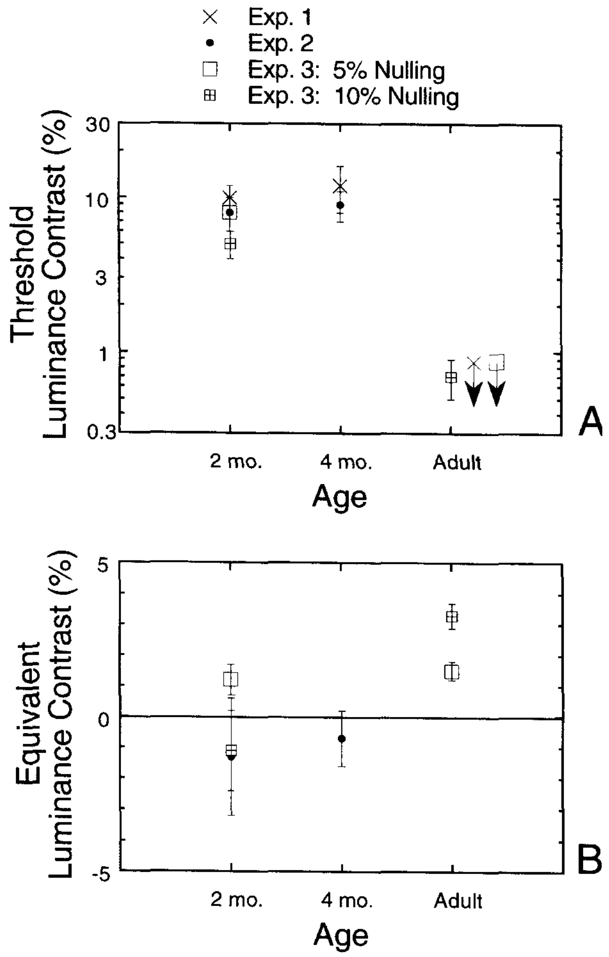

FIGURE 5. Summary of parameter values derived from all three experiments. The abscissae show the three age groups. (A) The threshold luminance contrast parameter, t. Threshold values are consistently much higher for infants than for adults. Downward pointing arrows show upper bound estimates. (B) The equivalent luminance contrast parameter, $e_{\max}$. For infants, across conditions, values of equivalent luminance contrast estimates cluster around zero. For adults, equivalent luminance contrast values are greater than zero, but vary with nulling contrast.

condition, the locations of the minima occurred at deviations of 5–10%.

Figure 4(C, D) shows group means for all five adult subjects. The group means show symmetrical minima that fall to 20 and 0% test responses for the 5 and 10% nulling conditions, respectively. For both, the minima are centered between 5 and 10% along the abscissae.

For 5% nulling contrast, the model was unable to fit the threshold parameter t, but consistently indicated a value $\ll 1\%$. A restricted model with a threshold value of 0.4 was used for this condition. (Similar parameter values were found for any threshold value from 0.1 to 1.2.) Values of model parameters for adults, for 5 and 10% nulling contrasts respectively, were: for the threshold, $t \ll 1\%$ and $0.7 \pm 0.2\%$; for the deviation, d, $7.4 \pm 0.5\%$ and $7.8 \pm 0.4\%$; and for the equivalent luminance contrast, $e_{\max}$, $1.5 \pm 0.3\%$ and $3.3 \pm 0.4\%$.

Thus, in contrast to the infants, the adult subjects showed small but statistically reliable, positive values of equivalent luminance contrast. In addition, there is an unpredicted but reliable effect of the nulling contrast on the equivalent luminance contrast. The difference between conditions was $1.8 \pm 0.5\%$ and is reliable, $t(8) = 3.7$, $P < 0.005$.

Figure 4(E, F) shows the data from all individual adult subjects. As in earlier figures, the individual data sets are shifted by the best-fitting individual values of d, to be centered at zero on the normalized luminance contrast axis. In each case, the solid line shows the prediction from the model, derived from the average values of t and $e_{\max}$ across subjects.

