

## Research Report

# COLOR-BASED MOTION PROCESSING IS STRONGER IN INFANTS THAN IN ADULTS

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**Abstract**—*One hallmark of vision in adults is the dichotomy between color and motion processing. Specifically, areas of the brain that encode an object's direction of motion are thought to receive little information about object color. We investigated the development of this dichotomy by conducting psychophysical experiments with human subjects (2-, 3-, and 4-month-olds and adults), using a novel red-green stimulus that isolates color-based input to motion processing. When performance on this red-green motion stimulus was quantified with respect to performance on a luminance (yellow-black) standard, we found stronger color-based motion processing in infants than in adults. These results suggest that color input to motion areas is greater early in life, and that motion areas then specialize to the adultlike state by reweighting or selectively pruning their inputs over the course of development.*

In the visual system of adults, information about object color and information about object motion are thought to be processed in separate, parallel pathways. Most notably, areas of the brain that encode an object's direction of motion (e.g., leftward or rightward) exhibit little selectivity for the color of that object (e.g., red or green; e.g., Livingstone & Hubel, 1988; Zeki, 1974; see Merigan & Maunsell, 1993, for review). This functional dichotomy between color and motion processing can be accounted for by the known segregation of anatomical projections in the visual system. Specifically, visual areas that encode object color have been shown to provide only marginal input to motion-processing areas of visual cortex (Livingstone & Hubel, 1988; Maunsell, Nealey, & DePriest, 1990). At the perceptual level, the consequence of this color-motion neural dichotomy is that motion perception is often impoverished when moving stimuli are defined solely by color, a phenomenon that has been well documented in the adult literature (see Dobkins & Albright, 1998, for review).

Although parallel processing for color and motion has been investigated extensively in adult subjects (both psychophysically and neurally), little is known about how it develops. Does the brain of a newborn start out with this segregation of function, or must rewiring or reweighting of connections take place over the course of development in order to produce the adultlike state? In order to address this question, we used psychophysical techniques to measure the strength of color-based motion perception in human infants, as compared with adults. Specifically, we measured subjects' ability to discern the direction of a moving red-black-green-black color grating, which could be accomplished only if information about color identity was employed, that is, matching red to red and green to green over time. To quantify the strength of color-based motion processing, we also tested subjects with a moving yellow-black "luminance" grating presented at varying levels of luminance contrast. The purpose of the luminance grating was

to obtain, for each subject, an *equivalent luminance contrast* (EqLC), defined as the luminance contrast in the yellow-black grating required to yield the same performance level (i.e., same percentage correct) elicited by the color grating.

These stimuli were designed with the special purpose of isolating the contribution of two different subcortical pathways of the visual system (see Merigan & Maunsell, 1993): one that encodes the color identity (red vs. green) of an object, the *parvocellular* (P) pathway, and one that is highly sensitive to luminance contrast yet unselective for object color, the *magnocellular* (M) pathway.<sup>1</sup> Our color stimulus is expected to isolate P pathway input to motion areas by requiring the use of color identity cues. By contrast, the effectiveness of our luminance stimulus should reflect M pathway input to motion areas, because the cells of this pathway are thought to underlie sensitivity to moving luminance stimuli (Lee, Pokorny, Smith, Martin, & Valberg, 1990; Shapley, 1990). The EqLC value obtained in our experiments thus reflects the strength of color-based motion with respect to luminance-based motion, with higher values indicating relatively more effective P pathway, compared with M pathway, contribution to motion processing.

## METHOD

### Subjects

A total of 35 infants participated in these studies: twelve 2-month-olds, thirteen 3-month-olds, and ten 4-month-olds. All the infants were born in families with no history of color blindness or color abnormalities. We also tested 6 color-normal adult subjects (ages 20–25) under nearly identical conditions so data from adults and infants could be compared.

