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 (e.g., Livingstone & Hubel, 1988; Merigan & Maunsell, 1993). Here, we investigated the development of this dichotomy by conducting psychophysical experiments in human subjects (2-, 3-, 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 relatively stronger color-based motion processing in infants as compared to adults. These results suggest relatively greater color input to motion areas early in life. Motion areas must then specialize to the adult-like state by re-weighting or selectively pruning their inputs over the course of development.
In the visual system of adults, information about object color and 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., 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 the topic of 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 re-wiring or re-weighting of connections take place over the course of development in order to produce the adult-like 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 to adults. Specifically, we measured subjects’ ability to discern the direction of a moving red/black/green/black (R/B/G/B) “color” grating, which could be accomplished only if information about color identity was employed, i.e., matching “red” to “red” and “green” to “green” over time. To quantify the strength of color-based motion processing, subjects were also tested with a moving yellow/black (Y/B) “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 percent correct performance as that 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 which encodes the color identity (red versus green) of an object -- the parvocellular (P) pathway, and one which is highly sensitive to luminance contrast yet unselective for object color -- the magnocellular (M) pathway1. 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, since 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, as compared to M pathway, contribution to motion processing.

**METHODS**

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 will not be discussed here.
Subjects. A total of 35 infants participated in these studies: 2-month-olds, n = 12; 3-month-olds, n = 13; 4-month-olds, n = 10. All infants were born in families with no history of color blindness or color abnormalities. For comparison to infant data, six color-normal adult subjects (ages 20-25) were tested under nearly identical conditions.

Stimuli. The “color” stimulus (Figure 1A) in these experiments consisted of moving red/black/green/black (R/B/G/B) sinusoidal gratings, for which the red and green stripes were equiluminant with each other. This novel stimulus was displaced 1/4 cycle (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 (Figure 1A). Note that the intervening black stripes, which were dimmer than the red and green stripes by 90%, provided an important function. Namely, their presence was expected to saturate the responses of M cells (Shapley, 1990; Movshon, Kiorpes, Hawken, Skoczynski, Cavanaugh, & Graham, 1997), thus rendering M cells useless in this task. This manipulation is crucial because, without the intervening black stripes, a conventional equiluminant red/green grating will 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, 1999). In addition, the intervening black stripes have the advantage of making any small luminance mismatch between the red and green stripes extremely difficult to notice. This is 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), however, these earlier studies employed conventional red/green gratings, which cannot isolate the contribution of P cells.]

The “luminance” stimulus (Figure 1B) consisted of yellow/black (Y/B) 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, 90%, adults: 0.5, 1, 2, 10, 20, 100% in order to obtain an “equivalent luminance contrast” (EqLC) for each subject (see below). Note that, since a 1/4 cycle in this stimulus translates into a smaller displacement per frame, the displacement occurred twice as frequently as in the color condition, in order to create identical speeds in the two conditions (i.e., 35°/sec). All other stimulus parameters were identical to the color stimulus.

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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 infant equiluminance values are known to be identical to those of adults (Brown, Lindsey, McSweeney, & Walters, 1995; Teller, Pereverzeva, Chien, & Palmer, 2000; Dobkins, Anderson, & Kelly, 2001).

3 Note that, although some of the higher luminance contrasts in the yellow/black grating could potentially saturate M cell responses, the equivalent luminance contrast values obtained in our subjects (see Figure 3) 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 no effect on our estimates.
Although we attempted to make the red and green stripes of the color grating equiluminant, the possibility remains that small luminance differences existed 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 (Y/B/y/B) "luminance control" stimulus (Figure 1C) in six 3-month-olds. The 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 & 40%. In all other respects, this stimulus was identical to the color stimulus.

![Figure 1: Stimuli.](image)

**Figure 1:** Stimuli. (A) Color stimulus (red/black/green/black, R/B/G/B). (B) Luminance stimulus (yellow/black, Y/B). (C) Luminance Control stimulus (bright-yellow/black/dim-yellow/black, Y/B/y/B). Each row represents one stimulus frame, with time going downward. In these examples, the stimuli are moving to the right. General stimulus parameters: distance from video monitor = 37 cm, stripe width = 1.9°, speed = 35°/sec, total stimulus size = 59° by 45°. Color stimulus: luminance of green and red stripes = 36.5 cd/m², luminance of black stripes = 1.92 cd/m². Note that, although the stripes that make up these gratings are depicted here as possessing sharp edges, the actual transition from red to black to green to black was sinusoidal in nature, in order to reduce the potential for chromatic aberration.

**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., Kremenitzer, Vaughtam, Kutzberg, & Dowling, 1979; Hainline, Lemerise, Abramov, & Turkel, 1984). Previous studies in adults have shown that eye movements can be used as an indicator of perceived motion direction (e.g., Kowler & McKee, 1987), and that this applies equally so for color- and luminance-defined moving stimuli (Brown, et al., 1995; Dobkins & Teller, 1996). On each trial, the color (Figure 1A) or the luminance (Figure 1B) 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, with chance performance equal to 50% correct). The stimulus remained present until a decision was made, and both percent correct and mean reaction time (i.e., the time it took the experimenter to judge the eye movement direction) were calculated for
each stimulus condition. On average, the total number of trials obtained were: 2-month-olds = 201 ± 25, 3-month-olds = 199 ± 14, 4-month-olds = 194 ± 28.