Summary of parameter values across all experiments

Finally, Fig. 5 shows summaries of the mean estimated values of two model parameters, the threshold and the equivalent luminance contrast, for all three age groups, derived from all experiments performed. As indicated above, Experiment 1 yields an estimate of only the threshold parameter; Experiment 2 yields an estimate of each of the three parameters; and Experiment 3 yields estimates of each parameter for each value of nulling contrast.

Thresholds. The mean estimated values of the threshold parameter, t, across all experiments, are shown in Fig. 5(A). Mean thresholds ranged between 5 and 12% for infants. Thresholds for 2- and 4-month-olds were similar rather than showing an improvement with age. We attribute this outcome to the two 4-month-olds who gave very flat psychometric functions in Experiment 1; as discussed above, use of medians for this age group reduced the average value of t from 12 to 7% in Experiment 1.

The infant threshold values reported here are about a factor of two higher than the values reported by Teller & Lindsey (1993) and Teller & Palmer (1996) for 2-month-olds. We have no insight to offer concerning this discrepancy. However, the present data are more consistent with the prior behavioral literature on infant contrast thresholds (see Brown, 1990 for a review).

Equivalent luminance contrasts. The mean estimated values for the equivalent luminance contrast parameter, $e_{\max}$, are shown in Fig. 5(B). Infant equivalent luminance contrast values were -1.1–1.2% for the three available estimates for 2-month-olds, and -0.7% in the single estimate for 4-month-olds. For adults, Experiment 2 yielded equivalent luminance contrast values too large to be estimated in the absence of a nulling grating, and Experiment 3 yielded equivalent luminance contrast values of 1.5 and 3.3%.

The reliability of the difference in $e_{\max}$ between infants and adults varies among conditions. For the 5% nulling contrast condition, $e_{\max}$ was $1.2 \pm 0.5\%$ and $1.5 \pm 0.3\%$ for the infants and adults, respectively. This difference is not reliable. For the 10% nulling contrast condition, $e_{\max}$ was -1.1 ± 1.3 and 3.3 ± 0.4 for the infants and adults, respectively. This difference of $4.4 \pm 1.8\%$ is reliable, $t(12) = 2.5$, $P < 0.025$, and remains reliable with a

Bonferroni correction for the presence of two tests ($P < 0.05$).

The difference in statistical outcome for the two values of nulling contrast is in part due to the unexpected variation of adult equivalent luminance contrast values with nulling contrast. The larger value found for the 10% nulling contrast in adults was easier to distinguish from the near zero values found for infants.

Deviations. Finally, in both Experiments 2 and 3, individual subjects in all three age groups showed response minima distributed across a range of luminance contrasts between −2 and +12% in the tritan grating series. Since photopic luminous efficiency varies slightly among adults and presumably among infants, these small variations were expected.

The average values of the deviation parameter, d, were about 5% for 2-month-olds and 4-month-olds and 8% for adults. That is, compared to V_λ, all age groups required a slightly higher relative luminance of the yellow–green with respect to the violet bars of the grating to generate their points of minimum performance. These data are in the direction expected if the responses to these large moving fields are relatively dominated by peripheral as opposed to foveal retina, with a consequent reduction in the density of macular pigment. These data further confirm the high degree of similarity of infant and adult photopic spectral efficiency functions seen in many previous studies (see Brown, 1990 for a review; see especially Teller & Lindsey, 1989; Bieber *et al.*, 1995; Brown *et al.*, 1995).

DISCUSSION

In the Discussion, we first address our main findings: that in infant subjects tested under our conditions, tritan stimuli do not drive directionally appropriate eye movements. We then discuss the implications of our findings on equivalent luminance contrasts, with regard to the question of uniform vs differential loss in infants vs adults. Finally, we discuss the implications of the results with regard to the magnitudes of possible "artifactual" luminance-channel signals generated by chromatic stimuli in infant subjects.