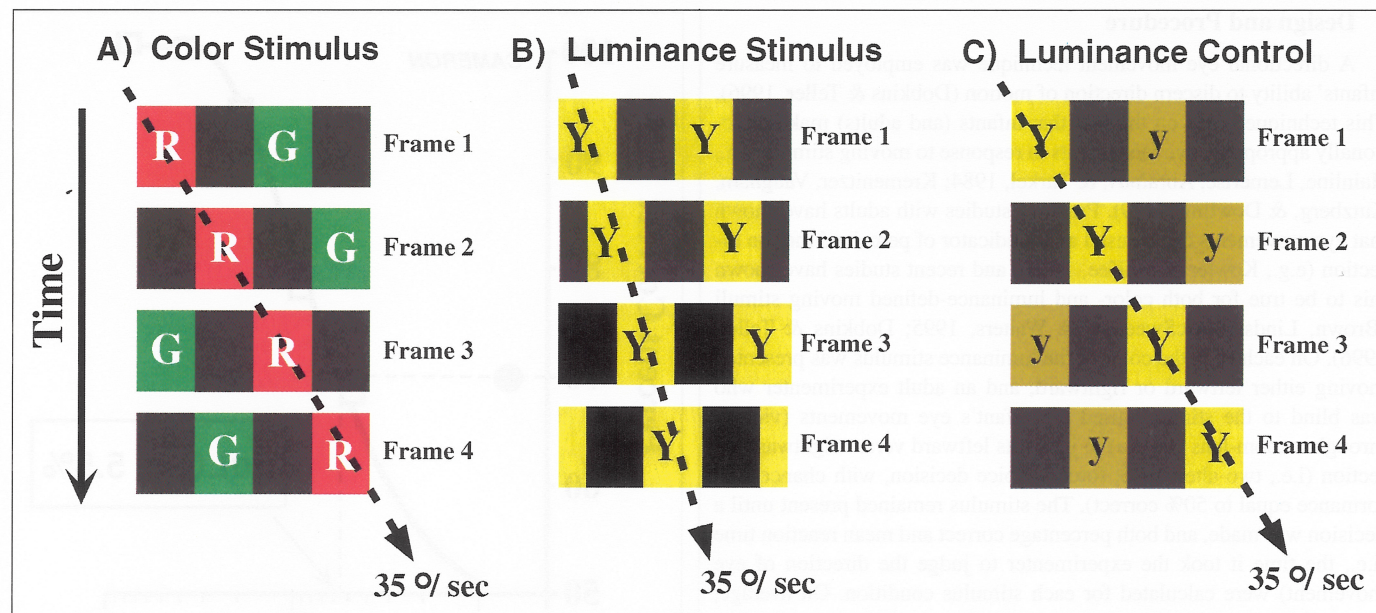
### Stimuli

The color stimulus (Fig. 1a) in these experiments consisted of moving red-black-green-black sinusoidal gratings; the red and green stripes were equiluminant.<sup>2</sup> This novel stimulus was displaced 1/4 cy-

1. There also exists a third subcortical pathway—the *koniocellular* (K) pathway—which is thought to encode "blue versus yellow" color information (see Hendry & Reid, 2000). However, the red and green colors employed in our experiments should not activate the K pathway, and thus it is not discussed here.

2. For all subjects (both infants and adults), the red and green stripes were set to be equiluminant based on the mean of settings from 15 adult subjects, obtained using a *minimally distinct motion* technique (Dobkins & Teller, 1996). The use of adult settings for infants is justified because infants' equiluminance values are known to be identical to those of adults (Brown, Lindsey, McSweeney, & Walters, 1995; Dobkins, Anderson, & Kelly, 2001; Teller, Perceverzeva, Chien, & Palmer, 2000).