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

Determining Equivalent Luminance Contrast (EqLC). For each subject, percent correct data obtained for the luminance (Y/B) stimulus were fitted with a Weibull function:

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P_c = 1 - 2^{[-(c/\mathcal{I})^b]} \tag{1}\]

where \(P_c\) is percent correct, \(c\) is contrast, \(\mathcal{I}\) is threshold (i.e., the contrast yielding 75% correct performance) and \(b\) is the slope parameter. From this equation, EqLC was computed as the luminance contrast in the Y/B grating that yielded the same performance as in the color condition (i.e., we solved for \(c\) given the percent correct, \(P_c\), generated in the color condition). As a secondary measure of EqLC, we also used reaction time data as follows: 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, the infant performed at 70% correct (filled circle). Percent correct data obtained for the luminance stimulus (open squares) were fitted with a Weibull function, which allowed us to determine the amount of luminance contrast required to yield 70% correct. For this infant, that value was 5.5%, reflecting his “equivalent luminance contrast” (EqLC).

![Figure 2: Example data from one 3-month-old. For this subject, performance on the color stimulus was at 70% correct (filled circle). 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 the EqLC for this individual.](image)
Sample data are presented in Figure 3. Shown are individual (open circles) and group mean (open triangles) EqLC values for 2-month-olds (n = 12), 3-month-olds (n = 13), 4-month-olds (n = 10), and adults (n = 6). As revealed in this plot, EqLC values decreased significantly with age (F(3,37) = 12.8, p < 0.0001). Specifically, mean EqLC values were 8.8%, 2.5%, 1.0%, and 0.02% for 2-, 3-, 4-month-olds, and adults, respectively. While the extremely low EqLC values observed for adults are to be expected – since 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 relatively stronger in the immature visual system.

![Figure 3: EqLCs plotted as a function of age. Data are shown for individual subjects (open circles) and group means (open triangles). Bars denote standard errors of the means.](image)

In addition to these results based on percent correct data, a significant decrease in EqLC with age was found when we used reaction time data (with adults tested separately on an unlimited-duration stimulus, see Methods) to compute a separate estimate of EqLC (F(3,37) = 3.66, p < 0.025). This secondary measure ensures that the color-based motion advantage seen in infants cannot be explained by a speed-accuracy tradeoff, or by some artifact of the limited-duration stimuli used for adults in the main experiment. Finally, the results of our luminance control experiment (Figure 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 that produced by the color stimulus. Because any mis-estimation of red/green equiluminance for our subjects was extremely unlikely to have exceeded this value, we feel confident that infants’ responses to the R/B/G/B stimulus reflect the use of color identity and not luminance differences.

These results provide the first demonstration that the 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, we must also consider another possibility based on changes in sensitivity to color and luminance stimuli that occur with age. That is, if the relative sensitivity of color versus luminance mechanisms decreases with age, we would also expect to find that the relative effectiveness of color-based, with respect to luminance-based, motion processing declines during development (without any need to entertain changes in the strength of input to motion detectors). However, this possibility is highly unlikely since the available data on development of color and luminance sensitivity tell a story opposite to this scenario. Specifically, the relative sensitivity to color versus luminance contrast has been shown to increase, not decrease, with age (Morrone, Burr, & Fiorentini, 1993; Kelly, Borchert, & Teller, 1997; Dobkins, et al., 2001) or at the very least, remain constant with age (Allen, Banks, & Norcia, 1993; Brown, et al., 1995; Teller & Palmer, 1996). Moreover, in further support that changes in sensitivity cannot account for our results, we found that absolute percent correct performance on the color-motion task actually 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 time period when color sensitivity is clearly improving, 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, i.e., 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 (Newsome, Wurtz, Dursteler, & Mikami, 1985; Braddick, Atkinson, Hood, Harkness, Jackson & Vargha-Khadem, 1992, but cf. Morrone, Atkinson, Cioni, Braddick, & Fiorentini, 1999) suggest that our eye movement measure is likely to be driven predominantly by cortical motion areas of the brain. With this in mind, we propose that the middle temporal area (MT) of visual cortex is a likely substrate since, 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 reflect relatively more effective P pathway input to area MT early in life, which then recedes over the course of development. This could occur either through 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 (Rodman & Consuelos, 1994; Callaway, 1998). 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). Of course, it is also possible that M pathway input to MT is selectively strengthened during development, either as a result of 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, such findings suggest the existence of re-wiring or re-weighting of inputs to motion areas over the course of development, with the ultimate result of segregated color and motion processing in the adult brain.
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