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Infant temporal contrast sensitivity functions (tCSFs) mature earlier for luminance than for chromatic stimuli: evidence for precocious magnocellular development?

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Abstract

In order to investigate the development of luminance and chromatic temporal contrast sensitivity functions (tCSFs), we obtained chromatic and luminance contrast thresholds from individual 3- and 4-month old infants, and compared them to previously obtained functions in adults. Stimuli were moving sinusoidal gratings of 0.27 cyc/deg, presented at one of five temporal frequencies: 1.0, 2.1, 4.2, 9.4 or 19 Hz (corresponding speeds: 3.8, 7.7, 15, 34, 69 deg/s). Previous studies, including our own, have shown that adult tCSFs are bandpass for luminance stimuli (peaking at 5–10 Hz), yet lowpass for chromatic stimuli (sensitivity falling at >2 Hz), and that the two functions cross one another near 4–5 Hz when plotted in terms of cone contrast. In the present study, we find that the shapes and peaks of the *luminance* tCSF in both 3- and 4-months-olds appear quite similar to those of adults. By contrast, *chromatic* tCSFs in infants are markedly different from those of adults. In agreement with our earlier report (Dobkins, K. R., Lia, B., & Teller, D. Y. (1997). *Vision Research*, *37*(19), 2699–2716), the chromatic function in 3-month-olds is rather flat, lacking the sharp high temporal frequency fall-off characteristic of the adult function. In addition, the luminance tCSF in 3-month-olds is elevated above the chromatic tCSF, and the two functions do not exhibit an adult-like cross-over within the range of temporal frequencies tested. By *4 months of age*, substantial development of chromatic contrast sensitivity takes place at the lowest temporal frequencies. Although still immature, the 4-month-old chromatic tCSF has begun to adopt a more adult-like shape. In addition, similar to adults, luminance and chromatic tCSFs in 4-month-olds cross one another near 5 Hz. In adults, magnocellular (M) and parvocellular (P) pathways are thought to underlie the bandpass luminance and lowpass chromatic tCSF, respectively (e.g. Lee, B. B., Pokorny, J., Smith, V. C., Martin, P. R., & Valberg, A. (1990). *Journal of the Optical Society of America* (*a*), *7*(12), 2223–2236). Based on this correspondence between psychophysical and neural responses in adults, our results suggest that the relatively slow development of the chromatic tCSF in infants may reflect immature chromatic responses in the P pathway and/or reliance on chromatic responses originating in the M pathway.

Keywords: Visual development; Temporal contrast sensitivity functions; Chromatic; Luminance; Parvocellular; Magnocellular

1. Introduction

In adults, temporal contrast sensitivity functions (tCSFs) differ for chromatic- and luminance-defined stimuli of low spatial frequency. Whereas luminance stimuli generally produce bandpass functions with a peak between 5 and 10 Hz (Robson, 1966; Kelly, 1971; Levinson & Sekuler, 1975; Burr & Ross, 1982; Anderson & Burr, 1985; Fiorentini, Burr & Morrone, 1991; Derrington & Henning, 1993; Gegenfurtner & Hawken, 1995; Dobkins & Teller, 1996a; Dobkins, Lia & Teller, 1997), chromatic stimuli generally yield lowpass functions with sensitivity declining sharply beyond about 2 Hz (Fiorentini et al., 1991; Mullen & Boulton, 1992; Derrington & Henning, 1993; Gegenfurtner & Hawken, 1995; Dobkins et al., 1997). When plotted in terms of cone contrast sensitivity, chromatic and luminance tCSFs cross near 4–5 Hz (Derrington & Henning, 1993; Gegenfurtner & Hawken, 1995; Dobkins et al.,

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1997, but cf. Metha & Mullen, 1996). Thus, adults are more sensitive to chromatic than luminance contrast for temporal frequencies below 4–5 Hz, and vice versa for higher temporal frequencies.

Although infants are far less sensitive to contrast than adults, it is known that the shape of the infant luminance tCSF is quite similar to that of adults, exhibiting a bandpass shape with a peak near 5–10 Hz (Swanson & Birch, 1990; Hartmann & Banks, 1992; Dobkins & Teller, 1996a; Rasengane, Allen & Manny, 1997). We have recently shown, however, that for red/green gratings, chromatic tCSFs differ vastly between 3-month-old infants and adults (Dobkins et al., 1997). Whereas adult chromatic curves fall in sensitivity by 10-fold (1 log unit) between 2 and 17 Hz, chromatic tCSFs in 3-month-olds exhibit at most a 1.6 fold (0.2 log unit) variation in sensitivity across this range of temporal frequencies. In this earlier study, infants were tested with *only* chromatic gratings, and results were compared to infant data previously obtained for luminance gratings (Dobkins & Teller, 1996a). Thus, comparisons were made across studies, using different infants and non-identical stimulus conditions (i.e. different mean luminances and chromaticities). In the present study, we obtained *both* chromatic and luminance thresholds from individual infant subjects, tested at one of five temporal frequencies. This within-subject design allowed us to directly compare the development of chromatic versus luminance tCSFs, as well as allowing us to investigate the existence of potential crossovers between the two functions, an issue that has yet to be addressed in the infant literature. In addition, the current study tested both 3- and 4-month-old infants, in order to follow the development of chromatic and luminance functions.

We are led to an interest in development of tCSFs as a potential way of tracking development of magnocellular (M) and parvocellular (P) pathways of the infant's visual system. In adults, the results from neurophysiological studies in macaque monkeys suggest that adult luminance tCSFs are subserved by activity within early stages of the M pathway, whereas chromatic tCSFs are subserved by activity in the P pathway (Lee, Martin & Valberg, 1989a; Lee, Pokorny, Smith, Martin & Valberg, 1990; Smith, Pokorny, Davis & Yeh, 1995). Unfortunately, neurophysiological data bearing on this topic in infant monkeys are extremely scarce, and for this reason psychophysical studies of chromatic and luminance tCSFs in infants may be a particularly valuable way of investigating the development of these visual pathways. In fact, recent psychophysical experiments investigating chromatic M:D (motion:detection) ratios in infants (Dobkins & Teller, 1996b; Lia, Dobkins, Palmer, & Teller, 1999) have provided evidence for the possibility that infant M, and not P, neurons might control chromatic detection thresholds, a situation that could arise if M neurons precede P neurons in the maturation of sensitivity.

In order to explore further the functional maturation rates for M versus P pathways in infants, we examined chromatic and luminance tCSFs in infants. The results of our experiments demonstrate that the shapes and peaks of the *luminance* tCSF in 3- and 4-month olds are quite similar to those of adults. By contrast, and confirming our earlier studies (Dobkins et al., 1997), we found that the *chromatic* tCSF of 3-month-olds is clearly *not* adult-like, i.e. the infant function lacks the high temporal frequency fall-off characteristic of the adult function. By 4 months of age, chromatic contrast sensitivity has improved substantially at all but the highest temporal frequency tested. Thus, the chromatic tCSF in 4-month-olds, while still not entirely mature in shape, begins to resemble that of adults.

Based on the link between chromatic tCSFs and P cell activity known to exist in adults, we propose that the relatively retarded development of the infant chromatic tCSF may reflect immature chromatic responses in the P pathway and possible reliance on chromatic responses originating in the M pathway. By 4 months, the advancement of the chromatic tCSF toward the adult signature may reflect development of chromatic contrast sensitivity in the P pathway.

2. Methods

2.1. Subjects

2.1.1. Infants

Male infants with a 25% or greater chance of dichromacy (based on family reports of incidences of color blindness on the mother's side) were excluded from the study. In addition, female infants with a 25% or greater chance of being a *carrier* for dichromacy were also excluded since their red/green color vision is unpredictable. (Specifically, it is known from adult studies that female carriers of dichromacy exhibit aberrant red/green luminance matches, e.g. Crone, 1959; Swanson, 1991.) All infants were born within 14 days of their due date and were reported to have uncomplicated births. A total of 58 *3-month-olds* and 56 *4-month-olds* participated in this study. Three 3-month-old infants and one 4-month-old failed to meet a minimum number of trials criterion ($n > 155$ trials). An additional four 3-month-olds failed to meet a minimum performance criterion (score of $> 85\%$ correct for the highest contrast stimuli). Data from these eight infants (7%) were not included in our analyses. Data from a total of 106 infants (51 3-month-olds and 55 4-month-olds) were retained. In this sample, 3-month-olds ranged from 84 to 98 days old on the first day of testing (average age = 89.0 days, S.D. = 3.3) and 4-month-olds ranged

from 118–132 days old (average age = 124.4 days, S.D. = 3.9). For all infants, testing was completed within a week.

