



Infants code the direction of chromatic quadrature motion

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Abstract

The present experiment uses a quadrature motion paradigm to investigate the motion correspondence cues used by young infants for coding the direction of motion of red/green isoluminant gratings. Three-month-old infants and adults were tested with 0.25 c/d luminance-modulated or red/green isoluminant gratings, either moving continuously or shifted in spatial quadrature. Both direction-of-motion and detection thresholds were measured, and motion:detection (M:D) threshold ratios were examined. Infants, like adults, could code the direction of motion of red/green quadrature-shifted gratings. In adults, M:D ratios were similar for continuous and quadrature motion. In infants, M:D ratios were higher for quadrature than for continuous motion, but elevations of similar magnitude were seen for both luminance-modulated and red/green gratings. The results suggest that frequency-doubled signals, such as those often seen in the magnocellular (M-cell) pathway, are not necessary for coding the direction of motion of isoluminant gratings in infant subjects. Two other theoretical options—mediation by the scatter of isoluminance points in the M-cell population, and parvocellular (P-cell) mediation—are discussed. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

It has long been known that very young infants are responsive to the direction of motion of luminance-modulated gratings (Gorman, Cogan & Gellis, 1957). More recently, it has been shown that 2- and 3-month-olds (but not 1-month-olds) are also responsive to the direction of motion of isoluminant red/green gratings (Teller & Lindsey, 1993a; Brown, Lindsey, McSweeney & Walters, 1995; Teller & Palmer, 1996; Dobkins & Teller, 1996a). The response measure used in these studies has been the infant's production of optokinetic nystagmus (OKN), or more generally directionally-appropriate eye movements (DEM), correlated with the direction of stimulus motion. These studies show that by 2 months postnatal the direction of motion of isoluminant red/green gratings is being analyzed by some component of the infant's visual system, and used

to guide the direction of eye movement responses to these stimuli.

However, these studies do not tell us which of several possible motion correspondence cues are employed by the infant in coding the direction of motion of isoluminant red/green gratings. That is, as shown in the top panels of Fig. 1, a continuously moving grating gives rise to both *signed* and *unsigned* motion correspondence cues. A *signed* motion correspondence cue is a cue based on matching the characteristics of the individual bars of the grating from one frame to the next: i.e. red-to-red and green-to-green for isoluminant red/green gratings. An *unsigned* (or border) cue is a cue arising from demarcating the locations of borders between the bars of the grating, without regard to the characteristics of the individual bars at the border. For example, red/green and green/red borders could both be coded simply as borders, without regard to the direction of the chromatic difference; and the changes of border locations from one frame to the next could then be used as a motion correspondence cue. Moreover, with re-

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spect to the spatial frequency of the initial grating, such unsigned border cues will be doubled in spatial frequency, and doubled in temporal frequency if the grating is moving. Thus, this form of unsigned cue leads to a frequency-doubled signal. For a continuously moving grating, both signed and unsigned cues provide unambiguous motion correspondence cues, and use of either cue would lead to the correct perception of the direction of motion of the grating.

A quadrature motion paradigm, shown in the bottom panels of Fig. 1, can be used to sort out signed from unsigned motion correspondence cues. Stimuli moving in spatial quadrature move with 90° phase shifts. Whenever the pattern moves, each new border appears exactly half the distance between two old borders, with the result that either direction of motion is a plausible interpretation of the unsigned cue. Thus, in the case of quadrature motion, unsigned borders provide an ambiguous motion correspondence cue; and any system that depends on the use of such unsigned border cues should fail to code the direction of motion of quadrature gratings. On the other hand, use of the signed chromatic cue—the colors of the individual bars in the grating—would allow the subject to code the direction of motion of the quadrature as well as the continuously moving grating.

In adult subjects, the quadrature motion paradigm has been used to sort out the motion correspondence cues used to code the direction of motion of isoluminant red/green gratings. It has been shown that adult subjects can correctly judge the direction of motion of quadrature shifted isoluminant red/green gratings (Gorea & Papathomas, 1989; Dobkins & Albright, 1993; Cropper & Derrington, 1996). Thus, in adults it is well established that signed chromatic cues are sufficient to code the direction of motion of isoluminant red/green gratings.

Part of the motivation for this study arises from physiological considerations. It is likely that the signals used for coding the direction of motion of luminance-modulated stimuli originate in the magnocellular or M-cell pathway (Merigan & Maunsell, 1993). However, the origins of the signals used for coding the direction of motion of isoluminant red/green stimuli have been a matter of controversy. There are three major alternatives. The first alternative is that these signals are signed, and arise in the parvocellular or P-cell pathway (Cavanagh & Anstis, 1991). The second alternative is that these signals are signed, but that they arise from non-frequency-doubled signals in the M-cell pathway (Dobkins & Albright, 1998). And the third alternative is that these signals are unsigned, and arise from the frequency-doubled non-linearities often reported in the M-cell pathway (Schiller & Colby, 1983; Dobkins & Albright, 1998; Lee, Martin & Valberg, 1989; Dobkins & Albright, 1994). These three options are discussed further in the Discussion section.

In the present experiment, we make use of the quadrature motion paradigm to test the unsigned cue hypothesis—the hypothesis that unsigned cues are necessary for coding the direction of motion of isoluminant red/green gratings—in 3-month-old infants.

