Spatial and temporal aspects of infant color vision

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Abstract

The present paper constitutes a review of the literature on young infants' chromatic discrimination capabilities. A series of early studies showed that infants as young as two months postnatal can make at least some chromatic discriminations between stationary, homogeneous fields of different wavelength compositions. Current studies of spatial and temporal contrast sensitivity functions (CSFs) for red/green isoluminant stimuli suggest that spatial chromatic CSFs show developmental changes in sensitivity and spatial scale, but not curve shape; while temporal chromatic CSFs (tCSFs) show developmental changes in sensitivity and curve shape, but not temporal scale. Infants can also code the direction of motion of moving isoluminant red/green gratings, for both continuous and quadrature motion. The possible mechanisms that underlie infants' chromatic discriminations are discussed. © 1998 Elsevier Science Ltd. All rights reserved.

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1. Introduction

An organism can be said to have color vision if it can discriminate between two stimuli of different wavelength composition, on the basis of the difference in wavelength composition alone. Historically, it has been easy to show that infants can respond differentially to a pair of objects of different colors. But most early studies were confounded by the 'brightness problem'; that is, by the problem that the infant's spectral luminous efficiency function was unknown, and there was no canonical way to equate the brightnesses (or luminances) of the two objects a priori. Thus, any differential responding might have been mediated by brightness (or luminance) differences rather than by wavelength differences per se.

In the mid 1970s, experimental paradigms that convincingly rule out brightness artifacts were developed independently in several laboratories ([1–5]; for critical reviews, see refs. [6,7]). Since that time, much has been learned about infants' photopic spectral luminosity functions and infants' capacity to make chromatic discriminations.

In the present paper, we review four groups of studies. In the first group, the range of chromatic discriminations that infants can make, and the times of onset of chromatic discriminations, are explored. In the second group are several studies of infants' photopic spectral luminous efficiency functions, showing that infants' photopic functions are highly similar to those of adults. The third group of studies concerns spatial and temporal contrast sensitivity functions in infant subjects, tested at adult isoluminance. The fourth group of studies shows that infants can code the direction of motion of moving red/green isoluminant stimuli, and explores paradigms that refine the study of direction-of-motion coding[1].

The capacity to make chromatic discriminations is served by the presence of three photoreceptor types, the long- (L), mid- (M) and short- (S-) wavelength-sensitive cones. Psychophysical theory suggests that signals from the three cone types are recombined in precortical visual processing to form a luminance channel and two chromatic channels, red/green and tritan [8]. At the physiological level, two major cell types and pathways

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[1] A fifth current issue, concerning whether infants show a uniform or a differential loss of sensitivity to luminance versus chromatic contrast, has been discussed extensively elsewhere [23,36,54].

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have been identified in early visual processing: the magnocellular (M) and parvocellular (P) pathways. In the simplest case—the detection of temporal modulation—the M pathway probably provides the detection of luminance modulation, and the P pathway the detection of chromatic modulation. However, under other conditions both M cells and P cells respond to both luminance modulation and chromatic modulation, and the more general mappings between psychophysically defined detection channels and physiologically identified neural pathways is not yet fully understood (for recent reviews see refs. [9,10]). In the final section of the present paper, we explore the degree to which the data on infant color vision shed light on psychophysical or neural mechanisms.

2. Chromatic discriminations with homogeneous stationary fields

In the chromatic discrimination paradigm most extensively used in later studies, Peeples and Teller [1] embedded a red field in a white surround. Using a forced-choice preferential looking (FPL) technique [11], they tested individual 2-month-old infants with each of a series of luminances of the red test field, centered around the adult red/white brightness match, but extending 0.4 log units above and below it in steps smaller than the infant's Weber fraction for luminance differences, as measured in situ. Each individual infant responded above chance at all luminances of the red field, including by inference that infant's brightness match, and thus infants were shown to have some form of color vision.

Using the Peeples and Teller paradigm, Teller et al. [12] tested 2-month-olds with a wide range of chromatic stimulus fields embedded in white surrounds. The Teller et al. data, replotted from the original stimulus specifications, are shown in MacLeod and Boynton [13] coordinates in Fig. 1. The infants discriminated broad-band reds, oranges, blue-greens and blues from a white surround, but failed in two regions centered in the yellow/green and mid-purple. The dashed line in Fig. 1 outlines the failure zone for the population of infants studied.

