

Categorical perception of color is lateralized to the right hemisphere in infants, but to the left hemisphere in adults

A. Franklin^{*†}, G. V. Drivonikou^{*}, L. Bevis^{*}, I. R. L. Davies^{*}, P. Kay^{†‡§}, and T. Regier[¶]

^{*}Department of Psychology, University of Surrey, Guildford, Surrey GU2 5XH, United Kingdom; [†]International Computer Science Institute, 1947 Center Street, Berkeley, CA 94704; [‡]Department of Linguistics, University of California, Berkeley, CA 94720; and [¶]Department of Psychology, University of Chicago, Chicago, IL 60637

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Both adults and infants are faster at discriminating between two colors from different categories than two colors from the same category, even when between- and within-category chromatic separation sizes are equated. For adults, this categorical perception (CP) is lateralized; the category effect is stronger for the right visual field (RVF)-left hemisphere (LH) than the left visual field (LVF)-right hemisphere (RH). Converging evidence suggests that the LH bias in color CP in adults is caused by the influence of lexical color codes in the LH. The current study investigates whether prelinguistic color CP is also lateralized to the LH by testing 4- to 6-month-old infants. A colored target was shown on a differently colored background, and time to initiate an eye movement to the target was measured. Target background pairs were either from the same or different categories, but with equal target-background chromatic separations. Infants were faster at initiating an eye movement to targets on different-category than same-category backgrounds, but only for targets in the LVF-RH. In contrast, adults showed a greater category effect when targets were presented to the RVF-LH. These results suggest that whereas color CP is stronger in the LH than RH in adults, prelinguistic CP in infants is lateralized to the RH. The findings suggest that language-driven CP in adults may not build on prelinguistic CP, but that language instead imposes its categories on a LH that is not categorically prepartitioned.

language and thought | nature/nurture | lateralization | perceptual development

Categorical perception (CP) of color is shown when two colors that belong to different color categories (between-category judgments) are discriminated faster, or more accurately, than two colors belonging to the same color category (within-category judgments), even when between- and within-category chromatic separation sizes are equated (1).^{||} This effect is found in adults (2–5), children and toddlers (6, 7), and infants (8–10). The role of language in the effect has been extensively debated (3–14). For example, some have advanced the hypothesis that the on-line use of language is the origin of the effect: comparing stimulus labels aids discrimination for between-category pairs and/or hinders discrimination for within-category pairs. In support of this hypothesis, for adult participants, CP is found only if the category boundary is marked in the participant's language (3, 12, 13), and verbal interference eliminates CP, but visual interference does not (4, 5, 13, 14). It has, however, been found that color CP occurs prelinguistically in toddlers and infants, who have no color language (6, 8–10).

A recent set of studies looking at hemispheric asymmetries in color CP has added a new perspective on the debate. Gilbert *et al.* (14), using a visual search task, found that the time to detect a colored target among differently colored distractors was faster when target and distractors were from different categories (e.g., blue1–green1) than when they were from the same category (blue1–blue2 or green1–green2), but only when the target was in the right visual field (RVF). As the RVF projects to the left

hemisphere (LH), which is dominant for most verbal tasks (15), Gilbert *et al.* (14), suggest the implicit use of lexical color codes as the likely reason for RVF CP. In support of this hypothesis, a verbal interference task selectively reversed the category effect for the RVF (between-category RT slower than within-category), whereas a visual interference task did not disrupt the original pattern of results.

