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Abstract

Early development is characterized by a period of exuberant neural connectivity followed by a retraction and reweighting of connections over the course of development. It has been proposed that this connectivity may facilitate arbitrary sensory experiences in infants that are unlike anything experienced by typical adults but are similar to the sensory experiences of adults with synaesthesia, a rare sensory phenomenon that has been associated with exuberant neural connectivity and that is characterized by strong arbitrary associations between different sensations. We provide the first evidence for this infant-synaesthesia hypothesis by showing that the presence of particular shapes influences color preferences in typical 2- and 3-month-olds, but not in 8-month-olds or adults. These results are consistent with the possibility that exuberant neural connectivity facilitates synaesthetic associations during infancy that are typically eliminated during development, but that a failure of the retraction process leads in rare cases to synaesthesia in adults.

Keywords

infant development, visual perception, brain

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The neonatal-synaesthesia hypothesis proposes that synaesthesia, a condition wherein stimulation of one sense involuntarily evokes an additional arbitrary stimulation of another sense, may be a universal experience in young infants that dissipates during the normal course of development (Maurer, 1993). The hypothesis suggests that synaesthesia may occur at high rates during infancy because of increased functional connectivity in the infant brain relative to the adult brain (e.g., Mills, Coffey-Corina, & Neville, 1997; Neville, 1995). The neural underpinning of increased functional connectivity may be the well-documented exuberant anatomical connectivity that occurs during infant development (e.g., Huttenlocher, de Courten, Garey, & Van der Loos, 1982; Rodman & Consuelos, 1994) or the potential decreased inhibition of feedback projections early in development (see Eagleman & Goodale, 2009, and Spector & Maurer, 2009, for discussion). Furthermore, if this increased functional connectivity does not dissipate over the course of development, it may result in synaesthesia in adults (e.g., Ramachandran & Hubbard, 2001; Rouw & Scholte, 2007). Although the neonatal-synaesthesia hypothesis has been discussed for nearly 20 years (Maurer, 1993), increased rates of synaesthesia in young infants have yet to be systematically demonstrated.

Recently, there have been a growing number of studies investigating synaesthetic-like associations in infants and children. For example, 2- to 3-year-old children associate

high-pitched sounds with small and light objects (Mondloch & Maurer, 2004), preliterate toddlers associate Xs with the color black and Os with white (Spector & Maurer, 2008), and 3-month-old infants associate high-pitched sounds with tall and sharp visual objects (Walker et al., 2010). Because some of these associations seem to be arbitrary, some researchers have proposed that, as opposed to being learned from the environment, these associations are remnants of neonatal synaesthesia. However, the associations in infants and children reported in previous studies have also been observed with similar prevalence in typical adults (Marks, Hammeal, & Bornstein, 1987; Melara & O'Brien, 1987; Spector & Maurer, 2008; Ward, Huckstep, & Tsakanikos, 2006). Thus, such results in infants and children do not fulfill one of the critical core predictions of the neonatal-synaesthesia hypothesis, namely, that synaesthetic associations decline with age as exuberant connections are pruned.

In contrast with previous studies, the study reported here examined the age-related decline in exuberant connectivity by testing associations in infancy that are thought to be very rare in adults. Specifically, our study focused on the best-documented

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form of synaesthesia in adults: grapheme-color synaesthesia. In grapheme-color synaesthesia, which is seen in only about 1% of adults, specific letters or numbers evoke idiosyncratic, largely individualized sensations of specific colors (Ramachandran & Hubbard, 2001).

Rather than using graphemes, which are complex and likely to be unfamiliar to young infants, we chose to use simple shapes. Our reasoning was that shape recognition in infants may be a precursor to grapheme recognition in adults, as both are thought to be processed in the same region of visual cortex (McCandliss, Cohen, & Dahan, 2003); in addition, it has recently been shown that the shapes of graphemes influence grapheme-color synaesthetic associations (Brang, Rouw, Ramachandran, & Coulson, 2011).

In our study, we presented shapes (circles or triangles) on backgrounds of two separate colors, either red versus green (see Fig. 1) or blue versus yellow. If a participant possessed shape-color associations, we expected the presence of shapes (either circles or triangles) to differentially affect the participant's background color preferences. This could happen in one of two ways. Suppose that a given infant associates triangles with red. First, the infant may prefer to look more to the red than to the green side of the screen when triangles are presented because red is congruent with this infant's associations. The alternative is that if the triangles actually "appear" red for this infant, they might stand out more (and thus be easier to detect) on the green rather than the red background. This would result in the infant preferring to look more often to the green than to the red side of the screen (see Smilek, Dixon, Cudahy, & Merikle, 2001, for evidence of this second type of phenomenon in an adult synaesthete).