1.1. Motion/detection (M:D) ratios

In order to further investigate infants' capacities to code the direction of motion of quadrature shifted gratings, we also used a motion:detection (M:D) ratio

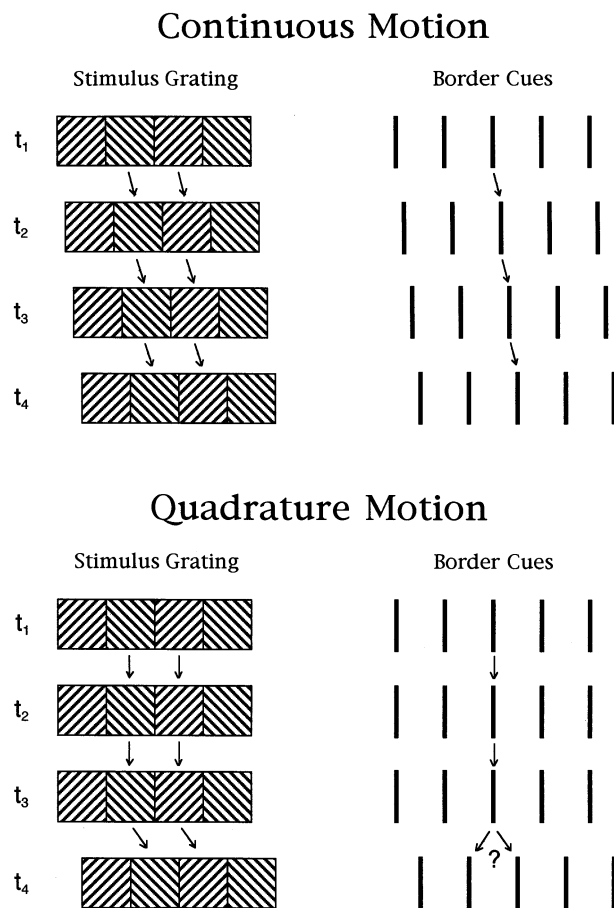


Fig. 1. Schematic depiction of the quadrature motion paradigm. Top panels: Continuous motion. Bottom panels: Quadrature motion. The left- versus right-diagonal shading represents the red versus green bars of the gratings. The sets of gratings on the left depict the locations of the stimulus in a series of four time frames, t_1 – t_4 . The arrows show the direction of motion implied by the use of *signed* cues; that is, by matching the colors of the bars from one time frame to the next. The sets of line segments on the right depict the locations of border cues for the same stimulus. The arrows show the direction of motion implied by use of the *unsigned* motion correspondence cue; that is, by matching the nearest border cue from one time frame to the next. For continuous motion, both signed and unsigned cues can be used for motion correspondence. For quadrature motion, the signed cues can be used for motion correspondence. However, the unsigned cue becomes ambiguous when the grating and its borders shift 90° in spatial phase at t_4 . Both stimuli move at the same overall velocity.

paradigm. In the M:D ratio paradigm, contrast thresholds for detecting a moving grating (D) are compared to contrast thresholds for direction-of-motion discrimination (M) for the same moving grating. M:D threshold ratios near 1 are taken to indicate that the mechanisms that detect the stimulus also code its direction of motion, while M:D threshold ratios greater than 1 indicate that mechanisms other than those that detect the stimulus must be activated in order to code its direction of motion (Graham, 1989).

In an earlier study from our laboratory, Dobkins and Teller (1996a) measured both direction-of-motion (M) and detection (D) thresholds for moving 0.25 c/d gratings, both luminance-modulated and red/green, in infants and adults. As previously reported by others (Watson, Thompson, Murphy & Nachmias, 1980; Lindsey & Teller, 1990; Gegenfurtner & Hawken, 1995), in adults the M:D ratio for luminance-modulated stimuli was near 1, while the M:D ratio for chromatic stimuli was elevated substantially above 1. In infants, however, the M:D ratios for both luminance-modulated and chromatic stimuli were similar, and both were near 1. This result suggested that infants detected both the chromatic and the luminance-modulated stimuli with a mechanism that is also sensitive to the direction of motion—probably a physiological pathway dominated by M-cell-initiated inputs. A similar suggestion arises from the bandpass shapes of infants' temporal contrast sensitivity functions for red/green chromatic gratings (Dobkins, Lia & Teller, 1997; Dobkins, Anderson & Lia, 1998).

In summary, the present project had two goals. First and most fundamentally, we wished to test infant subjects with quadrature-shifted red/green gratings, in order to find out whether or not signed motion correspondence cues are sufficient for coding the direction of motion in infants. And second, we wished to investigate the pattern of M:D ratios for both luminance-modulated and red/green gratings, shifting both continuously and in spatial quadrature in infants and adults, in order to search for more subtle deficits in infants' motion processing for quadrature-shifted chromatic gratings.

2. Methods

2.1. Subjects

2.1.1. Adults

Five adults (including the first and last authors) participated in these experiments (ages 19–59 years). All five had normal or corrected-to normal vision, and normal color vision by Ishihara plates. In addition, red/green isoluminance judgments were made by eleven adults, including two of the five subjects from the main

experiment. All adult subjects gave informed consent to participate.

2.1.2. Infants

Infants were recruited through the University of Washington Infant Studies Subject Pool. All infants were reported to have had uncomplicated births within ± 14 days of their due date. Each infant turned 12 weeks old during the test week and was tested over a period of 1–6 days. The mean age on the first day of testing was 83 days (S.D. = 2). Male infants with known family histories of color vision deficiencies were excluded. The parents of all infants gave informed consent for their infants to participate.

One hundred and six infants participated in these experiments. Infant subjects were excluded from further analysis if they failed to meet a minimum trial number criterion (≥ 60 trials/psychometric function) or if they failed to meet a minimum performance criterion ($\geq 80\%$ correct for trials using luminance-defined gratings of 100% contrast). Seven failed the minimum trial number criterion and ten failed the minimum performance criterion. These subjects were distributed across the series of experiments and roughly balanced across continuous and quadrature motion conditions. In addition, four subjects provided data sets that included two or more points that were below or near chance. These data sets resulted in extrapolated thresholds greater than three times the maximum chromatic contrast. These subjects were discarded. Data from 85 subjects (80%) were included in the final data set.

