

RESEARCH ARTICLE

Visual stimulus structure, visual system neural activity, and visual behavior in young human infants

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Abstract

In visual perception and information processing, a cascade of associations is hypothesized to flow from the structure of the visual stimulus to neural activity along the retinogeniculostrate visual system to behavior and action. Do visual perception and information processing adhere to this cascade near the beginning of life? To date, this three-stage hypothetical cascade has not been comprehensively tested in infants. In two related experiments, we attempted to expose this cascade in 6-month-old infants. Specifically, we presented infants with two levels of visual stimulus intensity, we measured electrical activity at the infant cortex, and we assessed infants' preferential looking behavior. Chromatic saturation provided a convenient stimulus dimension to test the cascade because greater saturation is known to excite increased activity in the primate visual system and is generally hypothesized to stimulate visual preference. Experiment 1 revealed that infants prefer (look longer) at the more saturated of two colors otherwise matched in hue and brightness. Experiment 2 showed increased aggregate neural cortical excitation in infants (and adults) to the more saturated of the same pair of colors. Thus, experiments 1 and 2 taken together confirm a cascade: Visual stimulation of relatively greater intensity evokes relatively greater levels of bioelectrical cortical activity which in turn is associated with relatively greater visual attention. As this cascade obtains near the beginning of life, it helps to account for early visual preferences and visual information processing.

Introduction

Before they have much (if any) experience, infants selectively attend visually to different stimuli in the environment. *Why?*

Understanding patterns of infant attention and information processing is important because the world offers myriad sources and types of stimulation and information, and central

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challenges for human infants from the start of life are to monitor the environment by deploying their attention selectively, extracting critical information from the environment, and at the same time avoid being overwhelmed by a rich environment of constantly changing stimulation [1]. The complementary task for students of early human sensory, perceptual, and cognitive development is to understand how young infants overcome those challenges. One early (but infrequently and not yet comprehensively tested) hypothesis suggests a cascade: infant visual attention to selective visual stimulation is mediated by excitation of neural tissue along the visual pathway [2,3]. Individual neurons as well as cell assemblies are known to respond selectively to different types of visual stimulation—orientation, direction, and hue, for example. Classic neurophysiology attests that, when the appropriate stimulus or “trigger feature” for a given neuron enters its receptive field, the rate of the neuron’s electrical discharge increases [4]. Stimuli that deviate from the neuron’s preferred trigger feature produce lower rates of firing or even inhibit neuronal excitation from its spontaneous level. This stimulus-response “dose” relation between specific stimulation and central nervous system activity is well established [5]. Notably, Hubel and Wiesel began their pathbreaking neurophysiological research with the straightforward assumption that turning on or turning off diffuse light in front of a cat’s eyes ought to affect the activity of cells in the cat’s brain. As Hubel recounted in his Nobel laureate lecture, to their surprise, however, Hubel and Wiesel found that neurons in the cat visual cortex were not excited by the mere presence or absence of light [6]. Instead, specific cells at specific cortical sites were excited by specific visual contours rotated to specific orientations moving in specific directions. Such specificities of stimuli, topography, velocity, and the like have since proven to be the rule in nervous system function [7,8]. On this classic principle, feature-detecting neurons code specific dimensions of environmental stimulation and mediate eventual behavior in the fashion of a cascade.

Although precise relations among environmental stimulation, neural coding, and perception and information processing are complex and still poorly understood, it has been hypothesized in developmental science, but not adequately nor comprehensively tested to date, that how much visual attention that a stimulus structure elicits from an infant may be governed by how much neural activity that stimulus structure excites. Here, in two related experiments we tested that proposition directly by examining both visual preference and cortical electroencephalographic (EEG) responses to variation in specific visual stimuli in human infants and (for comparison) adults. For reasons explained below, the visual structure we manipulated was chromatic saturation, the index of visual system neural activity at the cortex was event related spectral perturbation, and the measure of infant visual behavior was looking time. So, null hypotheses would be that stimulus saturation level has no effect on infant brain electrical activity and saturation level has no effect on infant looking behavior.

