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Infant Color Vision: Temporal Contrast Sensitivity Functions for Chromatic (Red/Green) Stimuli in 3-Month-olds

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In order to investigate the development of temporal contrast sensitivity functions (tCSFs) for chromatic (red/green) stimuli, we obtained chromatic contrast thresholds from 3-month-old infants and adults using behavioral techniques. Stimuli were moving or counterphase-reversing sinusoidal gratings of 0.25 c/deg. Five temporal frequencies were used: 0.7, 2.1, 5.6, 11 and 17 Hz (corresponding speeds = 2.8, 8.4, 22, 44 and 67 deg/sec). In order to compare chromatic results with those obtained under luminance-defined conditions, luminance tCSFs were also obtained from adults, and previously obtained infant luminance tCSFs were used (from Dobkins & Teller, 1996a). In accordance with previous studies, adults exhibited bandpass luminance tCSFs with peaks near 5 Hz and lowpass chromatic tCSFs that declined rapidly at temporal frequencies greater than 2 Hz, and the two curves crossed one another near 4 Hz. By contrast, infants exhibited *bandpass rather than lowpass* chromatic tCSFs with peaks near 5 Hz. These chromatic curves were quite similar in peak frequency and general shape to previously obtained infant tCSFs for luminance stimuli. Moreover, both chromatic and luminance tCSFs in infants were found to be quite similar in peak and shape to luminance tCSFs observed in adults. These findings point to the possibility that, for 3-month-old infants, both chromatic and luminance stimuli are detected by the same underlying mechanism under these conditions. We propose that such a mechanism is probably a physiological pathway dominated by magnocellular input. Earlier studies of infant color vision are discussed in this context. © 1997 Elsevier Science Ltd

Visual development Chromatic Luminance Infant color vision Motion
Temporal contrast sensitivity functions

INTRODUCTION

Psychophysical studies in adults have demonstrated that the shape of the temporal contrast sensitivity function (tCSF) is distinctly different for luminance vs chromatic stimuli of low spatial frequency. For luminance-defined stimuli, adult tCSFs are generally bandpass, with a peak between 5–10 Hz, for both low spatial frequency gratings (e.g., Robson, 1966; Levinson & Sekuler, 1975; Kelly, 1971a; Burr & Ross, 1982; Anderson & Burr, 1985; Fiorentini *et al.*, 1991; Derrington & Henning, 1993; Gegenfurtner & Hawken, 1995; Dobkins & Teller, 1996a), and homogeneous flickering fields (Kelly, 1969, 1971b; Kelly & van Norren, 1977; Swanson *et al.*, 1987; Lee *et al.*, 1989a, 1990; Smith *et al.*, 1995). For chromatic (red/green) stimuli, however, tCSFs are lowpass, with sensitivity declining beyond about 2 Hz, both for gratings (e.g., Fiorentini *et al.*, 1991; Mullen & Boulton, 1992; Derrington & Henning, 1993; Gegenfurtner & Hawken, 1995) and homogeneous fields (Kelly & van Norren, 1977; Swanson *et al.*, 1987; Lee *et al.*, 1989a, 1990; Smith *et al.*, 1995). Plotted in units of cone contrast, adult tCSFs for luminance and chromatic stimuli typically cross one another near 4 Hz (but cf. Metha & Mullen, 1996).

In infants, tCSFs for luminance stimuli have previously been described. Using behavioral techniques, it has been shown that tCSFs for luminance gratings of low spatial frequency are bandpass in 3–4 month olds, with a peak near 5 Hz (Hartmann & Banks, 1992; Rasengane *et al.*, 1997; Dobkins & Teller, 1996a; also see Swanson & Birch, 1990). In particular, we have emphasized that the bandpass tCSFs of 3-month-olds are quite similar in shape and peak temporal frequency to those of adults, although infant sensitivity is reduced by about 1.5 log units.

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In the present experiment, we wished to determine whether infant chromatic tCSFs are lowpass in nature, like those of adults, and whether they are subject to a sensitivity loss of a magnitude similar to that seen for luminance stimuli. Toward this end, we tested 3-month-old infants with isoluminant red/green gratings of different temporal frequencies, and compared the results with those obtained from adult subjects tested under identical viewing conditions.

We are led to an interest in the development of chromatic tCSFs for two different theoretical reasons. First, in our earlier study of luminance tCSFs (Dobkins & Teller, 1996a), we sought evidence for the presence of directionally selective mechanisms in infants by comparing detection thresholds for moving vs counterphase-reversing gratings in a summation-near-threshold paradigm (Levinson & Sekuler, 1975; Watson *et al.*, 1980; Graham, 1989). The results suggested that, over a certain range of temporal frequencies/speeds (5–17 Hz; 22–67 deg/sec), the most sensitive luminance contrast detectors in 3-month-olds are directionally selective.

In the present experiment, we similarly sought to compare infant chromatic sensitivity for moving vs counterphase gratings, as a means of addressing whether the most sensitive *chromatic* mechanisms for infants are directionally selective. Although our results were not fully definitive in addressing this particular question, this theoretical paradigm motivated the use of both moving and counterphase stimuli in the present experiment.

The second theoretical rationale for the present experiment concerns the physiological substrates for the detection of luminance vs chromatic stimuli in infants. As addressed further in the Discussion, adult (bandpass) tCSFs for luminance stimuli are thought to be subserved by activity within early stages of the magnocellular (M) pathway, whereas (lowpass) tCSFs for chromatic stimuli are thought to be subserved by parvocellular (P) activity (Lee *et al.*, 1989a, 1990; Smith *et al.*, 1995).

Most earlier discussions in the infancy literature have been built on the presumption that the P pathway precedes the M pathway in development (e.g., Atkinson, 1992). However, in a recent psychophysical experiment on motion:detection (*M:D*) ratios for grating stimuli, we found data consistent with the possibility that M neurons might control detection thresholds for chromatic as well as for luminance stimuli in 3-month-old infants (Dobkins & Teller, 1996b), and thus might precede P neurons in the maturation of sensitivity, at least for the detection of moving grating stimuli.

The present experiment was undertaken to explore further this question of functional maturation rates for M vs P pathways in infants, by examining the shapes and absolute sensitivities of tCSFs for chromatic stimuli. At least three possible scenarios can be envisioned. First, both M and P neurons in infants might show similar (and simple) losses of sensitivity compared with adults. If so, then infants' chromatic tCSFs should remain lowpass like those of adults, but show a loss of absolute sensitivity of approximately 1.5 log units, similar to the absolute sensitivity loss shown for luminance gratings in our earlier study. Second, infants' P cells might exhibit a larger (or smaller) loss of sensitivity than M cells, but P cells might still exhibit greater chromatic sensitivity than M cells. If so, then chromatic tCSFs should still be determined by P cells. In this scenario, infant chromatic tCSFs should show a larger (or smaller) loss of absolute sensitivity than infant luminance tCSFs, but remain lowpass in shape. And third, infants' P cells might be so insensitive that they are less sensitive than infants' M cells, even for chromatic stimuli. If so, then the infant chromatic tCSF could be subserved by M cells, and could be *bandpass* rather than *lowpass* in shape.

In the present experiment, infant chromatic tCSFs were found to be bandpass—not lowpass like those of adults—and similar in peak temporal frequency and general shape to the tCSFs we had previously obtained from infants tested with luminance gratings. The striking difference in curve shape between chromatic tCSFs in infants vs adults supports the third alternative hypothesis outlined above: that P cells in infants may be so insensitive that chromatic tCSFs are determined by M cells rather than by P cells. The data thereby lend support to the argument that, at least in terms of detection thresholds for temporally modulated stimuli, the M pathway precedes the P pathway in functional maturity.

METHODS

Subjects

Adults. Six adult subjects were tested under stimulus conditions nearly identical to those employed in our infant paradigm. Two authors (KRD and BL) and four naive viewers, aged 20–42 yr, participated in these experiments. Four of these subjects and an additional nine ($n = 13$), aged 20–55 yr, also provided psychophysical red/green isoluminance points to be used in the infant study (see below).

Infants. A total of 86 infants took part in this study. Male infants with family histories of color vision deficiencies were excluded from the study. All infants were born within 14 days of their due date, and were reported to have uncomplicated births. Each infant turned 12-weeks-old during the test week and was tested for 1–5 days within this period. The average age on the first day of testing was 82 days [standard deviation (SD) = 2].

Three infants failed to meet a minimum trial number criterion ($n \geq 120$ trials). Eighteen infants failed to meet a minimum performance criterion (score of $\geq 80\%$ correct for luminance-defined gratings at 80% contrast). Data from these 21 infants (which were fortuitously balanced across the temporal conditions) were not included in the analysis. Data from 65 infants were retained.

Apparatus and stimuli

Stimuli were generated on high resolution 19″ RGB monitors (either Barco model CDCT 6451 for the two infant apparatus or Barco model ICD 451B for the adult apparatus, 67 Hz, non-interlaced, 640×480 pixels)

driven by Mac II computers. The 8-bit video board allowed for 256 discrete levels of luminance. The CIE chromaticity coordinates for the Barco primaries were: Red (0.610, 0.340), Green (0.300, 0.590) and Blue (0.150, 0.060). The maximum output for the monitor was calibrated to equal energy white (CIE chromaticity coordinates = 0.333, 0.333), and the voltage/luminance relationship was linearized independently for each of the three guns in the display (Cowan, 1983).