2.2. Apparatus and stimuli

2.2.1. Apparatus

Both the adult apparatus and the infant apparatus were the same as those used in previous experiments (Dobkins & Teller, 1996a; Dobkins, Lia & Teller, 1997). Briefly, gratings were generated on high resolution 19 inch RGB monitors. The mean luminance of all stimuli was 17 cd/m². The space-average CIE chromaticity coordinates of the stimuli were set to (0.49, 0.43). These fields appear a desaturated yellow to color-normal observers. Stimuli were vertically oriented sinusoidal gratings of 0.25 c/d moving horizontally at 22°/s (5.6 Hz). At the 38 cm viewing distance used, the displays subtended 53 × 40°. Stimuli subtended either the full extent of the video display (infant direction-of-motion data in Experiment 1) or only one half of the screen or the other (all other experiments).

Motion was produced by phase-shifting the gratings at regular intervals (multiples of 15 ms) in synchrony with the vertical refresh of the monitor. For continuous motion, spatial offset was set at 0.33° of visual angle (30° phase shift) and the grating was shifted every 15 ms. Quadrature motion was generated by setting spatial

offset at 0.99° of visual angle (90° phase shift) and shifting the grating every 45 ms.

Luminance-modulated (yellow/black) gratings were made by sinusoidally modulating the red, green and blue primaries in the same spatial phase. Red/green gratings were made by sinusoidally modulating the red and green primaries 180° out of spatial phase. A small modulation of the blue primary in phase with the red primary served to silence the S cones. All stimuli were modulated through the mean yellow chromaticity, rather than through white, in order to maximize chromatic contrast.

For luminance-modulated gratings, contrast is defined as conventional Michelson contrast $[(L_{\max} - L_{\min}) / (L_{\max} + L_{\min})]$. For red/green gratings, cone modulations were computed as described in Dobkins, Lia & Teller (1997). We specify chromatic contrast in terms of root mean square (rms) cone contrast of the L and M cones $[\text{rms cone contrast} = \sqrt{(M^2 + L^2)/2}]$, in order to express chromatic and luminance contrast in comparable units (Mullen, 1985; Lennie & D'Zmura, 1988). The infant red/green stimulus was based on the mean adult isoluminance setting and limited by the gamut of the display. It had a maximum of 18% L cone contrast and 27% M cone contrast, resulting in a maximum rms cone contrast of 23%.

2.3. Isoluminance settings

To determine the mean isoluminance point for adults, 11 adult subjects were tested with a minimum motion technique (Moreland, 1980; Teller & Lindsey, 1993b; Dobkins & Teller, 1996a) in both the infant and the adult apparatus. Individual isoluminance values were estimated from the means of 25 trials per subject. For the main adult experiment, each adult subject's individual isoluminance value, as determined by his or her minimum motion settings in the adult apparatus, was used. For all infants, the mean of the individual isoluminance points of the eleven adults, determined in the infant apparatus, was used as the isoluminance setting.

As discussed in detail previously (Brown, Lindsey, McSweeney & Walters, 1995; Dobkins & Teller, 1996b), earlier studies indicate that the mean and range of isoluminance points for red/green stimuli are highly similar for infants and adults. For infants, we expect the maximum luminance contrast due to subject variability away from the adult average to be on the order of 2%. Since infant luminance contrast thresholds under our conditions are about 10% (see Section 3), 2% deviations from individual isoluminance should be negligible for infant subjects. In addition, in pilot data taken on infants, small variations around adult isoluminance revealed no systematic variations in quadrature motion thresholds. Further quantitative discussion of

this issue may be found in Brown, Lindsey, McSweeney and Walters (1995) and Dobkins and Teller (1996b).

2.4. Procedures

2.4.1. Adults

Five adult subjects were tested in the main experiment. Standard two-alternative forced-choice techniques with trial-by-trial feedback were used. For each condition, six contrast levels were used. 100 trials per contrast level were used, for a total of 600 trials per psychometric function. Contrast levels and left-right variables were randomized within blocks. To mimic the stimulus conditions used for infants, eye position was unrestricted and stimuli remained present on the display until a judgment was made.

2.4.2. Infants

Infant detection thresholds (D) were obtained with standard forced-choice preferential looking (FPL) techniques (Teller, 1979). Stimuli filled either the left or the right half of the monitor. Stimuli remained present on the display until a judgment was made, and auditory feedback was provided.

Infant direction-of-motion thresholds (M) were obtained using a directionally-appropriate eye movement (DEM) technique (Hainline, de Bie, Abramov & Camenzuli, 1987; Teller & Lindsey, 1993a; Dobkins & Teller, 1996a). In Experiment 1, in which direction-of-motion thresholds were initially evaluated for continuous versus quadrature motion, the grating filled the entire field of the display. In Experiment 3, in which M:D ratios were examined within subjects, the grating filled either the left or the right half of the display, as it did for detection. As in the case of detection thresholds, stimuli remained present until a judgment was made, and auditory feedback was provided.

For both FPL and DEM testing, luminance-modulated stimuli were presented at four contrast levels (5, 10, 20, and 100%). Chromatic stimuli were presented at three contrast levels (6.25, 12.5, and 23% rms cone contrast). To compensate for the fact that the highest cone contrast available on the monitor was near chromatic threshold for 3-month-olds, the highest cone contrast was presented twice as often as the other two, and a 100% contrast luminance grating was presented randomly on one out of every five trials. This strategy allowed some highly visible stimuli to be included in the stimulus sequence and afforded a measure of infant performance in the task with respect to our minimum criterion for retaining subjects ($\geq 80\%$ correct). These 100% luminance-contrast trials were excluded from the psychometric function for the chromatic gratings. In some instances, lower contrast levels were added during testing, in order to span the psychometric function. The mean number of trials per infant psychometric function

(exclusive of the high contrast luminance grating in the red/green conditions) was 98.