Further evidence for hemispheric asymmetries in color CP is provided in a study by Drivonikou *et al.* (16). The data from a previous study involving visual search for color (17) were reanalyzed according to whether targets appeared on the left or right. The pattern of results was similar to Gilbert *et al.* (14); CP was significantly stronger when the target was presented to the RVF than to the left visual field (LVF), although unlike Gilbert *et al.*, Drivonikou *et al.* found CP for both visual fields. Moreover, in a new experiment using a target detection task, RVF-LH-lateralized CP was again found. A single-colored target appeared briefly on a differently colored background, in one of 12 unmarked locations in a ring around a central fixation point (see Fig. 1*a*), and the task was to decide whether the target was to the left or to the right of fixation. Target-background pairs were either from the same category (e.g., blue1–blue2) or different categories (e.g., blue1–green1), but with equal target-background separations in all conditions. For the blue–green (BG) boundary, CP was found in both visual fields, but the category effect was ≈ 60 ms stronger in the RVF. For the blue–purple boundary, CP was found only for the RVF. Further support for the hypothesis that language can account for the RVF-LH bias in color CP is provided by cross-linguistic comparison of hemispheric asymmetries in color CP. LH-lateralized color CP has been shown to occur at those locations in color space where specific languages draw category boundaries, locations that vary from language to language (18, 19).

The idea that the LH has a categorical bias is not a new one. Research into hemispheric asymmetries for other domains has led to suggestions that the LH is geared to encoding categorical, or relational information, whereas the right hemisphere (RH) is geared toward encoding metric information. For example, a study by Kosslyn *et al.* (20) found that categorical judgments, such as on/off, left/right, or above/below, are faster for RVF than for LVF stimuli, whereas metric judgments, such as evaluations of distance, are faster for LVF than RVF stimuli (see also ref.

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[†]To whom correspondence may be addressed: E-mail: a.franklin@surrey.ac.uk or paulkay@berkeley.edu.

^{||}According to the original definition of CP, a requisite was that there is no within-category discrimination at all. However, this definition of CP in current research is no longer used, and CP is now defined as faster or more accurate between-category than within-category discrimination, when between- and within-category separations are equated (1).

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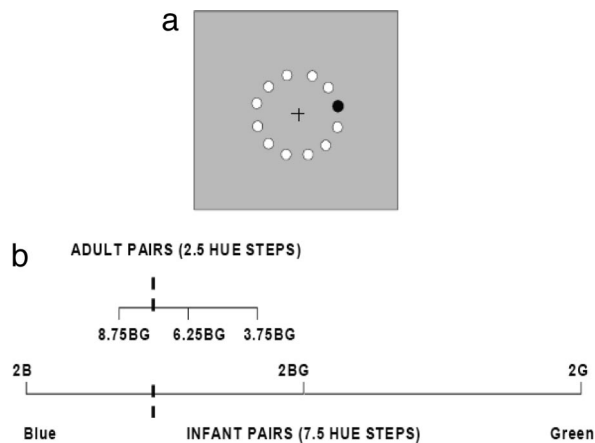


Fig. 1. Presentation and Munsell codes for target detection task stimuli. (a) Illustration of the display. The black circle indicates the target, and white circles show other possible target locations. (b) Munsell codes of the stimuli; stimuli varied in hue at constant value and chroma. Hue separations were 2.5 steps apart (adults) and 10 steps apart (infants). The target was either in the same color category as the background (e.g., 6.25BG and 3.75BG, both green) or in the adjacent category (e.g., 6.25BG on 8.75BG, green and blue). The dashed line indicates the category boundary.

21). Seger *et al.* (22) observed activation increases in the LH as participants learned to allocate colored checkerboard patterns to one of two artificial categories. A LH bias for color CP might therefore be one manifestation of general categorical encoding by the LH.

It is likely, however, given the evidence we have reviewed, that most color CP in adults, as for categorization, is mediated by language (23), and that the LH bias reflects this. At the same time, we have seen that color CP is also found in prelinguistic infants. The relation between prelinguistic and linguistic CP remains unclear. One possibility is that language makes fairly minor language-specific adjustments to a universal set of prelinguistically available categories. Another possibility is that language carves its categories into cognition *de novo*, without building on prelinguistically available categories.

One way to clarify the relation of linguistic and prelinguistic CP is to assess whether the hemispheric asymmetry favoring LH CP is present during infancy, before language is learned. If so, this would be compatible with the hypothesis that linguistic CP, which is lateralized to the LH, builds on prelinguistically available categorical distinctions in that hemisphere. In contrast, if the LH CP is not present in infancy, it would suggest that the linguistic categories that are eventually formed in the LH do not build on prelinguistic categorical distinctions.