Adult apparatus. In order to produce the low contrasts required to measure adult contrast thresholds, adult subjects were tested using an auxiliary field. The grating stimuli were produced on the main stimulus monitor (No. 1). A second Barco monitor (No. 2), which displayed a homogeneous yellow field, was placed at right angles to monitor No. 1. A piece of plate glass was placed between the two monitors at a 45 deg diagonal. Direct viewing of monitor No. 2 through the glass allowed approximately 90% transmittance of light from monitor No. 2 and 10% reflectance of light from monitor No. 1. The mean luminances on the two monitors (11.5 and 18.6 cd/m^2 for monitors Nos 1 and 2, respectively) were set such that the mean luminance of the combined display was 18 cd/m^2. Sinusoidal gratings presented on monitor No. 1 were thus reduced in contrast by 93%. At the eye, the combined chromaticity coordinates were 0.486, 0.421.

Infant apparatus. Infant subjects were tested on two different apparatus, which served to increase the number of subjects run per week. On Apparatus A, the mean luminance of the gratings and the background field was 18 cd/m^2, with mean chromaticity coordinates of 0.509, 0.416. On Apparatus B, the mean luminance of the gratings and the background field was 15 cd/m^2, with mean chromaticity coordinates of 0.515, 0.419.

Stimuli. All stimuli were horizontally oriented sinusoidal gratings. Spatial frequency was set at 0.25 c/deg. This spatial frequency was chosen because it is near the peak of the spatial contrast sensitivity function for infants 3 months of age (e.g., Atkinson *et al.*, 1977a; Banks & Salapatek, 1978), and because the effects of chromatic aberration are negligible below 1 c/deg (Flitcroft, 1989; Logothetis *et al.*, 1990; Cavanagh & Anstis, 1991). At a viewing distance of 38 cm, grating stimuli subtended 16 deg by 16 deg of visual angle (4 total cycles) and were centered 13 deg to either the left or right of center. The illuminated portion of the video monitor subtended 53 deg by 40 deg.

These experiments employed both moving and counterphase gratings, the generation of which have been described in detail in a previous report (Dobkins & Teller, 1996a). Briefly, moving gratings were produced by phase-shifting the gratings at regular intervals in synchrony with the vertical refresh of the video monitor. Vertical motion was employed in order to reduce the potential for optokinetic nystagmus (OKN) (Hainline *et al.*, 1984; Hainline & Abramov, 1985; Schwarzbach & Schwartze, 1991). As would be expected for the use of relatively small stimulus fields in conjunction with vertical motion, tracking or OKN eye movements were never observed in our infant subjects.

Counterphase gratings were produced using sinusoidal temporal modulation. A complete temporal cycle was created using the same number of discrete frames as required to cycle through a period of the moving stimulus. This ensured that the two types of stimuli (i.e., moving and counterphase) were equally sampled in time and space.

Temporal frequency and speed. Five temporal frequencies were used: 0.7, 2.1, 5.6, 11 and 17 Hz. Because spatial frequency was held constant, the speed of the moving gratings necessarily covaried with temporal frequency. Corresponding speeds were 2.8, 8.4, 22, 44 and 67 deg/sec, respectively. This range of temporal frequencies/speeds is identical to those we previously employed to obtain tCSFs for luminance-defined stimuli (Dobkins & Teller, 1996a).

Chromatic (red/green) gratings. Chromatic red/green gratings were produced by sinusoidally modulating the red and green primaries 180 deg out of phase, with a small amount of blue primary added in phase with the red portion of the grating so as to silence short-wavelength-sensitive (S) cones (see Dobkins & Teller, 1996b).

We specify the chromatic contrast in the red/green grating in two different ways. *Instrument contrast* describes the fraction of the potential chromatic modulation between the red and green phases of the grating. The point at which the red and green primaries are modulated by 100% of the available gamut is defined as 100% instrument contrast. *Cone contrast* describes the amplitude of response modulation in cone photoreceptors produced by the red and green phases of the stimulus, and is dependent on the chromaticity coordinates of the monitor's red and green primaries. The utility of converting to a cone contrast metric is that it standardizes across apparatus and laboratories, and allows for the expression of chromatic contrast and luminance contrast in comparable units (e.g., Mullen, 1985; Lennie & D'Zmura, 1988; Chaparro *et al.*, 1993; Derrington & Henning, 1993). Cone modulations were computed using the CIE coordinates of the primaries and the conversion functions provided by Boynton (1986), based on the cone action spectra provided in DeMarco *et al.* (1992).

Full modulation between the red and green primaries produced modulations of 14% and 34% in the L and M cones, respectively. Thus, the root mean square (r.m.s. = sqrt $[(M^2 + L^2)/2]$) of the independent modulations of the L and M cones was 26%. For our infant experiments, the maximum r.m.s. cone contrast employed was 26% (100% instrument contrast). In adult experiments, the auxiliary field reduced the maximum cone contrast produced at the eye to 1.8%.

Photometry: setting psychophysical isoluminance. Calibrations of standard CIE V_λ isoluminance were carried out using a Minolta TV-2150 photometer/colorimeter and a Gamma Spectroradiometer. Motion photometry (Moreland, 1982; Teller & Lindsey, 1993a) was used to determine psychophysical red/green iso-

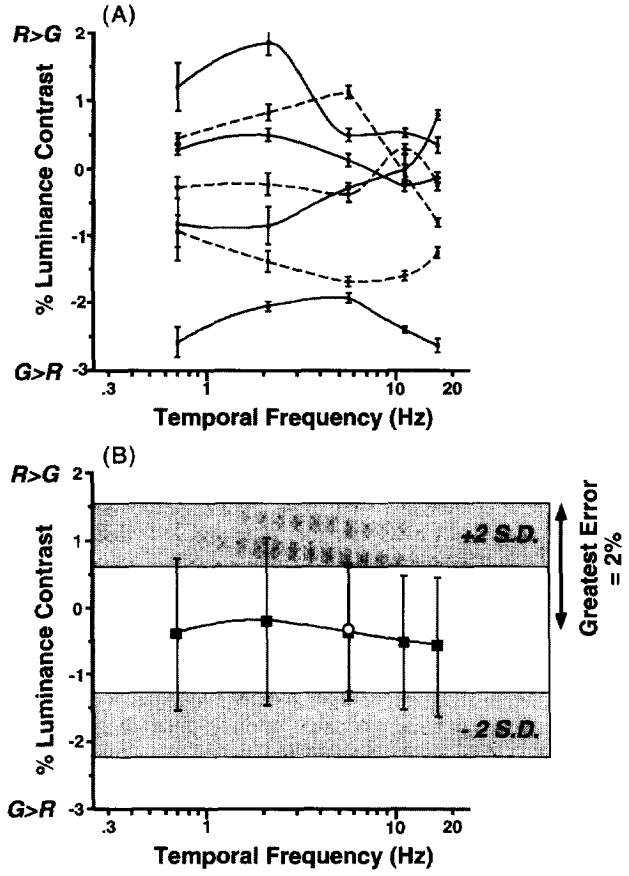

FIGURE 1. The effect of temporal frequency on isoluminance points determined by motion photometry. Zero on the ordinate indicates V_λ-based isoluminance. Positive luminance contrast values denote red brighter than green with respect to V_λ, and vice versa. (A) Individual means and standard errors for seven adult subjects. (B) Mean isoluminance points and population standard deviations (SD) across the seven subjects. The open circle shows the mean isoluminance point at 5.6 Hz determined from a larger sample of 13 subjects. This value was used for testing infants at all temporal frequencies. The shaded area, which represents 2 SD away from the mean of the 13 adults tested at 5.6 Hz, demonstrates that the greatest error that could exist for individual subjects is approximately 2% luminance contrast (see text for further details).

luminance points for individual adult subjects (see Dobkins & Teller, 1996b for details). Subjects fixated a small dot in the center of an upward or downward moving red/green grating (r.m.s. cone contrast = 1.35%) and adjusted the luminance contrast in the grating (contrast interval = 0.14%) until the percept of motion was least salient. Isoluminance points were determined from the mean of 20 trials.

The stimulus conditions for the motion photometry procedure were identical to those employed in the main adult experiments (i.e., same size, orientation, spatial frequency, and temporal frequencies). Typically, SD of motion photometry settings within a subject tested at a given temporal frequency were <0.2%, demonstrating that this technique yields rather precise estimates of isoluminance. Each subject's mean isoluminance point at each temporal frequency was used when testing the corresponding temporal frequency in the main adult experiment.

Choice of isoluminance settings for infants. In order to obtain an isoluminance setting for our infant subjects, isoluminance points were obtained from 13 adult subjects tested on the infant apparatus (r.m.s. cone contrast = 6.5%). Luminance contrast in the red/green grating could be stepped up and down in intervals of 0.5%. Seven of the subjects were tested at all five temporal frequencies on infant Apparatus A, whereas the other six subjects were tested only at 5.6 Hz.

The effect of temporal frequency on isoluminance point settings for the seven most extensively tested adult subjects is shown in Fig. 1(A). Although isoluminance settings were affected by temporal frequency, the effect was small (the largest variation in the mean isoluminance point across the temporal frequencies tested was ~1.6% for any individual), and the magnitude and direction of variation were not consistent across subjects. Mean isoluminance points and standard deviations for the seven subjects are plotted in Fig. 1(B). An ANOVA performed on the seven subjects' isoluminance estimates revealed no significant effect of temporal frequency ($F(4,24) = 0.51$, P = NS). Because the isoluminance point did not vary greatly within an individual adult subject across temporal frequency, and since the effect of temporal frequency on isoluminance point estimates was not significant for the population data, we chose to use only one red/green setting for all the temporal frequencies tested in the infant experiments. For this, we used the mean isoluminance point at 5.6 Hz (i.e., the median of the t.f. range) determined from a total of 13 subjects [Fig. 1(B), open circle]. These values were −0.25% (SD = 1.0%) and +2.31% (SD = 1.0%) with respect to V_λ isoluminance, on Apparatus A and Apparatus B, respectively. The low population standard deviations suggest that, for the conditions employed, individual isoluminance points varied relatively little across adult subjects.