2.1.2. Adults

Infant tCSFs were compared to those of adults (n = 6, ages 20–42) obtained from our previous study (Dobkins et al., 1997). Adult subjects were tested under nearly identical conditions to those of the present infant study (see below). To set the red/green stimuli for the infants of the present study, 24 adult subjects (ages 18–36) provided psychophysical red/green isoluminant points (see below).

2.2. Apparatus and stimuli

Stimuli were generated on a Nanao F2-21 monitor (1152 × 870 pixels, 75 Hz) driven by a PowerMac 7100 computer. The 8-bit video board allowed for 256 discrete levels of luminance. The CIE coordinates for the monitor primaries were: red (0.615, 0.342), green (0.282, 0.587), and blue (0.162, 0.069). 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), using a PR-650 Colorimeter (Photoresearch). The PR-650 was used for photometric measurements to standardize to V_λ isoluminance, as well as for spectroradiometric measurements to compute L and M cone modulations produced by our visual stimuli.

Stimuli were 0.27 cyc/deg horizontally-oriented sinusoidal gratings. 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, Braddick, & Moar, 1977; Banks & Salapatek, 1978) and because the effects of chromatic aberration are negligible below 1 cyc/deg (Flitcroft, 1989; Logothetis, Schiller, Charles, & Hurlbert, 1990; Cavanagh & Anstis, 1991). At a viewing distance of 38 cm, grating stimuli subtended 15 × 15° of visual angle (a total of four cycles) and were centered 15° to the left or right of screen center. The mean luminance of the display was 22 cd/m^2 with a mean chromaticity of 0.478, 0.425 in CIE color space. The illuminated portion of the video monitor subtended 59 × 45°.

2.2.1. Moving stimuli: temporal frequency and speed

Motion was produced by phase-shifting sinusoidal gratings at regular intervals in sync with the vertical refresh of the video monitor (75 Hz). Five different temporal frequencies were used: 1.0, 2.1, 4.2, 9.4, and 19 Hz (phase shift range = 5–90°). Because the spatial frequency was held constant (at 0.27 cyc/deg) the speed of moving stimuli necessarily covaried with temporal frequency. Corresponding speeds were: 3.8, 7.7, 15, 34, and 69 deg/s. To reduce the potential for optokinetic nystagmus (OKN), vertical motion was employed and counterbalanced by using upward and downward moving stimuli. Tracking or OKN eye movements were never observed in our subjects, as one would expect with relatively small, vertically moving stimuli (Hainline, Lemerise, Abramov, & Turkel, 1984; Hainline & Abramov, 1985; Schwarzbach & Schwartze, 1991). To avoid the intrusion of high temporal frequencies arising from an abrupt stimulus onset, stimulus contrast was ramped on, from zero to the specified contrast, in a sinusoidal fashion over the course of one motion cycle.

2.2.2. Chromatic (red/green) gratings

Chromatic red/green gratings were produced by sinusoidally modulating the red and green phosphors 180° out of phase, with a small amount of blue primary added in phase with the red portion of the grating so as to prevent modulation of the short-wavelength-sensitive (S) cones (Dobkins & Teller, 1996b). (S cone activation was approximately 0.003 units in MacLeod–Boynton chromaticity space (MacLeod & Boynton, 1979).)

We specify the chromatic contrast in the red/green grating in two ways. *Instrument contrast* refers to 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 phosphors. The benefit of converting to a cone contrast metric is that it standardizes across apparati and laboratories, and allows for the expression of chromatic and luminance contrast in comparable units (e.g. Mullen, 1985; Lennie & D'Zmura, 1988; Chaparro, Stromeyer, Huang, Kronauer, & Eskew, 1993; Derrington & Henning, 1993). Although our calibration techniques allowed us to request a specified amount of contrast, actual cone contrasts were confirmed for all chromatic stimuli using the PR-650 colorimeter. Cone modulations were computed by determining L and M cone excitations produced by the red and green peaks of our chromatic gratings, which were obtained by integrating the cross-product of stimulus spectral output of these stimuli by the Stockman, MacLeod and Johnson (1993) cone fundamentals. Based on these procedures, we calculate that full modulation between the red and green phosphors (i.e. 100% instrument contrast) produced modulations of 21.1 and 36.9% in the L and M cones, respectively. Thus, the root mean square cone contrast (r.m.s. = sqrt $[(M^2 + L^2)/2]$) was 27.5%.

2.2.3. Choice of isoluminance settings for infants

Red/green isoluminant stimuli were set for infants using mean isoluminance points determined for 24 adult subjects tested with motion photometry (Moreland, 1982; Teller & Lindsey, 1993b; Dobkins & Teller, 1996b). Adult subjects had normal color vision (as assessed by the Ishihara color plates) and no family history of color abnormalities. Subjects adjusted the luminance contrast (interval step = 0.5%) in a moving red/green grating (r.m.s. cone contrast = 7.2%) until the percept of motion was least salient. Isoluminance points were determined from the mean of twenty trials, separately for each of the five temporal frequencies used in this study. Across the population of 24 adult subjects, mean red/green isoluminant points were as follows: 1.0 Hz = −2.9% (S.D. = 1.5), 2.1 Hz = −0.17% (S.D. = 1.5), 4.2 Hz = 0.0% (S.D. = 1.6), 9.4 Hz = 0.3% (S.D. = 1.7), and 19 Hz = 0.1% (S.D./1.7), with respect to V_λ. These mean values were consequently used to set red/green isoluminance for infants tested under chromatic conditions.

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 highly similar red/green isoluminance points for infant and adult subjects (Maurer, Lewis, Cavanagh & Anstis, 1989; Teller & Lindsey, 1989; Morrone, Burr & Fiorentini, 1993; Bieber, Volbrecht & Werner, 1995; Brown, Lindsey, McSweeney & Walters, 1995). In our experiments, the variability across adults (in terms of S.D.) was $<1.6\%$ luminance contrast. Thus, we expect the amount of residual luminance contrast existing for infants (due to inter-subject variability) to be quite small. Because infants are typically not very sensitive to luminance contrast when tested behaviorally (e.g. Atkinson, Braddick & Braddick, 1974; Banks & Salapatek, 1981; Swanson & Birch, 1990; Hartmann & Banks, 1992; Teller, Lindsey, Mar, Succop & Mahal, 1992; Brown et al., 1995; Dobkins & Teller, 1996a), we expect such an error to have a minimal effect on the chromatic tCSF, an issue we return to in Section 4.1.1

2.2.4. Luminance (yellow/black) gratings

Luminance-defined gratings were produced by sinusoidally modulating the red and green phosphors in phase (with a small amount of blue gun also added in phase to match the mean chromaticity of 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. Although our calibration techniques allowed us to request a specified amount of contrast, the actual luminance contrast of all stimuli was verified using the PR-650 colorimeter.

2.3. Psychophysical paradigm

2.3.1. Infant procedure

Due 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 chromatic and luminance 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 on the left or right side of the video monitor (15° eccentricity), and the experimenter used cues such as the infant's head turning and gazing behavior to judge the left versus right location of the stimulus. To avoid the intrusion of high temporal frequencies arising from an abrupt stimulus onset, stimuli were ramped on slowly to their specified contrast (see above). Trials containing moving chromatic (isoluminant, red/green, cone contrast range = 3.5–27.5%) or luminance (yellow/black, cone contrast range = 1.5–86%) gratings were randomly interspersed throughout the experiment. Computer beeps provided feedback to the adult experimenter.

Four adult experimenters collected the infant data (author CMA and 3 assistants), all of whom were highly experienced in the FPL technique. Each experimenter tested approximately the same percentage of infants at each of the five temporal frequencies, and each temporal frequency group was balanced to include an approximately equal number of girls and boys. For 3-month-olds, data from 11, 10, 10, 10 and 10 infants tested at 1.0, 2.1, 4.2, 9.4 and 19 Hz, respectively, contributed to the results presented here (51 total subjects). The total number of trials obtained per 3-month-old ranged from 160 to 320, with an average of 224 trials/infant (112 trials per psychometric function). For 4-month-olds, data from 14, 10, 10, 11, and 10 infants tested at 1.0, 2.1, 4.2, 9.4, and 19 Hz, respectively, contributed to our results (55 total subjects). The total number of trials obtained per 4-month-old ranged from 160 to 285, with an average of 204 trials/infant (102 trials per psychometric function).