A series of studies using the Peeples and Teller paradigm was subsequently carried out using spectral stimuli, on infants 1–3 months of age. These studies included tests of infants' capacities to make Rayleigh discriminations and tritan discriminations, and thus were intended to probe for the presence of the red/green and tritan channels. The majority of 2-month-olds succeeded at both Rayleigh discriminations [14–16] and tritan discriminations [16,17]. In general, the majority of 1-month-olds failed to demonstrate chromatic discriminations with this paradigm, with the

possible exception of discriminating long wavelength (red) lights from those of other spectral compositions ([16]; but cf [18,19] using other testing paradigms). Larger field sizes enhance infants' chromatic discrimination performance [15,18].

The failure zone seen by Teller et al. [12] is suggestive of a tritan deficiency. Although later studies with monochromatic stimuli show that 2-month-olds can make tritan discriminations [16,17], we have also seen more recently that tritan modulations through white on a video monitor are difficult for infants to detect (Dobkins and Teller, unpublished obsrvations). The issue of when, how well, and with what mechanisms infants make discriminations among tritan stimuli is not yet well understood (reviewed in ref. [20]).

The responsiveness of infants 2 months and older to red/green chromatic differences, on the other hand, is well established. In addition to the earlier studies with homogeneous fields, studies of spatial and temporal contrast sensitivity functions (CSFs and tCSFs respectively), and direction-of-motion coding for red/green isoluminant gratings, have recently been undertaken with a variety of techniques. All of these studies, which will be reviewed below, show that the infant's visual system responds to red/green chromatic differences by 2 months postnatal.

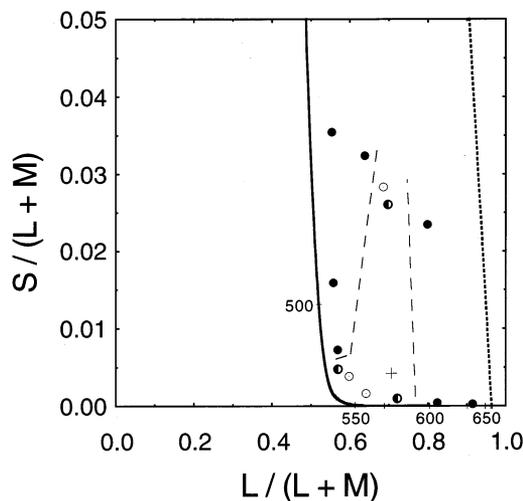### Data from Teller, Peeples & Sekel, 1978

Fig. 1. Chromatic discriminations in 2-month-old infants (from ref. [12]), replotted in MacLeod and Boynton [13] chromaticity space. The solid line shows the spectrum locus, with numbers indicating the locations of monochromatic stimuli from 500 to 650 nm. The dotted line connects the spectral extremes. Circles show the chromaticities of the stimuli, each tested against a white background (cross). Closed circles show successful discriminations; open circles show discrimination failures; and half-filled circles show cases in which some infants succeeded while others failed. The dashed line encloses all cases of discrimination failure. The failure zone encompasses a vertical line, suggesting the possibility of a failure of tritan discrimination.
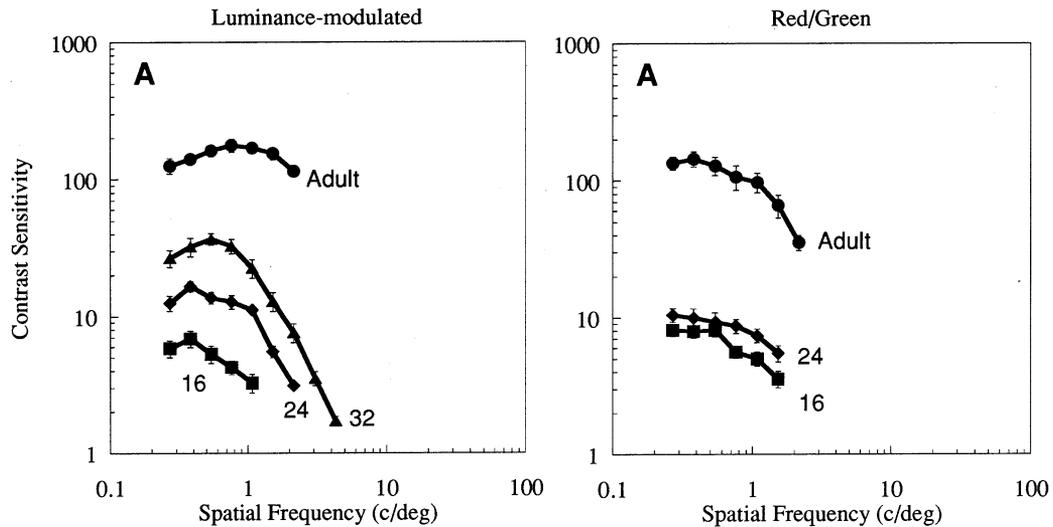
Fig. 2. Behaviorally measured CSFs for stationary gratings. (A): luminance-modulated gratings, in 16-, 24-, and 32-week infants, and adults (replotted from ref. [32]). (B): red/green isoluminant gratings in 16- and 24-week infants, and adults (replotted from ref. [35]).