There is evidence for prelinguistic hemispheric asymmetries in the processing of visual and auditory stimuli by infants (24–28). A study by Catherwood *et al.* (27) investigated hemispheric asymmetries for color recognition in 6-month-old infants. Infants were familiarized to a set of three colors (e.g., red, green, and yellow) over 24 trials. Familiarization was lateralized, with stimuli presented either to the RVF or LVF, for 250 ms per trial. After familiarization, a novel color (e.g., blue) was paired with one of the familiar colors, and looking time at the novel and familiar stimulus was recorded. There was significant novelty preference when colors were familiarized in the LVF, but not when familiarization occurred in the RVF. Catherwood *et al.* (27) concluded that there is a RH bias for color recognition at 6 months. Greater recognition memory in the right than LH for the different category colors (red, green, yellow, and blue) may actually indicate a RH bias for color categorization in infancy. However, if there was also greater recognition memory in the

RH than the LH for equivalently spaced within-category colors, then it would instead indicate a general RH bias for color memory, rather than a greater RH category effect. Based on the current evidence, as lateralized within-category color differences have not been tested in infants, an inference about hemispheric asymmetries in infant color CP cannot be made.

In the current study, we tested for hemispheric asymmetries in color CP for the BG boundary in 4- to 6-month-old infants, and in adults, using a version of the target detection task. The target detection task is appropriate as the task has been used to demonstrate CP in both infants and adults (10) and investigate hemispheric asymmetries in adult color CP with a reaction time measure (16). The original version of the target detection task explored color CP in infants and adults by using an eye-movement measure. For both infants and adults, the time taken to fixate the target was shorter for between-category target–background pairs than for within-category pairs (10). In the current study, we used as our performance measure the time that elapsed before an eye movement was initiated to the target from a central fixation point (initiation time). Targets were presented to the LVF or RVF for 4 s. We compared initiation times for targets on same- and different-category backgrounds (e.g., green1–green2; blue1–green1) and in LVF and RVF in infants and adults.

This method is unconventional for testing for hemispheric asymmetries. The conventional method is to present stimuli for ≈ 150 –250 ms and measure reaction time to these lateralized stimulus presentations (14, 16). Rapid stimulus presentation to one visual field ensures that direct projections of the stimulus are confined to the contralateral hemisphere. Free viewing of stimuli is problematic as once the stimulus is fixated it will no longer be lateralized. However, in the current study, although we had free viewing of the stimuli, participants were centrally fixated up until the initiation of the eye movement to the target, so there were no eye movements for the duration of the measure. Therefore, this method should be comparable to the method of studies that use rapid stimulus presentation and a reaction time measure (14, 16). We tested adults for confirmation. One benefit of the method is that the procedure and measure is identical for both infants and adults, enabling a clear comparison of the two groups. The only differences between the infant and adult experiments were that the target–background chromatic difference was larger for infants than adults (see Fig. 1b), because infants' chromatic sensitivity is much lower than adults' (29), and the number of trials for infants was half that for adults, because of their limited attention span.

CP would be indicated if initiation times were faster for between-category target–background pairs than for within-category pairs. Hemispheric asymmetry in CP would be indicated by a larger CP effect for one of the visual fields. It was expected that adults would show the same pattern of results as the adults in the Drivonikou *et al.* (16) and Gilbert *et al.* (14) studies, where reaction time was recorded and showed stronger CP for RVF than LVF targets. If there is a prelinguistic predisposition for LH CP, then infants should show the same pattern as adults, albeit with much slower initiation time (cf. ref. 10). Alternatively, if the adult LH bias for color CP depends on linguistic categorization that does not build on a base of prelinguistic categorization, then no such bias should be shown in infants. No LH bias in infant CP would be consistent with the hypothesis that a LH bias for color CP emerges with the development of language, perhaps reflecting the use of mediating lexical codes, and does not rely on prelinguistic categories. The strongest case for the LH bias in adults being language driven would be if infants show a reversed, RH bias for CP, which would imply that the effect of language is strong enough to overcome an initial RH bias.