Within each experiment, all conditions to be tested in the same infant were interleaved in a random order. In Experiment 3 (see below), in which detection thresholds were measured by FPL and direction-of-motion thresholds by DEM, the two types of trials were also randomly interleaved. An auditory cue informed the experimenter as to which kind of judgment to make on each trial.

2.5. Experimental design

2.5.1. Adults

All adult subjects were tested on all eight conditions of a $2 \times 2 \times 2$ experimental design. Quadrature versus continuous motion and luminance-modulated versus red/green gratings were randomized within blocks. Detection versus direction-of-motion tasks were tested in separate blocks, with each task tested in five separate sub-blocks of 480 trials, with different orders of tasks used on different subjects.

2.5.2. Infants

Three experiments were performed in infant subjects. In Experiment 1, contrast thresholds were measured for the direction-of-motion task (M), mainly in order to see whether infants had measurable thresholds for chromatic quadrature motion. Quadrature versus continuous motion was a within-subject variable, whereas luminance-modulated versus red/green stimuli were tested on separate groups of subjects. In Experiment 2, contrast thresholds were measured for the detection task (D). For this task (which allows more rapid judgments on the part of the adult observer), four conditions could be tested within a single infant; these were continuous versus quadrature motion and luminance-modulated versus red/green stimuli. By combining Experiments 1 (direction of motion) and 2 (detection), between-subject M:D ratios could be derived.

However, we have argued previously (Dobkins & Teller, 1996a) that a within-subjects design is more appropriate for testing M:D ratios in infants, particularly because the direction-of-motion judgments take longer than the detection judgments for the adult observer, suggesting that this condition may be more difficult for the infant. A within-subject design with interleaved trials keeps the subject's motivation as constant as possible across conditions. Moreover, as stated previously, field size differed between Experiment 1 (full field) and Experiment 2 (half field). For these reasons, Experiment 3 was performed, using quadrature motion only. In Experiment 3, direction-of-motion versus detection tasks were a within-subject variable, whereas luminance-modulated versus red/green gratings were a between-subjects variable. This design allowed us to

derive a second set of M:D ratios for quadrature motion, this time within subjects.

The data of Experiment 3 complement those of Dobkins and Teller (1996a), who carried out similar within-subjects experiments for continuous motion. Data from Dobkins and Teller (their Experiment 2, which is most comparable to the present data because the stimuli were modulated through yellow) are analyzed with those of the present Experiment 3 below.

2.6. Threshold estimates and M:D ratios

The data were fit with Weibull functions using a maximum likelihood criterion, as described in detail previously (Dobkins & Teller, 1996a,b). For adults, the slope parameter of the Weibull function was unrestricted. For infants, the slope parameter was fixed at 1.6 for all infant data sets. Log threshold values were used in calculating group means and for statistical analyses.

In evaluating the meaning of the statistical reliability of differences within infants versus within adults, one must keep in mind that the data from adults have higher statistical power than do those from infants, due to the steeper slopes of adult psychometric functions and the much larger number of trials per psychometric function (600 for adults and 98 for infants).

3. Results

3.1. Thresholds for direction-of-motion and detection tasks

Fig. 2 shows group mean threshold values for both direction-of-motion and detection tasks, for adults and for Experiments 1 and 2 in infants. Within each panel, thresholds are shown for both luminance-modulated (yellow/black) and chromatic (red/green) gratings, and for both continuous and quadrature motion tasks. Across all conditions, infants' contrast thresholds ranged from 6.5 to 20.5%, while adult thresholds ranged from 0.16 to 0.52%. Thus, as expected from many prior studies, infant thresholds are consistently more than an order of magnitude higher than are adult thresholds.

Fig. 2A, B show adult direction-of-motion and detection thresholds respectively. For direction-of-motion, for luminance-modulated gratings mean contrast thresholds were 0.16 and 0.18% for continuous and quadrature stimuli respectively; whereas for red/green gratings mean contrast thresholds were 0.42 and 0.52% for continuous and quadrature stimuli respectively. For detection, for luminance-modulated gratings mean contrast thresholds were 0.17 and 0.18% for continuous and quadrature stimuli respectively; whereas for red/