2.3.2. Adults

Adult data are taken from our previous study (Dobkins et al., 1997). Adults were tested on a mean yellow background of 18 cd/m^2 (CIE = 0.486, 0.421). Spatial frequency was 0.25 cyc/deg and temporal frequencies were: 0.7, 2.1, 5.6, 11, and 17 Hz. Note that these parameters are nearly identical to those of the present infant study. Contrast thresholds were obtained by standard forced-choice psychophysical techniques

with feedback. On each trial, a 16 × 16° moving stimulus (chromatic or luminance) appeared on the left or right side of the display and the subject reported its location. As for infants, eye position in our adult subjects was unrestricted and stimuli remained present on the screen until a decision was made. Unlike infants, each adult subject was tested at his/her individual red/green isoluminance point determined from motion photometry. Also, each adult subject was tested at all five temporal frequencies, presented in separate blocks.

2.4. Data analysis

2.4.1. Contrast thresholds and chromatic:luminance (C:L) sensitivity ratios

Psychometric curves were fit to infant data using Weibull functions and maximum likelihood analysis (Weibull, 1951; Watson, 1979). Upper asymptotes were fixed at 95% (which reflects the typical peak performance of infants in our laboratory) and contrast threshold was defined as the contrast yielding 72.5% correct performance (i.e. halfway between 50 and 95%). Although infant performance often reaches 90–95% correct for luminance stimuli (where cone contrasts of 100% are readily achievable), performance under chromatic conditions is often poorer due to the limited cone contrast attainable under these conditions (i.e. 100% instrument contrast = 27.5% r.m.s. cone contrast). In order to constrain the Weibull function (and thus improve the fit) under these relatively poor performance conditions, the slope parameter was fixed for all infant data sets. (Note that despite the potential for poor performance in the chromatic condition, data sets were retained as long as an infant performed at $>85\%$ correct on the most salient luminance gratings.) To increase the flexibility of this fixed slope method, as well as allow for inter-subject variability, two different fixed slope values (i.e. 1.0 and 2.0) were tried for each data set, and the threshold result from the fit that yielded the lowest error was retained. These fixed slope values were chosen based on results from unrestricted slope analyses for luminance data (e.g. Swanson & Birch, 1992; Brown et al., 1995; Dobkins & Teller, 1996a).

All thresholds were analyzed in terms of r.m.s. cone contrast. Contrast sensitivity was determined from the inverse of threshold (i.e. sensitivity = 1/threshold). In order to investigate the relative sensitivity to chromatic versus luminance stimuli (when equated via a cone contrast metric), a sensitivity ratio was determined for each subject (sensitivity ratio = $\text{sens}_{\text{Cromatic}}/\text{sens}_{\text{Luminance}}$, or $C{:}L$).

2.4.2. Temporal contrast sensitivity functions (tCSFS) and curve fitting

Chromatic and luminance tCSFs were obtained for all age groups by determining the geometric mean contrast sensitivity across subjects tested at the same temporal frequency. Curve fits to mean data were obtained by employing 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 (Kiorpes, Boothe, Hendrickson, Movshon, Eggers & Gizzi, 1987). These curves are of the form:

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

where ω is temporal frequency. The four 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.

3. Results

3.1. Psychometric functions

Representative psychometric functions from a 3-month-old subject tested under both chromatic and luminance conditions at 1.0 Hz are shown in the left panel of Fig. 1. Detection thresholds for this infant were 12.3% for luminance and 18.0% for chromatic gratings, resulting in a sensitivity ratio ($C{:}L$) of 0.68. Thus, this infant was found to be more sensitive to luminance than chromatic contrast. Data from a 4-

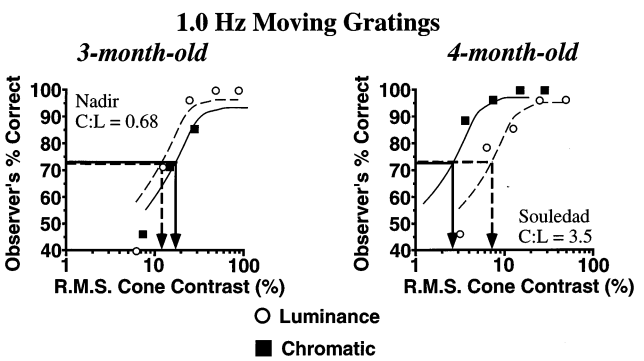

Fig. 1. Example psychometric functions from a *3-month-old* (left) and *4-month-old* (right) tested at 1.0 Hz. For both luminance (○) and chromatic (■) conditions, contrast is plotted in terms of r.m.s. cone contrast produced in L and M cones (see text). Contrast thresholds were obtained from Weibull functions fit to the data. In order to compare the relative sensitivity for the two types of contrast, a $\text{sens}_{\text{Chromatic}}/\text{sens}_{\text{Luminance}}$ ($C{:}L$) ratio was determined for each subject.

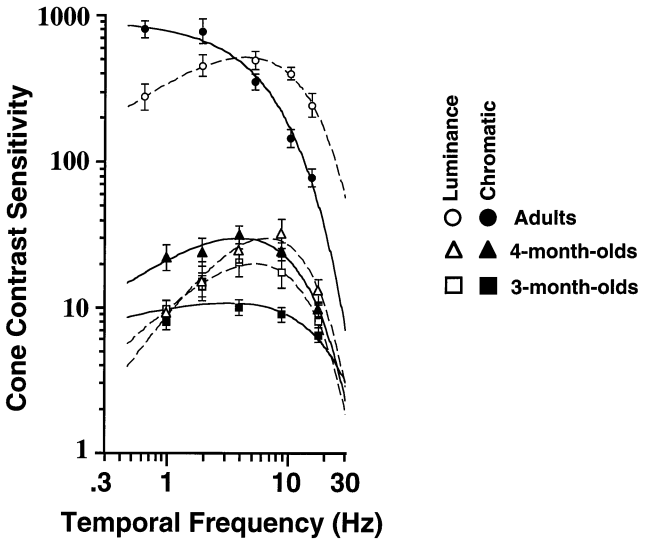

Fig. 2. Infant and adult temporal contrast sensitivity functions (tCSFs). Adults: Consistent with the literature, adults exhibit bandpass tCSFs for luminance gratings and lowpass tCSFs for chromatic gratings, and the two curves cross near 4–5 Hz. *3-month-olds:* Luminance tCSFs in 3-month-olds are bandpass, with a peak near 5 Hz, and are therefore quite adult-like in shape. By contrast, *chromatic* tCSFs in 3-month-olds are markedly different from those of adults. Specifically, whereas adult chromatic sensitivity falls by 10-fold (1 log unit) between 2.1 and 17 Hz, the chromatic function in 3-month-olds exhibits at most a 2.4-fold (0.37 log unit) variation in sensitivity across this range of temporal frequencies. In addition, unlike adults, the luminance tCSF in 3-month-olds is elevated above the chromatic tCSF, with no cross-over between the two functions. *4-month-olds:* At this age, substantial development of chromatic contrast sensitivity has taken place at all but the highest temporal frequency, suggesting maturation towards an adult-like shape. In addition, similar to adults, luminance and chromatic tCSFs in 4-month-olds cross one another near 5 Hz. Despite the trend of the 4-month-old chromatic tCSF towards the adult-like shape, however, the chromatic function at this age is clearly still immature, exhibiting only a 3.3-fold (or 0.5 log unit) variation across temporal frequency. Error bars denote standard errors of the means.

month-old subject tested under identical stimulus conditions are shown in the right panel of Fig. 1. Similar to others her age, this infant was more sensitive to chromatic than to luminance contrast at 1.0 Hz. Detection thresholds for this infant were 7.0 and 2.0% for luminance and chromatic gratings, respectively, and the resulting sensitivity ratio was 3.5.

3.2. Temporal contrast sensitivity functions (tCSFs)

Group mean tCSFs are shown for 3-month-olds ($n = 51$), 4-month-olds ($n = 55$) and adults ($n = 6$) in Fig. 2, for both luminance and chromatic gratings (3-month-olds, squares; 4-month-olds, triangles; adults, circles). The fitted curves show best fitting double exponential functions, the parameters and peak frequencies for which are presented in Table 1.