Infant responsiveness to tritan stimuli

For adult subjects in Experiment 2, moving tritan gratings clearly yielded both perceptual reports and eye movement responses appropriate to the direction of stimulus motion, throughout the tritan grating series. These data are consistent with prior observations that adult subjects can code the direction of motion of moving isoluminant tritan stimuli under forced-choice conditions (e.g. Lindsey & Teller, 1990; Palmer *et al.*, 1993). For infants, on the other hand, DEM performance dropped to chance in a region near V_λ isoluminance. Moreover, the estimated equivalent luminance contrasts for infants in Experiments 2 and 3 were very close to zero. These experiments thus provide no evidence that tritan gratings are effective as stimuli for eliciting appropriately directed eye movements in infant subjects.

As discussed in the Introduction, several earlier studies raise the possibility that infants may be relatively insensitive to S-cone-initiated signals. The chromatic adaptation based studies (Pulos *et al.*, 1980; Volbrecht & Werner, 1987) suggest the possibility of differentially elevated detection thresholds for S-cone-initiated signals. The chromatic discrimination studies either suggest failures of response to tritan differences (Teller *et al.*, 1978), or are ambiguous as to mechanism because of the possibility of rod intrusion (Varner *et al.*, 1985; Clavadetscher *et al.*, 1988; see also Brown, 1990; Knoblauch *et al.*, 1996); and the theoretical analyses of Banks and his colleagues (Banks & Bennett, 1988; Banks & Shannon, 1993) suggest a differential loss of sensitivity to tritan stimuli from an ideal observer perspective. The present results also show a marked insensitivity to tritan differences in infants, and suggest that this insensitivity extends to the case of direction-of-motion coding and eye movement response measures.

Mechanisms. Unfortunately the constellation of results to date has insufficient precision to allow any firm conclusions about the particular critical immaturities responsible for infants' apparent insensitivity to S-cone-initiated signals. This insensitivity could be caused by a loss of effective contrast at the level of the S cones themselves, in the early postreceptoral processing of all S-cone-initiated signals, in the processing of S-cone-initiated signals generated by moving (or time-varying) stimuli, in coding the *direction of motion* of moving tritan stimuli, or in the motor systems responsible for eye movement responses to tritan stimuli.

Interpretation of the data at present is especially difficult because comparisons across experiments are hampered by variations in stimulus parameters and response measures, and because S-cone-isolation may not have been achieved in the Varner *et al.* (1985) and Clavadetscher *et al.* (1988) experiments (Brown, 1990; Knoblauch *et al.*, 1996). Moreover, in recent preliminary experiments, we have found that it is difficult at best to measure tritan contrast thresholds in 3-month-olds within the range of S-cone contrasts achievable with modulation through white on standard color video systems (Dobkins and Teller, unpublished observations). The sorting out of tritan contrast thresholds for stationary vs moving stimuli, vs direction-of-motion thresholds for moving stimuli, vs the influence of response measures, remains a task for the future.

Equivalent luminance contrasts and the question of uniform vs differential loss

In adult subjects, in the nulling paradigm (Experiment 3), values of the equivalent luminance contrast parameter, $e_{\max}$, are small—1.5 and 3.3%—but reliably above zero. These values are lower than the value of 4% reported by Cavanagh & Anstis (1991). In infant subjects, the equivalent luminance contrast values for isoluminant tritan gratings (Experiments 2 and 3) are not reliably different from zero, when all four available estimates are taken together. Thus, unlike the case for red/green gratings (Teller & Lindsey, 1993; Teller & Palmer, 1996), infant equivalent luminance contrasts for tritan gratings are very close to zero, even in infants as old as 4 months postnatal.

However, interpretation of the data is complicated by two factors. First, the values of equivalent luminance contrast varied with variations in nulling contrast in both adults and infants; and at 5% nulling contrast were not reliably different for the two age groups. Second, if equivalent luminance contrast indeed varies with nulling contrast, the question arises, what choices of nulling contrasts for infants vs adults allow a legitimate comparison of equivalent luminance contrasts across age? It can be argued, for example, that the appropriate experiment would be to scale nulling contrasts to contrast thresholds at the two ages. Such experiments are beyond the scope of the present investigation.

In sum, the present experiments show that infants' equivalent luminance contrasts for isoluminant tritan gratings are very close to zero. However, the present experiments fail to settle the question of whether equivalent luminance contrast values for tritan stimuli are meaningfully lower in infants than in adults. The present experiments thus unfortunately contribute no definitive answer to the question of uniform vs differential loss for moving tritan vs luminance-modulated stimuli in infants with respect to adults.

