

Infants' visual system nonretinotopically integrates color signals along a motion trajectory

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Whereas early visual processing has been considered primarily retinotopic, recent studies have revealed significant contributions of nonretinotopic processing to the human perception of fundamental visual features. For adult vision, it has been shown that information about color, shape, and size is nonretinotopically integrated along the motion trajectory, which could bring about clear and unblurred perception of a moving object. Since this nonretinotopic processing presumably includes tight and elaborated cooperation among functional cortical modules for different visual attributes, how this processing matures in the course of brain development is an important unexplored question. Here we show that the nonretinotopic integration of color signals is fully developed in infants at five months of age. Using preferential looking, we found significantly better temporal segregation of colors for moving patterns than for flickering patterns, even when the retinal color alternation rate was the same. This effect could be ascribed to the integration of color signals along a motion trajectory. Furthermore, the infants' color segmentation performance was comparable to that of human adults. Given that both the motion processing and color vision of 5-month-old infants are still under development, our findings suggest that nonretinotopic color processing develops concurrently with basic color and motion processing. Our findings not only support

the notion of an early presence of cross-modal interactions in the brain, but also indicate the early development of a purposive cross-module interaction for elegant visual computation.

Introduction

The longer you look at something, the better you get to know it. In fact, the temporal integration of input signals is a useful strategy for the human visual system to improve its quality of perception. However, there is a problem. In daily life, the visual image of an object frequently jumps around the retina due to movements of the object or the observer's eyes. Temporally integrating the visual inputs across different retinal locations is a hard task for the early visual neural mechanisms, which normally have fixed receptive fields on the retinotopic coordinates. Recent studies of adult vision have suggested that the human visual system overcomes this problem by nonretinotopically integrating object information over time despite changes in the retinal location of the object by object movements or eye movements (Boi, Vergeer, Ögmen, & Herzog, 2011; Cavanagh, Holcombe, & Chou, 2008; Melcher &

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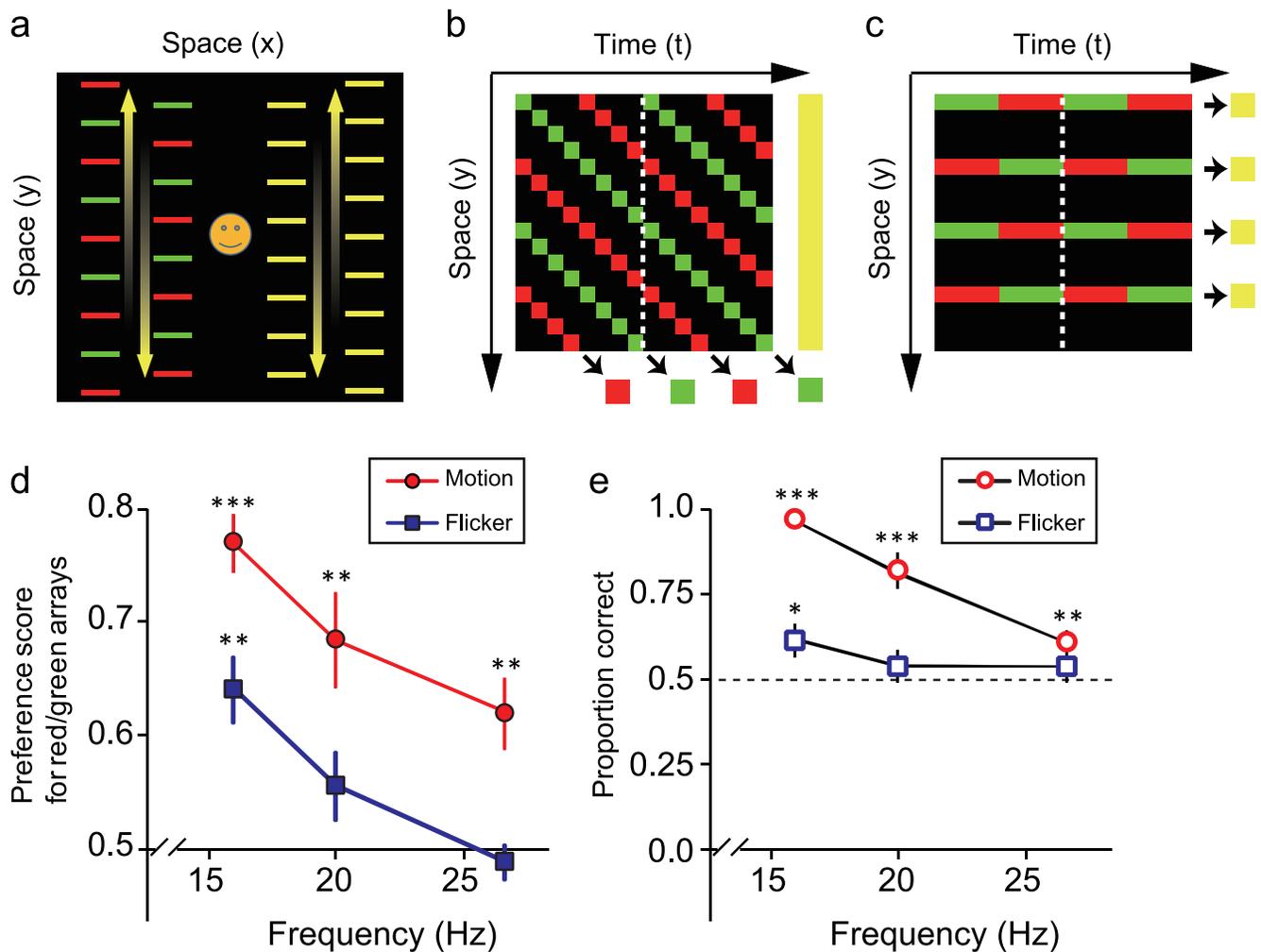