A brief review of the history of infant testing that anticipated this cascade proposition led us to these specific hypotheses. As long ago as the late 1950s, Berlyne observed that infants prefer to look at patterns with more contour, and he presciently speculated, based on then current physiological understanding, that patterns with more contour excite fibers along the visual system more [9]. This “high stimulating power,” Berlyne argued, accounts for the “high eye-drawing power of patterns.” Kessen and colleagues later recorded neonates’ eye-movement scanning and documented a preference for newborns crossing vertical edges; in turn, they speculated that that preference reflected greater neural stimulation provoked by vertical contours [10]. Subsequently, Karmel, Hoffman, and Fegy recorded visually evoked potentials (VEPs) from the cortex of infants who looked at checkerboards of different patterns [11]. The longest infant total looking times were to patterns that evoked maximum amplitude VEPs (see also [12]). Soon after, Karmel and Maisel confirmed that infants look more or less at patterns with more or less amounts of contour, and they hypothesized that patterns with more contour

optimally stimulated cells in the visual cortex tuned to contour detection [13]. With such data in hand, Haith advanced the principle that cortical firing rate guides infant vision, and he generated a series of related “rules” to account for infant visual search [3]. However suggestive, these studies together do not provide integrated support for a cascade from visual stimulus structure to neuronal activity along the retinogeniculostriate visual system to visual preferential looking in infants. The main purpose of the experiments presented here was to provide that more integrated and direct experimental test of the cascade.

Color is a basic domain of vision and a pervasive aspect of human visual experience. The subjective organization of color perception is tridimensional, encompassing hue, brightness, and saturation [14]; hue is most closely associated with dominant wavelength, brightness with luminance, and saturation with purity as physical variables [15]. Color is an esthetically impressive, perceptually appealing, and cognitively informative aspect of the visual world [14,16]. Colors possess influential affective qualities as they moderate mood [14]; they elicit and maintain visual attention, as they clarify and accentuate features of the visual environment [17]; and they aid detection, identification, encoding, learning, and communicating about visual attributes and objects in the world [18–21].

Chromatic saturation provides a functional stimulus dimension to test the cascade hypothesis. Saturation is the subjective density or vividness of color in a mixture with white and is a continuous variable. Saturation (*aka* chroma) corresponds to the physical property of purity. In the present experiments, we used levels of chromatic saturation to investigate neural responses and behavioral preferences for two reasons. First, neonates [22], 2-month-olds [23], and 4-month-olds [2] reliably discriminate among levels of chromatic saturation and discriminate saturated colors from white. Relevantly, the developmental literature indicates that young infants also pay more attention to more saturated colors than to less saturated ones [2,23,24]. When infants as young as 4 months of age are shown two otherwise equivalent visual stimuli, one of which is a saturated color and the other is either white, neutral gray, or less saturated, viewed against dark or achromatic surrounds, infants regularly look at (prefer) the more saturated color of the two [2,23,25–27]. Indeed, infants’ looking behavior obeys what has been called a *Maximum Saturation Rule*—that is, along the purity dimension from white to a chromatic saturation maximum, infants’ visual preference minimum lies at the white end of the dimension and their visual preference (looking) increases with increasing stimulus saturation [26,28–30].

One experiment assessed infants’ preferences among six chromatic stimuli versus white, all tested at physical isoluminance and adult-judgement isobrightness. Infants preferred all isoluminant chromatic stimuli to white and preferred all chromatic stimuli judged by adults to be equivalent to white in brightness [31]. The second reason we chose chromatic saturation as the stimulus test dimension is because the neurophysiological literature indicates that more saturated colors (a) stimulate activity in neurons in the visual system that are sensitive to color and (b) increase amplitude of the visually evoked cortical potential in human newborns. With respect to visual system activity, De Valois and Marrocco [32] determined that the frequency of discharge of color-sensitive cells in the lateral geniculate nucleus [33] of the primate *Macaca irus* increases monotonically with the saturation purity of visual chromatic stimulation. Cells sensitive to long wavelengths (“red”) fired to white light around the rate of their spontaneous discharge, but they fired to increasingly monochromatic long-wave ($\lambda = 640$ nm) light with increasing frequency. With respect to newborn cortical electrical activity, purity of saturation influences the amplitude of the VEP. Lodge, Armington, Barnet, Shanks, and Newcomb [34] studied the neonatal VEPs to white and long-wave ($\lambda > 580$ nm) light. When stimuli were equated for brightness, more purely saturated “orange” produced visually evoked potentials in newborns at an amplitude three times greater than to white.