As we have previously discussed (Dobkins & Teller, 1996b), our justification for using the adult mean isoluminance value in our infant experiments is based on previous experiments demonstrating that infant and adult mean isoluminance points measured by VEPs (Morrone *et al.*, 1993; Bieber *et al.*, 1995) and motion nulling (Maurer *et al.*, 1989; Teller & Lindsey, 1989; Brown *et al.*, 1995) are highly similar, especially in the red/green range. Moreover, Brown and colleagues argued quantitatively that the variability of isoluminance points across infant subjects is comparable with the variability across adult subjects, when measurement error is taken into account.

In our experiments, the variability across adults (in terms of SD) was <1.0% luminance contrast. Therefore, the maximal amount of luminance contrast expected to exist in the stimuli, for 95% of infants, due to inter-subject variability, is <2.0% (based on ±2 SD), a value which is less than behaviorally obtained luminance contrast thresholds observed in previous studies of 3-month-old infants (e.g., Atkinson *et al.*, 1974, 1977a,b; Banks & Salapatek, 1976, 1981; Swanson & Birch, 1990;

Hartmann & Banks, 1992; Teller *et al.*, 1992a; Brown *et al.*, 1995; Dobkins & Teller, 1996a,b). Thus, the maximum amount of luminance contrast expected to exist in our red/green stimuli should be well below threshold for the vast majority of infants.

Luminance-defined (yellow/black) gratings. Luminance-defined gratings were produced by sinusoidally modulating the red and green primaries in phase, and were of the same mean luminance and chromaticity as the chromatic gratings. For luminance stimuli, r.m.s. cone contrast values directly correspond to the conventional Michelson contrast: $[(L_{max} - L_{min})/(L_{max} + L_{min})]$, and cone contrasts up to 100% are readily produced.

For adults, luminance stimuli were employed for the purpose of obtaining luminance tCSFs. For infants, luminance gratings were employed for the purpose of obtaining a performance criterion (see below). Note that luminance tCSFs were not obtained from infant subjects in this experiment.

Psychophysical paradigm

Adult procedure. Adult subjects were situated in a chin-rest. Contrast thresholds were obtained by standard forced-choice psychophysical techniques with feedback. Each adult subject was tested at all five temporal frequencies (0.7, 2.1, 5.6, 11 and 17 Hz), presented in separate blocks. Trials containing moving gratings and counterphase gratings were interspersed throughout the session, and the moving stimuli were randomized as to direction of motion (upwards or downwards). Stimuli appeared on the left or right side of the monitor (centered 13 deg from the middle of the screen), and the subject reported the left vs right location after each trial. Adults were tested with both luminance and chromatic gratings, and this variable was also randomized across trials. Stimuli were presented in a random fashion at one of six chromatic contrasts or one of six luminance contrasts (contrast range = 0.06–1.8% r.m.s. cone contrast, 1.5 log unit, for both luminance and chromatic conditions). As was the case for infants, eye position in our adult subjects was unrestricted and stimuli remained present on the screen until a decision was made.

Infant procedure. Unlike the case for adults, and owing to the limited number of trials we could obtain from any individual infant, each infant was tested at only *one* of five temporal frequencies, but with both moving and counterphase gratings. Infant contrast thresholds were estimated using the forced-choice preferential looking (FPL) technique (Teller, 1979) with the method of constant stimuli, as described in detail previously (see Dobkins & Teller, 1996a,b). Briefly, an adult experimenter held the infant 38 cm away from the front of the stimulus monitor in the view of a video camera aimed at the infant's face. On each trial, the grating stimulus appeared abruptly on the left or right side of the video monitor (13 deg eccentricity), and the experimenter used cues such as the infant's head turning and gazing behavior to judge the left vs right location of the stimulus. Trials containing single moving gratings vs counterphase gratings were randomly interspersed throughout the experiment. Computer beeps provided feedback.

Stimuli were presented at one of three chromatic contrast levels, including the maximum available from our monitor (6.5, 13 and 26% r.m.s. cone contrast; 0.6 log unit range). In partial compensation for the limited maximum cone contrast, the highest chromatic contrast was presented twice as often as the lower two. Also, one-fifth of the stimulus trials consisted of a 40 or 80% contrast luminance-defined grating. The purpose of this stimulus was to provide some "easy" trials for the infant, and to obtain a performance criterion. (For the first 15 infants tested, we used a 40% contrast "easy" stimulus, and then decided to increase the contrast to 80%.) In addition to these randomly presented easy trials, the experimenter could call up the easy stimulus at any time in order to monitor the attentional state of the infant. An incorrect guess by the experimenter under this easy condition was taken to indicate that the infant was inattentive and required a break. Note that data obtained from the "easy" stimulus were not included in the Weibull fits (see below).

The five adult experimenters who collected the infant data (authors KRD and BL and three assistants) were all highly experienced in the FPL technique. Although we had originally tried to include about an equal number of infants per temporal frequency, we decided to use all data sets that met our minimal trials and performance criteria (described above). Thus, data from 10, 14, 20, 11 and 10 infants tested at 0.7, 2.1, 5.6, 11 and 17 Hz, respectively, contributed to the results presented here (65 total subjects). Each temporal frequency group was balanced to include an approximately equal number of girls and boys and a balance of subjects between the two infant apparatus and among the five observers. The total number of chromatic trials collected in retained data sets ranged from 123 to 224, with an average of 176 trials/infant (88 trials per psychometric function).

Data analysis

Contrast thresholds. Psychometric curves were fit to the data using Weibull functions and maximum likelihood analysis, the details of which have been previously described (Dobkins & Teller, 1996a,b). For adults, an upper asymptote of 100% was employed and the slope parameter of the Weibull function was unrestricted. (The mean slope value across adults tested over all conditions was ~3.0). For infants, upper asymptotes were fixed at 95%. Based on the asymptote values chosen for infants and adults, contrast threshold was defined as the contrast yielding 75% correct performance in adults and 72.5% correct performance in infants.

Owing to the limited range of available chromatic contrast, most infants did not perform above 90% correct, even at the highest available chromatic contrast (26% r.m.s. cone contrast). In order to improve the Weibull fit to the data under these conditions, the slope parameter was fixed at 2.0 for all infant data sets. This fixed slope