Figure 1. (a) Spatial configuration of stimuli used in color segregation experiment. (b) Space (y) – time (t) plot of the motion stimulus. The color integrated over time at each retinal position (yellow) is shown at the right, and the colors integrated along the motion trajectory (red and green) are shown at the bottom. The white dotted line indicates the cycle period of color alternation. (c) Space (y) – time (t) plot of the flicker stimulus, whose spatial configuration is the same as panel b. (d) Mean preference scores in infant color segregation experiment. The circles and the squares show the preference scores for the motion and flicker stimuli, respectively. Each data point shows the average for the seven infant observers. The error bars represent standard error. * $p < 0.05$. ** $p < 0.01$. *** $p < 0.001$. (e) Proportion correct of color change discrimination for motion (circles) and flicker (squares) stimuli in adult color segregation experiment. Each data point shows the average for six adult observers.

Morrone, 2003; Nishida, Watanabe, Kuriki, & Tokimoto, 2007; Ögmen & Herzog, 2010; Otto, Ögmen, & Herzog, 2010; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). For instance, the visual system temporally integrates the sensory signals of a moving object not only at the same retinal location, but also along the trajectory of a moving object. The trajectory integration serves a variety of useful visual functions, such as the reduction of motion smear (Burr, 1980; Burr & Morgan, 1997) and the veridical perception of the shape and color of moving objects (Nishida, 2004; Ögmen, Otto, & Herzog, 2006; Watanabe & Nishida, 2007).

We expected that a developmental study of the nonretinotopic signal integration in infant vision would

provide useful insights into the underlying neural mechanisms of this valuable visual function, which is a matter of ongoing investigation. Furthermore, such a study would also reveal a general picture of the development of visual modules. Nonretinotopic processing presumably includes tight and elaborate cooperation among the functional cortical modules for different visual attributes, in particular between motion processing and processing for other visual attributes. Interactions across functional modules for different visual attributes in infant vision have been discussed in relation to a synesthesia-like association (Maurer, Gibson, & Spector, 2012; Wagner & Dobkins, 2011). Infant synesthesia is thought to result from a normal developmental process involving an initial proliferation

of exuberant anatomical connectivity in the infant brain. However, unlike infant synesthesia, the elegant cooperative mechanisms for nonretinotopic processing are unlikely to emerge from random connections across functional modules or to disappear during the course of development. Meanwhile, if it matures early in development, nonretinotopic integration could be an effective mechanism for infants' visual system, whose visual acuity and sensitivity are very limited compared to adults (e.g., Atkinson, Braddick, & Braddick, 1974; Rasengane, Allen, & Manny, 1997), to extract reliable information from retinal images. However, little attention has been paid to the nonretinotopic aspects of infants' visual processing.