Although our data cannot distinguish between these two scenarios (which means our data cannot help us determine specific shape-color associations made by individual infants), this is not of concern; the objective of the study was to determine whether associations (regardless of their nature) are more prevalent in younger infants than in older infants. Furthermore, our methodology was designed to accommodate the likelihood that, like the highly individualized grapheme-color associations in adult synaesthetes (e.g., one adult synaesthete might associate "E" with green, and another might associate "E" with red), shape-color associations made by infants should also be highly individualized (e.g., one infant might associate

triangles with red, and another might associate triangles with green).

We also hypothesized that synaesthetic pairings of colors mediated primarily by the koniocellular pathway (blue and yellow) may occur later in development than pairings mediated by the parvocellular pathway (red and green). This prediction was made because sensitivity to red and green is present by 2 months of age (e.g., Dobkins, Anderson & Kelly, 2001), but sensitivity to blue and yellow is thought to emerge around 3 to 4 months of age (Crognale, Kelly, Weiss, & Teller, 1998; Suttle, Banks, & Graf, 2002). Thus, we chose to study 2- to 3-month-olds because color pathways are still actively developing in this age range, and in addition, they are developing differentially for red and green versus blue and yellow. Thus, synaesthetic associations for these two sets of colors may develop over different time courses. We also tested 8-month-olds and adults as older comparison groups, because we predicted that shape-color associations would be much more rare past 3 months of age.

Method

Participants

Infant participants were recruited by mass mailings to new parents in San Diego County. All infants were full term, between 38 and 42 weeks' gestation at birth, and participated within 1 week of their 2-month, 3-month, or 8-month birthday. Adult participants were 18 to 23 years old ($M = 20.4$ years) and received course credit for psychology classes at the University of California, San Diego. All participants were screened for color blindness via family-history interview (infants) or Ishihara color plates (adults).

Subjects were excluded from analysis if they completed less than 25 trials per condition (one 2-month-old, one 3-month-old, three 8-month-olds) or performed contrary to expectation on 15% or more of catch trials (five 2-month-olds, five 3-month-olds, two 8-month-olds, 6 adults). Most adult exclusions resulted from participants wearing glasses, which made it difficult to see their eye movements. Additionally, one 3-month-old was excluded because of parent interference with the task, and one 3-month-old was excluded because he had torticollis, making his eye and head movements difficult to interpret. After exclusions, participants were fifteen 2-month-olds (9 males, 6 females), fifteen 3-month-olds (9 males, 6 females), fifteen 8-month-olds (4 males, 11 females), and 16 adults (3 males, 13 females).

Stimuli

Stimuli were programmed in MATLAB (The MathWorks, Natick, MA) using Psychtoolbox 2 (Brainard, 1997) and were presented on a 17-in. EIZO monitor (Ishikawa, Japan) driven by a Dell PC laptop with an 8-bit ATI Radeon graphics card (AMD, Sunnyvale, CA). Each trial consisted of a field of 24 hollow circles or triangles (each subtending $\sim 6.4^\circ$, line width = 1.7° ,

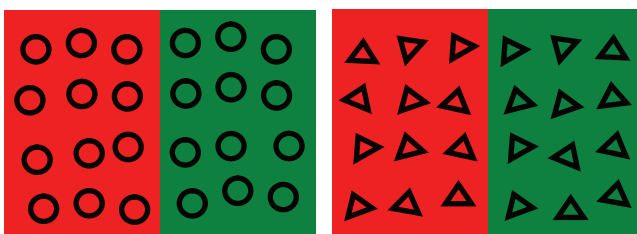


Fig. 1. Example stimuli used in the experiment. Twenty-four shapes (either circles or triangles) were presented on a background that was either red on one side and green on the other (shown here) or blue on one side and yellow on the other.

entire display = 56° × 42°) presented on a background consisting of separate colors on the left and right side of the display.

We chose to limit our investigation to four hues considered psychologically unique (red, green, blue, and yellow; Sternheim & Boynton, 1966); these colors were presented as two “chromatically opponent” pairs—red versus green and blue versus yellow—for three reasons. First, red-green contrast and blue-yellow contrast are mostly processed in separate visual pathways, and this phenomenon allowed us to compare the results of our different age groups with the known developmental time course of these pathways. Second, previous research on adult synaesthetes has shown that color naming is facilitated when graphemes are presented in a color congruent with each synaesthete’s associations, and interference is greatest when the graphemes are presented in a color chromatically opponent to each synaesthete’s associations (Nikolić, Lichti, & Singer, 2007). Thus, we felt that synaesthetic shape-color associations would affect looking behavior in participants to the greatest degree if we presented the shapes with both congruent and chromatically opponent colors simultaneously. Along a similar line, the fact that chromatically opponent colors are far apart in perceptual color space was also expected to increase the chance that synaesthetic shape-color associations would affect looking behavior.