3. Spectral luminous efficiency functions

Early studies of infants' sensitivity to lights of different wavelengths suggested that infant and adult spectral sensitivity functions are generally similar [6]. More recently, spectral luminous efficiency functions have been studied in 1- to 3-month-olds with techniques closely analogous to those used in adult subjects. Both motion nulling [21–23] and VEP-based flicker photometry [24] suggest a close similarity between infant and adult photopic spectral luminosity functions, especially in the mid to long wavelength region of the spectrum. The fact that infant Weber fractions are much larger than those of adults also suggests that small luminance differences between chromatic fields should not be detectable to infants.

These recent demonstrations of highly similar spectral luminosity functions in infants and adults have led to a change in the paradigm for testing infant chromatic discriminations. Rather than using systematic variations in relative luminance, as in the Peeples and Teller paradigm, it is now becoming standard practice to test infants just with chromatic fields that are set to adult isoluminance. The isoluminance criterion varies from study to study, but is typically the average flicker or minimum motion settings of adults in the apparatus used to test infants, under stimulus conditions as similar as possible to those used in the infant experiment. This shortcut, although adopted with some trepidation, makes it possible to test each infant on several spatial or temporal frequencies, and allows a much more rapid accumulation of data. In a few of the studies cited below, however, systematic variations of relative luminance have still been undertaken [20,25–27].

4. Spatial and temporal contrast sensitivity functions at (adult) isoluminance

Several recent studies have been concerned with describing infants' CSFs and tCSFs at adult isoluminance. We organize these studies around the question of whether, with respect to adults' functions, infants' functions are shifted vertically (in sensitivity), and/or horizontally (in spatial or temporal scale); and/or whether a change in curve shape, beyond shifts in sensitivity and scale, occurs during visual development [28]. In all cases, we have replotted the original data to a common scale and aspect ratio, and fitted the points with straight lines. Curvilinear fits and statistical analyses can be found in the original papers.

4.1. Spatial contrast sensitivity functions

When stationary luminance-modulated stimuli are used, adult CSFs are classically bandpass in shape. When human or monkey infants are tested behaviorally with these stimuli, similar bandpass functions are usually seen, but shifted downward in sensitivity and leftward in spatial scale [28–32]. There is also evidence from individual differences analyses that the underlying spatial channels, like the CSF as a whole, shift in spatial scale as well as in sensitivity during development [32,33]. Data from Peterzell et al. [32] are shown in Fig. 2(A).