In the current study, we tested infants' capability for nonretinotopic integration using a motion-induced color segregation phenomenon (Watanabe, & Nishida, 2007). In this phenomenon, with steady eye fixation by the observer, a retinal color alternation between red and green is perceptually segregated better when the color alternation is produced by a drifting motion of red and green bars (Figure 1a and b) than when it is produced by a stationary flicker of the two colors (Figure 1c). It is well known that red and green are perceptually fused into yellow when the two colors alternate on the retina at a rate beyond the critical fusion frequency. If the critical fusion frequency is solely determined by the retinal alternation rate, it should be the same for the motion and flicker conditions. However, if the two colors are nonretinotopically integrated along a motion trajectory, the critical fusion frequency should be higher (i.e., the two colors should be segregated more) for the motion condition than for the flicker condition. This is because in the motion condition, red and green signals are separate from each other in the integration along a moving motion path (diagonal path in Figure 1b), while in the flicker condition, red and green signals are mixed along a stationary motion path (horizontal path in Figure 1c). Therefore, better color segregation for the motion condition than for the flicker condition, which we named *motion-induced color segregation*, provides evidence supporting the trajectory integration mechanism in the human visual system, together with nonretinotopic color fusion along a motion trajectory of color alternating bars, which we named *motion-induced color mixture* (Nishida et al., 2007)

Using preferential looking, we examined whether motion-induced color segregation was observed in infants. Although one might expect a relatively slow maturation of the "smart" nonretinotopic processing after the establishment of basic processing for each visual attribute, our results showed that 5-month-old infants have the capability to integrate color signals along a motion trajectory.

General method

Participants

Seven infants aged 5 months (three males and four females, mean age = 162 days, ranging from 143 days to 171 days) participated in the infant color segregation experiments. Another seven infants aged 5 months (two males and five females, mean age = 156 days, ranging from 140 days to 179 days) participated in the artifact rejection experiments. This sample size was determined by the basis of sample sizes in previous studies of temporal contrast sensitivity in infants (e.g., Hartmann & Banks, 1992). No participant was ruled out from the data analysis. All infants were full term at birth and healthy at the time of testing. None of the participants' parents reported any family history of color deficiency. In addition, infants with color deficiency would have shown isoluminant points that significantly deviated from those of the other infants (Maurer, Lewis, Cavanagh, & Anstis, 1989), but no deviation was shown. These findings led us to assume that all the infants had normal color vision. All infants were recruited by advertisements in the newspaper. Nine adults (three males and six females, mean age = 26.1 years old) participated in the adult color segregation experiment. None of the participants reported any color deficiency. The experiments were approved by the ethics committee of Chuo University and conducted in accordance with the ethical standards in the 1964 Declaration of Helsinki. The parents of participants gave their informed written consent before the start of the experiment.

Apparatus

A 22-in. color CRT display (Mitsubishi Diamond Pro 2070SB, refresh rate 160 Hz, luminance range of 0.1–82 cd/m²) was used to display all stimuli. During experiments, each infant sat on his/her parent's lap at a distance of 60 cm from the front of the display monitor. The infant's looking behavior was recorded through a hidden video camera set below the CRT display. The experimenter observed the infant's behavior via a TV monitor behind the experimental booth and controlled the stimulus presentation by computer. The resolution of the CRT display was set at 800 × 600. Images were presented on the CRT display through a computer-controlled visual stimulus generator (ViSaGe; Cambridge Research Systems, Rochester, UK) with 12-bit gamma correction for each primary color (i.e., red, green, blue). The CIE *x* and *y* coordinates of the CRT phosphors, as measured by a ColorCal colorimeter (Cambridge Research Systems, Rochester, UK), were

(0.60, 0.35) for red, (0.29, 0.60) for green, and (0.15, 0.07) for blue.