3.3. Adults

As expected, the adult luminance tCSF (○, dashed line) is bandpass with peak sensitivity occurring at 4.7 Hz. By contrast, the adult chromatic tCSF (●, solid line) is lowpass, again as expected, with sensitivity falling dramatically above 2 Hz. Plotted in terms of cone contrast, adult chromatic and luminance curves cross one another at 4.3 Hz (data from Dobkins et al., 1997). Although one might argue that it be more appropriate to test adults at a higher spatial frequency (since infants and adults differ by 4-fold in their peak spatial frequency, e.g. Kelly, Borchert & Teller, 1997), note that spatial frequency has little effect on this task; adult data obtained at 0.25 cyc/deg (in the present study) look nearly identical to adult data previously obtained at 1 cyc/deg (Derrington & Henning, 1993; Gegenfurtner & Hawken, 1995). For this reason, we deemed it unnecessary to re-test adults at 1 cyc/deg.

3.4. 3-month-olds

Data from 3-month-olds largely confirm previous studies. These results, however, have the added benefit of presenting chromatic and luminance tCSFs from the *same* infants. Here, the luminance tCSF (□, dashed line) is bandpass, with the results from the double exponential fit yielding a peak at 5.7 Hz. As we have emphasized in the past, the bandpass tCSF of 3-month-olds is quite similar in shape and peak temporal frequency to that of adults, although infant sensitivity is reduced by about 1.45 log units. By contrast, the infant *chromatic* tCSF (■, solid line) is markedly different in shape from that of adults in that the infant function lacks a sharp high temporal frequency fall-off. With regard to the *low* temporal frequency portion of the curve, it is more difficult to ascertain whether the infant chromatic tCSF is bandpass or lowpass (see Movshon & Kiorpes, 1988 for further discussion). While the double exponential fit yields a peak at 3.5 Hz (see Table 1), the fitted function appears rather flat at low temporal frequencies. Regardless of the exact nature of the infant chromatic curve at low temporal frequencies, the important point is that, unlike the infant luminance tCSF, the infant chromatic tCSF does not appear adult-like in shape. In addition, another noteworthy finding is that within the range of temporal frequencies tested, infants are more sensitive to luminance than chromatic contrast (average across temporal frequencies = 1.4 × or 0.20 log units), and chromatic and luminance tCSFs do not cross one another, except perhaps at temporal frequencies below 1 Hz.

Table 1
Double exponential curve-fit parameters[a]

	a	*b*	*c*	*d*	Peak t.f.	Res. error
Luminance						
3-month-olds	49.46	0.16	0.92	0.84	5.68	0.006
4-month-olds	62.56	0.21	0.80	1.19	7.03	0.030
Adults	1181	0.14	0.86	0.58	4.70	0.003
Chromatic						
3-month-olds	18.40	0.07	0.94	0.21	3.49	0.204
4-month-olds	70.00	0.15	0.90	0.58	4.22	0.020
Adults	936	0.20	0.79	0.00	0.05	0.067

[a] Results from a double exponential curve-fitting procedure to the tCSF data. 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 falloff), 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 luminance (yellow/black) and chromatic (red/green) gratings are presented separately.

3.5. 4-month-olds

Data from 4-month-olds yield a luminance tCSF (Fig. 2, △, dashed line) that is bandpass in nature and quite similar in shape to that of 3-month-olds and adults, with the exception that the 4-month-old peak appears shifted to a somewhat higher frequency (i.e. 7.0 Hz). Interestingly, the overall luminance performance of 4-month-olds is not much better than that of 3-month-olds (average increase across temporal frequency = 0.11 log units), a finding that is supported by our statistical analyses (see below). By contrast, chromatic performance in infants changes substantially between 3 and 4 months at the lower temporal frequencies, remaining relatively unchanged at the highest temporal frequency tested (average increase across temporal frequency = 0.34 log units). Thus, the chromatic tCSF of 4-month-olds (▲, solid line) appears to be adopting a high temporal frequency fall-off characteristic of the adult curve (although the double exponential fit nonetheless yields a peak at 4.2 Hz, see Table 1). Also, similar to adults, chromatic and luminance tCSFs in 4-month-olds cross one another at 5.7 Hz. Despite the similarities, however, the 4-month-old chromatic function is still not fully mature in shape.

3.6. Temporal resolution

In addition to characterizing the general shapes of infant tCSFs, these data allow us to investigate temporal *resolution*, which we define as the temporal frequency at half curve height. Note that this definition is somewhat unconventional, chosen because, given the limited data points we obtained, it is less prone to error than is determining the intersection of the function with the *x*-axis (i.e. the conventional definition). For luminance stimuli, temporal resolution was 24.4, 26.6, and 39.8 Hz, for 3-month-olds, 4-month-olds, and adults, respectively. Thus, there is a 1.6-fold increase in temporal resolution between 3 months and adulthood and a 1.5-fold increase between 4 months and adulthood. For chromatic stimuli, temporal resolution was 29.0, 23.3, and 21.8 Hz, for 3-month-olds, 4-month-olds, and adults, respectively, thus demonstrating little change in temporal resolution (and perhaps even a *reverse* developmental trend) under chromatic conditions. This seemingly mature temporal resolution for chromatic stimuli is quite surprising in light of the markedly immature shape of the infant chromatic tCSF, and perhaps can be reconciled by proposing that a putative luminance mechanism underlies the high temporal frequency portion of the chromatic tCSF, an issue we return to in Section 4.

3.7. C:L sensitivity ratios

In order to determine relative sensitivity to chromatic versus luminance contrast, sensitivity ratios (*C*:*L*) were determined for each subject, and then averaged across subjects tested at the same temporal frequency. Here, a ratio of 1.0 indicates that chromatic and luminance sensitivity are identical in terms of cone contrast. The effect of temporal frequency on sensitivity ratios is shown for all three age groups in Fig. 3. For both 4-month-olds and adults, C:L ratios are greater than 1.0 for temporal frequencies below 4–5 Hz, and less than 1.0 for higher temporal frequencies. By contrast, 3-month-olds exhibit *C*:*L* ratios below 1.0 across the range of temporal frequencies tested.

In particular, at the lowest temporal frequency (infants, 1.0 Hz; adults, 0.7 Hz), mean *C*:*L* ratios are 0.82, 2.42, and 2.91 for 3-month-olds, 4-month-olds, and adults, respectively. Thus, at low temporal frequencies, there is a *reversal* of the *C*:*L* ratio between 3 and 4 months of age, which reflects the fact that for low temporal frequencies, there is substantial improvement

in chromatic sensitivity yet little improvement in luminance sensitivity between these ages. At high temporal frequencies (e.g. infants, 19 Hz; adults, 17 Hz), a different pattern of results is seen. Here, mean sensitivity ratios are 0.81, 0.75, and 0.32 for 3-month-olds, 4-month-olds, and adults, respectively. Thus, at high temporal frequencies, all age groups are more sensitive to luminance than to chromatic contrast.

3.8. Statistical analyses

In order to evaluate statistically the effects of temporal frequency, stimulus type (i.e. chromatic vs. luminance) and the interaction between the two, we performed two-factor ANOVAs, separately for the different age groups. Infant analyses were a mixed design since each infant was tested with both chromatic and luminance gratings, yet only at one of five temporal frequencies. For 3-month-olds, we found a main effect of temporal frequency ($F(4, 46) = 3.75$, $P = 0.01$) as well as stimulus type ($F(1, 46) = 12.98$, $P < 0.001$). This effect of stimulus type reflects the fact that 3-month-olds are more sensitive to luminance than to chromatic contrast (by about $1.4\times$ or 0.20 log units, averaged across temporal frequencies). In addition, an interaction was found between temporal frequency and stimulus type ($F(4, 46) = 2.65$, $P = 0.045$), suggesting that, grossly speaking, the shapes of the chromatic and luminance tCSFs are different from one another.

Results from 4-month-olds were generally quite similar. At this age, there was a main effect of temporal frequency ($F(4, 50) = 6.30$, $P < 0.001$) and stimulus type ($F(1, 50) = 5.83$, $P = 0.02$). Opposite to 3-month-olds, the effect of stimulus type arose because 4-month-olds are overall more sensitive to chromatic than to luminance contrast (by about $1.3\times$ or 0.11 log units). Again, an interaction between temporal frequency and stimulus type was found ($F(4, 50) = 7.96$, $P < 0.001$), suggesting different shapes for chromatic versus luminance tCSFs. For *adults*, the two-factor ANOVA was a within-subjects design. Here, we found a main effect of temporal frequency ($F(4, 20) = 38.04$, $P < 0.001$) but not stimulus type ($F(1, 20) = 2.36$, $P =$ NS), and a significant interaction between the two ($F(4, 20) = 38.3$, $P < 0.001$).