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**Fig. 1.** Stimuli used in the experiments: the color stimulus (a), luminance stimulus (b), and luminance control stimulus (c). Each row represents one stimulus frame, with time going downward. In these examples, the stimuli are moving to the right. Subjects viewed the stimuli at a distance of 37 cm from the video monitor. At this distance, the stripe width was  $1.9^\circ$  and the total stimulus size was  $59^\circ \times 45^\circ$ . The speed of movement was  $35^\circ/\text{s}$ . In the color stimulus, the luminance of the green and red stripes was  $36.5 \text{ cd}/\text{m}^2$ , and the luminance of the black stripes was  $1.92 \text{ cd}/\text{m}^2$ . Although the stripes that made up the gratings are depicted here as possessing sharp edges, the actual transition from red to black to green to black was sinusoidal, in order to reduce the potential for chromatic aberration. G = green; R = red; Y = bright yellow; y = dim yellow.

cle (i.e., the width of one stripe) at each successive time interval, with the result that a consistent direction of motion could be discerned only if color identity was employed (i.e., matching red to red and green to green over time). Note that the intervening black stripes, which were dimmer than the red and green stripes by 90%, provided an important function: Their presence was expected to saturate the responses of M cells (Movshon et al., 1997; Shapley, 1990), thus rendering M cells useless in this task. This manipulation was crucial because without the intervening black stripes, a conventional equiluminant red-green grating would produce residual (and usable) activity within the M pathway, in the form of responses to borders defined by red-green contrast (Valberg, Lee, Kaiser, & Kremers, 1992), as well as residual responses resulting from differential sensitivity to red versus green across the M cell population (Logothetis, Schiller, Charles, & Hurlbert, 1990). In addition, the intervening black stripes had the advantage of making any small luminance mismatch between the red and green stripes extremely difficult to notice because luminance discrimination is quite poor at high contrasts, in adults and especially in infants (Brown, 1994). Note that the use of an EqLC paradigm to quantify color input to motion processing has been described previously (Cavanagh & Anstis, 1991; Teller & Palmer, 1996; Thiele, Dobkins, & Albright, 1999), but these earlier studies employed conventional red-green gratings, which cannot isolate the contribution of P cells.

The luminance stimulus (Fig. 1b) consisted of yellow-black sinusoidal gratings, which were similarly displaced  $1/4$  cycle (i.e., half the width of one stripe) at each successive time interval. The luminance stimulus was presented at different luminance contrasts between the bright and dim stripes (infants: 2.5, 5.0, 10, 20, 50, and 90% contrast;

adults: 0.5, 1, 2, 10, and 20% contrast<sup>3</sup>) in order to obtain an EqLC for each subject. Because  $1/4$  cycle in this stimulus translates into a smaller displacement per frame than in the color stimulus, the displacement occurred twice as frequently as in the color condition, in order to create identical speeds in the two conditions (i.e.,  $35^\circ/\text{s}$ ). All other parameters of the luminance stimulus were identical to those of the color stimulus.

Although we attempted to make the red and green stripes of the color gratings equiluminant, the possibility remains that there were small luminance differences between the two colors, at least for some individuals. To ensure that performance could not be explained by luminance differences between the red and green stripes, we simulated the effects of this type of error using a moving bright-yellow/black/dim-yellow/black luminance control stimulus (Fig. 1c) in six 3-month-olds. This control stimulus was presented at five different levels of luminance contrast between the bright-yellow and dim-yellow stripes: 5.0, 7.5, 10, 20, and 40%. In all other respects, this stimulus was identical to the color stimulus.

3. Note that, although some of the higher luminance contrasts in the yellow-black grating could potentially saturate M cell responses, the EqLC values obtained were well below the values known to saturate M cells (i.e., adult saturation range: 10–20%, Shapley, 1990; infant saturation range: 20–30%, Movshon et al., 1997), and thus this factor should have had no effect on our estimates.