Color specification

We specified isoluminant red/green for each participant using the minimum motion paradigm (Teller & Lindsey, 1989). Four types of gratings, which were composed of counterphase red–green or monochrome (light gray–dark gray) square waves, were presented in a repeated sequence. The colors of the first and third gratings were red/green, and those of the second and fourth were monochrome. The sizes of all squares were the same, and the squares were subtended 1.0° in width and 10° in height. The vertical positions of the gratings were aligned, and each grating was presented with its position shifted sideways one-quarter cycle (half of a square width, 0.5°) from its predecessor. An apparent motion in a direction could be perceived depending on the relative luminance between the red and green stripes. When the red squares were perceived as darker than the green squares, the red squares in the first and third grating appeared to jump to the dark gray squares in the second and fourth grating, respectively. On the other hand, when the red squares were perceived as lighter, they appeared to jump in the opposite direction. If the red and green stripes were isoluminant, no clear direction of motion would be perceived. The rate of gratings update was 32 frames per second. The speed of one-directional motion, when visible, was $16^\circ/\text{s}$. The apparent motion induced optokinetic eye movements for infants. Accordingly, we were able to estimate the relative intensity of the red and green stripes that are isoluminant for each infant by observing the optokinetic nystagmus (OKN).

In the experiments, the participants' eye positions were monitored by a video camera and the movie images were sent to a TV monitor. A naïve observer watched the infants' eye movements on the monitor. Before the trials, a cartoon was displayed in order to gain the infant's attention. Immediately after the observer confirmed fixation, the gratings were presented until the observer judged whether the infants' eyes followed to the left or to the right. The five luminance ratios of green luminance to red luminance (0.20, 0.28, 0.36, 0.44, and 0.52 to 25 cd/m^2) were examined. Each luminance ratio was tested 20 times (100 trials total). One experimental block was composed of five trials for each ratio, and the ratios were presented in a randomized order. The obtained results in terms of the percent of trials in which the OKN indicated that green was perceived to be lighter were fitted to the cumulative Gaussian function using `psignifit` toolbox version 2.5.6 for MATLAB (<http://bootstrap-software.org/psignifit/>). The parameters α

(the 50% point), and β (steepness) were allowed to vary freely for the best fit on the basis of the maximum likelihood criterion. The lapse rates were fixed at 5%, which has been previously demonstrated to produce consistent and accurate threshold estimates in infants' psychometric function fitting (Teller, Mar, & Preston, 1992). The 50% point on the cumulative Gaussian function provided an isoluminant of red and green luminance for each participant.

Infant color segregation experiment

Method

Stimuli

We used two types of visual stimuli, motion and flicker. The motion stimulus was composed of four vertical arrays of bars presented on a dark background at 7.3° and 15.8° leftward or rightward from the fixation point. Each bar was subtended 4.4° in width and 0.2° in height. In each array, constant spatial intervals were inserted between bars. The two arrays at the left- or right-hand side were red/green alternating bars and the other two arrays were yellow bars (Figure 1a). The red bars (CIE, 1931; $x = 0.60$, $y = 0.35$) were equal to 20 cd/m^2 , and the green bars (CIE, 1931; $x = 0.29$, $y = 0.60$) were defined according to the individual isoluminant ratios of infant participants measured by the minimum motion method. The yellow was created by adding the red and green, each at 50% intensity. All bars shifted in a vertical direction every 6.25 ms by one bar height 0.19 deg (at a velocity of $31.0^\circ/\text{sec}$), with the color kept constant (Figure 1b). To minimize tracking eye movements, the inner and outer sides of the four bar arrays moved in opposite directions. Three interbar intervals were tested (0.38° , 0.57° , and 0.76° , which correspond to two, three, and four times the bar height, respectively). The corresponding color alternation rates at each retinal location were 26.7, 20.0, and 16.0 Hz. The initial bar positions were randomized. The flicker stimuli were red/green alternations with alternation rates of 26.7, 20.0, and 16.0 Hz, and the whole luminance energy of the stimulus was the same as that of the corresponding motion stimuli (Figure 1c).

Procedure

A preferential looking paradigm was used in the experiment. Before the experiment started, we followed the normal procedure for infant experiments by instructing the parents to close their eyes during the experiment. The eye movements of the infant participants were recorded with a video camera for analyses of looking directions. In order to fix the infant's gaze

on the center of the moving stimuli, each trial began with the presentation of a smiley face pattern at the center of the display accompanied by a short beep sound. Four moving (static) arrays of uniform yellow bars, whose vertical locations were randomized, were presented for the motion (flicker) condition at the time of the beep. We had an experimenter monitor the eye movements of the infants. Immediately after the experimenter confirmed that the infant participant was looking at the smiley face pattern presented at the center of the display, he/she changed the color of the two arrays at one side of the stimuli (left- or right-hand side) into equiluminant alternating red/green bars in the motion condition or into equiluminant red/green flicker in the flicker condition. The locations of the red/green bars in the array were alternated. When the eyes of the infant participant were static during the presentation, the red and green colors were superimposed on the retina. After 500 ms, the bars returned to yellow. Since it was crucial that the infant did not make eye movement while the red/green stimuli were presented, we monitored the eye movement of the infant and reduced the presentation duration from 1000 ms (Watanabe & Nishida, 2007) to 500 ms.