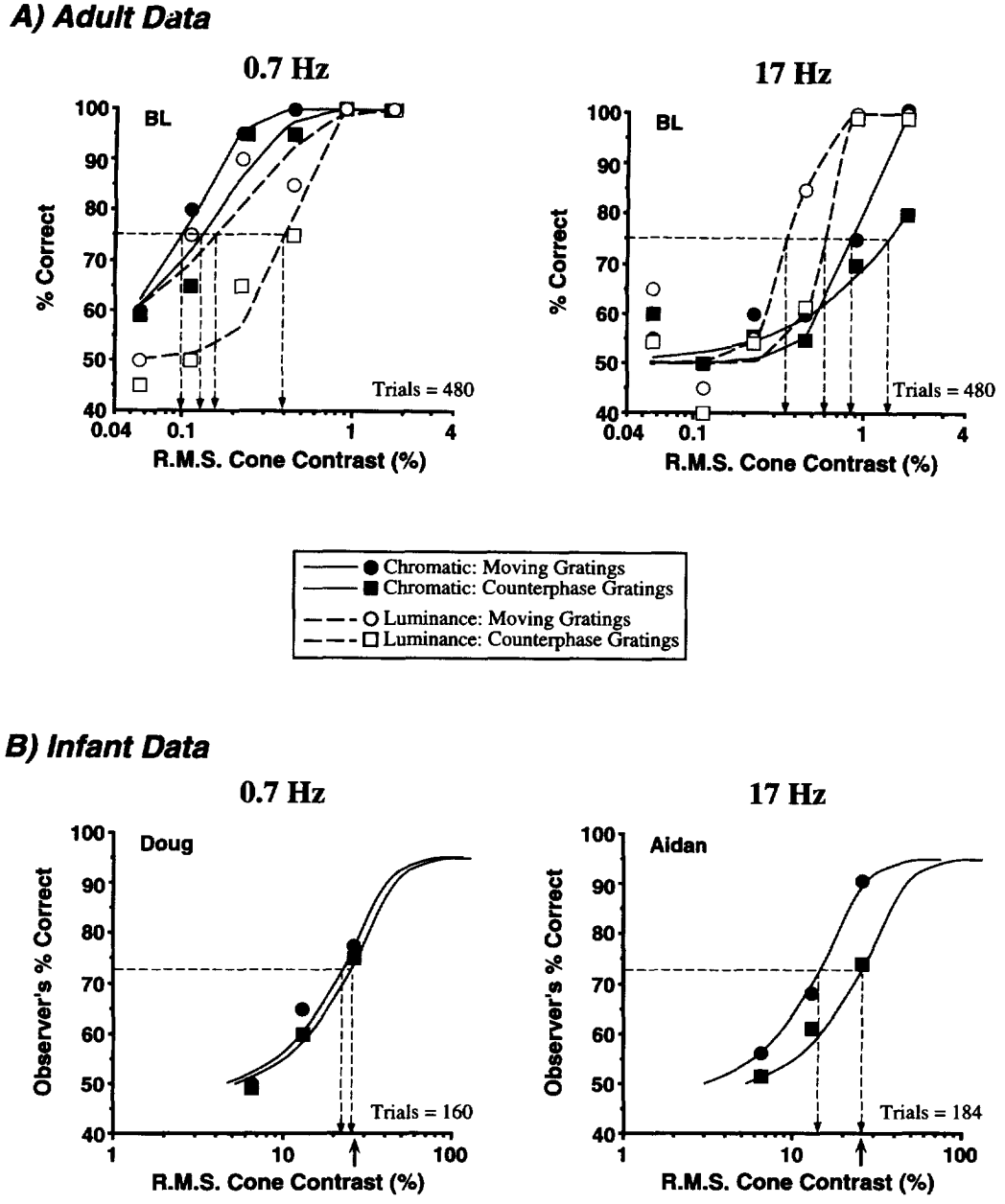

FIGURE 2. Psychometric functions. (A) Sample data from one adult subject tested with both chromatic (filled symbols, solid lines) and luminance (open symbols, long-dashed lines) gratings. Data are shown for two different temporal frequencies: 0.7 Hz (left) and 17 Hz (right). Weibull functions were fit to the data, using an unrestricted slope and an upper asymptote of 100%. Threshold = 75% correct. (B) Sample data from two infants, tested with chromatic gratings at 0.7 Hz (left) and 17 Hz (right). For infants, Weibull functions were fit to the data using a restricted slope of 2.0 and an upper asymptote of 95%. Threshold = 72.5% correct. Solid arrows under abscissae show the highest available r.m.s. cone contrast available for the chromatic stimuli on the infant apparatus.

value was chosen based on results from unrestricted slope analyses performed on earlier luminance data (Dobkins & Teller, 1996a), and is in agreement with slope values obtained in previous infant studies employing luminance gratings (e.g., Swanson & Birch, 1992; Brown *et al.*, 1995). Most importantly, for the sake of these analyses, fixing the slope parameter has negligible effects on estimates of threshold (McKee *et al.*, 1985; Teller *et al.*, 1992b).

In all but eight cases out of the 130 psychometric functions, the data were well fit by the fixed-slope Weibull functions, and estimated thresholds fell within the range of contrast values used. In seven of the eight exceptional cases, the estimated threshold fell beyond 52% r.m.s. cone contrast (twice the maximum available contrast of 26%). For these cases, thresholds were set to 52%. In the remaining case, the estimated threshold fell below 3.25% (half of the lowest contrast tested). In this case, threshold was set to 3.25%.

In our previous study (Dobkins & Teller, 1996a) we obtained tCSFs for 0.25 c/deg, 30 cd/m^2 luminance-defined gratings modulated through equal energy white

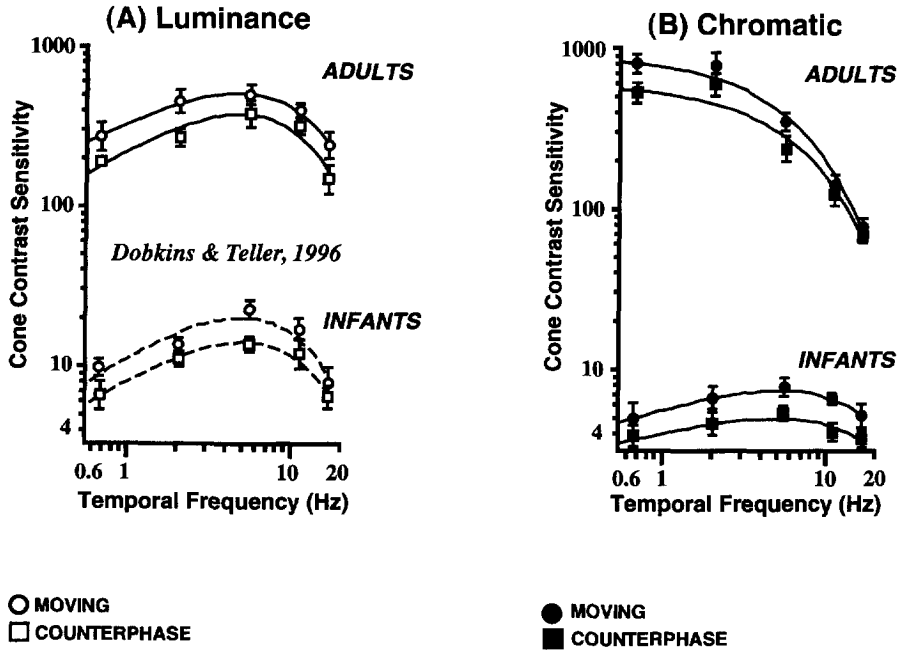

FIGURE 3. Temporal contrast sensitivity functions (tCSFs). (A) Luminance (yellow/black) tCSFs for adults (upper curves), tested with both moving (open circles) and counterphase (open squares) gratings. For comparison, luminance data from infants tested in Dobkins & Teller (1996a) are also shown (lower set of dashed curves). Curves are best-fitting double exponentials (see Methods for details). Error bars denote standard errors of the means. (B) Chromatic (red/green) tCSFs for adults (upper curves) and infants (lower curves), tested with both moving (filled circles) and counterphase (filled squares) gratings. As expected, adults exhibit bandpass tCSFs for luminance stimuli with a peak near 5 Hz and lowpass tCSFs for chromatic stimuli. By contrast, in infants, both chromatic and luminance tCSFs appear bandpass, with peak sensitivities near 5 Hz. For infants, the mean moving:counterphase sensitivity ratio (across temporal frequencies) is 1.3:1 for both chromatic and luminance stimuli. For adults, the mean moving:counterphase sensitivity ratio is 1.4:1 for luminance. Under chromatic conditions, however, the adult mean is 1.4:1 for the three lowest temporal frequencies, yet converges towards 1:1 at the two highest temporal frequencies.

(i.e., chromaticity coordinates 0.333, 0.333). The mean age for this group of infants was 88 days (SD = 2 days). These data will be used in the present study for comparison to the infant chromatic data. To maintain consistency of scoring between the luminance and chromatic analyses, data from this earlier study were re-analyzed, using fixed slope values of 2.0. The resulting mean tCSFs (Fig. 3) are essentially indistinguishable from those obtained earlier using Weibull functions for which the slope parameter was allowed to vary (see Fig. 6 of Dobkins & Teller, 1996a), lending further support to the assertion that fixing slope values has negligible effects on estimates of contrast threshold.

Curve fitting of tCSFs

In order to obtain curve fits for the tCSFs, we employed an iterative minimization procedure which fits tCSFs with a double exponential function, as has been previously described for spatial CSFs (Wilson, 1978; Movshon & Kiorpes, 1988). We attribute no specific theoretical significance to the double exponential function, but employ it merely on an empirical basis as one which fits CSFs well (see Kiorpes *et al.*, 1987). These curves are of the form:

$$a(\omega b)^{d}\exp(-c\omega b),$$

where ω is temporal frequency. The four free parameters of the double exponential function are a (which allows vertical shifts of sensitivity), b (which allows lateral shifts in temporal frequency), c (which affects the high-frequency fall-off), and d (which affects the low-frequency fall-off). In addition to providing values for these parameters, the double exponential fitting procedure also yields the peak temporal frequency for fitted curves. For these analyses, we used population-averaged data sets.

As a means of comparing curve similarity across the different tCSF data sets, the double exponential fits for the eight separate tCSFs were compared with a "multiple-fitting" procedure that provided a simultaneous best-fit common curve for several tCSF data sets fit *jointly*. For each tCSF, a, b, c and d were allowed to vary independently. For the multiple-fitting procedure, a and b (the sensitivity and temporal scale parameters) were fit independently to each tCSF, while c and d (the curve shape parameters) were constrained to be common across the selected data sets (for further details on this procedure, see Movshon & Kiorpes, 1988).

Multiple regression analysis (Judd & McClelland, 1989) was employed to determine whether the fits to separate data sets accounted for significantly more of the variance than the common curve fit across sets (i.e., whether allowing the curve shape parameters c and d to vary independently for each tCSF data set gave a significantly better fit than a multiple-fitting with a

TABLE 1. Results from a double exponential curve-fitting procedure performed on the tCSF data

	a	*b*	*c*	*d*	Peak t.f.	Res. error
Moving gratings						
Infant luminance	43.1	0.19	0.84	0.77	4.95	0.085
Infant chromatic	14.3	0.08	0.93	0.37	5.20	0.001
Adult luminance	1181	0.14	0.87	0.58	4.70	0.003
Adult chromatic	923	0.19	0.80	0.00	0.05	0.056
Counterphase gratings						
Infant luminance	31.1	0.16	0.86	0.69	5.15	0.019
Infant chromatic	10.1	0.07	0.95	0.32	4.95	0.011
Adult luminance	888	0.17	0.84	0.69	4.80	0.062
Adult chromatic	640	0.14	1.00	0.00	0.05	0.121

Curve fits are of the form: $a(\omega b)^d \exp(-c\omega b)$, where ω is temporal frequency. The four free parameters of the double exponential function are *a* (which allows vertical shifts of sensitivity), *b* (which allows lateral shifts in temporal frequency), *c* (which affects the high-frequency fall-off), and *d* (which affects the low-frequency fall-off). In addition to providing values for these parameters, the double exponential fitting procedure also yields the peak temporal frequency for fitted curves.

Results from individual fits for the moving and counterphase conditions are presented separately.

common curve shape, where *c* and *d* are constrained). If so, this would indicate that the separate tCSFs could not be fit by a common curve, suggesting that they are significantly different from one another. If, on the other hand, tCSF data sets are as well fit by a common curve as they are by their separately determined curves, this would suggest that the different tCSFs are of the same basic shape.