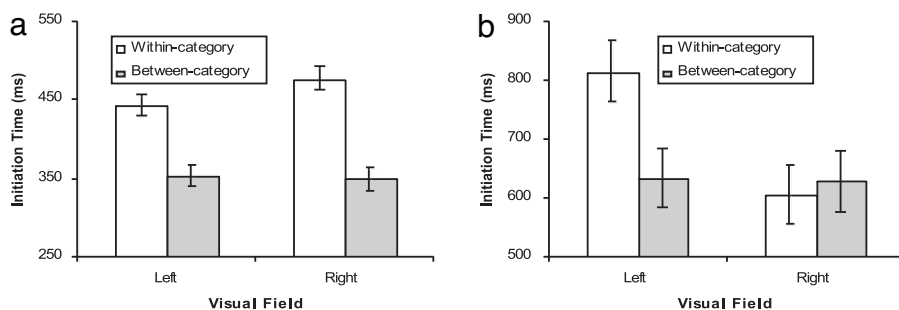


Fig. 2. The category effect for adults is significant in both visual fields, but is larger in the RVF than in the LVF. The category effect for infants using the same task and measure is only significant in the LVF. (a) For adults, the difference in time to initiate an eye movement to the target for within- and between-category is larger in the RVF than LVF. (b) For infants, the difference in time to initiate an eye movement to the target for within- and between-category is larger in the LVF than RVF. Error bars are within-subjects 95% confidence intervals (30).

Results

Adults. Trials were excluded if the eye-movement signal was lost (mean number of trials lost per participant = 2.39, SD = 3.16). Trials were also excluded if multiple eye movements around the screen were made before the eye movement to the target (mean number of trials lost per participant = 5.11, SD = 3.5), or if the target was not fixated at all (mean number of trials lost per participant = 0.22, SD = 0.24). There were on average 56.28 trials per participant (SD = 5.81), and all participants had at least 10 trials per condition.

The initiation time was calculated as: time from target onset up until the start of the eye movement to the target. ** Fig. 2a gives the mean time for adult initiation time (ms) for within- and between-category conditions for LVF and RVF targets. Between-category initiation time (mean = 352 ms, SD = 49) was significantly faster than within-category time (mean = 460 ms, SD = 50) [$F(1,17) = 130.02$, mean square error (MSE) = 1,618, $P < 0.001$, $\eta^2 = 0.88$], but there was no main effect of visual field [$F(1, 17) = 2.70$, MSE = 1,605, $P = 0.12$, $\eta^2 = 0.14$]. Although between-category initiation time was faster than within-category for both visual fields, [minimum $t(17) = 8.18$, $P < 0.001$], the interaction was significant [$F(1,17) = 9.14$, MSE = 777, $P < 0.01$, $\eta^2 = 0.35$]. The RVF category effect (between-within) was ≈ 40 ms greater than for the LVF [$t(17) = 3.02$, $P < 0.01$]. The greater RVF category effect was caused by the within-category target detection being slower in the RVF than in the LVF [$t(17) = 2.58$, $P < 0.05$], whereas between-category target detection did not differ [$t(17) = 0.497$, $P = 0.62$].

Infants. Trials were excluded if the eye-movement signal was lost (mean number of trials lost per infant = 7.77, SD = 4.90). Trials were also excluded if multiple eye movements around the screen were made before the eye movement to the target (mean number of trials lost per infant = 3.77, SD = 2.62) or if the target was not fixated at all (mean number of trials lost per infant = 2.9, SD = 1.8). This left on average 17.56 trials per infant (SD = 5.30), and all infants had at least two trials per condition.