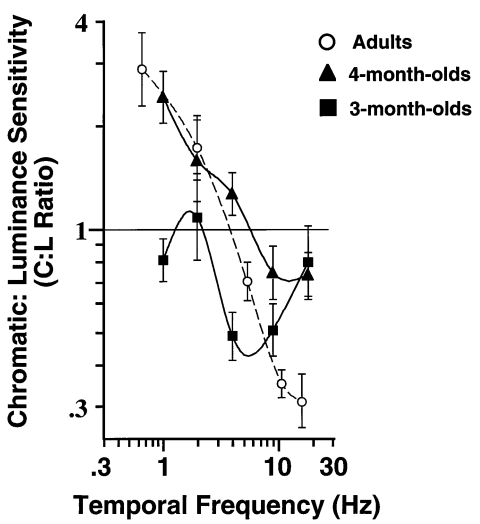

Fig. 3. Chromatic:luminance (C:L) ratios. Both adults and 4-month-olds exhibit C:L ratios greater than 1.0 for temporal frequencies below $\sim$4–5 Hz, and less than 1.0 for higher temporal frequencies. By contrast, 3-month-olds exhibit C:L ratios below 1.0 across the range of temporal frequencies tested. Thus, at low temporal frequencies, there is a *reversal* of the C:L ratio between 3 and 4 months of age. Error bars denote standard errors of the means.

A second set of analyses was performed to investigate changes between 3 and 4 months of age, separately for chromatic functions, luminance functions, and C:L sensitivity ratios. (Adults were not included in this analysis, due to differences in between vs. within subjects design.) To this end, two-factor ANOVAs were performed to look at the effects of age, temporal frequency and the interaction between the two. With regard to *luminance* data, there was a significant effect of temporal frequency ($F(4, 96) = 9.09$, $P < 0.001$). There was not, however, a significant effect of age ($F(1, 96) = 3.33$, $P =$ NS), indicating that there is little overall improvement in luminance sensitivity between 3 and 4 months of age (as can be observed in Fig. 2). As expected, there was no interaction between temporal frequency and age ($F(4, 96) = 0.797$, $P =$ NS), suggesting no change in the shape of the luminance tCSF between the two ages.

Under *chromatic* conditions, there was a significant effect of temporal frequency ($F(4, 96) = 8.05$, $P < 0.001$). Unlike the case for luminance stimuli, we found an effect of age ($F(1, 96) = 54.6$, $P < 0.001$), demonstrating significant improvement in chromatic contrast sensitivity between 3 and 4 months. Finally, no interaction was found between temporal frequency and age ($F(4, 96) = 1.910$, $P =$ NS), suggesting that, as for luminance tCSFs, there is little change in the *shape* of the chromatic tCSF between 3 and 4 months.

On the other hand, when a two-factor ANOVA was performed on C:L *sensitivity ratios*, we did find an interaction between temporal frequency and age ($F(4, 96) = 2.93$, $P = 0.025$), reflecting a change in the influence of temporal frequency on chromatic, relative to luminance, sensitivity as a function of age. (In addition, we found a main effect of temporal frequency ($F(4, 96) = 6.79$, $P < 0.001$) and age ($F(1, 96) = 18.6$, $P < 0.001$).) Thus, while neither the shape of the chromatic nor luminance curves alone differ significantly between 3 and 4 months, the shape of the sensitivity ratio versus temporal frequency curve does.

In sum, the results from these experiments demonstrate that the peaks and shapes of infant *luminance* tCSFs appear quite similar to those of adults (Fig. 2, dashed lines). By contrast, the peaks and shapes of

infant *chromatic* tCSFs are clearly different from those of adults, with a lowpass function dropping markedly at >2 Hz found only for adults (Fig. 2, solid lines).

4. Discussion

The goal of these experiments was to track the development of chromatic and luminance temporal contrast sensitivity functions (tCSFs) and to make direct comparisons between them. Our results demonstrate an earlier development of the luminance tCSF, as compared to the chromatic tCSF; whereas the luminance function is adult-like in shape by 3 months of age, the chromatic function is still quite immature at 4 months. These findings suggest that the neural mechanisms underlying temporal contrast sensitivity for chromatic stimuli develop relatively slowly.

These results are discussed in several contexts. First, we discuss our results in the context of earlier studies of chromatic and luminance tCSFs in infants and adults. With regard to chromatic stimuli, we address the potential contribution of residual luminance contrast in our chromatic red/green gratings. Second, we provide a further analysis of C:L sensitivity ratios. Comparisons of C:L ratios across different ages allow us to address the issue of uniform versus differential losses of chromatic, with respect to luminance, contrast sensitivity in infants. Third, we speculate on possible underlying neural mechanisms for the developmental time courses of luminance and chromatic tCSFs, and propose a simple physiological model of how activity in magnocellular (M) and parvocellular (P) pathways may account for our findings.

4.1. Development of temporal contrast sensitivity functions (tCSFs)

In adults, tCSFs obtained with low spatial frequency gratings are typically bandpass for luminance stimuli, with a peak between 5–10 Hz, and lowpass for chromatic (red/green) stimuli, with sensitivity declining rapidly at >2 Hz. When plotted in terms of a cone contrast metric, chromatic and luminance curves cross one another at around 4 Hz (Derrington & Henning, 1993; Gegenfurtner & Hawken, 1995). Interestingly, this pattern of results is maintained even when adults are tested under infant-like conditions (Dobkins et al., 1997, see upper set of curves in Fig. 2), suggesting that uncontrolled eye movements and extended viewing duration have little impact on the basic shape of tCSFs.

In accordance with previous infant psychophysical studies (Hartmann & Banks, 1992; Dobkins & Teller, 1996a; Rasengane et al., 1997, but cf. Teller et al., 1992), we find that the luminance tCSFs of 3- and 4-month-olds are bandpass in nature, with peaks near 5 Hz, and are thus quite similar in shape to those of adults. The mature shape of the infant luminance curve can be witnessed further by determining the difference between highest and lowest luminance sensitivity, which is approximately the same for all three ages groups (3-month-olds = 0.41 log units; 4-month-olds = 0.43 log units; adults = 0.31 log units). Thus, development of temporal contrast sensitivity between 3 months and adulthood 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).

Until recently, the shape of the infant *chromatic* tCSF was unknown. In accordance with our previous infant results (Dobkins et al., 1997), the present study found that the chromatic tCSF in 3-month-olds is quite different from that of adults, in that the infant curve lacks the severe high temporal frequency fall-off characteristic of the adult curve. More specifically, whereas adult chromatic sensitivity falls in sensitivity by 1.0 log unit between 2.1 and 17 Hz, the chromatic function in 3-month-olds exhibits at most a 0.37 log unit variation in sensitivity across this range of temporal frequencies. These chromatic tCSF results provide an important replication of our earlier study, with the exception that the chromatic function in the present study is flatter than before. In addition, the present study found no cross-over between chromatic and luminance functions in 3-month-olds, further emphasizing the immaturity of the chromatic tCSF at this age.

We also tested 4-month-olds in the present study. At this age, the chromatic tCSF has begun to adopt a more adult-like shape, which occurs due to a substantial increase in chromatic sensitivity at the lower temporal frequencies. Moreover, 4-month-olds exhibit a cross-over between chromatic and luminance functions near 5 Hz. Thus, like adults, 4-month-olds are more sensitive to chromatic than luminance contrast for low temporal frequencies, yet more sensitive to luminance contrast at higher frequencies (i.e. >4–5 Hz). Nonetheless, the shape of the chromatic tCSF is still not entirely mature in shape. Specifically, 4-month-olds exhibit a 0.5 log unit variation across the range of temporal frequencies tested, whereas adults exhibit a 1.0 log unit variation. Thus, unlike the case for luminance stimuli, it is clearly necessary to invoke changes in curve shape as well as changes in sensitivity to describe the development of chromatic tCSFs.