RESULTS

Psychometric functions

Psychometric functions from one adult subject are shown for two different temporal frequencies in Fig. 2(A). When tested at 0.7 Hz (left panel), which produced a speed of 2.8 deg/sec for the moving stimulus, chromatic detection thresholds for moving and counterphase gratings (filled circles and squares, respectively) were 0.10 and 0.13% r.m.s. cone contrast, respectively. For luminance gratings (open circles and squares), moving and counterphase thresholds were 0.16 and 0.41%, respectively. When tested at 17 Hz (right panel), which produced a speed of 67 deg/sec for the moving stimulus, chromatic detection thresholds for the moving and counterphase gratings were 0.86 and 1.36% r.m.s. cone contrast, respectively. For luminance gratings, moving and counterphase thresholds were 0.39 and 0.55%, respectively. Thus, for this subject, chromatic sensitivity was superior to luminance sensitivity at the low temporal frequency, yet the opposite was the case at the high temporal frequency.

Psychometric functions for chromatic stimuli from two 3-month-old infant subjects are shown in Fig. 2(B). For the data shown in the left panel, moving and counterphase stimuli were presented at 0.7 Hz. Detection thresholds for the moving and counterphase stimuli were 21.7 and 23.9% r.m.s. cone contrast, respectively. For the data shown in the right panel, moving and counterphase stimuli were presented at 17 Hz. At this temporal frequency, thresholds for moving and counterphase gratings were 14.4 and 24.5%, respectively.

Adult temporal contrast sensitivity functions (tCSFs)

Adult group mean tCSFs for moving and counterphase gratings are shown in Fig. 3 (upper curves), for both luminance and chromatic stimuli. The fitted curves show best fitting double exponential functions, the parameters and peak frequencies for which are presented in Table 1. For the luminance condition [Fig. 3(A)], adult tCSFs were bandpass as expected, with peak sensitivity occurring near 5 Hz. For the chromatic condition [Fig. 3(B)], adult tCSFs were lowpass, again as expected, with sensitivity falling dramatically above 2 Hz.

In addition, adults were an average of 0.11 log units more sensitive to moving than to counterphase gratings under luminance conditions and 0.16 log units more sensitive under chromatic conditions. In order to evaluate statistically the effects of stimulus type, temporal frequency and the interaction between the two, a two-factor ANOVA was performed. The results from this analysis, performed on both the luminance and chromatic data, revealed that adults were significantly more sensitive to moving than to counterphase gratings (chromatic: $F(1,5) = 41.02$, $P < 0.005$; luminance: $F(1,5) = 66.25$, $P < 0.005$). Furthermore, sensitivity was significantly affected by temporal frequency (chromatic: $F(4,20) = 117$, $P < 0.005$; luminance: $F(4,20) = 11.00$, $P < 0.005$), but no interaction was found between temporal frequency and stimulus type (chromatic: $F(4,20) = 0.91$, P = NS; luminance: $F(4,20) = 0.86$, P = NS).

Infant luminance tCSFs

Re-analyzed group mean tCSFs for luminance gratings from the data of Dobkins & Teller (1996) are shown in the Fig. 3(A) (lower dashed curves). The parameters and peak temporal frequencies for the double exponential curves fitted to the data are presented in Table 1. As previously established, infant luminance tCSFs were bandpass, with peak sensitivities near 5 Hz. The results from a two-factor ANOVA (mixed-design) revealed that infant luminance sensitivity was significantly greater for

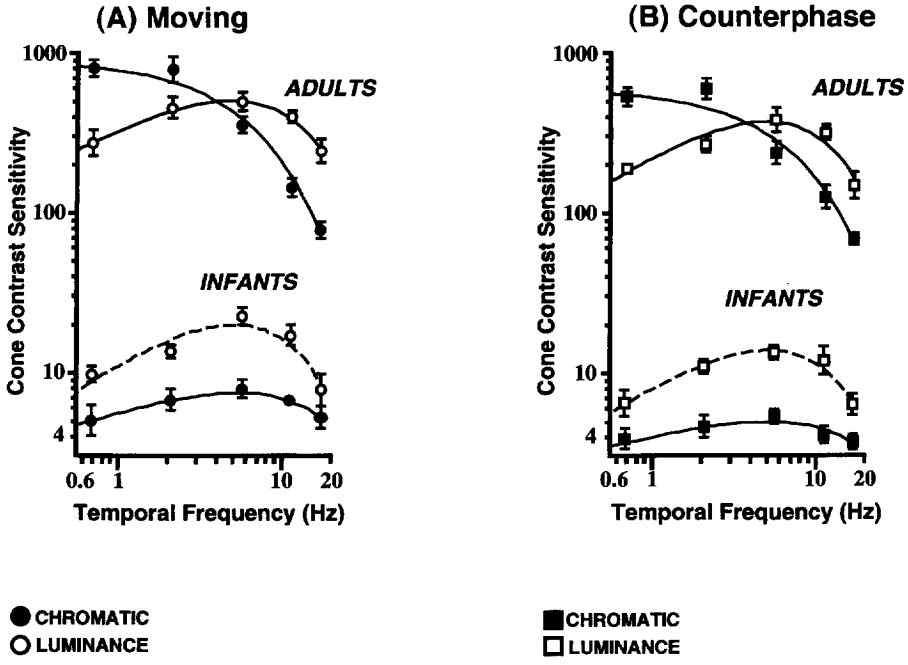

FIGURE 4. Infant and adult tCSFs, plotted separately for moving (A) vs counterphase (B) gratings (conventions as in Fig. 3). As expected, luminance tCSFs in adults are bandpass, while chromatic tCSFs are lowpass, and the luminance and chromatic curves cross one another near 4 Hz. By contrast to adults, chromatic tCSFs in infants are *bandpass* and chromatic and luminance curves do not cross one another.

moving than for counterphase gratings ($F(1,40) = 23.84$, $P < 0.001$). Averaged across temporal frequencies, infants were found to be a factor of 1.3 (or 0.12 log units) more sensitive in the moving grating condition (i.e., a *moving:counterphase sensitivity ratio* of 1.3:1). Furthermore, sensitivity was significantly affected by temporal frequency ($F(4,40) = 6.62$, $P < 0.001$), but no interaction was found between temporal frequency and stimulus type ($F(4,40) = 1.09$, P = NS).

Infant chromatic tCSFs

Finally, group mean chromatic tCSFs for infant subjects are shown in the Fig. 3(B) (lower solid curves). Infants were found to be more sensitive to moving than to counterphase gratings at all temporal frequencies, with the average difference being a factor of 1.3 (or 0.12 log units), a result which is identical to that found for luminance gratings. Surprisingly, for both counterphase and moving gratings, chromatic tCSFs appeared *bandpass rather than lowpass* with peak sensitivities near 5 Hz. Although the infant chromatic curves appear relatively flat, they nonetheless resemble infant luminance tCSFs, in terms of general shape and peak temporal frequency (see curve parameters in Table 1).

Similar to the results from the two-factor ANOVA performed for infant luminance data, analysis of chromatic data revealed that infants were significantly more sensitive to moving than to counterphase chromatic gratings ($F(1,60) = 29.08$, $P < 0.001$) and there was no interaction found between temporal frequency and stimulus type ($F(4,60) = 0.47$, P = NS). Unlike infant luminance data, sensitivity was not significantly affected by temporal frequency ($F(4,60) = 1.54$, P = NS). Nonetheless, a specific comparison based on contrast coding revealed that sensitivity at 5.6 Hz was significantly higher than that obtained at the two end temporal frequencies i.e., at 0.7 and 17 Hz ($F(1,60) = 6.02$, $P < 0.05$). This specific comparisons analysis, in conjunction with the results from our double exponential curve-fitting procedure (see below), reinforce the suggestion that chromatic tCSFs in infants are bandpass, and not lowpass, in nature.

Comparison of infant and adult tCSFs

For both the luminance and chromatic conditions, adults were found to be clearly more sensitive than 3-month-old infants, in accordance with previous behavioral studies (e.g., Banks & Salapatek, 1976, 1981; Atkinson *et al.*, 1977a,b; Hartmann & Banks, 1992; Brown *et al.*, 1995; Rasengane *et al.*, 1997; Dobkins & Teller, 1996a,b; but smaller sensitivity differences are observed between adults and infants tested with VEPs, e.g., Norcia *et al.*, 1990; Hamer & Norcia, 1994).

With regard to the peaks and shapes of functions, however, luminance tCSFs in infants appear quite similar to those of adults [Fig. 3(A)], with a 1.5 log unit sensitivity difference between the two ages existing across all temporal frequencies. By contrast, the peaks and shapes of infant and adult *chromatic* tCSFs are markedly different from one another [Fig. 3(B)]. Whereas adult chromatic tCSFs are lowpass, infant chromatic tCSFs are bandpass, with a peak near 5 Hz. Moreover, adult chromatic curves fall in sensitivity by 10-fold (1 log unit) between 2.1 and 17 Hz, whereas infant chromatic curves exhibit at most a 1.6-fold (0.2 log units) variation in sensitivity across this range of

temporal frequencies. Owing to these differences in curve shape, adult chromatic sensitivity is about 2.2 log units greater than that of infants at the two lowest temporal frequencies, but only 1.2 log units greater at the highest temporal frequency, further emphasizing the differences in chromatic temporal responses for the two age groups.