Each infant performed eight trials for each alternating frequency in each condition, in which the position of the test stimuli (left- or right-hand side) was reversed in half of the trials, and the order of test location was randomized. The motion directions of the inner and outer bar arrays (upward or downward direction) were counterbalanced for each infant in the motion condition. The motion and flicker conditions were tested in separate experimental blocks, and one block was composed of six trials, with two trials for each frequency in each condition. Eight experimental blocks were performed in total.

Date recording and analysis

An experimenter, who did not know on which side the red/green motion (flicker) stimulus was presented, analyzed the period of 2 s after the onset of red/green motion (flicker) stimulus using an offline video movie (30-Hz recording). We chose this recording timing since the latency of saccadic eye movement in 5-month-old infants is known to be about 400 ms (Matsuzawa & Shimojo, 1997). The infant's looking time during the period was classified into one of three behavioral categories—looking left, looking right, or no-looking—for each trial, and the duration of each category was estimated by pressing one of two keys assigned to the status of “looking left” and “looking right.” We calculated a preference score, which was the ratio of the looking time at the red/green side to the total looking time (looking left + looking right). When only “no-

looking” was recorded, the trial was excluded. Five trials were excluded based on this criterion.

In 29 of the 408 trials, we found vertical eye movements during the stimulus presentation. Immediately after the vertical eye movements, infants looked away from the CRT display in 28 of the 29 trials; in one trial the infant shifted his/her gaze to the right side. We excluded all 29 trials from the analysis.

Results

Figure 1d shows the mean preference score across the seven 5-month-old infants in the motion condition (circles) and in the flicker condition (squares). The results demonstrate that the preference scores for the red/green color were significantly higher than chance level for all motion stimuli, while a significant difference from chance level was observed only at 16.0 Hz for the flicker stimuli. Infants could segregate color alternations for a moving pattern at 26.6 Hz, but not for the static flicker at the same rate. We statistically analyzed the main effects of the two factors manipulated in this study: stimulus conditions (motion vs. flicker), and frequencies (16.0, 20.0, and 26.7 Hz), and their interactions. The analyses revealed that there were significant differences in the stimulus conditions, $F(1, 6) = 28.8, p < 0.01, \eta^2 = 0.315$, and in frequencies, $F(2, 12) = 34.6, p < 0.01, \eta^2 = 0.287$. No significant interactions were observed, $F(2, 12) = 0.01, ns$. Since, at each retinal location, visual stimuli with similar spatiotemporal patterns were presented by moving colors and static flickering colors, they should have generated a similar perception if they were integrated simply by the retinotopic coordinates (e.g., Coltheart, 1980). However, under all stimulus frequencies, the red–green alternations generated by the moving colors were more segregated perceptually than those generated by the static flickering color. These results suggest that the infant visual system has the capability to integrate color signals in nonretinotopic geometry (i.e., along a motion trajectory).

One may suggest that a similar performance enhancement in the motion condition could be produced by the infants' eye tracking of the stimulus movement. We, however, consider it unlikely that the infants' eye movement was the main factor producing the observed difference between the motion and flicker conditions. First, in order to not induce involuntary eye movements, we used a directionally balanced stimulus configuration (Figure 1a). Second, we video-monitored the infants' eye movements during each stimulus presentation, and screened out the trials in which vertical motion was detected. This method has been shown to effectively detect infants' tracking eye movements and OKN (e.g., Maurer et al., 1989; Teller

& Lindsey, 1989). In addition, while we found vertical eye movements in 29 trials, they did not affect the infants' preferential looking performance except in one trial. Video monitoring could not detect small eye movements including microsaccade, but eye movements in random directions should have enhanced color segregation in both the motion and flicker conditions. Third, the infants' performance was quantitatively similar to the adults' performance that was shown to be free from the eye movement artifacts (Watanabe & Nishida, 2007). Therefore, even if the eye movement had some effect on the infants' performance, the effect should be minor. Otherwise, such a high similarity would not have been obtained.