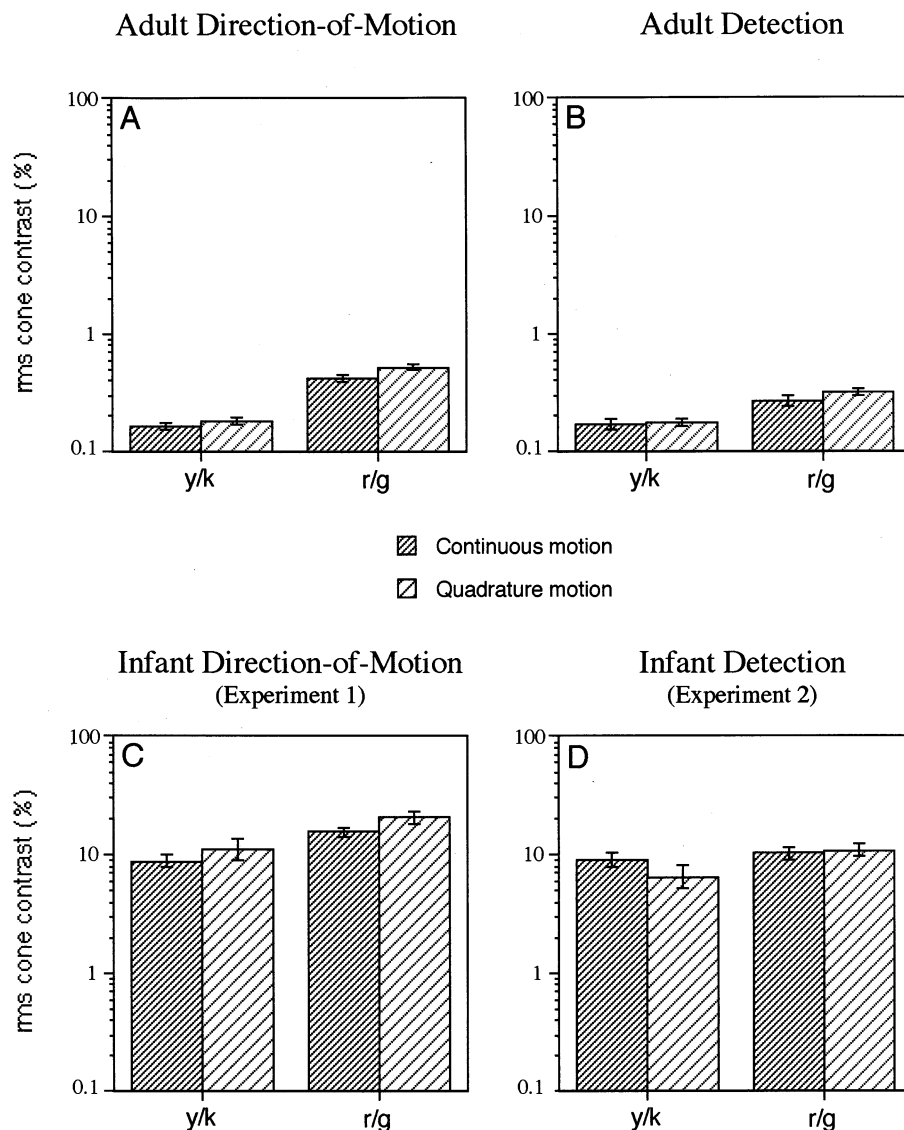


Fig. 2. Direction-of-motion versus detection thresholds. Direction-of-motion (left panels) and detection (right panels) thresholds for continuously moving (finely striped bars) and quadrature-shifted gratings (coarsely striped bars), in adults (top panels) and infants (bottom panels). Panel C is from infant Experiment 1 and panel D is from infant Experiment 2. Thresholds are expressed in terms of the root mean square (rms) cone contrast elicited in the long- and middle-wavelength cones (as defined in Section 2). Within each panel, the left and right pairs of bars show thresholds for luminance-modulated (yellow/black, or y/k) gratings and isoluminant red/green (r/g) gratings, respectively. The error bars show ± 1 standard error of the mean.

green gratings mean contrast thresholds were 0.27 and 0.32% for continuous and quadrature stimuli respectively.

Fig. 2C and D show infant direction-of-motion and detection thresholds respectively. For direction-of-motion, for luminance-modulated gratings mean contrast thresholds were 8.9 and 11.3% for continuous and quadrature stimuli respectively; whereas for red/green gratings mean contrast thresholds were 15.5 and 20.5% for continuous and quadrature stimuli respectively. For detection, for luminance-modulated gratings mean detection thresholds were 9.1 and 6.5% contrast for continuous and quadrature stimuli respectively; whereas for red/green gratings mean contrast thresholds were

10.3 and 10.9% for continuous and quadrature stimuli respectively.

Fig. 3 shows the results of infant Experiment 3 (within-subject measurements of direction-of-motion and detection thresholds for quadrature motion), along with the prior results of Dobkins and Teller (1996a) for continuous motion. Threshold values were similar to those shown in Fig. 2. For continuous motion (Dobkins & Teller, 1996a), for luminance-modulated gratings direction-of-motion and detection thresholds were respectively 11.0 and 9.2%; for red/green gratings these thresholds were 21.0 and 15.5%, respectively. For quadrature motion (the present Expt. 3), for luminance-modulated gratings direction-of-motion and detection

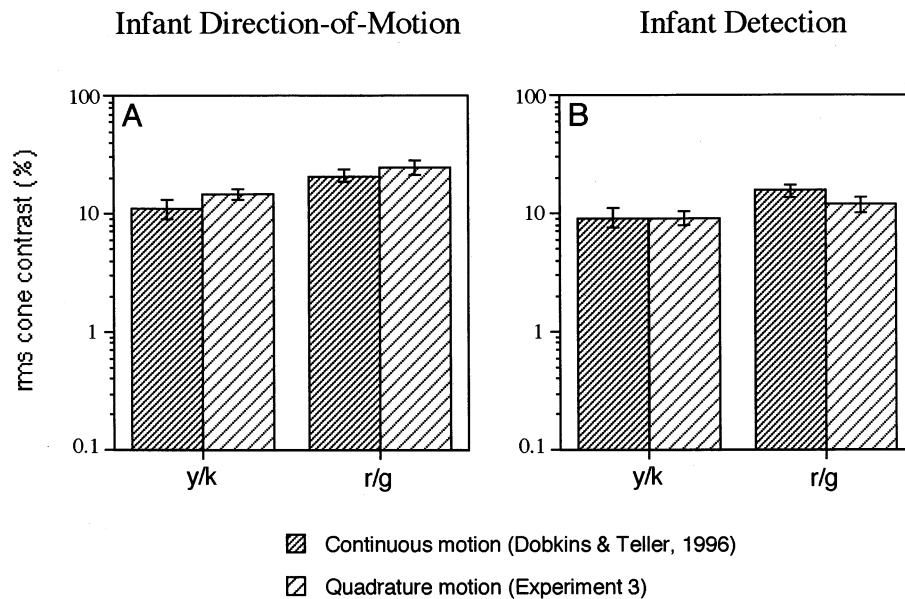


Fig. 3. Direction-of-motion and detection thresholds for continuously moving and quadrature-shifted gratings, tested within individual infant subjects. The data for continuous motion are replotted from Dobkins and Teller (1996a) (their Experiment 2). The data for quadrature motion are from the present infant Experiment 3. Other conventions as in Fig. 2

thresholds were respectively 14.6 and 9.0%; for chromatic gratings, these thresholds were respectively 24.6 and 11.8%.

