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Infant Motion: Detection (*M:D*) Ratios for Chromatically Defined and Luminance-defined Moving Stimuli

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In order to assess the relative contributions of chromatic vs luminance information to motion processing in infants, we employed a motion:detection (*M:D*) paradigm. Stimuli consisted of 27 deg by 40 deg, 0.25 c/deg sinusoidal gratings moving at 22 deg/sec (5.6 Hz), and were either chromatically defined or luminance-defined. Contrast thresholds for direction-of-motion (*M*) were obtained using a directional eye movement technique. Contrast thresholds for detection (*D*) were obtained using forced-choice preferential looking. *M:D* threshold ratios were obtained for individual infant subjects, and results were compared to those of adults.

As expected, adult *M:D* threshold ratios were near 1:1 for luminance-defined stimuli, but greater than 1:1 for chromatically defined stimuli. This suggests that, for adults, luminance-defined, but not chromatically defined, stimuli are detected by mechanisms labeled for direction of motion. By contrast, infant *M:D* ratios for chromatically and luminance-defined stimuli were approximately equal and close to 1:1, suggesting that, for infants, luminance- as well as chromatically defined stimuli are detected by mechanisms that are labeled for direction of motion. Copyright © 1996 Elsevier Science Ltd.

Visual development Chromatic motion processing Contrast thresholds Detection
Direction discrimination Infant chromatic vision Infant motion perception

INTRODUCTION

The use of chromatic information for motion processing has been a much debated topic in adult vision research. Many psychophysical investigations have demonstrated that motion processing is compromised when moving stimuli are defined solely by chromatic contrast, i.e., are *isoluminant* (e.g., Ramachandran & Gregory, 1978; Cavanagh *et al.*, 1984; Livingstone & Hubel, 1987; Lindsey & Teller, 1990; Teller & Lindsey, 1993a). Nonetheless, under most conditions, movement of chromatically defined stimuli can be detected and direction of motion can be accurately discriminated (e.g., Cavanagh & Favreau, 1985; Derrington & Badcock, 1985; Mullen & Baker, 1985; Lindsey & Teller, 1990; Simpson, 1990; Cavanagh & Anstis, 1991; Dobkins & Albright, 1993). Thus, in adults, there appear to exist at least minimal motion processing mechanisms that are sensitive to chromatic contrast.

To date, the question of how well infants use chromatic information for motion processing has been largely unexplored. Recently, however, the results from two infant studies have demonstrated that 2–3-month-old infants can make directionally appropriate eye movements in response to moving isoluminant red/green stimuli (Teller & Lindsey, 1993b; Brown *et al.*, 1995). Moreover, the equivalent luminance contrast of moving red/green gratings is approximately the same for infants and adults (Teller & Lindsey, 1993b; Teller & Palmer, 1996). Taken together, these findings suggest that infants, like adults, possess motion processing mechanisms that are sensitive to chromatic contrast.

In order to further investigate the extent to which infants use chromatic information for motion processing, we employed a motion:detection (*M:D*) paradigm, previously described in studies of adult vision. In a motion:detection *(M:D)* experiment, contrast thresholds for *detection* of a moving stimulus (*D*) are directly compared to contrast thresholds for *direction-of-motion discrimination* (*M*), for the same moving stimulus. In adults, *M:D* threshold ratios for luminance-defined stimuli are typically near 1:1, indicating that the amount

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of luminance contrast needed to detect a moving stimulus is also sufficient for discriminating its direction of motion (e.g., Watson *et al.*, 1980; Green, 1983; Graham, 1989). When stimuli are chromatically defined, however, *M:D* ratios range from 2:1 to 4:1 or larger, indicating that chromatic contrast levels sufficient for detection are *not* sufficient for discriminating direction of motion (Lindsey & Teller, 1990; Cavanagh & Anstis, 1991; Mullen & Boulton, 1992; Derrington & Henning, 1993; Palmer *et al.*, 1993; Teller & Lindsey, 1993a; Metha *et al.*, 1994; Gegenfurtner & Hawken, 1995). These *M:D* results demonstrate that, compared to luminance information, chromatic information provides limited input to motion possessing, thus supporting the notion that motion processing is impoverished when stimuli are defined solely by chromatic contrast.

At the theoretical level, luminance *M:D* ratios of 1:1 are taken to indicate that the most sensitive mechanisms for detecting luminance contrast are *directionally selective*, or labeled for direction of motion (e.g., see Thomas, 1985 and Watson & Robson, 1981 for a discussion of labeled lines). Conversely, chromatic *M:D* ratios greater than 1:1 indicate that the most sensitive mechanisms for detecting chromatic contrast are *not* labeled for direction of motion. Thus, the results from *M:D* experiments have implications for differential chromatic vs luminance contrast sensitivities of directional and non-directional mechanisms.

Because the results of *M:D* experiments have rich theoretical implications, we sought to use this paradigm in infants as a means of investigating chromatic vs luminance contrast sensitivities of developing directional and non-directional mechanisms. In the present experiment, we determined adult and infant *M:D* threshold ratios for chromatically defined and luminance-defined moving stimuli. For infants, contrast thresholds for direction-of-motion discrimination (*M*) were obtained using a directional eye movement technique (DEM). Infant contrast thresholds for detection (*D*) were obtained using forced-choice preferential looking (FPL). A within-subjects design was employed, in which both *M* and *D* thresholds were obtained within individual infant subjects. This infant protocol is directly analogous to that previously employed in adult M:D experiments, i.e., identical stimulus conditions, yet different tasks.

The contrast thresholds obtained in these experiments also allowed us to examine two other questions. First, using a cone contrast metric we were able to compare contrast thresholds for chromatically vs luminance-defined stimuli. The resulting chromatic:luminance (C:L) threshold ratios address the question of whether subjects are more sensitive to luminance or to chromatic contrast, under the present conditions (cf. Mullen, 1985; Stromeyer *et al.*, 1990; Chaparro *et al.*, 1993). And second, comparison of C:L ratios between the two age groups addresses the question of uniform vs differential loss of chromatic, with respect to luminance sensitivity (e.g., Banks & Bennett, 1988; Brown, 1989; Teller & Lindsey, 1993b). Equal C:L ratios at both ages would support the uniform loss model, while a larger C:L ratio in infants compared to adults would be evidence for a differential loss in infants of chromatic with respect to luminance sensitivity.

METHODS

Subjects

Infants. A total of 61 infants took part in this study. All infants were born within 14 days of their due date, and were reported to have normal, uncomplicated births. Male infants with family histories of color vision deficiencies were excluded from the experiment. Each infant was tested for 3–5 days within a 1 week time period. The average age on the first day of testing was 83 days (SD = 1.7 days). Data from 47 infants contributed to the results presented here (22 infants in Experiment 1 and 25 infants in Experiment 2). Six infants failed to meet the minimum trials criterion ($n \geq 120$) and eight infants failed to meet the minimum performance criterion (a score of $\geq 80\%$ correct on the easiest stimulus presented). These infants ($n = 14$) were therefore not included in the analysis.

Adults. Five naive adult subjects (ages 19–24 yr) were tested under stimulus conditions identical to those employed in our infant paradigm. Three of these subjects and an additional ten ($n = 13$) also provided psychophysical red/green isoluminance points. All subjects had normal or corrected-to-normal vision.

Visual apparatus and stimuli

Infant apparatus. Stimuli were generated on a high resolution RGB monitor (19″ Barco CDCT 6451, 67 Hz, non-interlaced, 640 × 480 pixels), driven by a Mac II computer. The 8-bit video board in the computer allowed for 256 discrete levels of luminance. The CIE chromaticity coordinates for the Barco primaries were: Red (0.610, 0.340), Green (0.300, 0.590) and Blue (0.150, 0.060). The maximum output for the monitor was calibrated to equal energy white (CIE chromaticity coordinates = 0.333, 0.333), and the voltage/luminance relationship was linearized independently for each of the three guns in the display (Cowan, 1983).

Adult apparatus. In order to produce the low chromatic and luminance contrasts required to span adult contrast thresholds, adult subjects were tested using an auxiliary field. A second Barco monitor (No. 2), which displayed a homogeneous yellow field, was placed at right angles to the main stimulus monitor (No. 1). A piece of plate glass (36 × 28 cm) was placed between the two monitors at a 45 deg diagonal, 24 cm from the center of each monitor. Direct viewing of monitor No. 2 through the glass allowed approximately 87% transmittance of light from monitor No. 2 and 13% reflection of light from monitor No. 1. The mean luminances on the two monitors (11 and 18 cd/m^2 for monitors Nos 1 and 2, respectively) were set such that the mean luminance of the combined display was 17 cd/m^2. Sinusoidal gratings presented on monitor No. 1 were thus reduced in contrast by 91%. For monitor

No. 1, the mean CIE chromaticity coordinates of the grating stimuli and the background field were fixed at 0.501, 0.412. For monitor No. 2, chromaticity coordinates were 0.509, 0.423. At the eye, the combined chromaticity coordinates were 0.508, 0.422.

Stimuli. All stimuli were vertically oriented sinusoidal gratings. Spatial frequency was set at 0.25 c/deg. This spatial frequency was chosen because it is near the peak of the spatial contrast sensitivity function for infants 3 months of age (Atkinson *et al.*, 1977a; Banks & Salapatek, 1978), and because the effects of chromatic aberration are negligible (Flitcroft, 1989). At a viewing distance of 38 cm, grating stimuli subtended 27 deg by 40 deg of visual angle (6.7 total cycles) and the illuminated portion of the video monitor subtended 53 deg by 40 deg.

Two replications of the experiment were carried out in infants. In Infant Experiment 1 the mean luminance of the gratings and the background field was set at 30 cd/m^2, with mean chromaticity coordinates of 0.417, 0.491. In Infant Experiment 2 the mean luminance of the gratings and the background field was set at 16 cd/m^2, with mean chromaticity coordinates of 0.514, 0.420. For adult experiments, which were designed to closely match the conditions of Infant Experiment 2, the mean luminance was 17 cd/m^2, with mean chromaticity coordinates of 0.508, 0.422.

Heterochromatic (red/green) gratings. Heterochromatic red/green gratings were produced by sinusoidally modulating the red and green primaries 180 deg out of phase. In order to create gratings that selectively modulate long-wavelength-sensitive (L) and medium-wavelength-sensitive (M) cones, but not short-wavelength-sensitive (S) cones, a small amount of sinusoidally modulated blue primary was added in phase with the red portion of the heterochromatic grating. The amount of blue primary required to null the modulation of S cones was calculated using cone fundamentals described in DeMarco *et al.* (1992): the change in S cone activation caused by varying from pure red to pure green phosphor was determined (approx. +16%), and was then counterbalanced with blue primary modulation to produce equal and opposite S cone modulation. Absolute S cone activation was 0.003 units, with 0% modulation, in MacLeod & Boynton (1979) chromaticity space.

Specification of chromatic contrast in the resulting heterochromatic grating is conducted in two ways. *Instrument contrast* in the heterochromatic red/green stimulus describes the fraction of the potential chromatic modulation between the red and green phases of the grating. The point at which the red and green primaries are modulated by 100% of the available gamut is defined as 100% instrument contrast. *Cone contrast* describes the amplitude of response modulation in cone photoreceptors produced by the red and green phases of the stimulus, and is dependent on the chromaticity coordinates of the monitor's red and green primaries. Cone modulations were computed using the CIE coordinates of the primaries and the conversion functions provided by Boynton (1986), based on the cone action spectra provided in DeMarco *et al.* (1992). Our calculations indicate that modulation between the red and green primaries produced maximum L and M cone modulations of 14 and 34%, respectively. Thus, the root mean square (r.m.s. = sqrt $((M^2 + L^2)/2)$) of the independent modulations of the L and M cones was 26% cone contrast. The utility of converting to a cone contrast metric is that it allows for the expression of chromatic contrast and luminance contrast in comparable units (e.g., Mullen, 1985; Lennie & D'Zmura, 1988; Chaparro *et al.*, 1993; Derrington & Henning, 1993).

In Infant Experiment 1, for which the background luminance level was 30 cd/m^2, 100% instrument contrast could not be achieved (due to limitations in the total luminance available in the red primary). In this experiment red/green gratings produced a maximum of 9 and 19% contrast modulation in L and M cones, respectively (r.m.s. cone contrast = 15%). In Infant Experiment 2, higher cone contrasts were achieved by employing a lower background luminance level (16 cd/m^2) that allowed for 100% instrument contrast. Under these conditions maximum L and M cone contrasts were 14 and 34%, respectively (r.m.s. cone contrast = 26%). In adult experiments the maximum r.m.s. cone contrast produced by the stimulus monitor was also 26%. The auxiliary field apparatus (see above) reduced the maximum cone contrast produced at the eye to 2.4%.

Photometry: Finding psychophysical isoluminance. Calibrations of Vλ isoluminance were carried out using a Minolta TV-2150 photometer/chromaticimeter and a Gamma Spectroradiometer. However, because isoluminance settings differ across subjects, as well as from Vλ, i.e., photometric isoluminance, we used a "minimal motion" method to determine psychophysical red/green isoluminance points in individual adult subjects. This technique relies on the fact that perceived motion is impoverished, slowed and/or jerky at the point of psychophysical isoluminance (Moreland, 1982; Cavanagh *et al.*, 1984; Mullen & Boulton, 1992; Teller & Lindsey, 1993a). Luminance contrast variation in the red/green gratings was created by differentially adjusting the amplitudes of the red and green phases, such that the mean luminance and chromaticity were held constant. Luminance contrast of the red/green grating is expressed as Michelson contrast: $[(L_{\text{red phase}} - L_{\text{green phase}}) / (L_{\text{red phase}} + L_{\text{green phase}})]$. Using this metric, luminance contrast can be either positive or negative, depending upon which of the two phases is brighter.