Further support of our argument is provided by the results of the artifact rejection experiments.

Adult color segregation experiment

To evaluate the magnitude of nonretinotopic color integration in infants, we asked adult observers to discriminate the same red/green alternating bars in motion and flicker stimuli and make a two-alternative forced-choice judgment (left or right).

Method

Stimuli

Individual isoluminant points were measured in the same minimum motion method. The stimuli were the same as those in the color segregation experiment for infants except for the 500-ms pre- and postmasks of stimulus onset/offset (instead of a continuously presented yellow). The mask pattern was a uniform yellow presented in the area of the bar arrays. The three interbar intervals were tested in the motion and flicker conditions (corresponding color alternation rates at each retinal location: 26.7, 20.0, and 16.0 Hz).

Procedure

At the initiation of a trial, we asked observers to fixate on the center of the display. In a trial, after yellow moving bars had been presented for 500 ms, half of them (on the left- or right-hand side) changed their color into alternating red/green for 500 ms, and then the color of the moving array returned to yellow for 500 ms. The observers had to make a two-alternative forced-choice judgment about which stimulus was the red/green array, and they indicated the left- or right-hand side orally. Motion and flicker conditions were examined. Each observer performed six trials for each alternation frequency in each condition. The motion

and flicker conditions were tested in separated experimental blocks.

Results

For all alternation rates, the proportions of correct judgment were higher in the motion condition than in the flicker condition (Figure 1e), in agreement with the previous study (Watanabe & Nishida, 2007). Although it is difficult to directly compare the performance of infants (duration ratio of preferential looking) and adults (proportion correct), a similar trend was observed. We statistically analyzed the main effects of the two factors manipulated in this study: stimulus conditions (motion vs. flicker), and frequencies (16.0, 20.0, and 26.7 Hz), and their interactions. The analyses revealed that there were significant differences in the stimulus conditions, $F(1, 8) = 28.2$, $p < 0.01$, $\eta^2 = 0.395$, and in frequencies, $F(2, 16) = 23.7$, $p < 0.01$, $\eta^2 = 0.217$. Significant interactions were observed, $F(2, 16) = 7.79$, $p < 0.01$, $\eta^2 = 0.099$. Post hoc comparisons revealed that the proportion corrects were higher in the motion condition than the flicker condition at the 16-Hz alternation and the 20-Hz alternation (Turkey's HSD test: $p < 0.01$ and $p < 0.05$, respectively). In addition, at the 16-Hz alternation in the motion condition, more than 75% of the looking duration was for the red/green direction in infants and the proportion correct was around 100%. At the 20-Hz alternation, the performance of both the infants and adults in the motion condition was significantly above chance level. Though the ratios of looking time and proportion correct were reduced at 26.6 Hz, they were still significantly above the chance level. Our results, therefore, imply that the ability of the infants to discriminate moving colors is comparable to that of human adults and that the underlying mechanism for the nonretinotopic color integration is already mature even at 5 months of age.

Artifact rejection experiments

We performed control experiments with seven other infant participants to test the validity of our interpretation.

Method

Four stimulus conditions coupled with the original motion and flicker conditions (20.0 Hz) were performed with the same procedure as in the infant color segregation experiment. The stimuli were the same as those in the infant color segregation experiment except

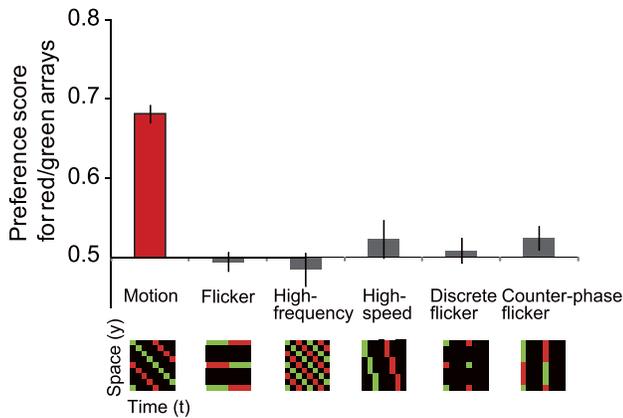


Figure 2. Mean preference scores in control experiments with the space–time plot of presented stimuli. From the left, data for motion, flicker, high-frequency, high-speed, discrete flicker, and counter-phase flicker controls are shown. Each data point shows the average for the seven infant observers. The error bars represent standard error. *** $p < 0.001$.

for the spatio-temporal arrangement of red and green colors.