## Color-Based Motion in Infants

## Design and Procedure

A directional eye movement technique was employed to measure infants' ability to discern direction of motion (Dobkins & Teller, 1996). This technique relies on the fact that infants (and adults) make directionally appropriate eye movements in response to moving stimuli (e.g., Hainline, Lemerise, Abramov, & Turkel, 1984; Kremenitzer, Vaughan, Kutzberg, & Dowling, 1979). Previous studies with adults have shown that eye movements can be used as an indicator of perceived motion direction (e.g., Kowler & McKee, 1987), and recent studies have shown this to be true for both color- and luminance-defined moving stimuli (Brown, Lindsey, McSweeney, & Walters, 1995; Dobkins & Teller, 1996). On each trial, the color or the luminance stimulus was presented moving either leftward or rightward, and an adult experimenter who was blind to the stimulus used the infant's eye movements (viewed through a zoom-lens camera) to judge its leftward versus rightward direction (i.e., two-alternative, forced-choice decision, with chance performance equal to 50% correct). The stimulus remained present until a decision was made, and both percentage correct and mean reaction time (i.e., the time it took the experimenter to judge the direction of eye movement) were calculated for each stimulus condition. On average, the total number of trials completed was  $201 \pm 25$  for 2-month-olds,  $199 \pm 14$  for 3-month-olds, and  $194 \pm 28$  for 4-month-olds.

For adults, data were obtained using the same directional eye movement technique (rather than direct reports from subjects), to ensure that any differences observed between infants and adults could not be attributable to differences in response measure. However, we modified the adult paradigm slightly to keep the percentage correct below ceiling (i.e., 100% correct), which was required in order to calculate EqLC. To this end, adults were tested with limited-duration stimuli (460 ms). In order to check that the use of limited-duration stimuli did not confound our results, we also tested each adult separately with unlimited-duration stimuli and recorded reaction times (as for infants). The purpose of obtaining reaction times in both adults and infants was to calculate a secondary (and confirmatory) estimate of EqLC. Adults were tested on a total of 320 trials, for both limited- and unlimited-duration stimuli.

## Determining EqLC

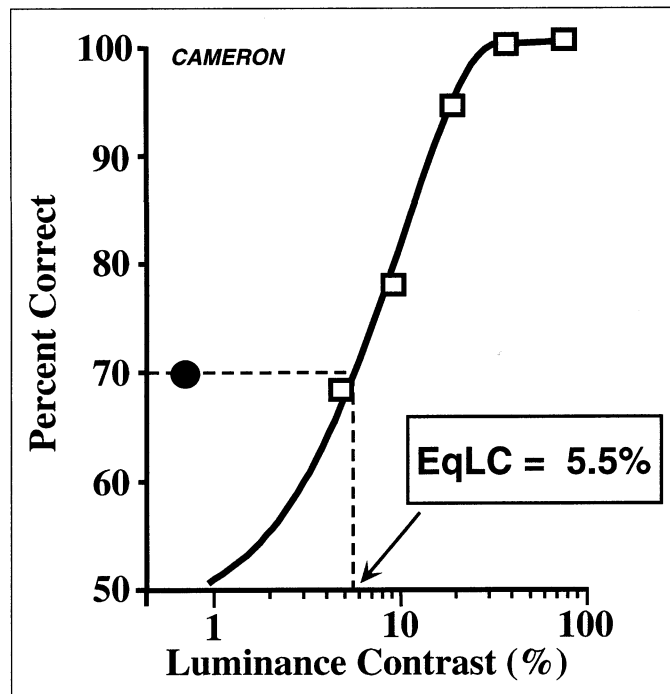
For each subject, the percentage-correct data for the luminance stimulus were fitted with a Weibull function:

$$P_c = 1 - 2^{-[(c/\alpha)^\beta]}$$

where  $P_c$  is percentage correct,  $c$  is contrast,  $\alpha$  is threshold (i.e., the contrast yielding 75% correct performance), and  $\beta$  is the slope parameter. From this equation, EqLC was computed as the contrast in the luminance grating that yielded the same performance as in the color condition (i.e., we solved for  $c$  given the percentage correct,  $P_c$ , generated in the color condition). We also used reaction time data as a secondary measure of EqLC: Reaction time data for the luminance condition were fitted with a logarithmic function, and the luminance contrast that yielded the same reaction time as in the color condition was taken as a second estimate of EqLC.