The luminance levels of the red-green and the blue-yellow background pairings were judged by the experimenters to be of approximately equal brightness. The resulting brightness matches produced variations in luminance by hue that were similar to previously observed brightness-to-luminance-ratio patterns (Burns, Smith, Pokorny, & Elsner, 1982; Teller, Civian, & Bronson-Castain, 2004). Although the different colors that adult synaesthetes experience with different graphemes are neither equally luminous nor equally bright (e.g., Beeli, Esslen, & Jänecke, 2007), we nonetheless thought a good starting point would be to present colors that were equally bright. The stimulus values employed are presented in Table 1. Shape type (triangle, circle), background-color pairing (red-green, blue-yellow), and left/right position of the background colors were randomized across trials.

Procedure

Color preferences in infants and adults were measured by an experimenter who could not see the display. The experimenter

used a variant of the forced-choice preferential-looking (FPL) technique (e.g., Dobkins et al., 2001) to judge which side of the display the participant looked toward first on each trial. Infants were tested individually in two to three sessions (15–60 min each) over 2 to 3 days within a single week. Each session lasted until the infant became bored or fussy or until all trials were completed (maximum of 60 trials per shape condition). Adults were tested in the same FPL format as infants were (McDonough, Choi, & Mandler, 2003) and completed the experiment in a single session lasting approximately 30 min (60 trials per shape condition). The design of the study was cross-sectional: No subject was included in more than one age group.

Catch trials

Thirty-two catch trials were interspersed throughout the experiment. They consisted of the same stimuli as in the main experiment, with two differences. First, the entire background was a single color (red, green, blue, or yellow), and, second, the shapes (circles or triangles) were presented on only one side of the video monitor (i.e., the other side of the video monitor was colored but contained no shapes).

These catch trials were employed to ensure that participants were paying attention. Only data from participants who looked toward the side of the monitor containing the shapes on more than 85% of catch trials were retained for further analysis. For retained participants, averaged across all trial types (i.e., different color backgrounds and different shapes), the mean percentage of correct responses for catch trials was 94.6% for 2-month-olds, 96.8% for 3-month-olds, 93.2% for 8-month-olds, and 92.1% for adults. The fact that these values are all above 90% indicates that participants were engaged in the FPL task.

Analysis

To represent the magnitude of shape influence on color preference, we calculated a synaesthesia index (SI) for each participant. For red-green trials, we subtracted the proportion of trials in which a participant preferred (i.e., looked toward) red (as opposed to green) on the circle trials from the proportion of trials in which that participant preferred red on triangle trials, and then took the absolute value of this difference, as follows: $SI = |p(\text{red})_{\text{triangles}} - p(\text{red})_{\text{circles}}|$.

The same procedure was repeated for blue-yellow trials. Note that the last step of the SI calculation (i.e., taking the absolute value) necessarily throws out information about the direction of the preference (e.g., whether red was preferred more when triangles were presented than when circles were presented or vice versa). This step was necessary because we assumed that, as is the case for adult synaesthetes, infants have individualized shape-color pairings. That is, half of the infants could prefer red more when presented with triangles than with circles, and the other half could prefer red more when

Table 1. Chromaticity and Luminance Values of the Colors Used in the Experiment

Color	Chromaticity		Luminance (cd/m ²)
	x	y	
Red	0.612	0.34	8.69
Green	0.287	0.597	13.9
Blue	0.153	0.066	4.94
Yellow	0.457	0.463	15.6

Note: Chromaticity is reported as the x and y coordinates from the Commission Internationale de l'Éclairage (CIE) 1931 chromaticity chart.

presented with circles than with triangles. In this scenario, if our SI did not have an absolute value, then averaging across individuals would cancel out any true effect. Of course, in taking an absolute value, we transformed our distribution in a way that violated the normality assumptions of most standard statistical tests. Thus, to determine whether the mean of these absolute values was greater than would be predicted by chance, we used a nonparametric analysis, a Monte Carlo simulation.