The time taken to initiate an eye movement to the target was calculated in the same way as for the adults. Fig. 2b shows the mean initiation time (ms) for each visual field and for within- and between-category conditions. A two-way repeated measures ANOVA with category (within/between) and visual field (left/right) was conducted on the time to initiate an eye movement to the target. As with the adults, responses were faster to between-

category targets (mean = 631 ms, SD = 239) than to within-category targets (mean = 711 ms, SD = 212) [$F(1,12) = 5.73$, MSE = 14,199, $P < 0.05$, $\eta^2 = 0.32$], and there was no effect of visual field [$F(1,12) = 2.38$, MSE = 62,371, $P = 0.15$, $\eta^2 = 0.17$]. The interaction was also significant [$F(1,12) = 18.49$, MSE = 7,265, $P < 0.005$, $\eta^2 = 0.61$] but reflected a significant LVF category effect [$t(12) = 3.71$, $P < 0.005$] and no RVF category effect [$t(12) = 0.74$, $P = 0.47$]. The visual field difference in CP was caused by slower RVF within-category responses than LVF responses [$t(12) = 2.61$, $P < 0.05$], whereas between-category responses did not differ [$t(12) = 0.078$, $P = 0.94$].

General Discussion. On a target detection task adults were faster to initiate an eye movement to a target if it was on a different-category than same-category background. A significant category effect was found in both visual fields. However, the category effect was significantly larger when targets appeared in the RVF than LVF. This RVF-LH bias in CP for adults replicates the findings of Drivonikou *et al.* (16), who used the same task but with rapid stimulus presentation, more trials, and reaction time rather than eye-movement initiation time as a measure, and Gilbert *et al.* (14), who used a reaction time measure on a similar task. Because of the time taken to initiate an eye movement to the target, some degree of interhemispheric communication was expected for the adults, which probably weakened the strength of the hemispheric bias found. Indeed, a number of studies suggest that the degree of LH color CP in adults is a function of the opportunity for transcallosal transfer. At one extreme, a study with an adult patient whose corpus callosum had been surgically severed, leaving effectively no such opportunity, showed clear color CP in the LH but none at all in the RH (ref. 14; for a second patient exhibiting the same pattern see ref. 31). In adults with an intact corpus callosum, LH CP is again consistently found, and the strength of RH CP increases with increased response time, and thus increased opportunity for transcallosal transfer (14, 16, 31). It appears then that in normal adults, color CP is based in the LH, and that RH CP when it occurs is largely caused by transcallosal transfer.^{††} An alternative account is that RH CP in adults is left over from infancy, although the complete lack of a RH category effect in patients with a severed corpus callosum makes this unlikely.

The lack of hemispheric integration until ≈ 24 months (33)

**The measure was normally distributed for both adult data [skew = 0.27, SE skew = 0.54, $Z = 0.50 < 1.96$; kurtosis = -0.31, SE kurtosis = 1.04, $Z = -0.03 < 1.96$; Shapiro-Wilk (18) = 0.98, $P = 0.95$] and infant data [skew = 0.48, SE skew = 0.62, $Z = 0.78 < 1.96$; kurtosis = -0.53, SE kurtosis = 1.19, $Z = -0.44 < 1.96$; Shapiro-Wilk (13) = 0.95, $P = 0.62$].

^{††}The picture is complicated by the fact that there are also some instances of RH CP in adults in circumstances that are probably not attributable to trans-callosal transfer. Notably, aphasics exhibit RH but not LH color CP (32), and sometimes normal adults performing visual search with a concurrent verbal interference task similarly exhibit RH CP and no LH CP (31). The relation of these RH CP findings to each other, to RH CP in infants, and to presumably trans-callosally mediated RH CP in adults, remains something of a mystery.

may ensure that the lateralization of targets will be more absolute for infants than adults. Indeed, in the present study, infants did show a more striking hemispheric asymmetry, a significant category effect was only found when targets appeared in the LVF but not the RVF. However, we found that the pattern of hemispheric asymmetry in CP was reversed in infants compared with adults, with infants showing a RH bias and adults showing a LH bias. One hypothesis that has been put forward to explain the LH bias in adult color CP is that the bias arises from the LH dominance for language, and that it is linguistic codes for color names that lead to a greater category effect in the LH than RH. The absence of CP in the RVF–LH of prelinguistic infants does not contradict the language hypothesis. One possibility is that LH CP develops as color terms are acquired, ≈ 2 –5 yrs (34) or later in childhood as access to lexical color codes becomes more automatic. Of course, the RH to LH shift in color CP may occur independently of learning color naming, and additional developmental studies are required to test this hypothesis.