Interestingly, qualitatively similar results were found by Morrone and colleagues who reported VEP amplitude measures of infants' responsiveness to both luminance and chromatic plaid patterns at various temporal frequencies (Morrone, Fiorentini & Burr, 1996). Although not emphasized in their results, 3-month-olds and adults exhibited nearly identical amplitude variations in luminance responsivity across the range of temporal frequencies tested (2–20 Hz), whereas adult

chromatic functions varied 3-fold more in responsivity than those of 3-month-olds, a result qualitatively similar to those of our own. Although their use of suprathreshold stimuli did not allow for threshold-based measurements of tCSFs—and thus were likely to invoke multiple, as opposed to single, mechanisms—it is nonetheless encouraging to observe general similarities in the relatively retarded development of chromatic temporal contrast sensitivity between the two studies.

4.1.1. Potential contribution of residual luminance contrast in red/green gratings

Due to our use of the adult mean isoluminance point for infants, we expect that (based on inter-subject variability) some infants may have been presented with red/green gratings that also possessed a small amount of luminance contrast (see Section 2). In addition to these expected errors, based on variability in red/green isoluminance points across individuals, we must also consider the possibility of an error regarding our assumption that the mean red/green isoluminance point in adults is the same as that for infants. There are a variety of factors that could lead to differences in isoluminance points as a function of age. For one, although we employed a relatively high background luminance level (i.e. 22 cd/m^2), rod responses (if they exist) are likely to contribute more in infants than in adults, which would have the effect of introducing luminance contrast into red/green gratings. In addition to this possibility, other differences (see Banks & Bennett, 1988 for a review) include: optical media (clearer in infants than adults), lens and macular pigment (greater in adults than infants) and optical density (lower in infants than adults). The expected influence of these factors has been elegantly modeled (Knoblauch, Bieber & Werner, 1998), the results of which predict shifts in infant L- and M-cone action spectra that, in turn, predict a 12% difference between infant and adult red/green isoluminance points in the worse-case scenario (with infants requiring relatively more red). Despite this prediction, these same investigators present empirical evidence demonstrating that infant L- and M-cone action spectra are indistinguishable from those of adults (Bieber, Knoblauch & Werner, 1998). These findings, in conjunction with other reports that infant and adult isoluminance points are indistinguishable (e.g. Brown et al., 1995), suggest that the effects of pre-retinal factors and optical density, should they exist, are sufficiently small as to not be measurable by current techniques.

Nonetheless, in light of the potential for errors in red/green isoluminance, it is important to consider the potential contribution of residual luminance contrast to infants' chromatic responses. If infants used residual luminance information, our measured chromatic contrast sensitivities would be over estimations of performance. Consequently, infant chromatic curves would need to be adjusted by shifting downwards accordingly. We have simulated the effects of this type of confound by shifting the chromatic curve by both a constant amount and by differing amounts at different temporal frequencies (based on the known luminance contrast sensitivity at each frequency). Never do these adjusted curves appear anything like the adult chromatic tCSF. In fact, this manipulation serves to flatten the chromatic curves, making them even *less* adult-like in shape, and moreover, makes the potential for a cross-over between luminance and chromatic curves less likely. For this reason, we feel strongly that residual luminance contrast (had it existed) could not explain the immature nature, and slow development, of the infant chromatic tCSF.

4.2. Chromatic:luminance (C:L) sensitivity ratios: differential or uniform loss?

The *C*:*L* ratios obtained in our study bear upon a long-debated question in the infant literature, i.e. do infants exhibit *uniform* or *differential* losses of chromatic, with respect to, luminance sensitivity (e.g. Banks & Bennett, 1988; Brown, 1989; Teller & Lindsey, 1993a)? Equal *C*:*L* ratios across ages supports a uniform loss model, while a lower *C*:*L* ratio in infants compared to adults is evidence for a differential loss. To date, the majority of studies that have addressed this issue support a uniform or near-uniform loss (Allen, Banks & Norcia, 1993; Teller & Lindsey, 1993a; Brown et al., 1995; Dobkins & Teller, 1996b; Teller & Palmer, 1996; Kelly et al., 1997; Lia et al., 1999, but cf. Morrone et al., 1993; Crognale, Kelly, Weiss & Teller, 1998).

The *C*:*L* results of the present experiment demonstrate that uniform versus differential losses depend heavily on both the age of the infant as well as the specific temporal frequency tested (see Kelly et al., 1997 for a similar argument in the *spatial* frequency domain). Specifically, we find the most obvious differential loss for 3-month-olds tested below 4 Hz. By contrast, 4-month-olds exhibit a near-uniform loss of sensitivity at low temporal frequencies, as evidenced by *C*:*L* ratios similar to those of adults.

Interestingly, both 3- and 4-month-olds exhibit *precocious* chromatic contrast sensitivity at the two highest temporal frequencies tested (i.e. 9.2 and 19 Hz), as evidenced by *C*:*L* ratios that are *higher* than those of adults. One possible explanation concerns the potential for residual luminance contrast to have artificially elevated the estimate of chromatic sensitivity in infants (as mentioned above). When we simulate the effects of residual luminance contrast, the infant *C*:*L* curves get shifted slightly downward with respect to the adult curve. Even with this correction, however, the *C*:*L* ratio

at the highest temporal frequency still remains slightly higher in infants as compared to adults.

4.3. Possible underlying neural mechanisms

Data from macaque monkeys, whose visual system is very similar to that of humans, have demonstrated the existence of two distinct subcortical pathways—parvocellular (P) and magnocellular (M)—which originate in the retina and remain segregated in the lateral geniculate nucleus (LGN) and up through layer 4C of area V1 (see Merigan & Maunsell, 1993 or Dobkins & Albright, 1998 for a recent review). In adult macaques, neurons most sensitive to luminance contrast are found within the M division, while neurons most sensitive to red/green chromatic contrast are found within the P division (Shapley, Kaplan & Soodak, 1981; Derrington & Lennie, 1984; Kaplan & Shapley, 1986; Lee, Martin & Valberg, 1988; Lee et al., 1989a, 1990; Shapley, 1990; Kremers, Lee & Kaiser, 1992; Lee, Martin, Valberg & Kremers, 1993; Croner & Kaplan, 1995). For this reason, it is tempting to attribute detection of luminance and chromatic stimuli to the M and P divisions, respectively. As we have emphasized in the past (Dobkins & Albright, 1993, 1994; Dobkins & Teller, 1996b; Dobkins et al., 1997), however, it is important to bear in mind that both M and P cell types respond to *both* luminance and chromatic (isoluminant, red/green) stimuli, but with different contrast thresholds.

4.3.1. Adult neural mechanisms

As mentioned in Section 1, 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 the macaque. These temporal contrast sensitivity data (from Lee et al., 1989a, 1989b) have been replotted in Fig. 4 (upper left panel). Shown are the mean cone contrast sensitivities for M and P cells tested with both chromatic (isoluminant, red/green) and luminance stimuli over a range of temporal frequencies (1–40 Hz).

For M retinal ganglion cells, the luminance tCSF is bandpass, with a peak between 10–20 Hz. For chromatic stimuli, the tCSF of M cells is also bandpass, with a peak near 10 Hz. Although M cells are more sensitive to luminance than to chromatic contrast (by about 3.2-fold), the overall shapes and peaks of the chromatic and luminance tCSFs are quite similar. When these same experiments are conducted on P retinal ganglion cells, the luminance tCSF appears bandpass, with a peak between 10–20 Hz. 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 contrast (by about 7.6-fold). [Across pathways, P cells are 5-fold more sensitive to chromatic contrast than are M cells. Likewise, M cells are 5-fold more sensitive to luminance contrast than are P cells.] In sum, the luminance tCSF of M cells and the chromatic tCSF of P cells have similar shapes as psychophysically-obtained adult luminance and chromatic tCSFs, respectively, with the exception that the neural functions have a much higher cut-off frequency than the psychophysical data.

4.3.2. Adult model

In order to account for psychophysically-obtained tCSFs based on neuronal data, we used a model originated by Lee and colleagues. Specifically, we passed P and M cell data of Lee et al. (1989a) through 2nd-order lowpass filters, which are meant to reflect the effects of neural filters higher up in visual processing. The corner frequencies (CF) of these lowpass filters were adjusted separately for P and M signals such that the output functions fit the psychophysical functions [filter attenuation $= 1.0 - 1.0/\mathrm{sqrt}(1/(f/\mathrm{CF})^2)$]. The results of passing P signals through a 5 Hz corner frequency, and M signals through a 15 Hz corner frequency (for luminance) and 10 Hz filter (for chromatic[1]) are shown in Fig. 4 (lower panels). For luminance data (lower left panel), the filtered P and M curves are bandpass, with M signals clearly dominating at all temporal frequencies. For chromatic data (lower right panel), the filtered P and M curves produce a lowpass envelope, with P signals clearly dominating at low temporal frequencies (< 10 Hz), and P and M cells contributing perhaps equally at higher temporal frequencies. When the envelopes of the filtered chromatic and luminance neural curves are scaled upward by about 1.4 log units, they nicely superimpose upon our adult tCSF data (upper right panel). In sum, this simple model demonstrates how adult luminance tCSFs are served by activity within M cells, whereas adult chromatic tCSFs are served by P cells.