Luminance "artifacts"

Finally, a distinction must be made between two concepts: a subject's responsiveness to isoluminant chromatic stimuli on the one hand, and any strong conclusions about the postreceptoral channels that mediate that response on the other. That is, isoluminant chromatic stimuli designed to isolate a chromatic channel can nonetheless generate extraneous or "artifactual" signals in a luminance channel. In fact, the degree to which motion signals generated by a moving isoluminant chromatic grating are confined to the intended chromatic channel must be evaluated separately for each experimental situation. For example, Cavanagh & Anstis (1991) convincingly argued that in adults, the equivalent luminance contrast of red/green stimuli should be attributed to a red/green chromatic channel; but could not definitively attribute the equivalent luminance contrast of tritan stimuli to a tritan channel.

Many potential sources of the putative extraneous luminance-channel signals have been identified. They include luminance mismatches caused by errors of estimation of lens or macular pigment density or cone action spectra, or unexpected rod or S-cone contributions to the luminance signal; spatial modulations caused by such factors as chromatic aberration; temporal modulations caused by such factors as differential phase lags for different photoreceptor types, or frequency-doubling non-linearities; inhomogeneity of isoluminance points among the sub-elements of the luminance channel; and variations of one or more of these factors with retinal eccentricity (see Cavanagh & Anstis, 1991; or Teller & Palmer, 1996 for further discussion).

Happily, the interpretation is simplified in the present case. In the present study, infants *failed* to generate an eye movement response to tritan stimuli, and showed an equivalent luminance contrast of zero. We are thus able to conclude that none of the available extraneous luminance-channel signals, either alone or in combination with tritan-channel signals, are sufficient to allow direction-of-motion coding in 2- or 4-month-old infants.

These data are useful in that they place an upper bound on the effectiveness of certain extraneous luminance-channel signals in infants. For example, signals initiated by the rods constitute one of the possible sources of extraneous luminance-channel signals. At the performance minimum of the average infant in the present experiments (d = about 5%), the rod contrast is about 16%. The present results show that under our conditions, this level of rod contrast is not sufficient to allow infants to code the direction of motion. Since the rod contrast generated by the red/green stimuli used by Teller & Palmer (1996) was about 17% at the infants' performance minimum, it is also unlikely that rod-initiated signals were a major contributor to infants' DEM to red/green gratings in that experiment, or in other experiments in which similar instrumentation and stimulus conditions have been used.

Moreover, tritan gratings involve the use of short-wavelength as well as mid- and long-wavelength light. For this reason, several other potential sources of extraneous luminance channel signals, including both chromatic aberration and variations in macular pigment density with retinal eccentricity, should be larger for tritan than for red/green stimuli. Thus, the failure of infants to produce DEM to tritan gratings also argues against any major contribution of these factors to the motion signals generated by red/green gratings in our earlier experiment.

On the other hand, some extraneous luminance-channel signals are larger for red/green than for tritan stimuli. In particular, Lee *et al.* (1989) have shown that isoluminant red/green gratings produce frequency-doubled signals in primate retinal M-type ganglion cells, while tritan gratings do not. Assuming that the same nonlinearities occur in human infants, the present study does not rule out such nonlinearities as the basis of infant's responses to the motion of isoluminant red/green gratings. This question is discussed further in Teller & Palmer (1996) and Dobkins & Teller (1996).

In summary, we have tested infant and adult subjects with moving tritan-modulated gratings, both alone and in a motion nulling paradigm. Our main findings are that under our conditions, tritan gratings do not elicit directionally appropriate eye movements in infants at either 2 or 4 months postnatal; and that the equivalent luminance contrast of tritan gratings for infants is very close to zero. Thus, in the present experiment infants show no evidence of being able to code the direction of motion of moving tritan stimuli. These results are consistent with earlier studies and analyses showing a reduced sensitivity to S-cone-initiated signals in infants, and extend this finding to the case of moving stimuli.

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