The fact that infant luminance contrast thresholds are on the order of 10% reaffirms the argument (see Section 2) that deviations on the order of 2% from the individual infant's isoluminance point should have negligible effects on infants' chromatic discrimination thresholds.

In sum, infants as well as adults have measurable thresholds for all four stimulus conditions. In particular, infants can respond to the direction of motion of red/green gratings moving in spatial quadrature. Moreover, although they are slightly higher than the thresholds in the other conditions, the direction-of-motion thresholds in the red/green quadrature motion condition show no striking elevation with respect to the other three stimulus conditions. This finding is contrary to the unsigned cues hypothesis.

3.2. M:D threshold ratios

Comparisons across upper and lower panels of Fig. 2 yield estimates of threshold ratios for direction-of-motion versus detection tasks (M:D threshold ratios), for adults and infants, for the four stimulus conditions: luminance-modulated versus chromatic stimuli, and continuous versus quadrature motion. Comparisons within Fig. 3 yield a second set of M:D ratios for infant subjects. All of these ratios are summarized and analyzed for statistical reliability in Table 1.

Adult M:D ratios are shown in the top rows of Table 1. As expected, M:D ratios for luminance-modulated

gratings are near 1.0. Also as expected, M:D ratios are higher for chromatic compared to luminance-modulated stimuli. Collapsing across motion conditions, the M:D ratio was 1.00 for luminance-modulation and 1.61 for chromatic modulation, a percentage increase of $61 \pm 6\%$ ($F(1,4) = 158$; $P < 0.001$). Thus, the present experiment replicates the finding that in adults, M:D threshold ratios are elevated above 1 for continuously moving chromatic gratings; and extends this finding to the quadrature motion case.

By comparison, the change from continuous to quadrature motion had little or no effect on the M:D ratios. Collapsed across color conditions, the M:D ratio was 1.24 for continuous motion and 1.30 for quadrature motion, an increase of only $5 \pm 4\%$ ($F(1,4) = 1.5$; $P > 0.1$). In addition, there was no indication of an interaction between these manipulations. For continuous motion, the change from luminance to chromatic modulation increased the M:D ratio by 63%; for quadrature motion, the same change increased the M:D ratio by 59%. These effects were not reliably different ($F(1,4) = 0.3$; $P > 0.1$). Thus, in adults the change from continuous to quadrature motion had no detectable effect either in general, or in particular for chromatic stimuli.

Infant M:D ratios from Experiments 1 and 2 derived from between-subjects comparisons are shown in the middle rows of Table 1. Collapsing across motion conditions, the M:D ratio was 1.3 for luminance modulation and 1.7 for chromatic modulation, an unreliable percentage increase of $30 \pm 33\%$ ($F(1,53) = 0.8$; $P > 0.1$). Thus, the increase of the M:D ratio seen on changing from luminance-modulated to chromatic stim-

Table 1

M:D threshold ratios for luminance-modulated or chromatic stimuli moving in either continuous or quadrature motion

	Continuous	Quadrature	
Adult experiment			
Luminance	0.97 ± 0.04	1.03 ± 0.04	1.00
Chromatic	1.58 ± 0.09	1.64 ± 0.06	1.61
	1.24	1.30	
Infant experiments 1 & 2 (between subjects)			
Luminance	1.0 ± 0.2	1.7 ± 0.6	1.3
Chromatic	1.5 ± 0.2	1.9 ± 0.4	1.7
	1.2	1.8	
Infant experiments (within subjects)			
Luminance	1.2 ± 0.2	1.6 ± 0.3	1.4
Chromatic	1.4 ± 0.1	2.1 ± 0.3	1.7
	1.3	1.8	

Marginal values collapsing across stimulus and across motion conditions are also shown: Upper table, values from adult experiment; middle table, values derived between subjects from infant Experiments 1 and 2; bottom table, values from within subjects experiments—previous data from Dobkins and Teller (1996a) (their Experiment 2) in the left column, and data from the current Experiment 3 in the right column.

uli cannot be distinguished either from zero or from the 61% increase observed for adults.

By comparison, the change from continuous to quadrature motion did have a significant effect on M:D ratios for infants. Collapsed across luminance-modulated and red/green stimuli, the M:D ratio was 1.2 for continuous motion and 1.8 for quadrature motion, a difference of $50 \pm 17\%$ ($F(1,53) = 11$; $P < 0.01$). There was also some uncertainty about the interaction between these manipulations. For continuous motion, the change from luminance to chromatic modulation increased the ratio by 54%; for quadrature motion, this change increased the ratio by only 8%. This difference was unreliable ($F(1,53) = 0.8$; $P > 0.10$), and is in the opposite direction of that expected if the change from continuous to quadrature motion had a greater effect for chromatic stimuli.

Finally, within-subject infant M:D ratios from Dobkins and Teller (1996a) for continuous motion, and from Experiment 3 for quadrature motion, are shown in the bottom rows of Table 1. Collapsing across continuous and quadrature motion conditions, the M:D ratio was 1.4 for luminance modulation and 1.7 for chromatic modulation, a percentage increase of $21 \pm 19\%$ ($F(1,50) = 1.5$; $P > 0.1$). This increase cannot be distinguished from zero, but it is reliably less than the corresponding 61% increase observed for adults. However, this difference is due to the inclusion of the Dobkins and Teller (1996a) data. If Experiment 3 is considered alone, the increase is $29 \pm 30\%$ and is not reliably less than the increase observed for adults.