The Monte Carlo simulation created a distribution of mean SIs that would be expected from chance given no shape influence on color preference, for each age group and color combination tested. First, we created “simulated participants,” with the number of simulated participants matching the actual number of participants for each age group. Then, we calculated observed color preferences, disregarding shape condition, and used the mean and standard deviation of these color preferences to create a distribution of simulated color preferences that was similar to the observed distribution of color preferences (disregarding shape condition). This was done separately for each age group and color condition (see Supplementary Information in the Supplemental Material available online for actual values). For each simulated participant, we then drew from this distribution to assign a simulated color preference, disregarding shape condition (e.g., 65% preference for red over green). Our null hypothesis was that participants would have the same color preference for both triangle and circle conditions; thus, the next step was to simulate for each participant a triangle and a circle color preference, both drawn from the same distribution.

To accomplish this, for each simulated trial, the model randomly assigned the trial as a circle or triangle trial, and then drew from a binomial distribution defined by each simulated participant’s color preference, which assigned that trial as a red or green preference. The resulting shape-condition color preferences, one for each of the circle and triangle conditions, allowed us to calculate individual SIs, and then group mean SIs. This simulation was repeated 100,000 times per each age group and color-pair condition. We then determined whether each observed group mean SI had less than a 5% chance of being drawn from the simulated distribution of group mean SI values.

Results

Figure 2 shows the group mean SI for each age group in each color condition. The results of the Monte Carlo simulation indicated that the group mean SI was greater than would be expected by chance (dashed lines in Fig. 2) in two cases: the red-green condition in 2-month-olds ($p = .015$) and the blue-yellow condition in 3-month-olds ($p = .006$). Note that there was also a clear pattern in the data sets; the group mean SI for the red-green condition declined monotonically past 2 months, and for the blue-yellow condition, it peaked at 3 months, declining steadily thereafter.

Note that because the mean number of trials differed somewhat from one age group to another, the mean of the simulated

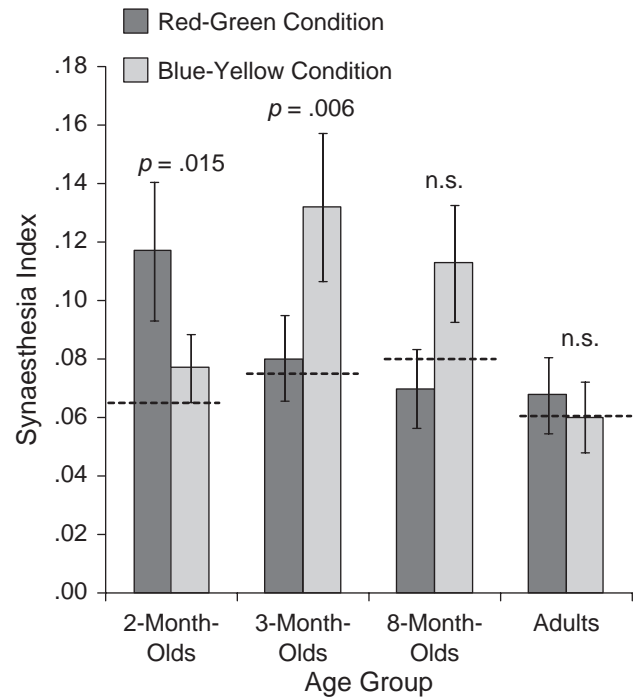


Fig. 2. Mean synaesthesia index as a function of age group and color condition. Synaesthesia indices were calculated by subtracting the proportion of trials in which a participant preferred red or blue (as opposed to green or yellow, respectively) in the circle condition from the proportion of trials in which that participant preferred red or blue in the triangle condition, and then taking the absolute value of this difference. The dashed lines denote the mean values that would be expected by chance, as determined by a Monte Carlo simulation. Means that are significantly greater than the simulated distributions are indicated. Error bars denote standard errors of the mean.

distributions varied somewhat across ages. To address the possibility that the observed age differences were an artifact of trial number, we repeated the analysis, but this time we equated trial number across participants by using only the first 25 trials per condition from each participant. The pattern of results was very similar to the pattern in our main analysis (group mean SI was greater than would be expected by chance in the red-green condition in 2-month-olds, $p = .039$, and in the blue-yellow condition in 3-month-olds, $p = .014$).

We conducted another analysis that determined whether, within an individual participant, there was a significant difference in the proportion of red versus green preference and blue versus yellow preference between the circle and triangle conditions. The findings from this analysis nicely mirror those of our Monte Carlo simulation (for details, see Supplementary Information and Fig. S1 in the Supplemental Material).