For adults, each subject's individual isoluminance point was determined, and was subsequently used in the *M:D* experiments. The stimulus conditions for the minimal motion isoluminance procedure were identical to those employed in the main *M:D* experiments (i.e., same size, speed and spatial frequency). Subjects fixated a small spot in the center of a moving red/green grating and adjusted the luminance contrast in the grating until the percept of motion was least salient. In the adult apparatus, luminance contrast could be stepped up and down in equal intervals of 0.18% and the total range of

possible contrasts varied from −3.5% (green brighter than red) to 3.5% (red brighter than green), with respect to Vλ isoluminance. Each subject made twenty settings. The standard deviation (SD) within a subject was typically < 0.8% luminance contrast, suggesting that this procedure yields extremely precise estimates of individual adult isoluminance.

For infant *M:D* experiments, a mean adult isoluminance point value was used. For this purpose, a total of thirteen adult subjects (three of whom also participated in the *M:D* experiments) were tested with the minimal motion procedure on the infant apparatus. Luminance contrast could be stepped up and down at equal intervals of 0.5%, and the total range of possible contrasts varied from −8.0% to 11.0%. Each subject made twenty settings at each of two luminance levels. Mean isoluminance points and standard deviations (SD) across the population of subjects were determined to be +2.8% (SD = 0.9%) and +2.3% (SD = 1.0%) at 16 and 30 cd/m^2, respectively. The low population standard deviations suggest that, for the conditions employed, individual isoluminance points varied relatively little across adult subjects.

Our justification for using the adult mean isoluminance value in our infant experiments is based on previous experiments demonstrating that infant and adult isoluminance points measured by VEPs (Morrone *et al.*, 1993; Bieber *et al.*, 1995) and motion photometry (Maurer *et al.*, 1989; Teller & Lindsey, 1989; Brown *et al.*, 1995) are highly similar, especially in the red/green range. Moreover, Brown and colleagues demonstrated that the variability of isoluminance points across infant subjects is comparable to the variability across adult subjects. In our experiments, the adult variability (in terms of SD) was < 1.0% luminance contrast. Therefore, the maximal amount of luminance contrast expected to exist due to inter-subject variability is < 2.0% (based on ±2 SD), a value which is far below behaviorally obtained luminance contrast thresholds observed herein and in previous studies of 3-month-old infants (e.g., Atkinson *et al.*, 1974; Banks & Salapatek, 1978; Swanson & Birch, 1990; Hartmann & Banks, 1992; Teller *et al.*, 1992a; Brown *et al.*, 1995; Dobkins & Teller, 1995). Thus, the small amount of luminance contrast expected to be present for any individual infant, due to the use of a single red/green setting for all subjects, should be undetectable.

Luminance-defined (yellow/black) gratings. Gratings that varied only in luminance were produced by sinusoidally modulating the red and green primaries *in phase* with one another (with a small amount of blue primary added in phase with the red and green primaries). Luminance-defined (yellow/black) gratings were of the same mean luminance and chromaticity as the chromatically defined (red/green) isoluminant gratings. Luminance contrast in the gratings was manipulated by varying the amplitude of the luminance sinusoid, and is expressed in terms of r.m.s. cone contrast elicited within L and M cones. For luminance-defined 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.

Motion generation. Moving stimuli were of the "apparent motion" type, i.e., movement was achieved by spatial phase offset at regular intervals occurring in synchrony with the vertical refresh of the video monitor (i.e., at multiples of 15 msec). Spatial offset was set at 0.33 deg visual angle (30 deg phase shift) and frame duration was set at 15 msec, which yielded an equivalent speed of 22 deg/sec, and a temporal frequency of 5.6 cyc/sec (Hz). For luminance-modulated stimuli, this spatiotemporal combination is known to be within the range that renders a clear percept of smooth motion in adult subjects (Burr *et al.*, 1986; Watson *et al.*, 1986), and is thought to invoke directional mechanisms in infants (Wattam-Bell, 1991; Hamer & Norcia, 1994; Dobkins & Teller, 1995) and adults (see Graham, 1989, pp. 464–465).

Psychophysical paradigm

Infant procedure. Infant contrast detection thresholds *(D)* were obtained using a standard forced-choice preferential looking (FPL) technique (Teller, 1979). Infant direction-of-motion contrast thresholds *(M)* were obtained using a "directional eye movement" (DEM) technique (e.g., Hainline *et al.*, 1987; Teller & Lindsey, 1993b; Brown *et al.*, 1995). DEM techniques rely on the fact that infants make directionally appropriate eye movements in response to moving stimuli (e.g., Dayton *et al.*, 1964; Kremenitzer *et al.*, 1979; Atkinson & Braddick, 1981; Hainline *et al.*, 1984; Roy *et al.*, 1989). These differential eye movements imply the existence of a mechanism that encodes direction of motion, and can, therefore, be used as a behavioral indicator of directional discrimination. We choose to use the term DEM, rather than a more narrow classification term like *optokinetic nystagmus* (OKN), to refer to the constellation of eye movement patterns (e.g., OKN, smooth pursuit and/or saccades) that can be elicited by a medium-sized (27 deg by 40 deg) moving stimulus.

An adult observer/experimenter (first author KRD or an assistant, BL or JDS) held the infant 38 cm away from the front of the stimulus monitor. Two video cameras were aimed at the infant's face. The experimenter was unable to see the stimulus display (an occluder obstructed the view), but could see the infant's face in two camera monitors suspended above the apparatus. Camera monitor No. 1 captured the entire face of the infant and was optimized for FPL judgments. Camera monitor No. 2 displayed an enlarged image of the infant's right eye and was optimized for DEM judgments.

Each trial began with the presentation of a computer-generated fixation target (which consisted of one of 40 moving or stationary pictures) in the center of the stimulus monitor. When the infant was judged to be looking centrally, the fixation target was extinguished and a 0.25 c/deg moving grating patch (27 deg by 40 deg) appeared and filled the left half, the right half or the center portion of the stimulus monitor. Trials containing

stimuli displaced to the left or right (centered 13 deg from the middle of the screen) required an FPL judgment. The experimenter used cues such as the infant's head turning and gazing behavior to judge the left vs right location of the stimulus. Trials containing stimuli appearing in the center of the screen required a DEM judgment. In this task, the experimenter used the pattern of the infant's eye movements to judge the left vs right direction of motion of the stimulus. FPL vs DEM trials were randomly interspersed throughout the experiment and auditory beeps signaled the trial type to the experimenter. The parent of the infant recorded the experimenter's verbal response by pressing one of two keys on the computer keyboard, and the response latency was recorded. Beeps from the computer provided feedback.

Individual infants were tested with either luminance-defined (black/yellow) or chromatically defined (isoluminant, red/green) gratings. For the luminance-defined condition, five different r.m.s. cone contrasts were employed (2.5–40%, 1.2 log unit range). For the chromatically defined condition, three different r.m.s. cone contrasts were employed, including the maximum contrast available (Infant Experiment 1: 3.7–15%, 0.6 log unit range; Infant Experiment 2: 6.5–26%, 0.6 log unit range). In partial compensation for the limited range of cone contrasts we could produce on our monitor, the highest chromatic contrast was presented twice as often as the lower two. To monitor the attentional state of the infant, the experimenter could call up an "easy" trial (i.e., an 80% contrast luminance-defined grating) at any time. An incorrect guess by the experimenter under this "easy" condition was taken to indicate that the infant was inattentive and required a break.

Chromatic and luminance groups were balanced to include an approximately equal number of girls and boys. In both Infant Experiments 1 and 2, two adult experimenters each tested approximately half of the infants from both the chromatic and the luminance groups. The total number of trials collected from each infant ranged from 141 to 280, with an average of 188 (94 trials/psychometric function).

Adult procedure. Five adult subjects participated in these experiments. Adult subjects were situated in a chin-rest, placed 38 cm away from the visual display. For each subject, a detection contrast threshold (D) and a (direction-of-motion) contrast threshold (M) were obtained by standard forced-choice psychophysical techniques with feedback. Trials containing stimuli displaced to the left or right required the subject to signal (by pressing a key pad) the left or right location of the stimulus. This provided the D threshold. Likewise, trials containing stimuli appearing in the center of the screen required the subject to signal the left or right direction of motion of the stimulus. This provided an M threshold. M and D trials were randomly interspersed throughout the experiment and each trial began with a differential beep to alert the subject to the task type.

Each subject was tested using both chromatically and luminance-defined stimuli. Chromatic and luminance trials were interspersed across trials, and presented at one of six contrasts (range = 0.07–2.4% r.m.s. cone contrast, 1.5 log units, for both chromatically and luminance-defined stimuli). As was the case for infant procedures, eye position in our adult subjects was unrestricted and stimuli remained present on the screen until a decision was made.

In addition to determining M and D psychophysical thresholds, contrast thresholds for DEM judgments were also obtained, in a manner analogous to that employed for infants. On trials for which subjects were required to report direction of motion, an experimenter/observer (first author, KRD) used the subject's eye movements to judge the left or right direction of the stimulus. Subjects were naive to the goal of the experiment. Prior to the onset of the experiment, subjects were informed that their right eye would be observed during direction-of-motion trials, and they were instructed to simply "watch the stripes" after they had given their key pad response. On these trials, the stimulus was extinguished after both the subject and experimenter responded, at which point the subject received visual feedback and the experimenter received auditory feedback.

Similar to the number of total trials obtained from our infant subjects, 240 trials were collected for chromatically defined, and 240 for luminance-defined stimuli (total = 480 trials/subject).

Data analysis

Contrast thresholds. Psychometric curves were fit to the data using Weibull functions (Weibull, 1951; Quick, 1974) and maximum likelihood analysis (Watson, 1979). We employed a particular variation of the Weibull formula, which contains a base 2 substitution and is modified for 2AFC experiments (see Graham, 1989):

$$P_c = u - ((u - v) * 2^{[-(x/t)\beta]})$$

where u is the upper asymptote, v is the lower asymptote (fixed at 0.5), β is the slope parameter of the psychometric function, x is the contrast in linear units, and t is the contrast threshold at the point halfway between u and v.

For adults, an upper asymptote of 100% was employed and the slope parameter of the Weibull function (β) was unrestricted. For infants, upper asymptotes were fixed at 95% correct performance, a value that reflects those observed in previous (Teller *et al.*, 1992b; Dobkins & Teller, 1995) and present data sets, and which has been shown to yield optimal threshold estimates for infant psychometric functions (Teller *et al.*, 1992b). Based on the asymptote values chosen for infants and adults, contrast threshold was defined as the contrast yielding 75% correct performance in adults and 72.5% correct performance in infants.

For infant data obtained under chromatically defined conditions it was often the case that, due to the limited range of available contrasts, we were unable to obtain full psychometric functions (i.e., even at the highest available chromatic contrast, infants were not performing at >90%

correct). In order to improve the goodness of the Weibull fit in this situation, slope parameters were fixed for all data sets. Fixed slope values were chosen based on mean unrestricted values determined separately for the DEM and FPL luminance-defined conditions of Infant Experiment 1 (where performance consistently varied from 50% to ~95% correct, yielding full psychometric functions). These values, which were 1.8 for the DEM data and 1.4 for the FPL data, are in agreement with slope values obtained in previous infant studies (e.g., Swanson & Birch, 1992; Brown *et al.*, 1995; Dobkins & Teller, 1995). Although it was not necessary to fix the slope for data sets obtained from the luminance-defined condition, we did so in order to maintain consistency between the luminance and chromatic analyses. Under these conditions, all infant data sets were well fit by Weibull functions.

Infant Experiments 1 and 2. In Experiment 1 the maximum r.m.s. cone contrast we could produce in the chromatically defined stimulus was 15%. This resulted in an overall poor performance by infants tested in the chromatically defined condition. For example, the mean infant performance at the highest cone contrast tested (15%) was 71% correct for the DEM trials and 72% for the FPL trials. These values were markedly lower than values obtained under the luminance-defined conditions. At the highest luminance contrast tested (40%), the mean infant performance was 96% correct for DEM trials and 93% for FPL trials.

To determine whether the lack of a full psychometric function for the chromatically defined data sets in Experiment 1 might have led to erroneous threshold estimates, we conducted a simulation analysis using data obtained from the luminance-defined DEM condition. Threshold values were estimated using only the three lowest luminance contrasts employed (i.e., 2.5, 5 and 10% contrast). Under these conditions, the mean peak performance (i.e., at 10% contrast) was only 82% correct. If threshold estimates are biased for data sets that do not span the full psychometric function, estimates should be different for data sets containing all five contrasts compared to those obtained for data sets containing only the bottom three contrasts. In fact, however, we found that mean threshold estimates obtained using the full data set were indistinguishable from those obtained using the three lowest contrasts. It is, therefore, likely that our threshold estimates for the chromatically defined condition in Experiment 1 were also unbiased.