As before, the change from continuous to quadrature motion did have a significant effect on the M:D ratios for infants. Collapsed across conditions, the M:D ratio

was 1.3 for continuous motion and 1.8 for quadrature motion, a difference of 45% ($F(1,50) = 5.6$; $P < 0.05$). There was also no sign of an interaction between these manipulations. For continuous motion, the change from luminance to chromatic modulation increased the ratio by 13%; for quadrature motion, the same change increased the ratio by 29%. In this case, the observed difference is in the direction expected if the change from continuous to quadrature motion had a greater effect for chromatic stimuli, but the difference is unreliable ($F(1,50) = 0.2$; $P > 0.1$).

In summary, the change from luminance-modulated to chromatic stimuli elevates M:D ratios reliably for adults but not reliably for infants; while the change from continuous to quadrature motion elevates M:D ratios for infants but not for adults. In neither case is there evidence for an interaction between these variables. In particular, there is no reliable evidence that M:D ratios are differentially elevated for red/green quadrature motion with respect to the other three stimulus conditions in either age group.

4. Discussion

These experiments will be discussed from four perspectives. First, we discuss the main result—infants' responsiveness to chromatic quadrature motion—and its implications for the potential mediation of infants' responses to chromatic gratings by frequency-doubled signals. Second, we explore briefly the implications of these experiments for infant motion processing and infant color vision. Third, we consider physiological mechanisms, including the possibility of a second form

of cross-activation of the M pathway by chromatic stimuli, and the possibility of P-cell mediation. And finally, we speculate briefly on the possibility that, even if infants' chromatic discriminations are P-cell mediated, infants might still be fundamentally color-blind.

4.1. Infants' responses to chromatic quadrature motion

Since luminance variations obviously provide a signed, luminance-based border cue, it is not surprising that infants can code the direction of motion of luminance-modulated quadrature-shifted gratings. On the other hand, one of the original options was that for isoluminant red/green gratings, unsigned border cues arising from chromatic modulation but carried in a luminance channel, might be solely responsible for coding the direction of motion in 3-month-olds. Since quadrature motion eliminates the effectiveness of unsigned border cues, this option predicts that direction-of-motion thresholds would be elevated (or even unmeasurable) for chromatic quadrature-shifted gratings. Similarly, this option predicts that the M:D ratio for quadrature-shifted chromatic stimuli would be very large relative to the M:D ratio for the other three stimulus conditions.

The most important result of the present experiments is that neither of these predictions was substantiated. Infants could do the direction-of-motion task with chromatic quadrature-shifted gratings; and their M:D ratios for chromatic quadrature gratings were not differentially elevated. Thus, signed cues arising from isoluminant chromatic stimuli must be available, and sufficient to allow direction-of-motion coding of chromatic stimuli, by 3-month-old infants under the present conditions.

4.2. Implications for infant motion processing and infant color vision

4.2.1. Infant motion processing

Table 1 shows that in adults, M:D ratios are highly similar for continuous versus quadrature motion. In contrast, in infants, M:D ratios are consistently higher for quadrature than for continuous motion. That is, infants' direction-of-motion thresholds are differentially elevated for quadrature-shifted gratings. We suggest that this outcome could result from a specific immaturity of infant motion processing; namely, a limited value of D_{\max} (Wattam-Bell, 1992).

The term D_{\max} is used in the motion literature to refer to the largest spatial displacement for which adult subjects report a clear perception of motion. Recently, Wattam-Bell (1992) measured D_{\max} in 2–4-month-old infants using random dot kinematograms (RDKs) and an FPL technique. He reported that under these conditions, the infant's D_{\max} is about 1/3 of the adult value,

suggesting that infants detect motion correspondences over shorter displacements than do adults (but cf. Kramer & Bertenthal, 1989). Although the absolute value for D_{\max} varies with stimulus parameters, it is reasonable to speculate that a similar difference in D_{\max} might also be found for sinusoidal gratings. Moreover, it is likely that direction-of-motion performance declines as D_{\max} is approached.

For the 0.25 c/d gratings used in the present experiment, a quadrature (90°) phase shift corresponds to a stimulus displacement of 1° of visual angle. If this value were near the infant's D_{\max} under the present stimulus conditions, the infant's performance could be differentially impaired for quadrature motion stimuli. This impairment would be restricted to the direction-of-motion task, and should not affect detection performance. Hence, it would lead to an elevation of the M:D ratio for quadrature motion in infants. Further experimentation will be needed to establish the validity of this suggestion.

4.2.2. Infant color vision

As reviewed in the Introduction, in the adult literature M:D ratios near 1 have been taken to indicate that the mechanism that detects the stimulus also codes its direction of motion; while M:D ratios above 1 have been taken to indicate that suprathreshold mechanisms must be activated to code the direction of motion (Graham, 1989). Adult M:D ratios are classically near 1 for luminance-modulated stimuli, and distinctly greater than 1 for chromatic stimuli. In contrast, our earlier work (Dobkins & Teller, 1996a) suggested that infants may show similar M:D ratios for both kinds of stimuli.

M:D ratios in infants are derived from two different forms of response: direction-of-motion thresholds from DEM measurements, and detection thresholds from FPL measurements. As discussed previously (Dobkins & Teller, 1996a), it is likely that the DEM response is a more difficult task for the infant and/or for the adult who is observing the infant's responses. If so, this factor would bias infant M:D threshold ratios in the direction of being too large. Thus, we have argued that the comparison of M:D ratios between stimulus conditions, rather than the absolute values of M:D ratios or their elevation above 1, is the most fundamental outcome measure in these experiments.

In our earlier study, the adult M:D ratio for chromatic stimuli was roughly double the M:D ratio for luminance-modulated stimuli, for an increase of about 100%. This increase was expected given those previously reported in the literature. In contrast, the infant M:D ratio for chromatic stimuli increased relative to the M:D ratio for luminance-modulated stimuli by only 10%. This increase was not reliably different from zero and was reliably less than the 100% increase observed for adults. In short, the chromatic inputs to motion

processing appeared to be better (or at least less degraded) in infants than in adults.