When adult subjects are tested with stationary red/green isoluminant stimuli, CSFs are typically low-pass rather than bandpass in shape [34]. A similar lowpass function has been found recently in our laboratory in 16- and 24-month-olds as well as in adults [35]. Data
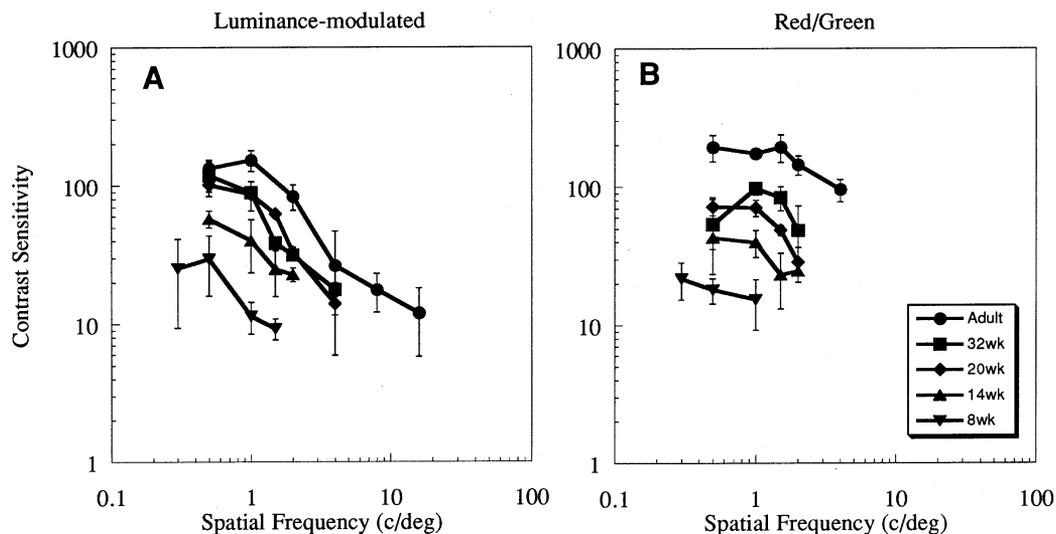
Fig. 3. CSFs for counter-phased gratings tested with VEP methods. (A): luminance-modulated gratings. (B): red/green isoluminant gratings. Ages: 8, 14, 20 and 32 weeks, and adults. (Replotted from ref. [36]).

from this study are shown in Fig. 2(B). Changes in sensitivity are evident. Although the data are not very powerful in this regard, similar lowpass curves will fit both infant and adult chromatic data. Changes in spatial scale are not obvious by eye; however, preliminary analyses suggest that the best-fitting curve for infants is shifted leftward on the spatial frequency axis for very young infants with respect to adults. Moreover, individual differences analyses suggest that, as in the case of luminance-modulated stimuli, the underlying spatial channels shift in spatial scale during development [35].

In addition to the behavioral studies of stationary gratings, two visual evoked potential (VEP) studies of CSFs for counter-phasing, luminance-modulated and red/green chromatic gratings have been published recently [25,36]. In adults, the use of counter-phasing stimuli typically leads to lowpass functions for both luminance-modulated and chromatic stimuli. In accord with this rule, the infant VEP studies also show lowpass CSFs for both luminance-modulated and chromatic stimuli. In both studies, a curve of a single fixed lowpass shape, shifting in sensitivity and spatial scale, is sufficient to fit both luminance and chromatic data at all ages. In both studies, at each age, absolute sensitivities to luminance-modulated and chromatic gratings are similar (although probably not identical) in cone contrast terms; and the shifts in spatial scale with age are also similar (and perhaps identical) for both kinds of stimuli. The data from Kelly et al. are shown in Fig. 3.

Thus, studies of spatial CSFs from a variety of techniques and laboratories give converging outcomes to date. Within a fixed stimulus paradigm and response measure, the data at all ages can be fit with curves of a fixed shape, shifting upward in sensitivity and rightward in spatial scale. We note, however, that support

for the constancy of curve shape across age for chromatic stimuli is not particularly powerful at this stage. In particular, the most extensive data come from VEP studies, in which all CSFs, for both luminance-modulated and red/green stimuli, are low-pass. More powerful tests of the constancy or non-constancy of curve shape would be provided by stimulus conditions in which a greater variety of curve shapes are observable.

4.2. Temporal CSFs (tCSFs)

In adults, studies of tCSFs for low spatial frequency stimuli typically yield bandpass functions for luminance-modulated stimuli and more nearly low-pass functions for chromatic stimuli [37]. Infants' tCSFs for luminance-modulated gratings have been studied by several groups of investigators [38,39]. tCSFs for low spatial frequency red/green stimuli have been studied recently in 3-month-olds by Dobkins et al. [40,41]. Combined data from Dobkins and Teller [39] and Dobkins et al. [40] are shown in Fig. 4.