Nonetheless, we replicated Experiment 1 in a second experiment in which the stimulus conditions yielded more complete psychometric functions. In Experiment 2, we produced red/green grating stimuli with higher chromatic contrasts (maximum = 26% r.m.s. cone contrast), by reducing the overall luminance of the display (16 cd/m^2). In addition to using higher chromatic contrasts, we also chose to modify our infant protocol in the following manner. In the chromatically defined condition, one-fifth of the stimulus trials consisted of a 40% contrast luminance-defined grating. The purpose of this stimulus was to provide some salient trials for the infant, and to obtain a performance criterion. Specifically, this procedure allowed us to distinguish infants who were insensitive to chromatic contrast from those who were generally inattentive. Infants who fell into the latter category (i.e., scored < 80% correct on the 40% luminance contrast trials, $n = 4$) were excluded from the analysis, a criterion that was also implemented for infants tested in the luminance-defined condition ($n = 4$). Under the chromatic conditions of Experiment 2, the mean infant performance at the highest cone contrast tested (26%) was 77% correct for the DEM trials and 81% for the FPL trials.

Infant and adult M:D *ratios.* For each subject, a motion:detection (*M:D*) threshold ratio was calculated. For infants, *M:D* threshold ratios were computed using DEM and FPL thresholds ($M{:}D = \mathrm{Thr}_{\mathrm{DEM}}/\mathrm{Thr}_{\mathrm{FPL}}$). For adults, *M:D* ratios were calculated in two ways. (1) An *M:D* ratio was calculated using psychophysically obtained *M* and *D* thresholds ($M{:}D = \mathrm{Thr}_{\mathrm{M}}/\mathrm{Thr}_{\mathrm{D}}$). (2) An *M:D* ratio was calculated using the psychophysically obtained threshold for *D*, but the DEM threshold for *M* ($M{:}D = \mathrm{Thr}_{\mathrm{DEM}}/\mathrm{Thr}_{\mathrm{D}}$). The purpose of computing this additional *M:D* ratio was to determine whether comparisons between chromatic and luminance *M:D* ratios would differ when eye movements, as opposed to perceptual direction-of-motion reports, were used for the motion threshold.

Note that in the case of infants, neither instructions nor verbal responses are available options; and different motor responses (FPL vs DEM) must be used for the two tasks. Change in task may itself bias the *M:D* threshold ratio. For example, if DEM judgments are harder than FPL judgments, *M:D* ratios will be biased greater than 1:1. Thus, the most fundamental outcome measurement will be the comparison of *M:D* ratios *between* chromatically and luminance-defined stimuli, and not the absolute value of *M:D* ratios *per se*.

RESULTS

M:D *ratios*

Representative results from one adult subject tested with both luminance- and chromatically defined stimuli are shown in Fig. 1(A). When the stimulus was luminance-defined (left), the subject exhibited *M* and *D* thresholds of 0.15 and 0.16% cone contrast, respectively. The resulting *M:D* ratio was 0.9, indicating that the luminance contrast level sufficient for detecting the stimulus was also sufficient for discriminating its direction of motion. When the stimulus was chromatically defined (right), the subject exhibited *M* and *D* thresholds of 0.58 and 0.31% cone contrast, respectively, with an *M:D* ratio of 1.9. Thus, for chromatically defined stimuli, the contrast level sufficient for detecting the stimulus was *not* sufficient for discriminating its direction of motion. The factor of two difference between the chromatic and luminance *M:D* ratios for this subject

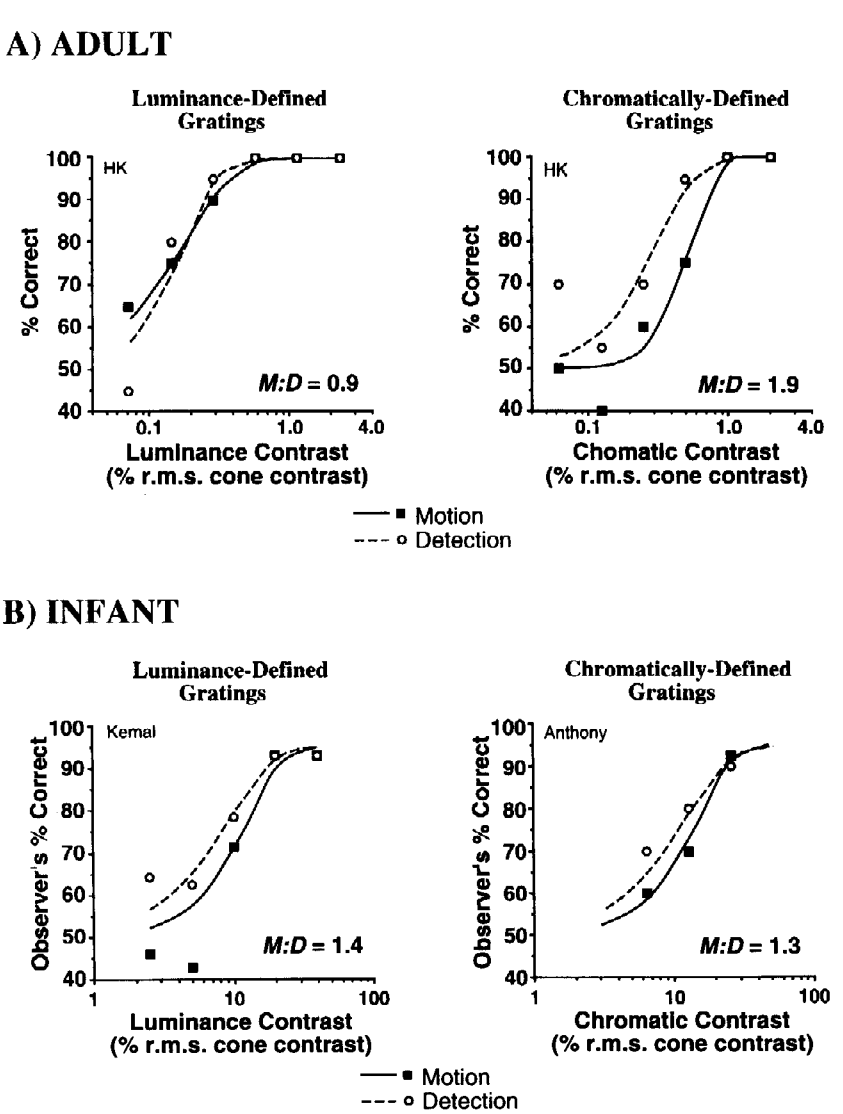

FIGURE 1. (A) Psychometric functions from an adult subject, tested with both luminance-defined and chromatically defined gratings. The stimulus consisted of a 0.25 c/deg grating moving at 22 deg/sec (5.6 Hz). For both chromatic and luminance data, percent correct is plotted as a function of r.m.s. cone contrast in the stimulus. Solid and dashed lines are best-fitting Weibull functions. When stimuli were luminance-defined (left), the subject exhibited approximately equal thresholds for direction-of-motion (*M*) and detection (*D*), with an *M:D* ratio of 0.9. By contrast, when stimuli were chromatically defined (right), the *M* threshold was higher than the *D* threshold, with an *M:D* ratio of 1.9. (B) Data obtained from two 3-month-old infants in Experiment 2. Data were collected using two task conditions: a directional eye movement (DEM) technique for obtaining direction-of-motion thresholds (*M*), and forced-choice preferential looking (FPL) for obtaining detection thresholds (*D*). All stimulus parameters and configurations were identical to those employed in adult experiments. The infant on the left, tested with luminance-defined gratings, exhibited a slightly higher threshold for DEM compared to FPL, with an *M:D* ratio ($M{:}D = \mathrm{Thr}_{\mathrm{DEM}}/\mathrm{Thr}_{\mathrm{FPL}}$) of 1.4. The infant on the right, tested with chromatically defined (red/green) gratings, exhibited an *M:D* ratio of 1.3.

suggests that, compared to luminance, chromatic information provides limited input to motion processing.

Results from two 3-month-old infant subjects in Experiment 2 are shown in Fig. 1(B). The infant on the left, tested with luminance-defined (yellow/black) gratings, exhibited DEM and FPL thresholds of 10 and 7% cone contrast, respectively. This resulted in an *M:D* ratio ($M{:}D = \mathrm{Thr}_{\mathrm{DEM}}/\mathrm{Thr}_{\mathrm{FPL}}$) of 1.4. The infant on the right, tested with chromatically defined (red/green) gratings, exhibited DEM and FPL thresholds of 13 and 10% cone contrast, respectively, with an *M:D* ratio of 1.3. Thus, both infants required slightly more contrast to discriminate direction of motion than to detect the moving stimulus.

Infant mean M:D *ratios*

M:D ratios were calculated for each infant, and group geometric mean *M:D* ratios were determined, separately for the chromatically defined and luminance-defined conditions. (All group means and statistical analyses were calculated using log values of the data.) If, compared to luminance information, chromatic information provides limited input to motion processing, mean *M:D* ratios for the chromatically defined stimuli should

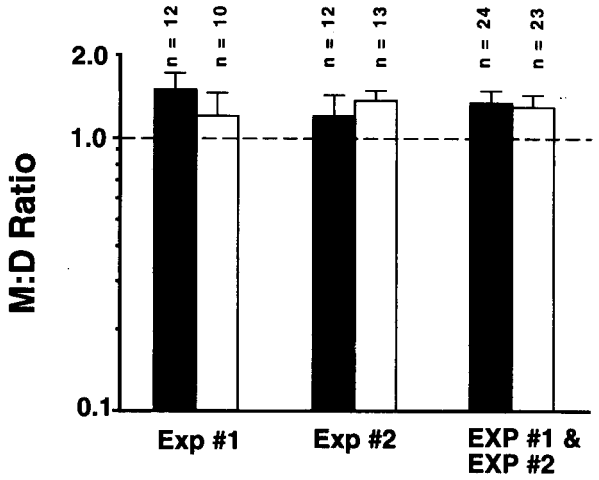

FIGURE 2. Infant group mean *M:D* ratios for luminance-defined (dark bar) and chromatically defined (light bar) stimuli. Error bars denote standard errors of the means. For each separate infant experiment (1 and 2), as well as for combined data, chromatic and luminance *M:D* ratios were statistically indistinguishable from each other.

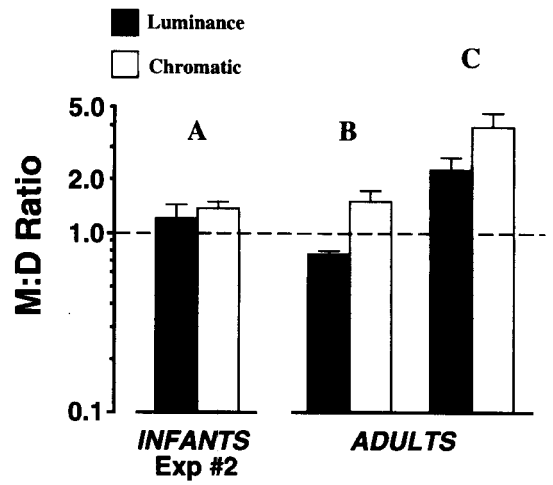

FIGURE 3. Group mean adult *M:D* ratios ($n = 5$) compared to infant *M:D* ratios from Experiment 2 ($n = 25$). Error bars denote standard errors of the means. (A) Infant data replotted from Fig. 2. (B) Adult *M:D* ratios computed using direction-of-motion reports as an *M* threshold (i.e., $M{:}D = \mathrm{Thr_M/Thr_D}$). (C) Adult *M:D* ratios computed using DEM judgments as an *M* threshold (i.e., $M{:}D = \mathrm{Thr_{DEM}/Thr_D}$). For adults (B and C), but not infants (A), *M:D* ratios for chromatically defined gratings are significantly higher, by about a factor of two, than those for luminance-defined gratings.

be elevated above those for the luminance-defined stimuli. If, on the other hand, chromatic and luminance information provide equivalent input to motion processing, *M:D* ratios should be the same for chromatically and luminance-defined stimuli.

Mean *M:D* ratios and standard errors from Experiment 1 are shown in Fig. 2 (left-most data set). *M:D* ratios for infants tested with luminance-defined ($n = 12$) and chromatically defined ($n = 10$) stimuli were 1.5 and 1.2, respectively. For both the luminance and chromatic conditions, mean *M:D* ratios were found to be significantly higher than 1.0 (luminance: $t_{11} = 9.30$, $P < 0.005$, 2-tailed; chromatic: $t_9 = 2.88$, $P < 0.025$, 2-tailed). With respect to each other, however, chromatic and luminance means were *not* significantly different ($t_{20} = 0.84$, P = NS).

Similar results were observed in Experiment 2. Mean *M:D* ratios for infants tested with luminance-defined ($n = 12$) and chromatically defined ($n = 13$) stimuli were 1.2 and 1.4, respectively (Fig. 2, middle data set). As was the case in Experiment 1, both luminance and chromatic *M:D* ratios were found to be significantly greater than 1.0 (luminance: $t_{11} = 3.77$, $P < 0.005$, 2-tailed; chromatic: $t_{12} = 16.59$, $P < 0.005$, 2-tailed), however, the chromatic *M:D* ratios were not significantly different from the luminance *M:D* ratios ($t_{23} = 0.62$, P = NS). Combined results from a total of 47 infants in Experiments 1 and 2 are shown on the right in Fig. 2. Mean luminance and chromatic *M:D* ratios were 1.33 and 1.28, respectively, with no significant difference between the two ($t_{45} = 0.23$, P = NS). In sum, the results from Experiments 1 and 2 demonstrate that infant *M:D* ratios for chromatically and luminance-defined gratings are very similar.