In sum, whereas adults exhibit lowpass chromatic and bandpass luminance tCSFs, both chromatic and luminance tCSFs in infants appear bandpass, with peak sensitivities near 5 Hz. Moreover, both luminance and chromatic tCSFs in infants resemble luminance tCSFs of adults in their general bandpass shapes and peak temporal frequencies, although infant chromatic curves may be slightly flatter than the others.

Comparison of luminance vs chromatic sensitivity

In order to facilitate comparison between luminance and chromatic sensitivity, infant and adult tCSFs have been replotted in Fig. 4, separately for moving [Fig. 4(A)] and counterphase [Fig. 4(B)] gratings. In adults, chromatic and luminance curves cross one another at around 4 Hz, in accordance with previous results. In infants, the luminance tCSFs (dashed lines) fall well above the chromatic tCSFs (on average, by a factor of ~ 2), and the curves do not cross at any temporal frequency within the range tested.

It should be noted that the infant luminance data (obtained 1 yr earlier from a different set of infants) were collected at a slightly higher mean luminance level (luminance: 30 cd/m^2 vs chromatic: ~ 16 cd/m^2), which could potentially contribute to the differences in absolute sensitivity for luminance vs chromatic stimuli demonstrated here (Dobkins and Teller, unpublished observations, and see Shannon *et al.*, 1996). Although large differences (e.g., 1–2 log units) in illuminance are also known to change the *shape* of the tCSF (e.g. de Lange, 1958; Kelly, 1961, 1971a; Swanson *et al.*, 1987; Lee *et al.*, 1990), the relatively small differences in mean luminance level for chromatic vs luminance stimuli in this infant study (~ 0.3 log units) should not confound interpretation of shape comparisons between chromatic and luminance curves.

Statistical comparisons of double exponential curve fits

In order to compare quantitatively the shapes of infant and adult tCSFs, statistical analyses were performed on the double exponential curves fit to the data. Using multiple regression, fits obtained for individual tCSF data sets were compared with those obtained for multiple-fittings across selected groups of data sets (see Methods). For fitting of individual tCSF data sets, the free parameters varied independently. The resulting a, b, c and d parameters and peak temporal frequencies for the individual data sets are presented in Table 1. For multiple-fitting of tCSFs, variables c and d were constrained for a simultaneous best fit of a common curve shape across the selected data sets. We reasoned that if the common best-fitting curve obtained from the multiple-fitting of two or more tCSF data sets could account for as much variance as when individual data sets are fit alone, the two (or more) tCSFs are of the same general shape.

For the *moving* grating condition, individual fits of parameters c and d to all four data sets (both infant and adult sets of chromatic and luminance tCSFs) were significantly better than their fit by a common curve among the four sets ($F(1,18) = 46.8$; $P < 0.001$). Given the obvious difference in the shape of the adult chromatic tCSF, this is to be expected. When the adult chromatic data set was left out of the multiple-fitting analysis, however, individual fits of c and d to the remaining three data sets were no better than their fit by a common curve ($F(1,13) = 0.074$; P = NS). Moreover, the peak temporal frequencies for the three remaining tCSFs for moving stimuli (i.e., adult luminance, infant luminance, infant chromatic) determined from these analyses were extremely close to one another, i.e., 4.7, 5.0 and 5.2 Hz, respectively. Taken together, the results from these analyses imply that the adult luminance, infant luminance, and infant chromatic tCSFs are of the same general bandpass shape and peak temporal frequency.

For the *counterphase* grating condition, it was again found that individual fits of parameters c and d to all four data sets were significantly better than their fit by a common curve among the four sets ($F(1,18) = 8.71$; $P < 0.01$). However, when the adult chromatic data set was taken out of the analysis, the outcome was not as described for moving gratings. Individual fits to the remaining three data sets were better than their fit by a common curve ($F(1,13) = 14.1$; $P < 0.005$). This is probably due to the fact that the infant chromatic curves are particularly flat compared with the infant and adult luminance curves. Nonetheless, the peak temporal frequencies for the three remaining tCSFs for counterphase gratings (i.e., adult luminance, infant luminance, infant chromatic) determined from this analysis were virtually identical to one another, i.e., 4.8, 5.2 and 5.0 Hz, respectively (and extremely close to those observed for the moving grating condition). Thus, while significant quantitative differences in shape exist between the adult and infant luminance tCSFs and the infant chromatic tCSF, these results still point to a general similarity between the adult luminance, infant luminance, and infant chromatic tCSFs, all of which are bandpass with a peak near 5 Hz.

DISCUSSION

The major purpose of the present experiment was to determine the shapes and absolute sensitivities of tCSFs for chromatic gratings in infants. We found that infant chromatic tCSFs are unexpectedly bandpass with a peak near 5 Hz, rather than lowpass. Moreover, the peaks and overall shapes of the infant chromatic tCSFs are quite similar to previously obtained infant luminance tCSFs. Most importantly, infant chromatic tCSFs are drastically different from those of adults, and instead resemble adult and infant luminance tCSFs. These findings point to the possibility that, in contrast to adults, infants detect both

chromatic and luminance stimuli via a common neural mechanism.

These results are discussed in four contexts. First, the results are compared with the earlier literature on tCSFs for luminance and chromatic stimuli in infants and adults. Second, we provide a further analysis of the data in regard to the question of summation-near-threshold. Third, we speculate on possible underlying neural mechanisms for the developmental time courses of luminance and chromatic tCSFs. And fourth, we assess the implications of these results for the interpretation of earlier studies of infant color vision.

Infant temporal contrast sensitivity functions (tCSFs)

Luminance stimuli. The results from several infant psychophysical studies have demonstrated that by 3 months of age, infant tCSFs for low spatial frequency luminance-defined stimuli are bandpass in shape with a peak near 5 Hz (Hartmann & Banks, 1992; Rasengane *et al.*, 1997; Dobkins & Teller, 1996a, but cf. Teller *et al.*, 1992a), a value close to that observed in adults. Moreover, the peak temporal frequency observed at 3 months is relatively fixed, despite a three-fold variation in *spatial* frequency across studies (see Dobkins & Teller, 1996a, Fig. 7), suggesting that temporal frequency (as opposed to speed) is likely to be the crucial factor for determining sensitivity, as is the case for adults (Kelly, 1979; Burr & Ross, 1982).

Chromatic stimuli. The chromatic data reported herein are, to our knowledge, the only threshold-based chromatic tCSFs yet measured in infants. Unlike the lowpass chromatic tCSFs commonly seen in adults, we found that chromatic tCSFs in 3-month-olds are bandpass in shape, and bear a close resemblance to luminance tCSFs at the same age.

In a related study, Morrone *et al.* (1996) have reported VEP amplitude measures of infants' responsiveness to both luminance and chromatic plaid patterns at various temporal frequencies. In general, both luminance and chromatic amplitude functions were found to be lowpass at 8 weeks of age, falling to half height at about 4 Hz. By 12–14 weeks, luminance VEP amplitude functions became bandpass, with a peak near 5 Hz, in agreement with the present study and other behavioral studies cited earlier. However, in contradiction to the results from the present study, chromatic VEP amplitude functions remained lowpass at 12–14 weeks for most infants.

A possible explanation for differences in curve shape between the Morrone *et al.* and the present study is that the Morrone study employed a VEP amplitude measure in response to suprathreshold stimuli of fixed contrast. Because suprathreshold stimuli were employed, it is likely that the recorded VEP response combined inputs from several physiological mechanisms. By contrast, the threshold paradigm we employed was more likely to isolate a single mechanism, i.e., the most sensitive mechanism for the detection of each stimulus. In addition, differences between the two studies could be due to other factors, such as different eccentricities and/or differences in attentional demands. It will be interesting to see whether, at 3 months postnatal, chromatic tCSFs defined by VEP threshold measures—isolating the single, most sensitive mechanism—turn out to be bandpass, like the behavioral tCSFs in the present study, or lowpass, as they are for suprathreshold VEP amplitude measures.

In any event, an important commonality between our data and those of Morrone *et al.* is the finding that, in early infancy, chromatic and luminance responses appear quite similar to one another. Thus, the results from both studies point to a common underlying mechanism for chromatic and luminance stimuli, although the nature of this mechanism—be it lowpass or bandpass—apparently varies with the testing techniques and stimulus parameters.

Comparison with adults. As reviewed in the Introduction, adult tCSFs for luminance stimuli are bandpass with peaks between 5 and 10 Hz. For chromatic (red/green) stimuli, adult tCSFs are lowpass (at least down to 0.7 Hz), with sensitivity declining rapidly at >2 Hz. When adult tCSFs are compared in terms of a cone contrast metric, chromatic and luminance curves typically cross one another at around 4 Hz. These results were confirmed in our adult studies (see Fig. 4), despite the fact that our experiments were carried out in an "infant-like" fashion. Thus, large fields, uncontrolled eye movements and extended viewing duration appear to have surprisingly little impact on the basic shape of tCSFs in adults.

The results from our previous infant experiments conducted under luminance conditions yielded tCSFs with peaks and shapes quite similar to those of adults in the present study, although adults were about 1.5 log units more sensitive at all temporal frequencies (see Figs 3 and 4). Thus, the development of temporal contrast sensitivity for luminance-defined stimuli can be described as an increase in sensitivity (i.e., a vertical shift), with no change in tCSF shape or temporal scale (i.e., no horizontal shift). These temporal data stand in contrast to the development of *spatial* contrast sensitivity for luminance stimuli, which undergoes changes in both sensitivity and spatial scale (Brown *et al.*, 1987; Banks & Bennett, 1988; Boothe *et al.*, 1988; Movshon & Kiorpes, 1988; Wilson, 1988; Banks & Crowell, 1993; Morrone *et al.*, 1993; Wilson, 1993; Peterzell *et al.*, 1995; Peterzell & Teller, 1996; Kelly *et al.*, 1997; and similar developmental changes are found for spatial contrast sensitivity with *chromatic* stimuli, e.g., Allen *et al.*, 1993; Morrone *et al.*, 1993; Kelly *et al.*, 1997). Thus, while spatial tuning is quite immature at 3 months of age, temporal tuning for luminance stimuli appears relatively adult-like.