For adult subjects, these data confirm earlier results in showing bandpass functions for luminance-modulated stimuli and lowpass functions for chromatic stimuli. For infants, luminance-modulated stimuli also yield a bandpass function, differing from the adult function only by a change in sensitivity, with no evidence of a change of curve shape or temporal scale. For chromatic stimuli, surprisingly, the shape of the infants' tCSF does not match the lowpass data of the adults; but is instead bandpass, like the data for luminance-modulated stimuli. Thus, a change of curve shape during development is found for red/green stimuli, but not for luminance-modulated stimuli. Despite the change in curve shape, no change in temporal scale is seen (see Table 1 in [40]).
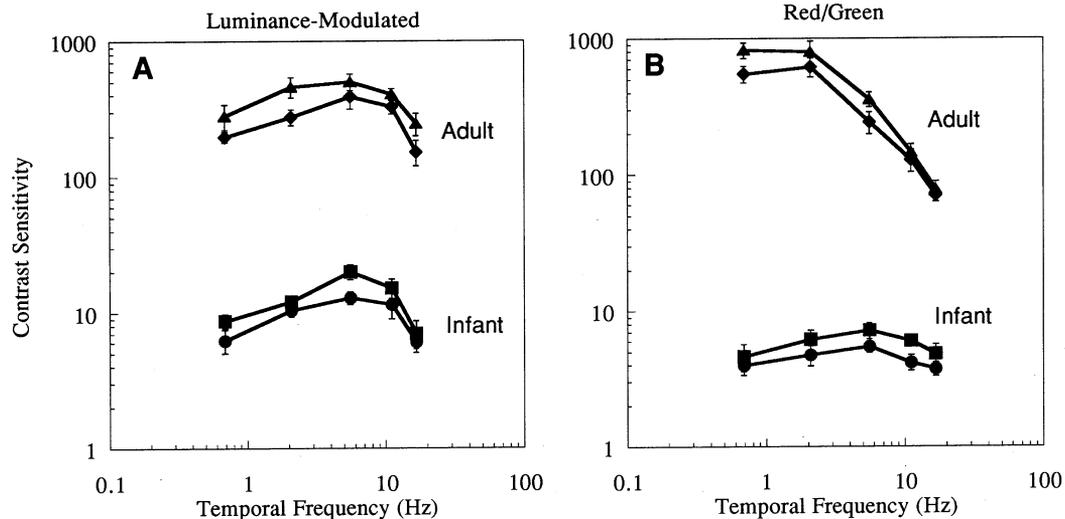
Fig. 4. tCSFs for luminance-modulated (A) and isoluminant red/green (B) gratings, in 3-month-old infants and adults. Both moving and counter-phasing gratings were tested. Surprisingly, the shape of the chromatic tCSF for infants resembles the bandpass tCSF for luminance-modulated gratings in adults and infants, and not the lowpass tCSF for chromatic gratings in adults. (Replotted from ref. [40]).

5. Direction-of-motion coding

Large fields of moving, low-spatial-frequency, high contrast red/green gratings elicit OKN-like, direction-ally-appropriate eye movements (DEM) in both adults and 2- to 3-month-old infants, but not in 1-month-olds [23,26,27]. Thus, for 2- and 3-month-olds, these red/green gratings must produce a motion correspondence cue that is sufficient for the infant's eye movement system to analyse the direction of motion of the grating. Chromatic motion nulling [42] was also tested in these studies [26,27], and the equivalent luminance contrast of red/green gratings—the luminance contrast required to null the motion of a high contrast red/green grating—was found to be about the same in infants as in adults. Since most 1-month-olds failed to produce DEM in these studies, this paradigm, like the earlier FPL paradigm, suggests the onset of effective red/green chromatic discrimination between 1 and 2 months postnatal.

In a later study, Teller et al. [20] showed the opposite result for tritan stimuli: tritan stimuli failed to elicit DEM in both 2- and 4-month-old infants, and 2-month-olds have an equivalent achromatic contrast very near zero. This study re-emphasizes the generalization that infants have trouble with tritan stimuli.