Infant M:D *ratios: Effects of different task procedures (DEM vs. FPL)*

For both chromatically and luminance-defined stimuli, we found that infant *M:D* ratios were slightly, yet significantly, above 1:1. As discussed in the Methods, this result may be due to the DEM task being more difficult for the experimenter than the FPL task. Differences in the degree of difficulty for the two tasks are supported by the fact that the mean response latency for DEM judgments was 8.2 sec, while the mean response latency for FPL judgments was 4.6 sec. That direction of eye movements may be inherently defficult to judge is further supported by results from adult experiments, which demonstrate that contrast thresholds obtained using DEM-like techniques are consistently higher than *M* thresholds obtained from perceptual reports (Hainline *et al.*, 1987; Brown *et al.*, 1995; and see Fig. 4 herein). Thus, even for adult subjects who are attentive and actively participating, DEM judgments tend to underestimate perceptual sensitivity.

In sum, we suspect that the elevation of *M:D* ratios above 1:1 should be attributed to differences in response difficulty between FPL and DEM tasks. In any case, our main finding–infant *M:D* ratios for chromatically and luminance-defined stimuli are not different from each other—cannot be explained by differential task difficulty.

Adult mean M:D *ratios*

As was performed for infant data, individual adult *M:D* ratios for luminance- and chromatically defined stimuli were averaged across subjects ($n = 5$). To facilitate comparison, infant group mean *M:D* ratios (obtained in Experiment 2, replotted from Fig. 2) and adult group

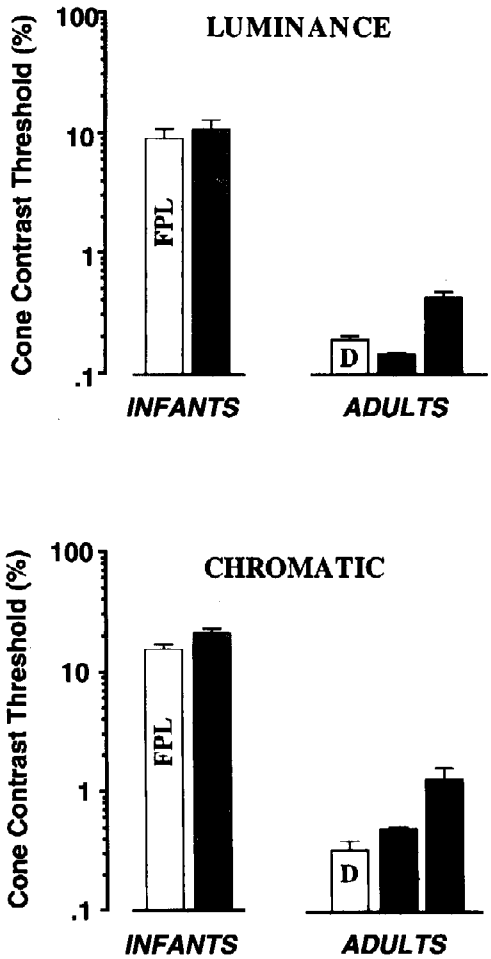

FIGURE 4. Infant and adult group mean cone contrast thresholds for luminance-defined (A) and chromatically defined (B) stimuli. Error bars denote standard errors of the means. All thresholds are expressed in terms of the r.m.s. cone contrast elicited in L and M cones (see methods and text). Infant contrast thresholds are plotted for FPL and DEM. Adult thresholds are plotted for *D*, *M* and DEM. Under all test conditions, adults were found to be more than a log unit more sensitive than infants.

means are shown in Fig. 3. Adult mean *M:D* ratios defined using direction-of-motion reports for the *M* threshold [Fig. 3(B) $M{:}D = \mathrm{Thr_M/Thr_D}$] were significantly elevated for chromatically defined compared to luminance-defined stimuli ($t_4 = 3.24$, $P < 0.05$, 2-tailed). In accordance with previous reports (Cavanagh & Anstis, 1991; Mullen & Boulton, 1992; Derrington & Henning, 1993; Palmer *et al.*, 1993; Gegenfurtner & Hawken, 1995 but cf. Lindsey & Teller, 1990), adult *M:D* ratios for chromatically defined gratings were about twice those observed for luminance-defined gratings. This result in adults is markedly different from that observed in infants [Fig. 3(A)]; infant *M:D* ratios for chromatically defined gratings were only a factor of 1.1 higher than those for luminance-defined gratings, and the difference was not significant.

To determine whether the differences observed between infants and adults might be due to the fact that we employed eye movements as a behavioral indicator of directional discrimination in infants, we used adult DEM contrast thresholds as a substitute for *M* thresholds. Accordingly, adult chromatic and luminance *M:D* ratios were determined by dividing DEM thresholds by detection (*D*) thresholds (i.e., $M{:}D = \mathrm{Thr_{DEM}/Thr_D}$). The resulting chromatic and luminance mean *M:D* ratios are shown in Fig. 3(C). *M:D* ratios obtained using DEM data for an *M* threshold were qualitatively the same as those obtained using psychophysical measures; *M:D* ratios for chromatically defined gratings were significantly elevated above and about twice those for luminance-defined gratings ($t_4 = 2.91$, $P < 0.05$, 2-tailed).

Interestingly, for adults the mean psychophysically obtained *M:D* ratio for luminance-defined stimuli [Fig. 3(B), dark bar] was found to be *less* than 1.0. This result, which has been observed in previous *M:D* experiments (e.g., Derrington & Henning, 1993), is seemingly unrealizable, since it implies that the observer can discriminate direction of motion of a stimulus that is not seen. In fact, however, this non-intuitive result is resolved in models of detection/identification, in which factors such as the specific psychophysical procedure employed and the degree to which stimuli differ along a particular stimulus dimension are shown to influence the threshold values obtained (see Thomas, 1985).

Infant and adult absolute contrast thresholds. Next, to examine absolute r.m.s. cone contrast thresholds for luminance- and chromatically defined stimuli, individual threshold values were averaged across subjects, separately for infants and adults. Group means and standard errors are shown in Fig. 4, for luminance-defined (A) and chromatically defined (B) stimuli.* Infant luminance FPL and DEM thresholds were 9.2 and 11% r.m.s. cone contrast, respectively. Infant chromatic FPL and DEM thresholds were 15 and 21%, respectively.

Adult mean *D*, *M* and DEM thresholds for luminance-defined stimuli were 0.2, 0.2 and 0.4%, respectively. Mean chromatic *D*, *M* and DEM thresholds were 0.3, 0.5 and 1.3%, respectively. In general, adults were found to be greater than a log unit more sensitive than 3-month-old infants, in accordance with previous behavioral studies employing luminance-defined (e.g., Banks & Salapatek, 1978; Atkinson *et al.*, 1977a,b; Hartmann & Banks, 1992; Brown *et al.*, 1995; Dobkins & Teller, 1995) and chromatically defined (Brown *et al.*, 1995) stimuli.

*For the purpose of comparing threshold values between infants and adults, we present only the mean cone contrast thresholds from Infant Experiment 2 (since the conditions of Experiment 2, and not Experiment 1, matched the adult testing conditions). Cone contrast thresholds from Infant Experiment 1 were, on average, 1.5-fold lower than those of Experiment 2. This decrease is roughly consistent with the square root law, where a 1.83-fold increase in luminance (i.e., from 16 cd/m^2 in Experiment 2 to 30 cd/m^2 in Experiment 1) predicts a 1.35-fold decrease in threshold (e.g., Walvaren & Bouman, 1966; van Nes & Bouman, 1967; Koenderink *et al.*, 1978; Swanson *et al.*, 1987; Yeh *et al.*, 1993; Shannon *et al.*, 1996).

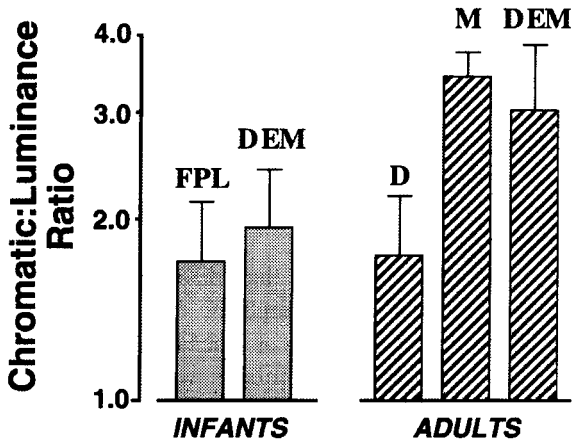

FIGURE 5. Group mean chromatic:luminance (C:L) contrast threshold ratios for infants and adults. Error bars denote standard errors of the means. For all conditions and for both age groups, r.m.s. cone contrast thresholds for chromatically defined gratings were higher than those for luminance-defined gratings, as evidenced by C:L ratios greater than 1.0. These data suggest that, at the particular spatiotemporal frequency tested, both infants and adults are more sensitive to luminance than to chromatic contrast.

Relative thresholds for chromatically vs. luminance-defined gratings: Chromatic:luminance (C:L) ratios

Because the contrasts of our chromatically and luminance-defined stimuli are expressed in the same units (i.e., r.m.s. cone contrast), we can make direct comparisons between the two types of stimuli by dividing chromatic thresholds by luminance thresholds. Chromatic:luminance (C:L) threshold ratios were calculated using between-subjects data for infants and within-subjects data for adults. Group mean C:L ratios and standard errors are presented in Fig. 5.

For infant FPL data, chromatic thresholds were significantly higher than luminance thresholds ($t_{23} = 2.30$, $P < 0.05$, 2-tailed), with a mean C:L ratio of 1.7. Likewise, for infant DEM data, chromatic thresholds were significantly higher than luminance thresholds ($t_{23} = 2.93$, $P < 0.025$, 2-tailed), with a mean C:L ratio of 1.9. A similar pattern was observed in adults. For adult detection (*D*) data, the mean C:L ratio was 1.7. Although the difference between chromatic and luminance detection thresholds was not significant ($t_4 = 2.15$, $P < 0.10$, 2-tailed), further statistical analysis revealed that the mean C:L ratio was significantly greater than 1.0 ($t_4 = 8.64$, $P < 0.005$, 2-tailed). For adult motion (*M*) data, chromatic thresholds were significantly higher than luminance thresholds ($t_4 = 11.50$, $P < 0.005$, 2-tailed), with a mean C:L ratio of 3.4. For adult eye movement (DEM) data, the C:L ratio was similarly elevated, with a mean C:L ratio of 3.0 ($t_4 = 3.88$, $P < 0.025$, 2-tailed).

In sum, for all conditions and for both age groups, cone contrast thresholds were higher for chromatic than for luminance stimuli, as evidenced by C:L ratios greater than 1.0. In accordance with previous adult data obtained for stimuli moving at similar speeds and/or temporal frequencies (Stromeyer *et al.*, 1990; Derrington & Henning, 1993; Gegenfurtner & Hawken, 1995), our data suggest that both infants and adults are more sensitive to luminance than to chromatic contrast when a r.m.s. cone contrast metric is used.

DISCUSSION

The major results from these experiments (Fig. 3) demonstrate that chromatic and luminance *M:D* ratios are highly similar and near 1:1 for 3-month-old infants. By contrast, chromatic *M:D* ratios in adults are significantly elevated above and about twice those for luminance. Unlike the case for adults, therefore, chromatic motion processing in infants does not appear to be impoverished relative to luminance motion processing. This difference between infants and adults may be explained by positing that, for adults, the most sensitive mechanisms for detecting luminance, but not chromatic, contrast are labeled for direction of motion; in contrast, for infants, the most sensitive mechanisms for detecting *both* luminance and chromatic contrast are labeled for direction of motion.

In addition to providing information about motion processing *per se*, the chromatic and luminance cone contrast thresholds obtained in our experiments allow us to look at C:L ratios, in terms of a cone contrast metric. The C:L ratios (Fig. 5) demonstrate that, for the spatiotemporal parameters employed, both infants and adults are more sensitive to luminance than to chromatic information. Moreover, comparisons between C:L ratios of infants and adults allow us to address the question of uniform vs differential contrast sensitivity losses in infants.

Errors in isoluminance settings?

Before proceeding with the discussion of the results and their significance, it is necessary to evaluate the possibility that our chromatically defined stimuli were not, in fact, precisely isoluminant for each individual subject. If our presumed chromatically defined stimuli contained detectable residual luminance contrast, our chromatic results would be confounded and less interpretable. With regard to the choice of individual isoluminance points, different strategies were used in adults and in infants. In adults, we used individual isoluminance point settings, which were obtained with motion photometry using stimuli of the same spatiotemporal frequency as that employed in the *M:D* study. For this reason we feel it highly unlikely that errors in individual isoluminance settings existed for our adult subjects. For infants, we used the mean isoluminance point setting from adult experiments. Under such conditions, our calculations (cf. Brown *et al.*, 1995) indicate that the largest likely error in isoluminance for any individual infant subject was no more than 2% luminance contrast (see Methods). Because this luminance contrast level is well below behavioral luminance contrast thresholds observed in 3-month-old infants of the present and previous studies (Banks & Salapatek, 1978; Atkinson *et al.*, 1977a,b; Swanson & Birch, 1990; Hartmann & Banks, 1992; Teller *et al.*, 1992a; Brown *et*

al., 1995; Dobkins & Teller, 1995), we feel certain that our heterochromatic stimuli did not produce any noticeable luminance contrast for infant subjects.