In the present study, this difference between infants and adults is not as clear. First, the adults in this study showed an increase of only 61% (rather than 100%) when changing from luminance-modulated to chromatic stimuli. Thus, the effect for adults was smaller than that observed by Dobkins and Teller (1996a). Second, the infants in Experiments 1 and 2 showed increases of $30 \pm 33\%$ (rather than 10%). This value is halfway between an increase of zero and the increase of 61% observed for adults, and is not reliably different from either. Third, the infants in Experiment 3 showed an increase of $29 \pm 30\%$ which again falls halfway between zero and the adult value of 61% and is not reliably different from either. Thus, while all measurements of the increase in the M:D ratio for chromatic versus luminance-modulated gratings have been less than the corresponding increases in adults, only the original Dobkins and Teller (1996a) study found a statistically reliable difference. We conclude that both studies show that the chromatic input to motion processing is relatively no worse in infants than in adults. The question remains as to whether the chromatic input to motion processing is relatively better in infants than in adults, as suggested by Dobkins and Teller (1996a).

4.3. *Physiological mechanisms*

Prior studies from our laboratory (Dobkins & Teller, 1996a,b; Dobkins, Lia & Teller, 1997) have suggested to us that infants might detect and code the direction of motion of temporally varying chromatic stimuli by means of M-cell- rather than P-cell-initiated signals. To this end, we have suggested that immature P-cells might be differentially insensitive in infants, and in particular less sensitive than are M-cells to moving or temporally counterphasing chromatic patterns. However, the present finding—that infants can code the direction of motion of quadrature shifted chromatic gratings—argues that frequency-doubled signals are not necessary for coding the direction of motion in infants. Thus, infants' direction-of-motion coding is probably not mediated by the frequency-doubled signals commonly seen in the M-cell pathway.

The earlier data could be reconciled with the present data in two ways. The first alternative is to take another look at the M-cell pathway. As noted in the Introduction, signed, non-frequency-doubled, chromatically-initiated responses also occur in the M-cell population; and these responses could still contribute to chromatic motion coding. Most relevant to this discussion, it is well known that the null planes of M-cells, and their red/green balance points—the luminance contrasts for which red and green phases of the stimulus elicit responses of equal magnitude—vary across the

population of M-cells, in both the retina and the LGN of adult macaque monkeys (Schiller & Colby, 1983; Derrington, Krauskopf & Lennie, 1984; Logothetis, Schiller, Charles & Hurlbert, 1990; Lee, Martin, Valberg & Kremers, 1993). This variability assures that, as a population, M-cells can never be truly silenced (Logothetis, Schiller, Charles & Hurlbert, 1990; Dobkins & Albright, 1998). In other words, even if some of the M-cells are silenced at each particular red/green luminance ratio, other M-cells will remain active. Moreover, this population response will be signed; i.e. different for the red versus green phases of the grating, or for the transition from red to green versus green to red. This M-cell population code could provide a chromatically-initiated motion cue. Evaluation of the reasonableness of this line of argument awaits a more quantitative model of M-cell population responses in infants.

The remaining alternative is to attribute infant chromatic motion processing to signals initiated in the P-cell pathway. In that case, to reconcile the present data with the apparent luminance signatures seen in our earlier papers, one could argue that immature P-cells might bear a temporal signature much like that of M-cells, and change their temporal response properties between infancy and adulthood. Further experiments will be needed to differentiate between these two options.

4.4. *Developmental cerebral achromatopsia?*

In broader terms, it is possible to frame three different definitions of infant color vision. The first is that infants should be said to have color vision if they respond differentially to lights of different wavelength compositions on the basis of the difference in wavelength composition. The second is that infants should be said to have color vision only if these responses are P-cell mediated. And the third is that infants should be said to have color vision only if these signals lead to variations in perceived hue.

By the first definition—wavelength discrimination—infants have been known to have color vision for at least a quarter century. The second definition—P-cell mediation—is addressed (although not definitively answered) by the present experiments on quadrature motion of isoluminant chromatic gratings. Yet, regardless of the interpretation of the present experiment, the third definition remains unaddressed: infant's responses to wavelength differences might not be accompanied by variations of perceived hue.

Such a lack of appreciation of hue in infants might be analogous to recent reports of patients with acquired cerebral achromatopsia. Such patients typically have bilateral occipito-temporal lesions leaving the dorsal cortical processing stream intact. These patients can correctly report the direction of quadrature motion of red/green isoluminant stimuli, but cannot report the

colors of the stimuli (Cavanagh, Henaff, Michel & Landis, 1994; Heywood, Cowey & Newcombe, 1994). That is, these patients are able to use signed chromatic cues for motion correspondence, and even for forms of unconscious inference (Troscianko, Davidoff, Humphreys, Landis, Fahle, Greenlee, Brugger & Phillips, 1996), despite being unable to identify the colors of the grating.

It is interesting to speculate that young infants, like the acquired cerebral achromatope, might process differences in wavelength composition without being able to appreciate variations of subjective hue. This phenomenon could occur if areas of the brain from which neural signals are mapped to perceived hue were to mature later than those areas that use chromatically-initiated signals for other purposes such as motion processing. Although not yet conclusive, metabolic imaging studies using 2-deoxyglucose techniques in infant macaque monkeys suggest that the higher order areas of both the dorsal and the ventral cortical streams become functionally mature at later ages than do lower order cortical areas, with the dorsal stream maturing on the whole a bit earlier than the ventral stream (Distler, Bachevalier, Kennedy, Mishkin & Ungerleider, 1996). The young infant might conceivably turn out to be another case, like the acquired cerebral achromatope, of the separability of chromatic motion processing from the appreciation of perceived hue.

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