4.3.3. Infant neural mechanisms

Although neural data from infants are relatively scarce, the literature generally supports (although not without exception, e.g. Chalupa, Meissirel & Lia, 1996; Hickey, 1977) faster M pathway, with respect to P pathway, development (Mates & Lund, 1983; Lachica & Casagrande, 1988; Florence & Casagrande, 1990;

[1] Note that, to best fit our adult tCSF data, the M cell chromatic function had to be passed through a lower CF filter (10 Hz) than that used for the M cell *luminance* function (15 Hz). More filtering for M chromatic, as compared to M luminance, signals is physiologically plausible if, for example, phase variability across cells is greater for chromatic than for luminance responses generated in M cells.

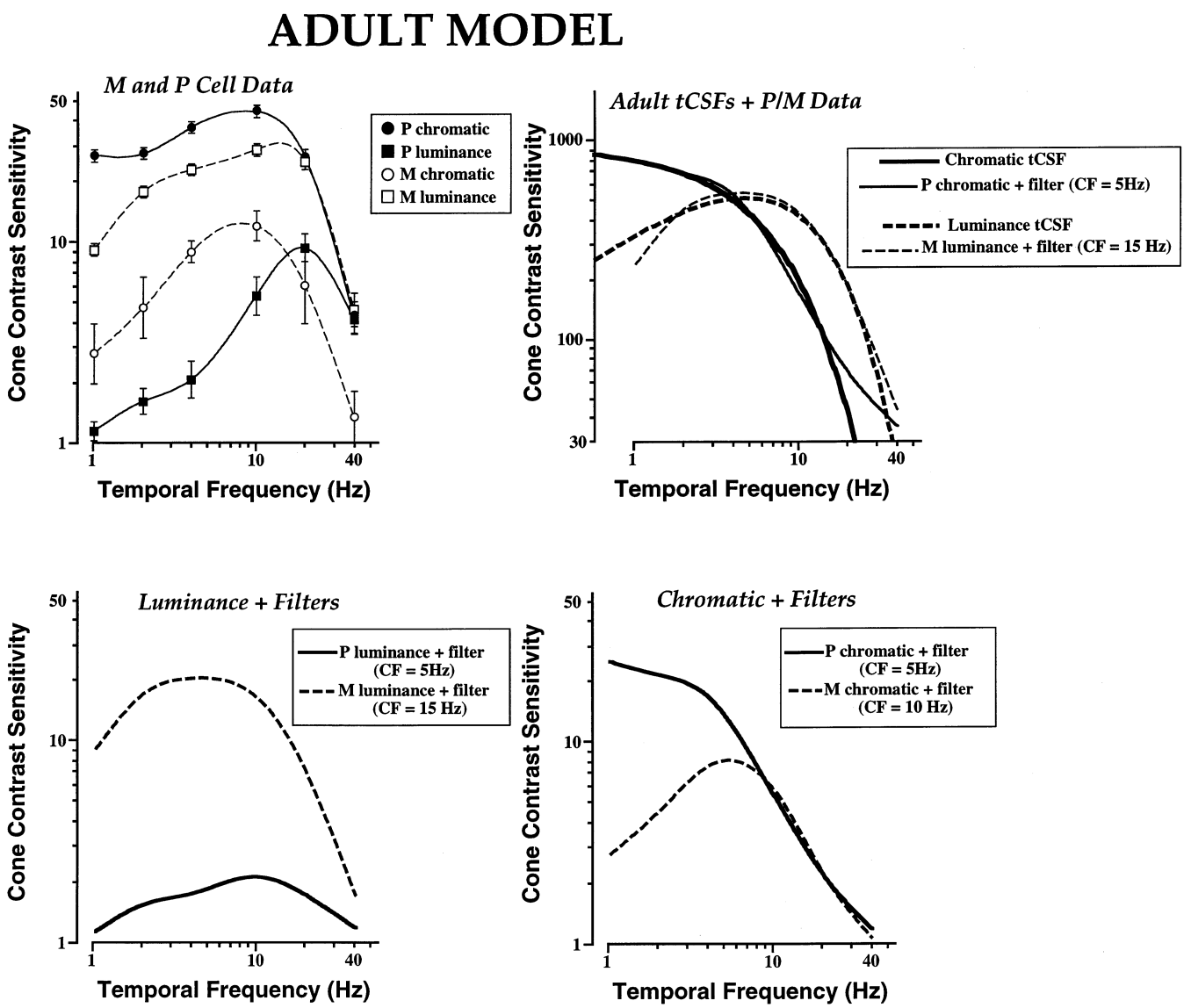

Fig. 4. Adult model. Mean cone contrast sensitivities are shown for adult P and M retinal ganglion cells tested with both chromatic (red/green) and luminance stimuli from 1 to 40 Hz (from Lee et al., 1989a, upper left). (Error bars denote standard errors of the means.) In order to model our adult tCSF data, we have passed the P and M neural functions through lowpass filters of different corner frequencies (CF), which are meant to reflect the effects of neural filters higher up in visual processing (lower panels). When the envelopes of the filtered chromatic and luminance curves are scaled upward by about 1.4 log units, they nicely superimpose upon our adult tCSF data (upper right). In sum, adult luminance and chromatic tCSFs obtained psychophysically can be modeled by activity within M and P pathways, respectively.

Lund & Harper, 1991; Lund & Holbach, 1991; Burkhalter, Bernardo & Charles, 1993; Pospichal, Florence & Kaas, 1994; Distler, Bachevalier, Kennedy, Mishkin & Ungerleider, 1996). Perhaps most relevant are recent findings from single-unit neurophysiological experiments performed in the LGN of 1–4-week-old infant macaque monkeys (using *luminance* stimuli only). These studies found that temporal resolution and peak temporal frequency in M cells are nearly adult-like by 4 weeks (an age which is comparable to a 4-month-old human). By contrast, P cell temporal resolution is still quite immature, differing from adult values by about 3-fold (Movshon, Kiorpes, Hawken, Skoczenski, Cavanaugh & Graham, 1997). In addition, as for adults, infant monkey M cells are more sensitive to luminance contrast than are P cells (in accordance with earlier reports, Hawken, Blakemore & Morley, 1997). Thus, this precocious M cell temporal resolution can support the adult-like shape of the infant luminance tCSF revealed psychophysically.

In light of the relatively limited amount of data on M and P functional maturation, infant psychophysical studies may be a particularly valuable tool for accessing the relative development of these two pathways. In fact, we have previously made the argument, on psychophysical grounds, that contrast sensitivity in the infant M

pathway may develop faster than that of the P pathway (Dobkins & Teller, 1996b). In these studies, we used a motion:detection (M:D) paradigm to quantify chromatic and luminance input to motion processing in infants and adults. 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, 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 (but cf. Lia et al., 1999 for slightly different results under *quadrature* motion conditions), 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 (Merigan & Maunsell, 1990; Maunsell, Nealey & DePriest, 1990), 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. In the past, we have proposed that such a situation could arise if M cell contrast sensitivity develops faster than that of P cells.