It should be mentioned, however, that even when stimuli are truly isoluminant, there are a number of ways in which such isoluminant stimuli can still potentially create luminance signals at various stages of visual processing. These possibilities include: chromatic aberration (e.g., Flitcroft, 1989), rod contamination (e.g., Brown, 1990; Lindsey, 1990; Mullen, 1991; Dobkins & Albright, 1993), variations in isoluminance points across neurons (Schiller & Colby, 1983; Lee *et al.*, 1988; Saito *et al.*, 1989; Logothetis *et al.*, 1990; Dobkins & Albright, 1994, 1995; Gegenfurtner *et al.*, 1994), variations in isoluminance across the retina due to variations in macular pigment or L/M cone ratios with eccentricity (e.g., Wooten *et al.*, 1975; Marc & Sperling, 1977; Stabell & Stabell, 1980, 1981; Viénot, 1980; Noorlander *et al.*, 1983; Livingstone & Hubel, 1987; Nerger & Cicerone, 1992), and temporal phase lags between the responses to red and green (e.g., Lindsey *et al.*, 1986; Smith, 1991). For the most part, the potential luminance signals produced by such factors are not thought to determine direction of motion discrimination of red/green isoluminant gratings [see Cavanagh & Anstis (1991) for adult discussion and Teller & Palmer (1996) for infant discussion].

Relative sensitivity for chromatically vs luminance-defined stimuli

Using a cone contrast metric, several investigators have demonstrated that, for slowly moving stimuli, adult contrast sensitivity for direction-of-motion discrimination is better for chromatic than for luminance stimuli (Stromeyer *et al.*, 1990; Derrington & Henning, 1993; Metha *et al.*, 1994; Gegenfurtner & Hawken, 1995; Stromeyer *et al.*, 1995), a seeming contradiction to the more common view that motion is impoverished when stimuli are defined solely by chromatic contrast. At temporal frequencies greater than about 4 Hz, however, subjects are more sensitive to luminance than to chromatic contrast, for both moving (Stromeyer *et al.*, 1990; Derrington & Henning, 1993; Gegenfurtner & Hawken, 1995) and flickering (Kelly & van Norren, 1977; Noorlander *et al.*, 1981; Smith *et al.*, 1995) stimuli. In our experiments, stimulus speed was set at 22 deg/sec (5.6 Hz). As would be expected for this speed/temporal frequency, we found both infants and adults to be more sensitive to luminance than to chromatic contrast, as evidenced by chromatic:luminance (C:L) threshold ratios greater than 1.0 (see Fig. 5).

It is worthwhile pointing out, however, that even under conditions for which both detection and direction-of-motion discrimination are better for chromatic than for luminance stimuli (i.e., at low speeds/temporal frequencies), discrimination:detection *(M:D)* ratios are nonetheless 1:1 for luminance-defined stimuli and greater than 1:1 for chromatically defined stimuli (e.g., Metha *et al.*, 1994; Gegenfurtner & Hawken, 1995). Despite the overall better performance for chromatically defined stimuli, therefore, such results still support the view that, relative to luminance input, chromatic input to direction-of-motion processing is limited. This notion has recently been reinforced by neurophysiological recordings in directionally selective neurons of extrastriate visual area MT of rhesus monkeys. Mirroring the perceptual effect at high temporal/low spatial frequencies, neurons in MT are clearly more sensitive to luminance than to chromatic contrast (Dobkins & Albright, 1994; Gegenfurtner *et al.*, 1994).

Infant chromatic vision: Uniform or differential loss?

Several psychophysical experiments have demonstrated that infant chromatic vision is poor [see Brown (1990) and Teller & Bornstein (1987) for a review]. It is not entirely clear, however, whether the poor chromatic vision exhibited by infants reflects a uniform loss of both chromatic and luminance contrast sensitivity or a differential loss of chromatic, with respect to luminance, sensitivity (Banks & Bennett, 1988; Brown, 1989, 1990; Banks & Shannon, 1993; Teller & Lindsey, 1993b). To distinguish between uniform vs differential loss hypotheses for red/green stimuli, several studies (Allen *et al.*, 1993; Morrone *et al.*, 1993; Teller & Lindsey, 1993b; Brown *et al.*, 1995; Kelly *et al.*, 1995; Teller & Palmer, 1996) have examined the development of chromatic (red/green) mechanisms with respect to luminance mechanisms. Although the issue remains controversial, the majority of studies to date report a uniform or near-uniform loss (but cf. Morrone *et al.*, 1993 for a more complex view).

By comparing infant chromatic:luminance threshold ratios (C:L) with those of adults, our experiments allow us to address the issue of uniform vs differential loss, for both detection and direction-of-motion tasks. If infants possess a differential loss for chromatic vision, C:L ratios should be higher in infants compared to adults. If, on the other hand, infant chromatic vision is poor due to a uniform contrast deficit, C:L ratios in infants should be the same as those of adults.

The results of C:L ratio comparisons differ for the two different tasks. In the detection task, we found comparable C:L ratios for infants and adults (compare "FPL" and "D" in Fig. 5). Thus, our detection data support a uniform, as opposed to a differential, loss for the detection of moving stimuli. In the direction-of-motion task, we found that infant C:L ratios were about a factor of 1.7 *lower* than those of adults (compare infant "DEM" and adult "M" and "DEM" in Fig. 5), a result which is qualitatively the same as that previously reported by Brown *et al.* (1995). In other words, when direction-of-motion discrimination is used as a behavioral assay, the data show a reverse trend, i.e., a differential precocity for chromatic with respect to luminance vision. Note that this effect observed under direction-of-motion conditions is expected from the fact that, in contrast to adult data, chromatic *M:D* ratios in infants are *not* elevated compared to luminance *M:D* ratios.

Interestingly, the C:L results from the direction-of-motion task in the present study and that of Brown *et al.* (1995) lead to a somewhat different conclusion from that of Teller & Lindsey (1993b), who used a motion nulling technique to address the issue of uniform vs differential losses. The stimulus in their experiments consisted of a 0.15 or 0.3 c/deg luminance-modulated (yellow/black) and a chromatically modulated (red/green) grating, superimposed and moving in opposite directions at a speed of 25 deg/sec. Using an eye movement-based technique similar to that described in the present study, they judged the direction of eye movements to determine the point of motion nulling, in 1-month-olds, 2-month-olds and adults. The results from this study, which were further analyzed in a more recent manuscript (Teller & Palmer, 1996), showed that 15% contrast luminance-defined gratings were about equally effective in nulling the motion of the red/green grating in infants and adults, and that the equivalent luminance contrast of the red/green grating (8–10%) was approximately the same for all ages. These results therefore suggest that, with respect to processing direction-of-motion signals, infants exhibit a uniform contrast sensitivity loss for luminance- vs chromatically defined stimuli.

Since the spatial frequency and speed values used in the present study were similar to those used in the Teller and Lindsey study, differences in results cannot be attributed to these factors. It is possible, however, that the differences may be attributable to different age groups used between studies (1–2-month-olds vs 3-month-olds). Another possible reason for the different results between studies concerns the fact that the motion nulling paradigm uses *suprathreshold* stimuli, whereas the *M:D* study is a *threshold* experiment. In other words, whereas the present study is designed to isolate the most sensitive contrast mechanisms, the motion nulling paradigm may call upon a broader range of mechanisms. Due to this difference, chromatic input to motion processing may appear similar for infants and adults when stimuli are above, but not at, detection threshold.

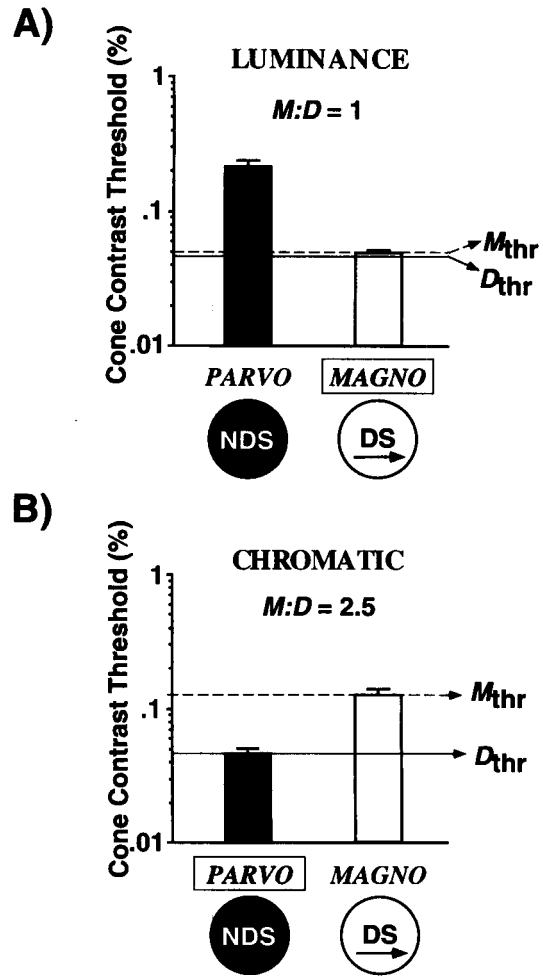

FIGURE 6. Adult model: contrast sensitivities of parvocellular and magnocellular neurons may account for psychophysically determined *M:D* ratios. The solid and open bars show the mean cone contrast thresholds for a population of parvocellular ("parvo") and magnocellular ("magno") retinal ganglion cells in mature macaque monkeys tested with 4 Hz flickering stimuli. Responses to luminance-defined and chromatically defined stimuli are shown in (A) and (B), respectively. Means and standard errors were estimated from neurophysiological data presented in Fig. 3 of Lee *et al.* (1989a). Note that magnocellular is designated as directionally selective (DS, and arrow), while parvocellular is designated as non-directionally selective (NDS) (see text). For each condition (i.e., luminance and chromatic), the most sensitive pathway is highlighted below in gray. (A) Luminance-defined stimuli: when stimuli are luminance-defined, magnocellular neurons are more sensitive than parvocellular neurons. Hence, the directionally selective magnocellular pathway is expected to underlie both detection (*D*, solid horizontal line) and direction-of-motion (*M*, dashed horizontal line) thresholds, producing *M:D* ratios near 1:1. (B) Chromatically defined stimuli: by contrast, when stimuli are chromatically defined, parvocellular neurons are more sensitive than magnocellular neurons. Thus, the parvocellular pathway is expected to underlie detection. However, since the parvocellular pathway is not directionally selective, it can not provide a direction-of-motion signal; hence, the directionally selective magnocellular pathway will underlie direction-of-motion thresholds. Owing to the 2.5-fold difference in chromatic contrast thresholds between magnocellular and parvocellular neurons, chromatic *M:D* ratios are expected to be near 2.5:1.

Model of underlying mechanisms: Adults

At the theoretical level, an *M:D* ratio of 1:1 has been taken to indicate that the mechanism responsible for detection (i.e., the most sensitive mechanism) is one that, when activated, is sufficient to signal direction of motion. In other words, the mechanism must be directionally selective, and the output of individual analyzers must be labeled for direction of motion (e.g., Watson & Robson, 1981; Thomas, 1985). Because adult *M:D* ratios for luminance-defined stimuli are typically near 1:1, it is accepted that the most sensitive luminance contrast detectors in adults are directionally selective. Conversely, adult *M:D* ratios for chromatically defined stimuli, which are typically greater than 1:1, indicate that the most sensitive chromatic contrast detectors in adults are *not* directionally selective.

Because much is known regarding the neural processing of chromatic, luminance, and motion information in the adult visual system of primates, we are afforded the opportunity to speculate about the neural origins of the *M:D* ratios observed in adults. A wealth of anatomical and neurophysiological data from monkeys has demon-

strated the existence of two distinct pathways—parvocellular and magnocellular—which originate in the retina and remain segregated through several levels of visual processing [see Van Essen (1985) and DeYoe & Van Essen (1988) for a review]. With regard to luminance and chromatic contrast sensitivity, the results from several investigations have demonstrated that, at early stages of visual processing (i.e., in the retina and LGN), neurons most sensitive to luminance contrast are found within the magnocellular pathway, while neurons most sensitive to chromatic contrast are found within the parvocellular pathway (Shapley *et al.*, 1981; Derrington & Lennie, 1984; Kaplan & Shapley, 1986; Lee *et al.*, 1988, 1989a, 1990; Kremers *et al.*, 1992; Lee *et al.*, 1993; Croner & Kaplan, 1995). It is important to emphasize, however, that this separation is not absolute: in fact, both magnocellular and parvocellular neurons respond to both luminance-defined and red/green chromatically defined stimuli, although with different contrast thresholds.

To illustrate the differential luminance vs. chromatic contrast sensitivities, we have calculated mean contrast thresholds of magnocellular and parvocellular retinal ganglion cells based on neurophysiological data from mature macaque monkeys (Lee *et al.*, 1989a). Mean contrast thresholds and standard errors for a population of magnocellular and parvocellular neurons are shown in Fig. 6. When the stimulus consists of a luminance-defined patch flickering at 4 Hz, magnocellular neurons exhibit luminance contrast thresholds that are, on average, 4.3-fold lower than those of parvocellular neurons [Fig. 6(A)]. When the stimulus is defined by chromatic contrast (red/green), however, magnocellular neurons exhibit chromatic contrast thresholds that are, on average, 2.7-fold *higher* than those of parvocellular neurons [Fig. 6(B)]. The chromatic response observed in magnocellular retinal ganglion cells is one of "frequency-doubling", i.e., magnocellular neurons respond with equal zeal to the onset of either the red or green phase of the stimulus (Lee *et al.*, 1988, 1989a,b,c). These frequency-doubled responses, which are also observed in magnocellular neurons of the LGN (Schiller & Colby, 1983; Derrington *et al.*, 1984; Logothetis *et al.*, 1990), provide a signal for the existence of chromatic contrast, without conveying information about the nature of the chromatic signal *per se* (e.g., see Dobkins & Albright, 1993, 1994).