First, we increased the local color alternation rate of moving bars to 40.0 Hz by reducing the spatial interval between the bars (high-frequency control), with the velocity of the movements of the color bars unchanged. Even under the motion condition, adult observers cannot segregate colors at 40.0 Hz (Watanabe & Nishida, 2007). We expected to see the same result if the trajectory integration mechanism also produced the infants' motion enhancement of color segregation. If the infants could segregate colors even at 40.0 Hz, their performance might be based on some artifacts, such as eye movements.

Second, we made the speed of moving bars three times higher by making the interbar interval three times larger (high-speed control at the 20-Hz alternation). Since the speed of the bars in this condition exceeded the infants' upper limit speed for motion perception (Wattam-Bell, 1992), and since color segregation is associated with motion perception, we expected that the enhancement of the color segregation would not be observed in this case.

One might suspect that flicker stimuli have higher luminance energy than motion stimuli at each retinal location, and that the difference in the luminance energy caused the difference in the preference score. To rule out such concerns, we lastly presented the flicker stimuli made from the motion stimulus by removing the bars that were to be presented in the interbar areas (discrete flicker control at the 20-Hz alternation), and the counter-phase red–green square wave grating stimuli (counter-phase flicker control at the 20-Hz alternation). These two flicker controls, having the same temporal pattern as the motion stimulus at the local points on the

retina, were alternative versions of the flicker stimulus. In order to compare their results with those of the color segregation experiment, motion stimulus and flicker stimulus at the 20-Hz alternation were also presented in the artifact rejection experiments.

Seven new infants participated in the artifact rejection experiments. As in the color segregation experiment, we obtained an isoluminant pair of red and green for each infant using the minimum motion paradigm. In this experiment, one block was composed of six conditions (motion, flicker, high-frequency, high-speed, discrete flicker, and counter-phase flicker), and eight blocks were performed in total for each infant. The data were analyzed and preference scores were calculated in the same way as in the infant color segregation experiment (nine trials were excluded, or 2.7% of all trials).

Results

The results for the motion and the high-frequency control conditions (the first and third bars from the left in Figure 2) show that, while the preference score in the motion condition was significantly higher than the chance level again, the effect of motion on the color segregation was dramatically reduced in the high-frequency control. The lack of enhancement in the high-frequency control suggests that the enhancement in color segregation is mediated by the same mechanism in adults and infants.

The results for the high-speed control condition (the fourth bar from the left in Figure 2) show that the effect of motion on the color segregation was dramatically reduced when the motion of the bars could not be perceived. The lack of enhancement for the high-speed stimulus indicates that motion perception is crucial for the enhancement of the color segregation.

The results for the discrete flicker and counter-phase flicker conditions (the first and second bars from the right in Figure 2) demonstrate that the preference scores in the two flicker control were not different from the chance level or from the flicker condition (the second bars from the left in Figure 2), suggesting that the enhancement of color segregation cannot be ascribed to differences in the luminance energy of the visual stimuli.

Discussion

Our series of experiments demonstrated that 5-month-old infants could segregate the alternations of equiluminant red–green colors better (i.e., with less mixture) for a moving pattern than for a static

flickering one, indicating that color signals can be integrated along a motion trajectory (nonretinotopic integration of color signals) even in immature chromatic visual processing.

In infant studies, how each module of sensory attributes, such as motion, form, and color, is established has been investigated intensively, and recent research has focused on the development of the modules' hierarchical organization within a single attribute (Wattam-Bell et al., 2010). However, few studies have examined the visual module interactions, except for those by Dobkins and colleagues (Dobkins & Anderson, 2002; Dobkins & Teller, 1996; Wagner & Dobkins, 2011). Going against the notion that motion and color modules are independent in the visual system of adults (Livingstone & Hubel, 1987; Zeki, 1978) and also of infants (Wilcox, Haslup, & Boas, 2010), they demonstrated visual module interactions between color and motion in infant vision. They suggested that exuberant neural connectivity in the young infant brain may facilitate arbitrary association between different attributes, which gradually disappear during the course of development due to retraction of the connection (infant-synesthesia hypothesis) (e.g., Wagner & Dobkins, 2011). Our findings, in agreement with this hypothesis, indicate an early presence of cross-modal interactions in the brain. However, our findings differ critically from the infant-synesthesia hypothesis in that the motion–color interaction in motion trajectory integration cannot accidentally emerge from random exuberant neural connections. Instead, it requires elegant direction-selective motion processing and an integrative process of motion and color signals.