4.3.4. Infant model

Given the known relationship between P and M cell responses and tCSFs in adults, it may be possible, in an inverse fashion, to predict the tuning and absolute sensitivities of infant P and M cells based on infant psychophysically-obtained chromatic and luminance tCSFs. A simple model of P and M cell development that may account for the luminance and chromatic tCSFs observed in 3-month-olds is presented in Fig. 5. Here, we plot hypothetical infant P and M response curves using the same lowpass-filtered neural functions employed in the adult model, with the exception that the infant data are plotted in terms of relative sensitivity. Under luminance conditions (left panel), the infant

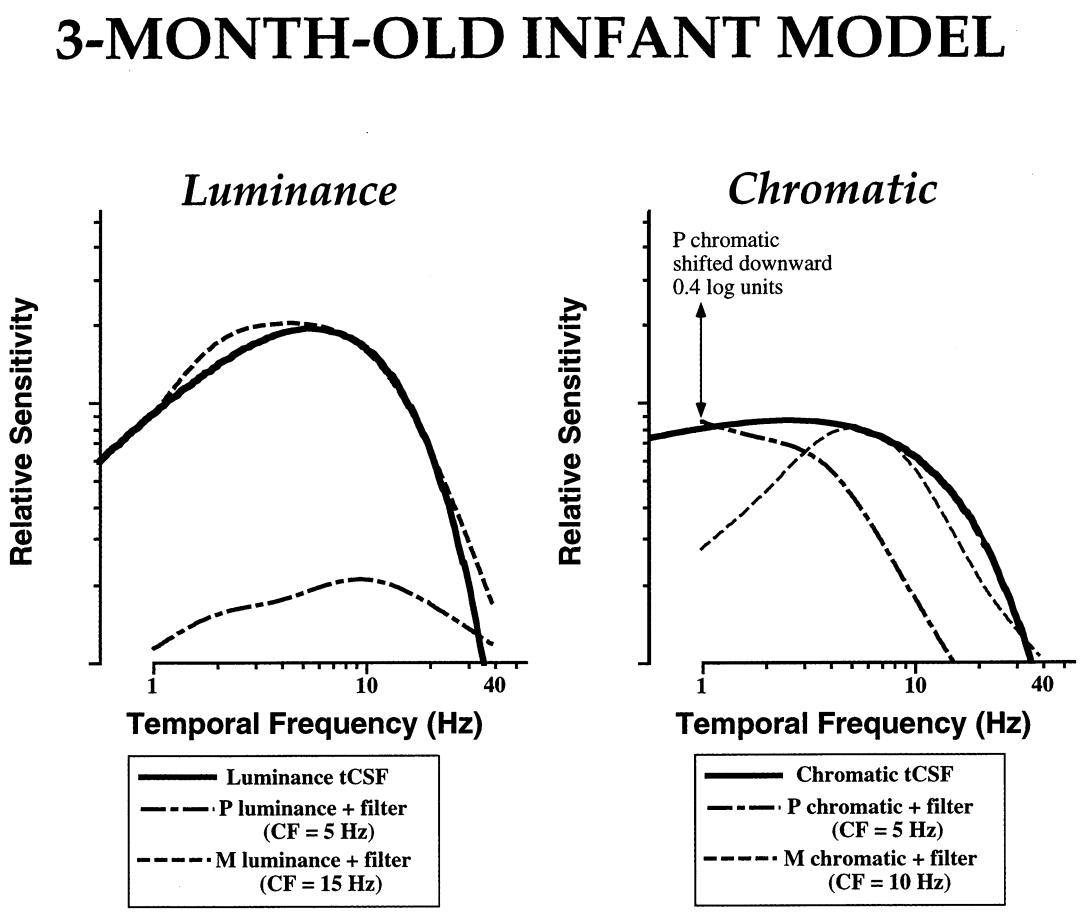

Fig. 5. 3-month-old infant model. Here, we plot hypothetical infant P and M neural functions using the same lowpass-filtered cell responses used in the adult model. Under *luminance* conditions (left panel), the infant psychophysical tCSF nicely corresponds to the filtered M cell envelope, without requiring a shift of the (adult) M cell peak to lower temporal frequencies. Under *chromatic* conditions, we have downwardly-shifted the P cell filtered response function, with respect to the M cell function, by a factor of 0.4 log units (right panel). Here, P cells are superior to M cells at the lowest temporal frequencies (i.e. < 3 Hz), yet inferior to M cells at higher temporal frequencies. In this scenario, the chromatic tCSF of 3-month-olds is well fit by the upper envelopes of P and M functions. Thus, the infant chromatic tCSF revealed psychophysically can be modeled by proposing a relatively retarded development of chromatic responses in P cells.

tCSF nicely corresponds to the filtered M cell envelope, without requiring a shift of the (adult) M cell peak to lower temporal frequencies. This mature shape of the infant M cell function predicted by the model is consistent with results from infant monkey neurophysiological studies demonstrating relatively adult-like temporal resolution in M cells by 4 weeks of age (Movshon et al., 1997).

In order to model the chromatic tCSF of 3-month-olds, we have downwardly-shifted the P cell chromatic response function, with respect to the M cell function, by a factor of 0.4 log units (right panel). In this scenario, there is a larger loss of P cell chromatic sensitivity with respect to M cell sensitivity, but P cell chromatic sensitivity is nonetheless superior to that of M cells at the lowest temporal frequencies (i.e. 1–2 Hz). By contrast, at greater than $\sim$3 Hz, M cells are superior to P cells and thus M cells are expected to underlie chromatic detection at these higher temporal frequencies. Under these conditions, the infant chromatic tCSF (bold curve) is well fit by the upper envelopes of filtered P and M functions. In this sense, the infant chromatic curve may reflect a hybrid of lowpass P responses and bandpass M responses. Thus, the infant chromatic tCSF revealed psychophysically can be modeled by proposing a relatively retarded development of chromatic sensitivity in P cells, such that infant M cells underlie chromatic sensitivity at temporal frequencies above $\sim$3 Hz. The model also predicts that as the P cell function elevates in sensitivity, it will eventually dominate at higher temporal frequencies. Finally, another feature of the model is that infant C:L ratios (obtained at frequencies $\sim$ $>$3 Hz) derive from a *single* (magnocellular) mechanism (unlike adult C:L ratios, which derive from separate P and M mechanisms). This difference could potentially underlie the somewhat surprising finding of *higher* C:L ratios in infants as compared to adults at high temporal frequencies (see Fig. 3).

4.3.5. Other potential underlying mechanisms

It is important to point out that the model depicted in Fig. 5 is only one of several possibilities. For example, in our model, we passed the infant M and P cell signals through lowpass filters identical to those used for adults, thereby assuming mature *cortical* filters in infants. An alternative model might predict comparable developmental rates of sensitivity in M and P cells, yet greater loss of P, with respect to M, signals at the *cortical* level. For example, the signals generated from P cells may be subject to far more central lowpass temporal filtering in infancy than in adulthood. Thus, in our model, had we not shifted the sensitivity of the P cell function, but simply passed it though a very stringent lowpass filter (e.g. with an extremely low corner frequency), a reasonable fit to the psychophysical data may have resulted.

Another possibility concerns the issue of intrinsic noise. In adult monkeys, parvocellular LGN neurons contain higher levels of intrinsic noise than do magnocellular neurons (Movshon, Hawken, Kiorpes, Skoczenski, Tang & O'Keefe, 1994). Perhaps this M/P difference is exaggerated in infants, such that infant P neurons are subject to particularly high levels of intrinsic noise (although recent data do not seem to support this notion—J.A. Movshon, personal communication). A related possibility concerns the potential for enhanced phase variability in infant P cell chromatic responses compared to that observed in adult P cells (Lee, Martin & Valberg, 1989b; Lee et al., 1990), which would serve to degrade the signal through convergence downstream. Phenomena of this sort could also result in magnocellular control of chromatic contrast detection, even if the signals from P cells early on in visual processing are more sensitive to chromatic contrast than are M cell signals.

Finally, it is also conceivable that the chromatic tCSF we observed for infants could still be subserved by *P* cells in infants (as in adults) if infant P cells are more sensitive than M cells at all temporal frequencies yet the P cell tCSF is immature in *shape*. In this scenario, P cell functions may start out somewhat flat with a sharp high temporal frequency fall-off developing later in time. If this were the case, however, we would nonetheless assert that development of temporal contrast sensitivity in the P pathway is slowed relative to that of the M pathway.

4.4. Summary

In adults, magnocellular (M) and parvocellular (P) pathways are thought to underlie the bandpass luminance and lowpass chromatic tCSF, respectively (Lee et al., 1989a, 1990; Smith et al., 1995). Given the known relationship between P and M cell responses and tCSFs in adults, it may be possible to model the tuning and absolute sensitivities of infant P and M cells based on infant psychophysically-obtained chromatic and luminance tCSFs. The basic proposal of our model is that the relatively retarded development of the infant chromatic tCSF revealed psychophysically reflects immature chromatic responses in the P pathway and thus partial reliance on chromatic responses originating in the M pathway. By 4 months, the advancement of the chromatic tCSF toward the adult signature may reflect development of chromatic sensitivity in the P pathway.

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