## RESULTS AND DISCUSSION

Example data from one 3-month-old subject are shown in Figure 2. When tested with the color stimulus, this infant was correct on 70% of

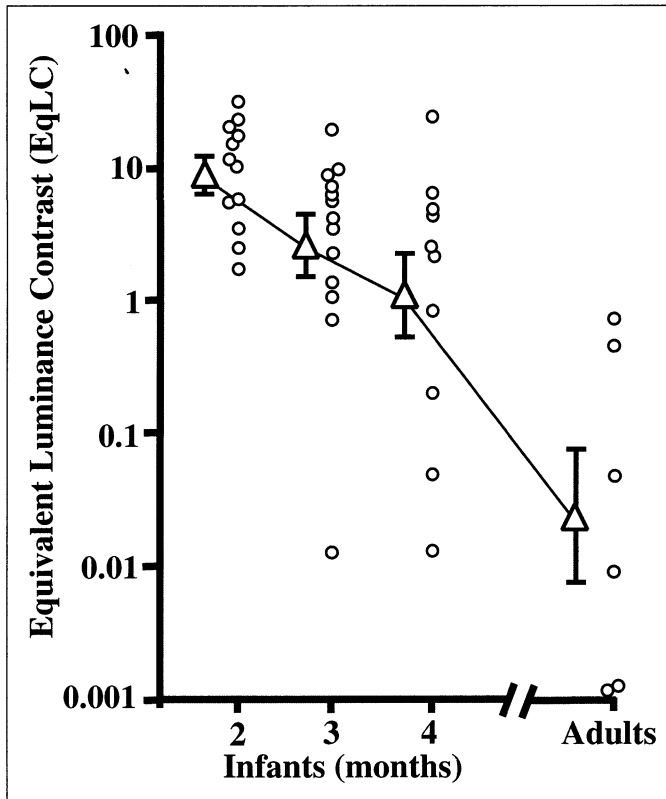


**Fig. 2.** Example data from one 3-month-old. This subject was correct on 70% of the trials with the color stimulus (filled circle). The subject's luminance data (open squares) were fitted with a Weibull function, and the luminance contrast that yielded 70% correct performance (i.e., 5.5% in this case) was defined as his equivalent luminance contrast (EqLC).

the trials. Percentage-correct data for the luminance stimulus were fitted with a Weibull function, which allowed us to determine the amount of luminance contrast required to yield correct performance on 70% of the luminance trials. For this infant, that value was 5.5%, reflecting his EqLC.

Figure 3 shows individual and group mean EqLC values for the 2-month-olds, 3-month-olds, 4-month-olds, and adults. As revealed in this plot, EqLC values decreased significantly with age,  $F(3, 37) = 12.8$ ,  $p < .0001$ . Specifically, mean EqLC values were 8.8%, 2.5%, 1.0%, and 0.02% for 2-, 3-, and 4-month-olds and adults, respectively. Although the extremely low EqLC values observed for adults were expected—because motion-processing areas in adults are known to receive minimal information about object color—the surprisingly high EqLC values for infants suggest that color input to motion processing is stronger in the immature visual system.