5.1. M/D ratios

Another paradigm that has been used in adult subjects is that of measuring two contrast thresholds for the same moving stimuli: the detection threshold (D), and the threshold for judging the direction of motion (M). For adults, for speeds of 1 deg/s and above, the ratio of direction-of-motion threshold to detection

threshold—the M/D ratio—has been shown to be near one for luminance modulated stimuli, suggesting that the mechanisms that detect moving stimuli also code the direction of motion (for a review see ref. [43]). But for chromatic stimuli, the M/D ratio is typically greater than one, suggesting that the mechanisms that detect moving chromatic gratings do not code the direction of motion [44]. Chromatic contrasts above the detection threshold, which presumably activate additional mechanisms beyond those that underlie the detection threshold, must be used before adults can code the direction of motion of isoluminant red/green gratings.

Dobkins and Teller [45] applied this paradigm to 3-month-old infants. FPL judgments were used to measure detection thresholds, while DEM judgments were used to measure direction-of-motion thresholds. These authors showed that in infants, the M/D ratios for luminance-modulated and red/green stimuli are equal and close to one. That is, infants' M/D ratios for both kinds of stimuli are similar to the adult M/D ratio for luminance-modulated stimuli, rather than to the adult ratio for chromatic stimuli.

5.2. Quadrature motion

Finally, Lia et al. [46] have carried out a study of 3-month-old infants' abilities to code the direction of motion of continuous versus quadrature-shifted stimuli [47]. In continuous motion, both the red and green bars of the grating and the borders between them shift continuously across the retina, with the result that either the colors of the bars or the locations of the red/green borders could be providing the motion correspondence cue. In quadrature motion, however, the location of the grating shifts by 90° of spatial phase

(one quarter of the period of the grating) from one time frame to the next. In consequence, the locations of red/green borders in each frame fall halfway between the locations of red/green borders in the previous frame. Thus, the locations of borders provide an ambiguous motion cue. Successful discrimination of the direction of quadrature motion would therefore suggest that the remaining motion correspondence cue—the colors of the bars—is sufficient for analysing the direction of motion.

In the Lia et al. study, both adults and 3-month-olds succeeded at the quadrature motion task. For infants, contrast thresholds for discriminating the direction of motion were slightly higher for quadrature than for continuous motion, but this was true for both luminance-modulated and red/green stimuli; no deficit specific to chromatic gratings was seen for quadrature motion. These data suggest that the colors of the bars provide a sufficient motion correspondence cue for infants, as they do for adults.

6. Discussion

6.1. Chromatic discriminations

In summary, there is converging evidence from several different stimulus configurations and response paradigms that by 2 months postnatal, infants can respond to high contrast isoluminant red/green chromatic differences, whether modulated in space, in time, or in space and time together. It is quite certain, therefore, that infants possess neural machinery sufficient to allow the preservation of red/green chromatic stimulus differences and the expression of that information through a variety of response systems. There is also direct evidence that this neural machinery includes both L- and M-cones [48] and a red/green opponent mechanism [49].

The results for tritan discriminations seem more variable across studies. However, all of the published studies are consistent with the generalization that 2-month-old infants succeed in making tritan discriminations when tested with highly saturated stimuli (i.e. monochromatic tritan pairs) embedded in a homogeneous background field; but have difficulty with less saturated stimuli, including the desaturated stimuli used by Teller et al. [12], and with stimuli presented on video monitors. Direct evidence that infants have functional S-cones has been provided by Volbrecht and Werner [50], but rods are also present [51], and may well play a role in the detection of tritan stimuli [7,16]. A more definitive investigation of tritan discriminations and the mechanisms that underlie them remains for the future.

6.2. CSFs and tCSFs

As noted above, developmental changes in CSFs and tCSFs can take several forms: changes in sensitivity, in spatial or temporal scale, and/or in curve shape. At the empirical level, changes in sensitivity are universally large and easy to see. However, at the theoretical level, changes in sensitivity are of least interest, because there are so many stages of processing, sensory and post-sensory, at which losses of sensitivity could be imposed.