By contrast, for *chromatic* stimuli, the shape of the tCSF appears to change dramatically between 3 months and adulthood, being bandpass in infants and lowpass in adults. Whereas adult chromatic tCSFs fall in sensitivity by a factor of 10 (1 log unit) between 2.1 and 17 Hz, infant chromatic tCSFs exhibit at most a 1.6-fold (0.2 log unit) variation in sensitivity over the same temporal

frequency range. Stated with a different emphasis, between 3 months of age and adulthood, contrast sensitivity at low temporal frequencies increases by a full two log units, whereas at higher temporal frequencies the change is closer to one log unit. Thus, to describe the development of chromatic tCSFs, it is clearly necessary to invoke changes in curve shape as well as changes in sensitivity.

Summation near chromatic contrast threshold

One of the approaches used in adult psychophysics to demonstrate the presence of directionally selective mechanisms is the summation-near-threshold paradigm (Levinson & Sekuler, 1975; Watson *et al.*, 1980; Graham, 1989). Summation experiments take advantage of the fact that a counterphase-reversing grating of contrast C is physically identical to the sum of two grating components of contrast $C/2$ moving in opposite directions. As detailed in our previous study using luminance stimuli (Dobkins & Teller, 1996a), probability summation models predict moving:counterphase sensitivity ratios between 2:1 and 1:1, with the exact value depending on the slope of the psychometric functions generated by the moving grating condition.

For luminance gratings moving at relatively fast speeds, data from both adults (Levinson & Sekuler, 1975; Stromeyer *et al.*, 1978; Kelly, 1979; Murray *et al.*, 1983) and infants (Dobkins & Teller, 1996a) yield moving:counterphase sensitivity ratios between 2:1 and 1:1, consistent with the presence of independent directionally selective mechanisms, provided that probability summation is taken into account (Watson *et al.*, 1980; Dobkins & Teller, 1996a). Thus, tested with the summation-near-threshold paradigm, the most sensitive *luminance* contrast detectors in both adults and infants are directionally selective.

Infant chromatic summation. One purpose of the present study was to address the existence of directionally selective mechanisms at *chromatic* contrast threshold, and thresholds for both moving and counterphase gratings were measured with this goal in mind. Inspection of Fig. 3 shows that infants' chromatic sensitivity for single moving gratings falls above their sensitivity for counterphase gratings. The average moving:counterphase sensitivity ratio (across all temporal frequencies) for the chromatic gratings is 1.3:1 (0.12 log units)—a value virtually identical to that found for luminance gratings (0.12 log units in the re-analyzed luminance data, and 0.14 in the original report).

In the case of chromatic thresholds, the available cone contrasts were unfortunately too low to allow the upper parts of the infant psychometric functions to be measured definitively. Thus it was necessary to fix the slopes of the Weibull functions to obtain estimates of chromatic thresholds. This difficulty prevented a detailed probability summation analysis of the present data. As discussed in the Methods, we chose a fixed slope value of 2.0 as this reflected the average slope across all data sets from the previously conducted infant luminance experiment. Thus, individual slope parameters were not utilized for the infant Weibull functions in this study.

If we use the fixed slope value of 2.0 in a probability summation analysis (assuming it reliably describes the actual slopes of the infant data), then the predicted sensitivity ratio is 1.4:1 (see Dobkins & Teller, 1996a, Appendix A for details of this calculation). The average moving:counterphase sensitivity ratio (i.e., 1.3:1) was quite close to (although slightly below) the probability summation prediction for both luminance and chromatic data. Thus, this suggests that our results are consistent with the presence of directionally selective mechanisms at chromatic contrast threshold as well as at luminance contrast threshold. To perform this analysis optimally, however, one needs to know the actual mean slope value and its variation. Moreover, these values need to be obtained separately for each temporal frequency/speed, since different answers are found under different speed conditions (e.g., Graham, 1989; Dobkins & Teller, 1996a). Nonetheless, for chromatic as for luminance gratings, the hypothesis of complete summation (i.e., motion:counterphase sensitivity ratios of 1:1) can be rejected by the present data. In addition, the identical sensitivity ratio for both luminance and chromatic data suggests similar summation characteristics in the two cases.

Adult chromatic summation. To our knowledge, the summation-near-threshold paradigm has not previously been used with chromatic stimuli in adult subjects. Interestingly, in the present data for adults, moving:counterphase sensitivity ratios were about 1.4:1 at the three lowest temporal frequencies, but converged toward 1:1 at the two highest temporal frequencies tested (at 11 and 17 Hz). Although this difference is just a trend (i.e., the ANOVA did not produce a significant interaction between stimulus type and temporal frequency), it suggests that under the present conditions, the most sensitive chromatic contrast detectors are directionally selective at temporal frequencies below, but not above, 10 Hz. As this differential effect of temporal frequency is contradictory to results from recent adult motion:detection (*M:D*) studies employing chromatic stimuli (see Fiorentini *et al.*, 1991; Derrington & Henning, 1993; Gegenfurtner & Hawken, 1995, but cf. Mullen & Boulton, 1992), further studies conducted under more closely similar stimulus and observational conditions will be needed to resolve this discrepancy.

Possible underlying neural mechanisms

Anatomical and neurophysiological data from monkeys have demonstrated the existence of two distinct subcortical pathways—parvocellular (P) and magnocellular (M)—which originate in the retina and remain segregated up through layer 4C of area V1 (see Merigan & Maunsell, 1993 for a recent review). In adult monkeys, neurons most sensitive to luminance contrast are found within the M division, while neurons most sensitive to chromatic contrast are found within the P division (Shapley *et al.*, 1981; Derrington & Lennie, 1984;

Kaplan & Shapley, 1986; Lee *et al.*, 1988, 1989a, 1990; Shapley, 1990; Kremers *et al.*, 1992; Lee *et al.*, 1993; Croner & Kaplan, 1995). Based on these data, it is tempting to attribute detection of luminance and chromatic stimuli to the M and P divisions, respectively. It is important to emphasize, however, that both M and P cell types respond to both luminance and chromatic (red/green) stimuli, but with different contrast thresholds.

The response to isoluminant chromatic stimuli observed in magnocellular neurons of the retina (Lee *et al.*, 1988, 1989a–c; Dacey, 1996) and LGN (Schiller & Colby, 1983; Derrington *et al.*, 1984; Logothetis *et al.*, 1990) is typically one of *frequency-doubling*, i.e., magnocellular neurons respond to changes both from red to green and from green to red. In addition to these frequency-doubled responses, variation in red/green "balance" points across magnocellular neurons can produce a viable population response to isoluminant stimuli. This variability guarantees that, even at some psychophysically determined isoluminance point, some magnocellular neurons will continue to signal a luminance imbalance between the two colors (Logothetis *et al.*, 1990). In sum, frequency-doubled responses and/or inter-neuron variability may provide a signal for the presence of chromatic contrast, without necessarily conveying information about the colors themselves (see Dobkins & Albright, 1997 for further discussion). By contrast, P neurons, by virtue of their *selectivity* for color, are thought to convey information about color identity.

Adult tCSFs and neural mechanisms. As mentioned in the Introduction, activity in the P pathway is thought to underlie the lowpass chromatic tCSF revealed psychophysically in adults, whereas activity in the M pathway is thought to underlie the bandpass luminance tCSF (e.g., Lee *et al.*, 1990; Smith *et al.*, 1995). Especially relevant are studies by Lee and colleagues (Lee *et al.*, 1989a, 1990), which have directly determined tCSFs for M and P retinal ganglion cells of adult macaques. The results from these studies demonstrate that M retinal ganglion cells exhibit bandpass tCSFs for luminance stimuli, with a peak between 10 and 20 Hz, in accordance with results obtained from magnocellular neurons of the LGN (e.g., Hicks *et al.*, 1983; Derrington *et al.*, 1984). For chromatic (red/green) stimuli, tCSFs of M cells (which are obtained from their frequency-doubled responses mentioned above) are also bandpass, with a peak near 10 Hz. Although M cells are more sensitive to luminance than to chromatic modulation (by a factor of 3 to 4, see Lee *et al.*, 1989a), the overall shapes and peaks of the chromatic and luminance tCSFs are extremely similar.

When these same experiments are conducted on P retinal ganglion cells, tCSFs for luminance stimuli appear bandpass, with a peak near 10 Hz, in accordance with earlier results from parvocellular LGN neurons (e.g., Hicks *et al.*, 1983; Derrington *et al.*, 1984). For chromatic stimuli, however, P cells exhibit tCSFs that are *lowpass* in nature. As expected, P cells are more sensitive to chromatic than to luminance modulation (by a factor of ~ 8, see Lee *et al.*, 1989a). Interestingly, the existence of multiple underlying channels for chromatic and luminance detection has recently been supported by psychophysical results (Metha & Mullen, 1996). These channels possess temporal tuning similar to those described for physiological M and P data.