With regard to motion sensitivity, all lines of evidence suggest that directional selectivity is a property that emerges within cortical stages of the magnocellular, and not the parvocellular, pathway (e.g., Dubner & Zeki, 1971; Dow, 1974; Zeki, 1978; Maunsell & Van Essen, 1983; Albright, 1984; Van Essen, 1985; Mikami *et al.*, 1986; Schiller *et al.*, 1990). Moreover, there exists substantial evidence that the magnocellular-dominated areas of cortex, such as extrastriate area MT, provide signals required for direction-of-motion discrimination (e.g., Newsome *et al.*, 1985, 1989; Britten *et al.*, 1992; Salzman *et al.*, 1992; Celebrini & Newsome, 1994). Thus, whereas activity in *either* the magnocellular or parvocellular pathway is expected to be sufficient for signalling detection of a moving stimulus, only when the magnocellular (motion) pathway is active can direction-of-motion in the stimulus be discriminated. Following this logic, because the magnocellular pathway is the most sensitive system for detecting luminance contrast, but not chromatic contrast, direction of motion should be discernable at detection threshold for luminance-defined stimuli, but not for chromatically defined stimuli.

Bearing this in mind, we propose a simple model that can explain adult *M:D* ratios in terms of activity within magnocellular and parvocellular pathways. The essential characteristics of this model are illustrated in a schematized form in Fig. 6, using known contrast thresholds of magnocellular and parvocellular neurons in mature macaque retina (Lee *et al.*, 1989a). Note that the magnocellular, and not the parvocellular, pathway is designated as directionally selective.

For luminance-defined stimuli [Fig. 6(A)], the directionally selective magnocellular pathway is expected to underlie both detection (*D*) and direction-of-motion (*M*) psychophysical thresholds, thus producing *M:D* ratios near 1:1. For chromatically defined stimuli [Fig. 6(B)], the non-directionally selective (NDS) parvocellular pathway is expected to underlie detection, however, the magnocellular pathway will continue to underlie direction-of-motion thresholds. Owing to the 2.5-fold difference in chromatic contrast thresholds between magnocellular and parvocellular neurons, chromatic *M:D* ratios are expected to be near 2.5:1. Thus, this model can sufficiently account for the results of present and previous experiments in adult subjects; luminance *M:D* ratios near 1:1 and chromatic *M:D* ratios of 2:1 or more.

Model of underlying mechanisms: Infants

In our infant experiments, we found that *M:D* ratios were near 1:1 for luminance-defined stimuli (see Fig. 2 and earlier discussion of task difficulty). A speculative model to account for infant luminance data is shown in Fig. 7(A). Here, we have plotted mean contrast thresholds of magnocellular and parvocellular LGN neurons based on neurophysiological data from a 2-month-old infant macaque monkey (Hawken *et al.*, 1996). For luminance-defined 0.25 c/deg gratings (temporal frequency range = 3–6 Hz), magnocellular neurons are about twice as sensitive as parvocellular neurons. Moreover, Hawken *et al.* report that many parvocellular LGN neurons in the newborn and 2-month-old monkey fail to respond, even at the highest contrasts. In addition, recent neurophysiological experiments in infant macaque monkeys have demonstrated that magnocellular divisions of infant extrastriate cortex exhibit the type of directionally selective responses observed in adults (Distler *et al.*, 1990; Rodman *et al.*, 1991, 1993), suggesting that the infant's magnocellular pathway signals direction-of-motion. As was the case for adults, therefore, infant *M:D* ratios near 1:1 for luminance-defined stimuli can be explained by the fact that the magnocellular pathway, which provides signals for direction-of-motion, is more

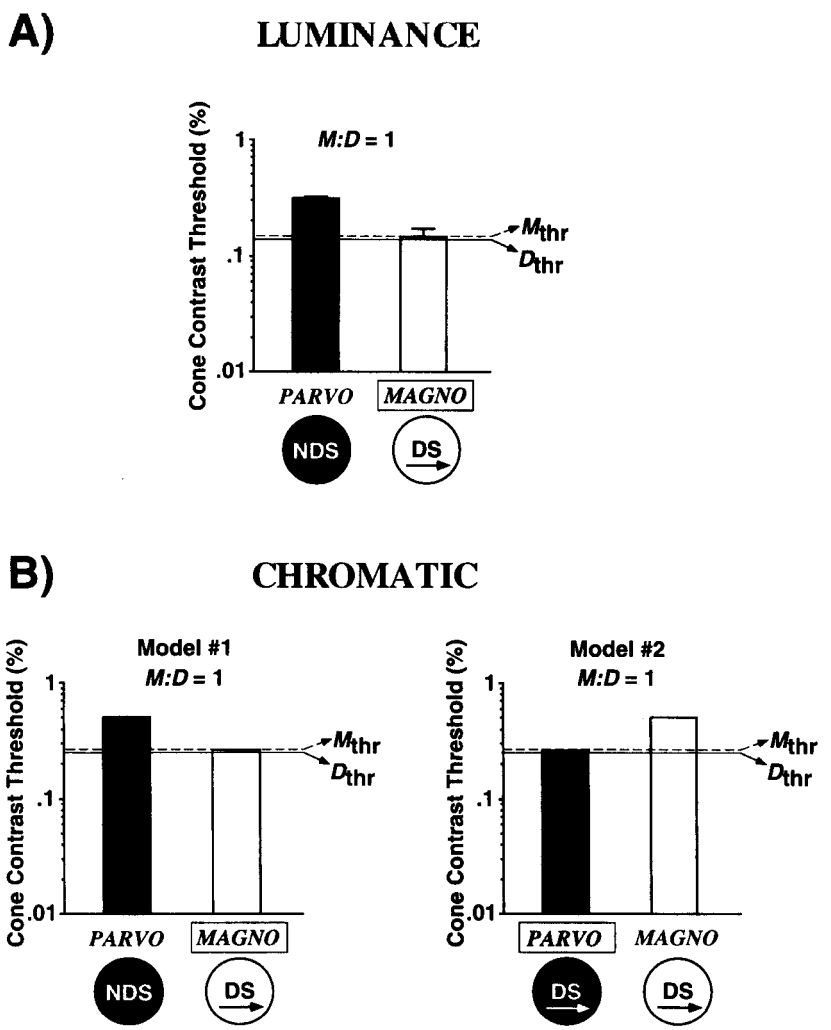

FIGURE 7. Infant model: response properties of parvocellular and magnocellular neurons may account for psychophysically determined *M:D* ratios. All conventions are the same as in Fig. 6. (A) Luminance-defined stimuli: mean cone contrast thresholds are shown for magnocellular and parvocellular LGN neurons in a 2-month-old macaque monkey (Hawken *et al.*, 1995). For luminance-defined 0.25 c/deg gratings (temporal frequency range = 3–6 Hz), magnocellular neurons are about twice as sensitive as parvocellular neurons. If the infant's magnocellular pathway is directionally selective (DS), as is the case for adults, magnocellular responses in infants will underlie both detection and direction-of-motion thresholds, thus producing luminance *M:D* ratios near 1:1. (B) Chromatically defined stimuli—two models: model 1 (left) posits a superior sensitivity of infant magnocellular neurons to chromatic contrast. In this scenario, the magnocellular pathway in infants underlies both detection and direction-of-motion thresholds, resulting in a chromatic *M:D* ratio of 1:1. Model 2 (right) posits that parvocellular neurons are more sensitive to chromatic contrast than are magnocellular neurons, but that the infant's parvocellular pathway contributes to motion processing (note the "DS" and arrow below "parvo"). In this scenario, the parvocellular pathway in infants underlies both detection and direction-of-motion thresholds, again resulting in a chromatic *M:D* ratio of 1:1.

sensitive to luminance contrast than is the parvocellular pathway.

With respect to the chromatic data, the surprising finding of the present study is that infant chromatic *M:D* ratios are also near 1:1. This result suggests that, in infants, as distinct from adults, chromatic contrast thresholds for both detection and direction-of-motion are determined by the *same* mechanism, and that this mechanism is directionally selective. There are at least two different potential scenarios that could give rise to such a situation, which are schematized in Fig. 7(B). The first model supposes that, in infants, the developing magnocellular pathway shows a relatively enhanced sensitivity to chromatic contrast, so that is it as sensitive or more sensitive to chromatic contrast than is the developing parvocellular pathway. By contrast, the second model supposes that the developing parvocellular pathway is the most sensitive pathway for detecting chromatic contrast, and that this pathway also plays a significant transient role in motion processing early in development.

Model 1: Magnocellular neurons exhibit relatively enhanced chromatic sensitivity. The first model proposes that, opposite to adults, magnocellular neurons are as or more sensitive to chromatic contrast than are parvocellular neurons [Fig. 7(B), left]. In this scenario, chromatic *M:D* ratios near 1:1 can be explained by positing that the magnocellular pathway in infants underlies both detection and direction-of-motion discrimination of moving chromatically defined stimuli, as it does for luminance-

defined stimuli [cf. Fig. 7(A)]. This situation could come about if infant magnocellular neurons are uniformly functionally more mature than parvocellular neurons, exceeding them in sensitivity under all conditions. Alternatively, it is possible that a superior magnocellular sensitivity to chromatic stimuli exists only at specific spatiotemporal frequencies (i.e., those employed in our experiments, 0.25 c/deg, 5.6 Hz), but not all.

The possibility of enhanced maturity for the magnocellular with respect to parvocellular pathway is supported by the finding that, for luminance-defined stimuli, magnocellular neurons are generally more responsive than parvocellular neurons (Hawken *et al.*, 1996). (It is possible, of course, that the dull responses observed in infant parvocellular neurons may be due to the fact that luminance stimuli are not optimal for eliciting responses in these cells.) Further evidence that the infant magnocellular pathway may be functionally more mature than the parvocellular pathway comes from recent anatomical studies in infant macaques. Synapse maturation occurs earlier for magnocellular-recipient neurons in area V1, compared to parvocellular-recipient neurons (Lund & Harper, 1991; Lund & Holbach, 1991), suggesting that the magnocellular system develops faster.

Alternatively, a relatively enhanced chromatic contrast sensitivity for magnocellular neurons could arise if the signals generated from parvocellular neurons are subjected to more low-pass temporal filtering than are magnocellular neurons, as has been previously described for adult neurophysiological data (e.g., Lee *et al.*, 1990). In this scenario, parvocellular neurons might be more sensitive to chromatic contrast than magnocellular neurons at an *early* stage of visual processing (e.g., in the LGN), yet a lower corner frequency filter for parvocellular signals, compared to magnocellular signals, would result in a relatively superior magnocellular sensitivity at a later stage of visual processing. Regardless of whether the enhanced magnocellular sensitivity occurs at an early or late stage, model 1 suggests that, at the spatiotemporal frequency tested, the magnocellular pathway in infants is responsible for both detection *and* discrimination of chromatically defined stimuli, as is the case for luminance-defined stimuli.

Model 2: Transient parvocellular contribution to motion processing. Alternatively, if neurons at early stages of the infant's parvocellular pathway are more sensitive to chromatic contrast than are magnocellular neurons (as is the case for adults), how might we explain infant chromatic *M:D* ratios near 1:1? Our second model proposes that the infant parvocellular pathway, unlike that of the adult, plays a significant role in motion processing. Such a situation could occur if, early in development, parvocellular neurons provide input to cortical areas involved in motion processing, but that these inputs are retracted later in development. In support of the general feasibility of this idea, several studies in infant monkeys have demonstrated the existence of immature branching patterns, which later become more refined (e.g., Callaway & Katz, 1990; Florence & Casagrande, 1990; Burkhalter, 1993; Pospichal *et al.*, 1994), as well as transient cortical connections (e.g. Dehay *et al.*, 1984, 1988a,b, 1989; Webster *et al.*, 1991; Rodman & Consuelos, 1994).

For example, it is possible that in infants, parvocellular geniculocortical neurons project to magnocellular-recipient layers of area V1, which, in turn, project to motion processing areas. This possibility is rather tenuous, however, since parvocellular and magnocellular geniculocortical axons in newborn monkeys are restricted to their respective recipient layers in V1, as is the case for adults (Florence & Casagrande, 1990; Littlejohn & Casagrande, 1994; Pospichal *et al.*, 1994). Another potential site where parvocellular signals might mingle with motion detectors is in motion-processing area MT. For example, neurophysiological experiments in adult monkeys have demonstrated a weak parvocellular input to extrastriate area MT (Maunsell *et al.*, 1990). Whether these connections are more prominent in infant animals is yet unknown. In any event, it seems that there are many means by which inputs from infant parvocellular neurons might have transient access to motion detectors, such that parvocellular contribution to motion is relatively stronger in infants than in adults. Interactions of this sort could create motion detectors in infants that possess chromatic contrast sensitivity reflective of the parvocellular pathway, which, in turn, might result in chromatic *M:D* ratios near 1:1.