A significant decrease in EqLC with age was also found when we used reaction time data (with adults tested separately on an unlimited-duration stimulus) to compute an estimate of EqLC,  $F(3, 37) = 3.66$ ,  $p < .025$ . This secondary measure ensures that the color-based motion advantage seen in infants cannot be explained by a speed-accuracy trade-off, or by some artifact of the limited-duration stimuli used for adults in the main experiment. Finally, the results with the luminance control stimulus (Fig. 1c), which simulated the effects of potential luminance mismatches between the red and green stripes, demonstrated that, on average, 27% luminance contrast between the bright- and dim-yellow stripes was required to reach performance that matched



**Fig. 3.** Equivalent luminance contrast as a function of age. Individual subjects' data (open circles) and group means (open triangles) are shown. Bars denote standard errors of the means.

that produced by the color stimulus. Because any misestimation of red-green equiluminance for our subjects was extremely unlikely to have exceeded this value, we feel confident that the infants' responses to the color stimulus reflect the use of color identity and not luminance differences.

These results provide the first demonstration that the relative strength of color-based, with respect to luminance-based, motion processing is greater in infants than in adults. A simple way to account for these findings is to propose that the relative strength of P pathway (color-based) versus M pathway (luminance-based) input to motion detectors changes over the course of development, with the strongest P pathway input occurring early in life.

Before accepting this *differential-input hypothesis*, however, we must also consider whether the results can be accounted for by changing sensitivity to color and luminance stimuli. That is, if the relative sensitivity of color versus luminance mechanisms decreases with age, the relative effectiveness of color-based, with respect to luminance-based, motion processing would be expected to decline during development (and there would be no need to appeal to changes in the strength of input to motion detectors to explain the results). However, this possibility is highly unlikely because the available data on development of color and luminance sensitivity tell the opposite story. Specifically, the relative sensitivity to color versus luminance contrast has been shown to increase, not decrease, with age (Dobkins, Anderson, & Kelly, 2001; Kelly, Borchert, & Teller, 1997; Morrone, Burr, & Fiorentini, 1993) or, at the very least, remain constant with age (Allen,

Banks, & Norcia, 1993; Brown et al., 1995; Teller & Palmer, 1996). Moreover, we found that the absolute percentage correct on the color-motion task declined with age (2-month-olds: 74.7%; 3-month-olds: 70.1%; 4-month-olds: 68.3%), although this effect was not significant. In other words, infants exhibited a decrement in color-motion performance over a developmental period during which color sensitivity clearly improves, an outcome that is entirely consistent with a decrease in the strength of color input to motion detectors with age.

In sum, the results of our experiments support the differential-input hypothesis; that is, they suggest that the relative strength of P versus M pathway input to motion processing is greater in infants than it is in adults. Although we cannot rule out the possibility that subcortical areas known to be involved in eye movement generation contribute to these effects, the results from previous studies (Braddick et al., 1992; Newsome, Wurtz, Dursteler, & Mikami, 1985; but cf. Morrone, Atkinson, Cioni, Braddick, & Fiorentini, 1999) suggest that the eye movement measure we used is likely to be driven predominantly by cortical motion areas of the brain. We propose that the middle temporal area (MT) of visual cortex is likely to contribute to the effects obtained in the present study because, in adults, this area is known to play a key role in motion processing (see Albright, 1993), and receives predominantly M pathway input, with only a small contribution from the P pathway (Maunsell et al., 1990). Thus, our results may indicate that P pathway input to area MT is relatively more effective early than late in life, and therefore recedes over the course of development. This decrease in input could occur through either a decrease in the synaptic strength of P cell connections to MT or anatomical pruning of those connections.

This latter possibility is consistent with the general principle that developing brains produce exuberant connections, some of which are later retracted (Callaway, 1998; Rodman & Consuelos, 1994). And, in fact, pruning of anatomical connections during development has similarly been used to account for other aspects of infant visual development, specifically the onset of stereo vision (Held, 1993; see Johnson & Vecera, 1996, for discussion). Of course, it is also possible that M pathway input to MT is selectively strengthened during development, as a result of either an increased number of connections or strengthening of synapses. In either case, the results of these experiments suggest that infants may not be born with a strict color-motion dichotomy. Rather, the findings suggest that inputs to motion areas are rewired or reweighted over the course of development, ultimately resulting in segregated color and motion processing in the adult brain.

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