If language can account for the LH bias in adults, what can account for the strong RH bias in infants? Strong hemispheric asymmetries in infancy are not unusual (24–28), and some researchers have even argued for a RH dominance in infancy caused by greater RH than LH cerebral blood flow (35). Changes in side of lateralization across development are also not unusual and are found for other domains such as some aspects of language processing (26, 36). Further research is needed to understand the neuro-physiological basis of early hemispheric asymmetries and their development. Additionally, further investigation of infant hemispheric asymmetries in CP for domains other than color, for example, CP of facial expressions (37), may shed light on whether the effects found here are indicative of a general RH categorical bias in infancy or restricted to color CP. Comparisons with other domains may lead to a greater understanding of why there is hemispheric specialization in infant color CP and why this changes across development.

Evidence suggesting that color CP varies cross-linguistically, and that color CP is eliminated by verbal interference, has supported the hypothesis that color CP depends on access to lexical codes for color (3–5, 12–14). However, the finding of color category effects in prelinguistic infants and toddlers has led others to argue that language cannot be the only origin of the effect (6, 9, 10). The current study finds evidence to support both positions. Color CP is found in 4- to 6-month-old infants, replicating previous infant studies (8–10). However, the absence of a category effect in the LH for infants, but the presence of a greater LH than RH category effect for adults, suggests that language-driven CP in adults may not build on prelinguistic CP, but that language instead imposes its categories on a LH that is not categorically prepartitioned.^{‡‡} The current findings may therefore suggest a compromise between the two positions: there is a form of CP that is nonlinguistic and RH based (found in infancy) and a form of CP that is lexically influenced and biased to the LH (found in adulthood). Color CP is found for both infants and adults, but the contribution of the LH and RH to color CP appears to change across the life span.

Materials and Methods

Adults. Participants. Eighteen adults (7 males, 11 females) took part in the study (mean age = 21.83, SD = 3.85). All adults had normal color vision as assessed

^{‡‡}Color category boundaries observed to date in infant CP coincide rather closely with color boundaries arising frequently in the languages of the world, namely green/blue, blue/purple, and purple/pink (8, 9). We suggest that this circumstance is not caused by linguistic categories building on prelinguistic partitions, but instead may be attributable to the same general organizing principles operating independently in both LH and RH, producing similar (but not identical) categorizations of color. Notably, general clustering principles operating over the irregular shape of perceptual color space have been shown to produce color category systems like those found in the world's languages (38) and might in principle also account for prelinguistic CP.

Table 1. CIE 1931 Y, x, y chromaticity coordinates of the stimuli

Stimulus	Y	x	y
8.75BG 6/8	19.47	0.214	0.304
6.25BG 6/8	19.47	0.220	0.322
3.75BG 6/8	19.47	0.228	0.342
2B 6/8	19.47	0.209	0.282
2BG 6/8	19.47	0.235	0.355
2G 6/8	19.47	0.286	0.431
Gray	19.47	0.336	0.344

White point of monitor as measured on screen: $Y = 64.80$ cd/m², $x = 0.326$, and $y = 0.335$. The stimuli emulated a reflectance of 30.05.

by the City Color Vision Test (39), were right-handed, and spoke English was their native language. All were students at the University of Surrey and received course credits for their participation.

Apparatus and experimental set-up. The experiment was conducted in a dark room. Stimuli were displayed on a calibrated Sony Trinitron monitor (model GDM-F520) and measured with a Cambridge Research Systems ColorCal colorimeter. Participants were seated 50 cm away and at eye level to the monitor. Eye movements were recorded with an ASL 504 pan/tilt eye-tracking camera, tracking at 0.5° accuracy, placed under the monitor recording at 50 Hz. The eye-movement output gave a video of what the participant was shown with “cross-hairs” superimposed. Cross-hairs are two crossing lines (one vertical and one horizontal), and where they cross indicates point of gaze. The output was digitized by using an analogue-to-digital video converter (Canopus ADVC-300), and the digital video was analyzed with i-Movie 2.1.2 software.