SUMMARY

In summary, the results from these studies demonstrate that, unlike adults, 3-month-old infants do *not* exhibit chromatic *M:D* ratios that are elevated above those for luminance-defined stimuli. In other words, in contrast to the case for adults, chromatic input to motion processing does not appear to be selectively impaired in infants. In theoretical terms, these findings suggest that, for adults, the most sensitive mechanisms for detecting luminance contrast, but *not* chromatic contrast, are directionally selective. In contrast, in infants, the equally low *M:D* ratios for chromatic and luminance conditions suggest that infants' most sensitive mechanisms for detecting chromatic contrast *are* directionally selective. The low chromatic *M:D* ratios in infants lead us to predict that neural immaturities will be found in infant primates, such that the neural pathway most sensitive to chromatic contrast is also involved in signalling direction-of-motion.

REFERENCES

Albright, T. D. (1984). Direction and orientation selectivity of neurons in visual area MT of the macaque. *Journal of Neurophysiology, 52*, 1106–1130.

Allen, D., Banks, M. S. & Norcia, A. M. (1993). Does chromatic sensitivity develop more slowly than luminance sensitivity? *Vision Research, 33*, 2553–2562.

Atkinson, J. & Braddick, O. J. (1981). Development of optokinetic nystagmus in infants: An indicator of cortical binocularity? In Fisher, D. F., Monty, R. A. & Senders, J. W. (Eds), *Eye movements: Cognition and visual perception*. Hillsdale, NJ: Erlbaum.

Atkinson, J., Braddick, O. & Braddick, F. (1974). Acuity and contrast sensitivity of infant vision. *Nature, 247*, 403–404.

Atkinson, J., Braddick, O. & Moar, K. (1977a). Development of contrast sensitivity over the first 3 months of life in the human infant. *Vision Research, 17,* 1037–1044.

Atkinson, J., Braddick, O. & Moar, K. (1977b), Contrast sensitivity of the human infant for moving and static patterns. *Vision Research, 17,* 1045–1047.

Banks, M. S. & Bennett, P. J. (1988). Optical and photoreceptor immaturities limit the spatial and chromatic vision of human neonates. *Journal of the Optical Society of America A, 5,* 2059–2079.

Banks, M. S. & Salapatek, P. (1978). Acuity and contrast sensitivity in 1-, 2-, and 3-month-old human infants. *Investigative Ophthalmology & Visual Science, 17,* 361–365.

Banks, M. S. & Shannon, E. (1993). Spatial and chromatic visual efficiency in human neonates. In Granrud, C. E. (Ed.), *Visual perception and cognition in infancy* (pp. 1–46). Hillsdale, NJ: Laurence Erlbaum.

Bieber, M., Volbrecht, V. & Werner, J. (1995). Spectral efficiency measured by heterochromatic flicker photometry is similar in human infants and adults. *Vision Research,* 35, 1385–1392.

Boynton, R. M. (1986). A system of photometry and colorimetry based on cone excitations. *Color Research and Application, 11,* 244–252.

Britten, K. H., Shadlen, M. N., Newsome, W. T. & Movshon, J. A. (1992). The analysis of visual motion: A comparison of neuronal and psychophysical performance. *Journal of Neuroscience, 12,* 4745–4765.

Brown, A. M. (1989). Issues in human color development. In Kulikowski, J. (Ed.), *Seeing contour and colour.* Oxford: Pergamon Press.

Brown, A. M. (1990). Development of visual sensitivity to light and color vision in human infants: A critical review. *Vision Research, 30,* 1159–1188.

Brown, A. M., Lindsey, D. T., McSweeney, E. M. & Walters, M. M. (1995). Infant luminance and chromatic contrast sensitivity: Optokinetic nystagmus data on 3-month-olds. *Vision Research, 35,* 3145–3160.

Burkhalter, A. (1993). Development of forward and feedback connections between areas V1 and V2 of human visual cortex. *Cerebral Cortex, 3,* 476–487.

Burr, D. C., Ross, J. & Morrone, M. C. (1986). Smooth and sampled motion. *Vision Research, 26,* 643–652.

Callaway, E. M. & Katz, L. C. (1990). Emergence and refinement of clustered horizontal connections in cat striate cortex. *Journal of Neuroscience, 10,* 1134–1153.

Cavanagh, P. & Anstis, S. (1991). The contribution of color to motion in normal and color-deficient observers. *Vision Research, 31,* 2109–2148.

Cavanagh, P. & Favreau, O. E. (1985). Color and luminance share a common motion pathway. *Vision Research, 25,* 1595–1601.

Cavanagh, P., Tyler, C. W. & Favreau, O. E. (1984). Perceived velocity of moving chromatic gratings. *Journal of the Optical Society of America A, 1,* 893–899.

Celebrini, S. & Newsome, W. T. (1994). Neuronal and psychophysical sensitivity to motion signals in extrastriate area MST of the macaque monkey. *Journal of Neuroscience, 14,* 4109–4124.

Chaparro, A., Stromeyer, C. d., Huang, E. P., Kronauer, R. E. & Eskew, R. J. (1993). Colour is what the eye sees best. *Nature, 361,* 348–350.

Cowan, C. B. (1983). An inexpensive scheme for calibration of a colour monitor in terms of CIE standard coordinates. *Computer Graphics, 17,* 315–321.

Croner, L. J. & Kaplan, E. (1995). Receptive fields of P and M ganglion cells across the primate retina. *Vision Research, 35,* 7–24.

Dayton, G. O., Jones, M. H., Aiu, P., Rawson, R. A., Steele, B. & Rose, M. (1964). Developmental study of co-ordinated eye movements in the human infant. I. A study based on induced optokinetic nystagmus recorded by electroculography. *Archives of Ophthalmology, 71,* 865–870.

Dehay, C., Bullier, J. & Kennedy, H. (1984). Transient projections from the fronto-parietal and temporal cortex to areas 17, 18 and 19 in the kitten. *Experimental Brain Research, 57,* 208–212.

Dehay, C., Horsburgh, G. & Kennedy, H. (1989). Maturation and connectivity of the visual cortex in monkey is altered by prenatal removal of retinal input [see comments]. *Proceedings of the National Academy of Science USA, 86,* 8093–8097.

Dehay, C., Kennedy, H. & Bullier, J. (1988a). Characterization of transient cortical projections from auditory, somatosensory, and motor cortices to visual areas 17, 18, and 19 in the kitten. *Behavioural Brain Research, 29,* 237–244.

Dehay, C., Kennedy, H., Bullier, J. & Berland, M. (1988b). Absence of interhemispheric connections of area 17 during development in the monkey. *Journal of Comparative Neurology, 272,* 68–89.

DeMarco, P., Pokorny, J. & Smith, V. C. (1992). Full-spectrum cone sensitivity functions for X-chromosome-linked anomalous trichromats. *Journal of the Optical Society of America A, 9,* 1465–1476.

Derrington, A. M. & Badcock, D. R. (1985). The low level motion system has both chromatic and luminance inputs. *Vision Research, 25,* 1879–1884.

Derrington, A. M. & Henning, G. B. (1993). Detecting and discriminating the direction of motion of luminance and colour gratings. *Vision Research, 33,* 799–811.

Derrington, A. M., Krauskopf, J. & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology (London), 357,* 241–265.

Derrington, A. M. & Lennie, P. (1984). Spatial and temporal contrast sensitivities of neurones in lateral geniculate nucleus of macaque. *Journal of Physiology (London), 357,* 219–240.

DeYoe, E. A. & Van Essen, D. C. (1988). Concurrent processing streams in monkey visual cortex. *Trends in Neuroscience, 11,* 219–226.

Distler, C., Ungerleider, L. G., Bachevalier, J. & Mishkin, M. (1990). Functional development of the cortical visual pathway for motion analysis in rhesus monkeys. *Society for Neuroscience Abstracts, 16,* 5.

Dobkins, K. R. & Albright, T. D. (1993). What happens if it changes color when it moves?: Psychophysical experiments on the nature of chromatic input to motion detectors. *Vision Research, 33,* 1019–1036.

Dobkins, K. R. & Albright, T. D. (1994). What happens if it changes color when it moves?: The nature of chromatic input to macaque visual area MT. *The Journal of Neuroscience, 14,* 4854–4870.

Dobkins, K. R. & Albright, T. D. (1995). Behavioral and neural effects of chromatic isoluminance in the primate visual motion system. *Visual Neuroscience, 12,* 321–332.

Dobkins, K. R. & Teller, D. Y. (1995). Infant contrast detectors are selective for direction of motion. *Vision Research, 36,* 281–294.

Dow, B. (1974). Functional classes of cells and their laminar distribution in monkey visual cortex. *Journal of Neurophysiology, 37,* 927–946.

Dubner, R. & Zeki, S.M. (1971). Response properties and receptive fields of cells in an anatomically defined region of the superior temporal sulcus in the monkey. *Brain Research, 35,* 528–532.

Flitcroft, D. I. (1989). The interactions between chromatic aberration, defocus and stimulus chromaticity: Implications for visual physiology and colorimetry. *Vision Research, 29,* 349–360.

Florence, S. L. & Casagrande, V. A. (1990). Development of geniculocortical axon arbors in a primate. *Visual Neuroscience, 5,* 291–309.

Gegenfurtner, K. R. & Hawken, M. J. (1995). Temporal and chromatic properties of motion mechanisms. *Vision Research, 35,* 1547–1563.

Gegenfurtner, K. R., Kiper, D. C., Beusmans, J. M., Carandini, M., Zaidi, Q. & Movshon, J.A. (1994). Chromatic properties of neurons in macaque MT. *Visual Neuroscience, 11,* 455–466.

Graham, N. V. S. (1989). *Visual pattern analyzers.* New York: Oxford University Press.

Green, M. (1983). Contrast detection and direction discrimination of drifting gratings. *Vision Research, 23,* 281–289.

Hainline, L., de Bie, J., Abramov, I. & Camenzuli, C. (1987). Eye movement voting: A new technique for deriving spatial contrast sensitivity. *Clinical Vision Science, 2,* 33–44.

Hainline, L., Lemerise, E., Abramov, I. & Turkel, J. (1984).

Orientational asymmetries in small-field optokinetic nystagmus in human infants. *Behavioural Brain Research, 13*, 217–230.

Hamer, R. D. & Norcia, A. M. (1984). The development of motion sensitivity during the first year of life. *Vision Research, 34*, 2387–2402.

Hartmann, E. E. & Banks, M. S. (1992). Temporal contrast sensitivity in human infants. *Vision Research, 32*, 1163–1168.

Hawken, M. J., Blakemore, C. & Morley, J. W. (1996). Development of contrast sensitivity and temporal frequency in primate lateral geniculate nucleus. *Experimental Brain Research*, in press.

Kaplan, E. & Shapley, R. M. (1986). The primate retina contains two types of ganglion cells, with high and low contrast sensitivity. *Proceedings of the National Academy of Science USA, 83*, 2755–2757.

Kelly, D. H. & van Norren, D. (1977). Two-band model of heterochromatic flicker. *Journal of the Optical Society of America, 67*, 1081–1091.

Kelly, J. P., Borchert, K. & Teller, D. T. (1995). The development of chromatic and achromatic contrast sensitivity in infancy as tested with the sweep VEP. *Vision Research*, submitted.

Koenderink, J. J., Bouman, M. A., Beuno-de-Mesquita, A. E. & Slappendel, S. (1978). Perimetry of contrast detection thresholds of moving spatial sine wave patterns: IV. The influence of mean retinal illuminance. *Journal of the Optical Society of America, 68*, 860–865.

Kremenitzer, J. P., Vaugham, H. G. J., Kutzberg, D. & Dowling, K. (1979). Smooth-pursuit eye movements in newborn infants. *Child Development, 50*, 442–448.

Kremers, J., Lee, B. B. & Kaiser, P. K. (1992). Sensitivity of macaque retinal ganglion cells and human observers to combined luminance and chromatic temporal modulation. *Journal of the Optical Society of America A, 9*, 1477–1485.

Lee, B. B., Martin, P. R. & Valberg, A. (1988). The physiological basis of heterochromatic flicker photometry demonstrated in the ganglion cells of the macaque retina. *Journal of Physiology (London), 404*, 323–347.

Lee, B. B., Martin, P. R. & Valberg, A. (1989a). Sensitivity of macaque retinal ganglion cells to chromatic and luminance flicker. *Journal of Physiology (London), 414*, 223–243.

Lee, B. B., Martin, P. R. & Valberg, A. (1989b). Amplitude and phase of responses of macaque retinal ganglion cells to flickering stimuli. *Journal of Physiology (London)*, 245–263.

Lee, B. B., Martin, P. R. & Valberg, A. (1989c). Nonlinear summation of M- and L-cone inputs to phasic retinal ganglion cells of the macaque. *Journal of Neuroscience, 9*, 1433–1442.

Lee, B. B., Martin, P. R., Valberg, A. & Kremers, J. (1993). Physiological mechanisms underlying psychophysical sensitivity to combined luminance and chromatic modulation. *Journal of the Optical Society of America A, 10*, 1403–1412.

Lee, B. B., Pokorny, J., Smith, V. C., Martin, P. R. & Valberg, A. (1990). Luminance and chromatic modulation sensitivity of macaque ganglion cells and human observers. *Journal of the Optical Society of America A, 7*, 2223–2236.

Lennie, P. & D'Zmura, M. (1988). Mechanisms of color vision. *Critical Reviews in Neurobiology, 3*, 333–400.

Lindsey, D. T. (1990). Linear analysis of eccentricity-dependent changes in the null-based isoluminant plane. *Optical Society of America Annual Meeting, 15*, 166.