Discussion

The results from this study provide the first evidence that fulfills both of the core predictions of the neonatal-synaesthesia hypothesis: They demonstrate synaesthetic-like associations early in life and demonstrate that they decline with age. Furthermore, the observed synaesthetic shape-color associations occurred

later in development with blue-yellow than with red-green stimuli. This could result from the fact that blue-yellow sensitivity, mediated by the koniocellular subcortical pathway, develops later than red-green sensitivity, mediated by the parvocellular subcortical pathway (e.g., Crognale et al., 1998; Suttle et al., 2002). As part of its delayed development, the blue-yellow pathway may also retract later from shape-grapheme areas than the pathway underlying red-green processing does. Thus, the time course of shape-color associations may be later for the blue-yellow than for the red-green condition. Furthermore, in the red-green condition, the observed decline in synaesthetic associations observed between 2 and 3 months is consistent with prior evidence that the red-green pathway may retract from other cortical areas (specifically, motion areas) around the same time, between 2 and 4 months (Dobkins & Anderson, 2002).

It is important to point out that the supporting evidence for this conclusion, namely, the age-related decline in shape-color associations, cannot be accounted for by age-related improvements in shape discrimination (Slater, Mattock, & Brown, 1981) or color discrimination (Dobkins et al., 2001); if anything, such improvements would predict an increase in shape-color associations rather than a decline with age. Also note that the study reported here focused on the four unique colors: red, green, blue, and yellow. However, many associations made by adult synaesthetes involve other, nonunique colors (such as purple). In our paradigm, a synaesthetic experience of even a nonunique color will be perceptually more similar to a synaesthetic experience of one of the two colors in our pairs (i.e., more similar to blue than to yellow), and thus we expected our design to be sensitive to some of these nonunique associations. We recognize, of course, that our paradigm may not be sensitive enough to pick up on all nonunique color associations, nor would it be sensitive in circumstances in which an individual makes similar color associations with both shapes (triangles and circles). Thus, the results reported here, if anything, likely show an underestimation of the prevalence of neonatal synaesthesia. Especially in light of these limitations, we believe that our results provide strong evidence for synaesthetic shape-color associations in young infants.

The results reported here join a wealth of previous data demonstrating behavioral abilities declining during infancy, including discrimination of nonnative phonetic categories (Werker & Tees, 1984), nonnative spatial categories (Choi, 2006; Hespos & Spelke, 2004), other-race faces (Kelly et al., 2007), and other-species faces (Pascalis, De Haan, & Nelson, 2002). Age-related declines have also been reported in the ability to match other-species vocalizations to mouth movements (Lewkowicz, Sowiński, & Place, 2008) and use of color information for motion processing (Dobkins & Anderson, 2002). Our results demonstrate that this domain-general developmental learning process, in which extraneous abilities are lost, might also produce arbitrary synaesthetic associations in infancy that dissipate with age.

In sum, our finding of an age-related decline in shape-color associations is consistent with the previously proposed

possibility that neonatal synaesthesia is caused by exuberant anatomical connectivity, and that a failure of the retraction process leads in rare cases to synaesthesia in adults (Maurer, 1993; Spector & Maurer, 2009). Furthermore, even in nonsynaesthetes, retraction may not be 100% complete, leaving them with a weaker form of synaesthesia, as previously reported in typical children and adults (Spector & Maurer, 2008, 2009). In addition to the hypothesis of anatomical exuberance and retraction, another suggestion is that synaesthesia results from decreased inhibition from feedback projections (e.g., Eagleman & Goodale, 2009), and thus it is also possible that the age-related decline in shape-color associations observed in the study reported here reflects age-related changes in inhibitory feedback connections (for discussion, see Spector & Maurer, 2009). More information about the time course of anatomical exuberance and retraction (e.g., Huttenlocher et al., 1982) and development of feedback pathways (e.g., Burkhalter, 1993) will be necessary to differentiate between these possibilities.

On a final note, the presence of widespread synaesthetic associations has important implications for typical development. It suggests that the infant perceptual experience is fundamentally different from that of typical adults, in that young infants experience a “blooming, buzzing confusion” (James, 1890, p. 488) from intermingling of sensations. Although this intermingling would not appear to be beneficial in and of itself, it may be that exuberance followed by retraction is the most efficient way to form neural connections (and sensory associations) that are ultimately useful (Checkik, Meilijson, & Ruppín, 1999; and see Dobkins, 2009). Thus, although this intermingling might create a confusing experience for infants, this confusion may be dwarfed by the advantage gained in the ability to learn most efficiently about their world.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information may be found at <http://pss.sagepub.com/content/by/supplemental-data>

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