Changes in spatial or temporal scale are of more interest, because they suggest changes in the spatial or temporal integration properties of the underlying detection mechanisms. And changes in curve shape are perhaps the most interesting, because they suggest changes in the contrast sensitivity function of the underlying detection mechanism. That is, a change in curve shape during development suggests either a developmental change in the shape of the spatial or temporal CSF of a single mechanism, or a shift from detection by one mechanism to detection by another during the course of development. To date, spatial CSFs show shifts of sensitivity and spatial scale, but not curve shape; while temporal CSFs show shifts of sensitivity and curve shape, but not temporal scale.

In the case of spatial CSFs, postnatal changes in the packing density of foveal photoreceptors [52] and in eye size, provide appealing models [53–55] of the changes in spatial scale observed for both luminance-modulated and red/green stimuli. For a fixed stimulus type, the apparent developmental constancy of curve shape suggests (but does not prove) that the same detection mechanisms, shifting in scale as the fovea develops, are at work in both infants and adults.

The most surprising aspect of the recent studies remains the developmental change in curve shape for the tCSF for red/green chromatic stimuli: from bandpass in infants to lowpass in adults. This change in curve shape led Dobkins et al. [40] to suggest that temporally modulated red/green chromatic stimuli may be detected by a different mechanism in infants than in adults. The agreement of curve shape between the infant tCSF for chromatic stimuli and the adult and infant tCSFs for luminance-modulated stimuli led to the further suggestion that chromatic stimuli are detected by M-pathway-initiated signals in infancy, switching to detection by P-pathway-initiated signals in adulthood. The most likely mediator would be the frequency-doubled response often seen in M cells at isoluminance [56].

The recent findings with moving stimuli complicate the argument. The finding that M/D ratios for chromatic stimuli in infants are near one, like the M/D ratios for luminance-modulated stimuli in adults, initially led Dobkins and Teller [45] to argue that moving chromatic stimuli might be detected by M-cell-initiated

signals; and the data on tCSFs are consistent with this interpretation. But the finding that infants can follow the direction of motion of moving quadrature gratings [46] provides an apparent contradiction. That is, if the motion correspondence cue used for red/green gratings is a frequency-doubled response initiated in M cells [56], then the infant should fail to perform the direction-of-motion task with the quadrature motion stimulus. The success of the infant on the quadrature motion task suggests that red/green chromatic differences per se, presumably coded by P-cell-initiated signals, can provide a sufficient motion correspondence cue for direction-of-motion coding in infant subjects. But if so, one might expect P-cell-initiated signals to be available for detecting stationary counter-phasing gratings as well. Alternatively, some other motion correspondence cue, provided by non-frequency-doubled M cell signals or by signals in some other cell class, could be mediating the infant's performance on this task. Further empirical and theoretical work aimed toward reconciling these differences is in progress.

6.3. Perceptual aspects

Finally, we return to the definition of infant color vision. At the outset we defined color vision as the capacity to discriminate among stimuli that differ in wavelength composition, on the basis of the difference in wavelength composition alone. By this definition, there is now abundant evidence that infants have at least red/green color vision by 2 months postnatal.

However, some might choose to make the definition of color vision more stringent. At present, it is probably widely believed that in adults, 'true' color vision—the perception of chromatic differences—arises as a consequence of signals that pass through the P-cell pathway; while an M-cell mediated response to wavelength differences could be accompanied by a visual 'happening' that is not predominantly a variation of perceived color per se. If isoluminant temporal chromatic changes are indeed detected by M-cell-mediated signals, then perhaps infants' responses to these stimuli are not indications of chromatic discrimination, but just indications of the detection of temporal 'happenings'. Just as brightness cues had to be ruled out in the 1970s, M-cell mediation of infants' chromatic discriminations remains to be ruled out in the 1990s.

Infants' responses to stationary, spatial chromatic changes are much more likely to reveal the presence of true color differences in the infant's perceptual world. But when two chromatic stimuli are juxtaposed in space, it remains conceivable that eye movements could still yield perceptual 'happenings' at the edges of the stimuli, sufficient to produce the fixation behavior required for FPL responses [57]. Ironically, although they have not been pursued systematically, experimental paradigms in which the stimuli being discriminated are separated in space and/or time [2,4,5] may well provide the most direct and definitive evidence of P-cell mediated color vision in infants. As is the case in adults, continuing work will be required to establish the neural basis of infants' responses to chromatic stimuli.

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