Lindsey, D. T., Pokorny, J. & Smith, V. C. (1986). Phase-dependent sensitivity to heterochromatic flicker. *Journal of the Optical Society of America A, 3*, 921–927.

Lindsey, D. T. & Teller, D. Y. (1990). Motion at isoluminance: Discrimination/detection ratios for moving isoluminant gratings. *Vision Research, 30*, 1751–1761.

Littlejohn, C. D. & Casagrande, V. A. (1994). Axon development in striate cortex (V1) of prenatal macaque monkeys. *Investigative Ophthalmology and Visual Science Suppl, 35*, 1773.

Livingstone, M. S. & Hubel, D. H. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *Journal of Neuroscience, 7*, 3416–3468.

Logothetis, N. K., Schiller, P. H., Charles, E. R. & Hurlbert, A. C. (1990). Perceptual deficits and the activity of the color-opponent and broad-band pathways at isoluminance. *Science, 247*, 214–217.

Lund, J. S. & Harper, T. R. (1991). Postnatal development of thalamic recipient neurons in the monkey striate cortex: III. Somatic inhibitory synapse acquisition by spiny stellate neurons of layer 4C. *Journal of Comparative Neurology, 309*, 141–149.

Lund, J. S. & Holbach, S. M. (1991). Postnatal development of thalamic recipient neurons in the monkey striate cortex: I. Comparison of spine acquisition and dendritic growth of layer 4C alpha and beta spiny stellate neurons. *Journal of Comparative Neurology, 309*, 115–128.

MacLeod, D. I. & Boynton, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America, 69*, 1183–1186.

Marc, R. E. & Sperling, H. G. (1977). Chromatic organization of primate cones. *Science, 196*, 454–456.

Maunsell, J. H., Nealey, T. A. & DePriest, D. D. (1990). Magnocellular and parvocellular contributions to responses in the middle temporal visual area (MT) of the macaque monkey. *Journal of Neuroscience, 10*, 3323–3334.

Maunsell, J. H. & Van Essen, D. C. (1983). Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. *Journal of Neurophysiology, 49*, 1127–1147.

Maurer, D., Lewis, T. L., Cavanagh, P. & Anstis, S. (1989). A new test of luminous efficiency for babies. *Investigative Ophthalmology & Visual Science, 30*, 297–303.

Metha, A. B., Vingrys, A. J. & Badcock, D. R. (1994). Detection and discrimination of moving stimuli: The effects of color, luminance, and eccentricity. *Journal of the Optical Society of America A, 11*, 1697–1709.

Mikami, A., Newsome, W. T. & Wurtz, R. H. (1986). Motion selectivity in macaque visual cortex. I. Mechanisms of direction and speed selectivity in extrastriate area MT. *Journal of Neurophysiology, 55*, 1308–1327.

Moreland, J. D. (1982). Spectral sensitivity measured by motion photometry. *Documenta Ophthalmologica Proceedings Series, 33*, 61–66.

Morrone, M. C., Burr, D. C. & Fiorentini, A. (1993). Development of infant contrast sensitivity to chromatic stimuli. *Vision Research, 33*, 2535–2552.

Mullen, K. T. (1985). The contrast sensitivity of human colour vision to red–green and blue–yellow chromatic gratings. *Vision Research, 27*, 829–839.

Mullen, K. T. (1991). Colour vision as a post-receptoral specialization of the central visual field. *Vision Research, 31*, 119–130.

Mullen, K. T. & Baker, C. J. (1985). A motion aftereffect from an isoluminant stimulus. *Vision Research, 25*, 685–688.

Mullen, K. T. & Boulton, J. C. (1992). Absence of smooth motion perception in color vision. *Vision Research, 32*, 483–488.

Nerger, J. L. & Cicerone, C. M. (1992). The ratio of L cones to M cones in the human parafoveal retina. *Vision Research, 32*, 879–888.

Newsome, W. T., Britten, K.H. & Movshon, J. A. (1989). Neuronal correlates of a perceptual decision. *Nature, 341*, 52–54.

Newsome, W. T., Wurtz, R. H., Dursteler, M. R. & Mikami, A. (1985). Deficits in visual motion processing following ibotenic acid lesions of the middle temporal visual area of the macaque monkey. *Journal of Neuroscience, 5*, 825–840.

Noorlander, C., Heuts, M. J. & Koenderink, J. J. (1981). Sensitivity to spatiotemporal combined luminance and chromaticity contrast. *Journal of the Optical Society of America, 71*, 453–459.

Noorlander, C., Koenderink, J. J., den Ouden, R. J. & Edens, B. W. (1983). Sensitivity to spatiotemporal colour contrast in the peripheral visual field. *Vision Research, 23*, 1–11.

Palmer, J., Mobley, L. A. & Teller, D. Y. (1993). Motion at isoluminance: Discrimination/detection ratios and the summation of luminance and chromatic signals. *Journal of the Optical Society of America A, 10*, 1353–1362.

Pospichal, M. W., Florence, S. L. & Kaas, J. H. (1994). The postnatal development of geniculocortical axon arbors in owl monkeys. *Visual Neuroscience, 11*, 71–90.

Quick, R. F. (1974). A vector–magnitude model of contrast detection. *Kybernetic, 16*, 65–67.

Ramachandran, V. S. & Gregory, R. L. (1978). Does colour provide an input to human motion perception? *Nature, 275*, 55–56.

Rodman, H. R. & Consuelos, M. J. (1994). Cortical projections to anterior inferior temporal cortex in infant macaque monkeys. *Visual Neuroscience, 11*, 119–133.

Rodman, H. R., Scalaidhe, S. P. & Gross, C. G. (1993). Response properties of neurons in temporal cortical visual areas of infant monkeys. *Journal of Neurophysiology, 70*, 1115–1136.

Rodman, H. R., Skelly, J. P. & Gross, C. G. (1991). Stimulus selectivity and state dependence of activity in inferior temporal cortex of infant monkeys. *Proceedings of the National Academy of Science USA, 88*, 7572–7575.

Roy, M. S., Lachapelle, P. & Leporé, F. (1989). Maturation of the optokinetic nystagmus as a function of the speed of stimulation in fullterm and preterm infants. *Clinical Visual Science, 4*, 357–366.

Saito, H., Tanaka, K., Isono, H., Yasuda, M. & Mikami, A. (1989). Directionally selective response of cells in the middle temporal area (MT) of the macaque monkey to the movement of equiluminous opponent color stimuli. *Experimental Brain Research, 75*, 1–14.

Salzman, C. D., Murasugi, C. M., Britten, K. H. & Newsome, W. T. (1992). Microstimulation in visual area MT: Effects on direction discrimination performance. *Journal of Neuroscience, 12*, 2331–2355.

Schiller, P. H. & Colby, C. L. (1983). The responses of single cells in the lateral geniculate nucleus of the rhesus monkey to color and luminance contrast. *Vision Research, 23*, 1631–1641.

Schiller, P. H., Logothetis, N. K. & Charles, E. R. (1990). Role of the color-opponent and broad-band channels in vision. *Visual Neuroscience, 5*, 321–346.

Shannon, E., Skoczenski, A. M. & Banks, M. S. (1996). Retinal illuminance and contrast sensitivity in human infants. *Vision Research, 36*, 67–76.

Shapley, R., Kaplan, E. & Soodak, R. (1981). Spatial summation and contrast sensitivity of X and Y cells in the lateral geniculate nucleus of the macaque. *Nature, 292*, 543–545.

Simpson, W. A. (1990). The use of different features by the matching process in short-range motion. *Vision Research, 30*, 1421–1428.

Smith, V. C. (1991). Origin of perceptually measured phase shifts in the visual system. In Valberg, A. & Lee, B. B. (Eds), *From pigments to perception*. New York: Plenum Press.

Smith, V. C., Pokorny, J., Davis, M. & Yeh, T. (1995). Mechanisms subserving temporal modulation sensitivity in silent-cone substitution. *Journal of the Optical Society of America A, 12*, 241–249.

Stabell, B. & Stabell, U. (1981). Absolute spectral sensitivity at different eccentricities. *Journal of the Optical Society of America, 71*, 836–840.

Stabell, U. & Stabell, B. (1980). Variation in density of macular pigmentation and in short-wave cone sensitivity with eccentricity. *Journal of the Optical Society of America, 70*, 706–711.

Stromeyer, C. F., Eskew, J. R. T. & Kronauer, R. E. (1990). The most sensitive motion detectors in humans are spectrally-opponent. *Investigative Ophthalmology & Visual Science Suppl, 31*, 240.

Stromeyer, C. F. I., Kronauer, R. E., Ryu, A., Chaparro, A. & Eskew, R. T. (1995). Contributions of human long-wave and middle-wave cones to motion detection. *Journal of Physiology, 485*, 221–243.

Swanson, W. H. & Birch, E. E. (1990). Infant spatiotemporal vision: Dependence of spatial contrast sensitivity on temporal frequency. *Vision Research, 30*, 1033–1048.

Swanson, W. H. & Birch, E. E. (1992). Extracting thresholds from noisy psychophysical data. *Perception and Psychophysics, 51*, 409–422.

Swanson, W. H., Ueno, T., Smith, V. C. & Pokorny, J. (1987). Temporal modulation sensitivity and pulse-detection thresholds for chromatic and luminance pertubations. *Journal of the Optical Society of America A, 4*, 1992–2005.

Teller, D. Y. (1979). The forced-choice preferential looking procedure: A psychophysical technique for use with human infants. *Infant Behavior and Development, 2*, 135–153.

Teller, D. Y. & Bornstein, M. H. (1987). Infant color vision and color perception Vol. I. From sensation to perception. Salapatek, P., Cohen, L. (Eds), *Handbook of infant perception* (pp. 185–236). Orlando, FL: Academic Press.

Teller, D. Y. & Lindsey, D. T. (1989). Motion nulls for white versus isochromatic gratings in infants and adults. *Journal of the Optical Society of America A, 6*, 1945–1954.

Teller, D. Y. & Lindsey, D. T. (1993a). Motion at isoluminance: Motion dead zones in three-dimensional color space. *Journal of the Optical Society of America A, 10*, 1324-1331.

Teller, D. Y. & Lindsey, D. T. (1993b). Infant color vision: OKN techniques and null plane analysis. In Simons, K. (Eds), *Infant vision: Basic and clinical research* (pp. 143–162). New York: Oxford University Press.

Teller, D. Y., Lindsey, D. T., Mar, C. M., Succop, A. & Mahal, M. R. (1992a). Infant temporal contrast sensitivity at low temporal frequencies. *Vision Research, 32*, 1157-1162.

Teller, D. Y., Mar, C. & Preston, K. L. (1992b). Statistical properties of 500-trial infant psychometric functions. In Werner, L. A. & Rubel, E. W. (Eds), *Developmental psychoacoustics* (pp. 211–227). Washington D.C.: American Psychological Association.

Teller, D. Y. & Palmer, J. (1996). Infant color vision: Motion nulls for red/green vs. luminance-modulated stimuli in infants and adults. *Vision Research, 36*, 955–974.

Thomas, J. P. (1985). Detection and identification: How are they related? *Journal of the Optical Society of America A, 2*, 1457–1467.

Van Essen, D. C. (1985). Functional organization of primate visual cortex. In Peters, A. & Jones, E. G. (Eds), *Cerebral cortex* (pp. 259–329). New York: Plenum Press.

van Nes, F. & Bouman, M. A. (1967). Spatial modulation transfer of the human eye. *Journal of the Optical Society of America, 57*, 401–406.

Viénot, F. (1980). Relations between inter- and intra-individual variability of color-matching functions. Experimental results. *Journal of the Optical Society of America, 70*, 1476–1483.

Walvaren, P. L. & Bouman, M. A. (1966). Fluctuation theory of color discrimination of normal trichromats. *Vision Research, 6*, 567–586.

Watson, A. B. (1979). Probability summation over time. *Vision Research, 19*, 515–522.

Watson, A. B., Ahumada, A. J. & Farrell, J. E. (1986). Window of visibility: A psychophysical theory of fidelity in time-sampled visual motion displays. *Journal of the Optical Society of America A, 3*, 300–307.

Watson, A. B. & Robson, J. G. (1981). Discrimination at threshold: Labeled detectors in human vision. *Vision Research, 21*, 1115–1122.

Watson, A. B., Thompson, P. G., Murphy, B. J. & Nachmias, J. (1980). Summation and discrimination of gratings moving in opposite directions. *Vision Research, 20*, 341–347.

Wattam-Bell, J. (1991). Development of motion-specific cortical responses in infancy. *Vision Research, 31*, 287–297.

Webster, M. J., Ungerleider, L. G. & Bachevalier, J. (1991). Lesions of inferior temporal area TE in infant monkeys alter cortico-amygdalar projections. *Neuroreport, 2*, 769–772.

Weibull, W. (1951). A statistical distribution function of wide applicability. *Journal of Applied Mechanics, 18*, 292–297.

Wooten, B. R., Fuld, K. & Spillmann, L. (1975). Photopic spectral sensitivity of the peripheral retina. *Journal of the Optical Society of America, 65*, 334–342.

Yeh, T., Pokorny, J. & Smith, V. C. (1993). Chromatic discrimination with variation in chromaticity and luminance: Data and theory. *Vision Research, 33*, 1835–1845.

Zeki, S. M. (1978). Uniformity and diversity of structure and function in rhesus monkey prestriate cortex. *Journal of Physiology (London), 277*, 273–290.

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