Lee and colleagues elegantly demonstrated that the luminance tCSFs of M cells and the chromatic tCSFs of P cells have the same shapes as psychophysically obtained luminance and chromatic tCSFs, respectively, with the exception that the neural functions have a much higher cut-off frequency than the psychophysical data. The discrepancy at the high temporal frequencies is likely to result from the existence of central filters with corner frequencies of about 10 and 20 Hz, for parvocellular and magnocellular responses, respectively. In sum, correspondences of both absolute sensitivity and curve shape strongly suggest that in adults, luminance tCSFs are served by activity within magnocellular neurons, whereas chromatic tCSFs are served by parvocellular neurons.

Infant tCSFs and neural mechanisms. At the anatomical and physiological level, evidence is mixed on the question of relative maturation levels for M vs P systems in infant primates. The possibility of enhanced development for the magnocellular with respect to the parvocellular pathway is supported by the finding that synapse maturation occurs earlier for magnocellular-recipient neurons in layer $4C_\alpha$ of V1, compared with parvocellular-recipient layer $4C_\beta$ neurons (Mates & Lund, 1983; Lund & Harper, 1991; Lund & Holbach, 1991). With respect to morphological development, the issue of differential M vs P development is somewhat controversial; whereas some studies have reported that axon arbors of magnocellular LGN neurons mature faster than those of parvocellular neurons (e.g., Lachica & Casagrande, 1988; Florence & Casagrande, 1990; Pospichal *et al.*, 1994) and that layer 4B of V1 (which receives from $4C_\alpha$) develops relatively fast in human newborns (Burkhalter *et al.*, 1993), others have shown that the primate parvocellular stream is morphologically set up relatively early in development, and perhaps even earlier than the magnocellular stream (Hickey, 1977; Chalupa *et al.*, 1996). Thus, in the absence of definitive anatomical/physiological data on maturation, a number of scenarios are possible to account for the current pattern of psychophysical results.

The finding that both chromatic and luminance tCSFs in infants are bandpass, with the same peak frequency, raises the possibility that chromatic and luminance stimuli are detected at threshold by the same underlying neural mechanism. Because both chromatic and luminance tCSFs in infants are quite similar in shape to luminance tCSFs of adults (see Fig. 4), the simplest alternative is that 3-month-old infants may rely solely on magnocellular responses for the detection of both chromatic and luminance stimuli. This scenario could arise if magnocellular responses mature (with respect to contrast sensitivity) earlier in development than do parvocellular responses.

We (Dobkins & Teller, 1996b) have recently made a

similar argument regarding development of parvocellular/magnocellular functionality, also on psychophysical grounds. In these experiments we used a motion:detection (*M:D*) paradigm to quantify chromatic and luminance input to motion processing in infants and adults (stimuli = 0.25 c/deg, 5.6 Hz moving gratings). In infants, contrast thresholds for *direction-of-motion (M)* and *detection (D)* were obtained using a directional eye movement technique and forced-choice preferential looking, respectively. As expected from previous studies, adult *M:D* threshold ratios were near 1:1 for luminance stimuli, yet near 2:1 for chromatic stimuli. This result suggests that, for adults tested under these specific spatiotemporal frequency conditions, the most sensitive mechanisms for detecting luminance contrast, but *not* chromatic contrast, are directionally selective. By contrast, infant *M:D* ratios for chromatic and luminance stimuli were approximately equal and close to 1:1, suggesting that, for infants, both luminance and chromatic stimuli are detected by directionally selective mechanisms. Because directionally selective mechanisms in primate cortex are believed to rely largely on input from the magnocellular subcortical division (Maunsell *et al.*, 1990; Merigan & Maunsell, 1990, but cf. Merigan *et al.*, 1991), these *M:D* results point to the magnocellular division as the most sensitive detection system available to the infant for chromatic, as well as for luminance, stimuli.

Other potential underlying mechanisms. There are also more complicated ways in which magnocellular responses could dominate behavioral tCSFs for both luminance and chromatic stimuli early in development. For example, if the signals generated from parvocellular neurons are subject to far more central lowpass temporal filtering in infancy than that described for adult neurophysiological data (e.g., Lee *et al.*, 1990; Kremers *et al.*, 1993), a relatively diminished chromatic contrast sensitivity in the parvocellular pathway could result. Thus, at all temporal frequencies, parvocellular neurons might be more sensitive to chromatic contrast than are magnocellular neurons, yet a very low centrally imposed corner frequency for parvocellular signals, compared wih magnocellular signals, might result in magnocellular activity subserving contrast sensitivity at high temporal frequencies. In other words, it may be that, for infants, chromatic sensitivity at low vs high temporal frequencies is governed separately by parvocellular vs magnocellular activity, respectively.

A related possibility concerns the issue of intrinsic noise. In adult monkeys, parvocellular LGN neurons contain higher levels of intrinsic noise than do magnocellular neurons (Movshon *et al.*, 1994). Perhaps this magnocellular/parvocellular difference is exaggerated in infants, such that their parvocellular stream is subject to particularly high levels of intrinsic noise. This phenomenon might also result in magnocellular control of chromatic contrast detection.

Alternatively, the bandpass chromatic tCSFs we observed for infants could be controlled by *parvocellular* neurons in infants as they are in adults (cf. Morrone *et al.*, 1996). In this scenario, bandpass chromatic psychophysical tCSFs in infants could be explained if, unlike the case for adults, tCSFs for infant parvocellular neurons were themselves *bandpass* in nature for chromatic stimuli. Perhaps parvocellular tCSFs later become lowpass, with sensitivity increasing substantially more for low than for high temporal frequencies during the course of development. (It is unlikely that *luminance* tCSFs in infants are also subserved by *parvocellular* responses, since neurophysiological data have demonstrated that, in infants as in adults, magnocellular neurons are more sensitive to luminance contrast than are parvocellular neurons, e.g., Hawken *et al.*, 1997).

In any event, the differences we observed between infant and adult chromatic tCSFs lead us to predict that neural immaturities will be found in infant primates, such that either a single neural pathway subserves both chromatic and luminance contrast sensitivity, or a neural mechanism for chromatic sensitivity changes its tuning curve from bandpass to lowpass during development.

Implications for infant color vision

It has been argued that the responses of magnocellular neurons to isoluminant red/green stimuli convey information about the spatial and temporal locations of chromatic changes, but not about color *per se* (e.g., Dobkins & Albright, 1994, 1997). On the other hand, parvocellular responses are thought to convey information about color identity. Thus, we expect parvocellular rather than magnocellular activity to underlie the adult human capacity to identify and categorize stimuli on the basis of color differences. In the present paper, we have argued that magnocellular activity may underlie infants' tCSFs for both luminance and chromatic (red/green) temporally modulated gratings. Thus, we suggest that a demonstration of chromatic contrast detection may not necessarily constitute a demonstration of parvocellular-mediated color vision.

Many earlier experiments have shown that infants can respond to isoluminant chromatic differences (reviewed in Teller & Bornstein, 1987; Brown, 1990; Teller, 1997). Based on our arguments, it is possible that in some of these earlier experiments, infants may have been using magnocellular rather than parvocellular activity as the basis of chromatic discrimination. To pursue this notion, we here briefly review the prior work in infant red/green color vision (conducted in infants aged 2–4 months). We divide this work into three categories, presented in order of decreasing likelihood that the infants' chromatic discrimination performance depends on magnocellular activity, and hence in order of increasing likelihood that the chromatic discrimination reveals the presence of a functional parvocellular pathway.

In the first category are experiments that demonstrate infants' sensitivity to moving or counterphase flickering red/green stimuli (Allen *et al.*, 1993; Morrone *et al.*, 1993; Teller & Lindsey, 1993b; Brown *et al.*, 1995; Kelly *et al.*, 1997). Since these stimuli are quite similar to those

employed in the present experiment, and since frequency-doubled responses of magnocellular cells arise from such temporal modulation, it seems likely that magnocellular activity contributes to the infants' responses under these conditions.

In the second category are experiments that employ a stationary test field of one chromaticity embedded in an isoluminant surround of a second chromaticity (e.g., Peeples & Teller, 1975; Teller *et al.*, 1978; Hamer *et al.*, 1982; Packer *et al.*, 1984; Clavadetscher *et al.*, 1988). In this case, it is possible to argue that the motion of isoluminant chromatic edges across the retina, caused by the infants' eye and head movements, might produce transient responses in the magnocellular pathway sufficient to allow the infant to detect and stare at the embedded chromatic field. Although this possibility seems unlikely, it cannot be ruled out *a priori*.

In the third category are experiments that employ stimulus fields of varying chromaticity that are separated in space or time—for example, the stimulus displays used to date in habituation, preference, or conditioned learning paradigms (e.g., Bornstein, 1975; Oster, 1975; Schaller, 1975; Bornstein *et al.*, 1976; Adams & Courage, 1995). Under these conditions, it seems highly unlikely that stimulus fields of different chromaticities would give rise to differentiable magnocellular-based signals. Thus, this last category of experiments appears to be the most secure demonstration of the presence and use of parvocellular neurons for chromatic discrimination in infants.

With regard to the third category, we note that the apparent parvocellular-mediated color vision in young infants is not inconsistent with our proposal (based on the data presented herein) that the infants' parvocellular system is relatively immature, at least for temporally modulated stimuli. It may simply be that whereas the infants' parvocellular system is functioning at an early age, chromatic contrast sensitivity of the parvocellular system is inferior to that of the magnocellular system. In this scenario, magnocellular responses would underlie the infants' ability to detect the presence of moving or flickering chromatic stimuli *at threshold*, but parvocellular responses would also be available at higher chromatic contrasts and/or under other stimulus conditions. Such parvocellular responses would allow the infant to discern different colors. In sum, it will be of interest to sort out the extent to which infants rely on responses generated in parvocellular vs magnocellular neurons in making chromatic discriminations in various paradigms at different ages.

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