Stimuli and design. As shown in the top half of Fig. 1*b*, there were three stimuli that varied only in Munsell hue with Munsell value and chroma kept constant (value = 6, chroma = 8). Adjacent stimuli were separated by 2.5 Munsell hue units and straddled the BG boundary (7.5BG). Two stimuli were green (3.75BG, 6.25BG), and the third was blue [8.75BG; see Table 1 for Commission on Illumination (CIE) 1931 Y, x, y chromaticity coordinates]. Adjacent stimuli were paired, giving one within-category and one between-category pair (see Fig. 1*b*). For each pair, one stimulus was used as the target (diameter = 3 cm, visual angle of 3.5°) and one as the background (40 × 30 cm), with both stimuli in a pair appearing equally as the target or background. The target appeared at 1 of 12 locations arranged radially around a central point, with 6 locations to the left of the central point and 6 to the right (Fig. 1*a*). For both within- and between-category pairs, the location of the target was randomized, with the constraint that the target appeared equally as often on the left and right. There were thus four conditions (within-category left, within-category right, between-category left, between-category right), and there were 16 trials per condition presented in a randomized order. Each trial began with the presentation of a looming and contracting black and white central attention-getter presented on a gray screen (see Table 1 for Y, x, y chromaticity coordinates). This attention-getter was presented until eye-movement cross-hairs indicated that the participant was fixating the central point. A blank gray screen was then presented for 250 ms, followed by the presentation of the target and background for 4 s.

Procedure. Adults' eye movements were calibrated by using a nine-point procedure, where adults were instructed to look at nine points on the computer screen shown consecutively, and the corneal reflection and pupil signal were recorded at each point. The accuracy of calibration was then assessed by asking participants to look at five more randomly chosen points on the screen, and if the crosshairs indicating point of gaze hit each of these five points then calibration was deemed accurate. If calibration was not accurate then the procedure was repeated (see ref. 10 for further details). Once eye movements were calibrated, participants were told to “fixate the flashing bulls-eye when it is shown, but other than that, just look at the screen, keeping your head as still as possible.” No other instructions were given.

Infants. Participants. Twenty-six infants took part in the study. Of these, 13 were not included in the final study because of general fussiness such as crying or excessive head movement (6 infants), no accurate calibration achieved (3 infants), or not enough completed trials for one or more of the conditions (4 infants). The mean age of the final sample was 20.61 weeks (SD = 2.66), and there were five females and eight males. The mean birth weight of the sample was 3,850 g (SD = 820).

Apparatus and experimental set-up. The apparatus was the same as for the adults. Infants were seated and strapped into an infant car seat 50 cm away from and

at eye level to the monitor. All other aspects of the experimental setup remained the same, except that there were no verbal instructions.

Stimuli and design. The stimuli and design were the same as for the adults, with the exception that the stimuli were separated by 10 Munsell hue units rather than 2.5 (see Fig. 1*b* and Table 1 for Y , x , y chromaticity coordinates). There were also 32 rather than 64 trials in total, with 8 trials per condition.

Procedure. Infant eye movements were calibrated with a two-point procedure where the black and white attention-getter was shown consecutively at two points (top left, bottom right), and the pupil signal and corneal reflection were recorded for each point. The accuracy of calibration was then assessed by showing the attention-getter at three more randomly chosen points, and if the crosshairs indicating point of gaze was centered on the attention-getter for each of these three points then calibration was deemed accurate. If

calibration was not accurate then the procedure was repeated (see ref. 10 for further details). After calibration, infants were shown the 32 experimental trials. The target and background were only shown once infants were fixating on the central attention-getter. If an infant's attention waned and the infant didn't fixate on the central attention-getter, black and white cartoon animals that moved in synchrony with noises were shown in between trials to refocus the infant on the screen. Once the infant was focused on the screen the attention-getter was shown, and once this was fixated the next trial began.

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