Our interpretation is consistent with recent findings on the development of the infant visual system. Although sensitivity to chromatic temporal contrast is still immature in 2- to 4-month-old infants (Kelly, Borchert, & Teller, 1997; Morrone, Fiorentini, & Burr, 1996; Teller, 1998 for a review), the foundational functions of color vision, such as the color opponent process (Brown & Teller, 1989), and color constancy (Yang, Kanazawa, Yamaguchi, & Kuriki, 2013), are well established at 5 months of age or earlier. Local motion processing in infant vision is relatively mature at 4 to 6 months, and that the integrative process for the local motion signals follows rapidly (e.g., Braddick & Atkinson, 2009; Dobkins, Fine, Hsueh, & Vitten, 2004; Hou, Gilmore, Pettet, & Norcia, 2009; Kanazawa, Shirai, Ohtsuka, & Yamaguchi, 2006). Taking the previous studies into account, the infant visual system has the potential ability to use direction-selective motion information for integrating color signals.

From a different viewpoint, one might argue that the color integration along a motion trajectory could be achieved by the color-sensitive neurons that have spatio-temporal receptive fields and are also sensitive to

motion signals. However, only a small proportion of visual neurons seem to have these properties in the visual cortex (Gegenfurtner, Kiper, & Fenstemaker, 1996; Tamura, Sato, Katsuyama, Hata, & Tsumoto, 1996). Consequently, we conjecture that a possible underlying mechanism might be a global interaction between direction-selective motion processing and its integration with color signals (Watanabe & Nishida, 2007).

Our results demonstrated that a motion-induced color segregation phenomenon could be observed in 5-month-old infants at a similar extent of adults. Previous researches have shown that infants in the early postnatal period have poor spatial and temporal contrast sensitivity (Dobkins & Teller, 1996; Hartmann & Banks, 1992; Kelly et al., 1997; Rasengane et al., 1997; Swanson & Birch, 1990; Teller, 1998 for a review). For instance, 3-month-old infants have only 1/50th of the maximum contrast sensitivity of adults (Brown & Lindsey, 2009). And the fusion rate of 3-month-old infants is 20.0 Hz, which is obviously lower than adults (Rasengane et al., 1997). Similar to spatial contrast sensitivity, 3-month-old infants are far less sensitive to chromatic temporal contrast than adults (Dobkins, Anderson, & Lia, 1999; Dobkins, Lia, & Teller, 1997; Morrone et al., 1996). A longitudinal study (Kelly et al., 1997) showed increased chromatic contrast sensitivity from 2- to 8-month-old infants, but in 5-month-old infants, the chromatic temporal contrast sensitivity is still lower than in adults. Unlike previous studies on contrast sensitivity, the performance of 5-month-old infants shown in the present study was comparable to that of adults.

As shown in Figure 1, both infants and adults could segregate color alternations significantly better for moving patterns than 16.0 Hz (i.e., ISI was <25 ms). This implies that the nonretinotopic integration we examined operates in the timescale considerably faster than those found in other studies. For example, figural attribution (a vernier offset) based on Ternus-Pikler apparent motion was demonstrated with the ISI of 100 m (Öğmen et al., 2006), and the transsaccadic integration of motion signals was made with the ISI of 150 ms (Melcher & Morrone, 2003). The performance of reporting pair of color and motion direction was better when attention moved to track the same combination at successive locations (4.9 Hz) than when it was stationary (2.2 Hz) (Cavanagh et al., 2008). It is still an open question whether infants can also integrate form/motion/color information nonretinotopically over time in these phenomena reported to occur in different time scales.

Our findings present the first evidence supporting the early development of cross-module interaction for elegant visual computation. The results suggest that nonretinotopic processing involving a tight motion–

color interaction develops simultaneously with basic motion and color processing and matures surprisingly early. Accordingly, this early onset of the contribution of motion to color perception might be a reasonable strategy taken by the brain to reinforce premature color vision in infants as effectively as possible.

Keywords: infant vision, motion, color, nonretinotopic processing, flicker, temporal frequency

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