On the basis of these kinds of data, we hypothesized, first, that infants would preferably attend to (look at) otherwise equivalent more saturated than less saturated chromatic visual stimuli and, second, that infants would show greater cortical neural electrical activity to otherwise equivalent more saturated than less saturated chromatic visual stimuli. To test the first hypothesis, in Experiment 1 infant visual looking times (attention) to less and more saturated versions of the same chromatic visual stimuli were assessed where wavelength and brightness of those stimuli were held constant. To test the second hypothesis, in Experiment 2 infants' and adults' cortical EEG activity was monitored while they looked at the same visual stimuli of less and more chromatic saturation.

General methods

Participants

Infants in the two experiments were born at term and 6 months of age and healthy at the time of testing. We recruited infants aged 6 months because research confirms that by this age infants have trichromatic color vision [35–39]. Moreover, infants in this age range have the abilities to control their attention [40], and the design of these experiments implemented an infant-controlled visual perception procedure. Infants were recruited through the use of purchased mailing lists of newborns in a suburban metropolitan area and represented families of middle to upper socioeconomic status. Sample sizes in these experiments were determined by reference to previous related research and are consistent with a predominance of infant visual attention studies [41,42]; data collection ceased when planned sample sizes were reached; and attrition rates were comparable to other published looking time and EEG studies [41,43]. Adults were recruited from Institutional staff. Each participant in these studies (infants and adults alike) were first-time participants; these were the only such studies in which they participated; and all participants were naïve as to the hypotheses of the experiments. Participants were tested in accordance with ethical principles of the Declaration of Helsinki, and the research Clinical Protocol 04-CH-0250 was approved (11/16/2011) by the Institutional Review Board of the *Eunice Kennedy Shriver* National Institute of Child Health and Human Development. The recruitment period of the study was 5/1/2010–11/14/2013. Infant participants' parents and adult participants were informed about study procedures before participating. Consent for participation by infants was obtained by parents' signature, and for adults by each participant's signature.

Stimuli. The same chromatic stimuli were used in Experiments 1 and 2. [Table 1](#) shows their CIE Yxy coordinates. Two 17.4° by 22.6° chromatic fields were generated by a computer program (E-prime; Psychology Software Tools, Pittsburgh, PA) with the same 630 nm dominant wavelength (“red”) and equivalent brightness and presented on a computer monitor (Dell Ultra-Scan P1110 21”; Dell Technologies, Round Rock, TX) against a black background (as has been done previously; [37,44]). Each stimulus field contained a simple circular schematic face in

Table 1. CIE Yxy coordinates for chromatic stimuli used in Experiments 1 and 2.

Chromatic Stimulus	Y	x	y
“Red” more saturated	17.66	0.64	0.33
“Red” less saturated	15.71	0.45	0.34
“Green” more saturated	37.26	0.30	0.60
“Green” less saturated	36.08	0.31	0.48

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black outline that was 8.7° in diameter and centered within the field (Fig 1). The faces were intended to maintain infants' engagement with the task without biasing attention, and they were sized to be salient in relation to infants' developing acuity while still fitting parafoveal limits when centrally fixated. One field was more saturated and the other field less saturated. Because stimulus brightness can vary independent of saturation [45] and affect infant attention, brightness (as well as wavelength—hue) was held constant with the use of isoluminant chromatic stimuli. This selection enables interpretation of any observed behavioral and psychophysiological differences as occurring in relation to saturation uniquely. Infant and adult isoluminance values are similar [46], and infant and adult spectral sensitivity for video generated stimuli are also similar. Moreover, the amplitudes and latencies of the major components of chromatic onset responses represent robust to large (even intentional) luminance mismatches [47,48].

Specific methods and results

Experiment 1A. Experiment 1A assessed infants' spontaneous looking preferences between the more and less saturated stimuli when presented side by side. Ruff [49] presented 4.5-month-olds with paired high-contrast geometric stimuli, and she argued that infants' gaze shifts indexed active efforts to process and compare paired stimuli. Infants may be more

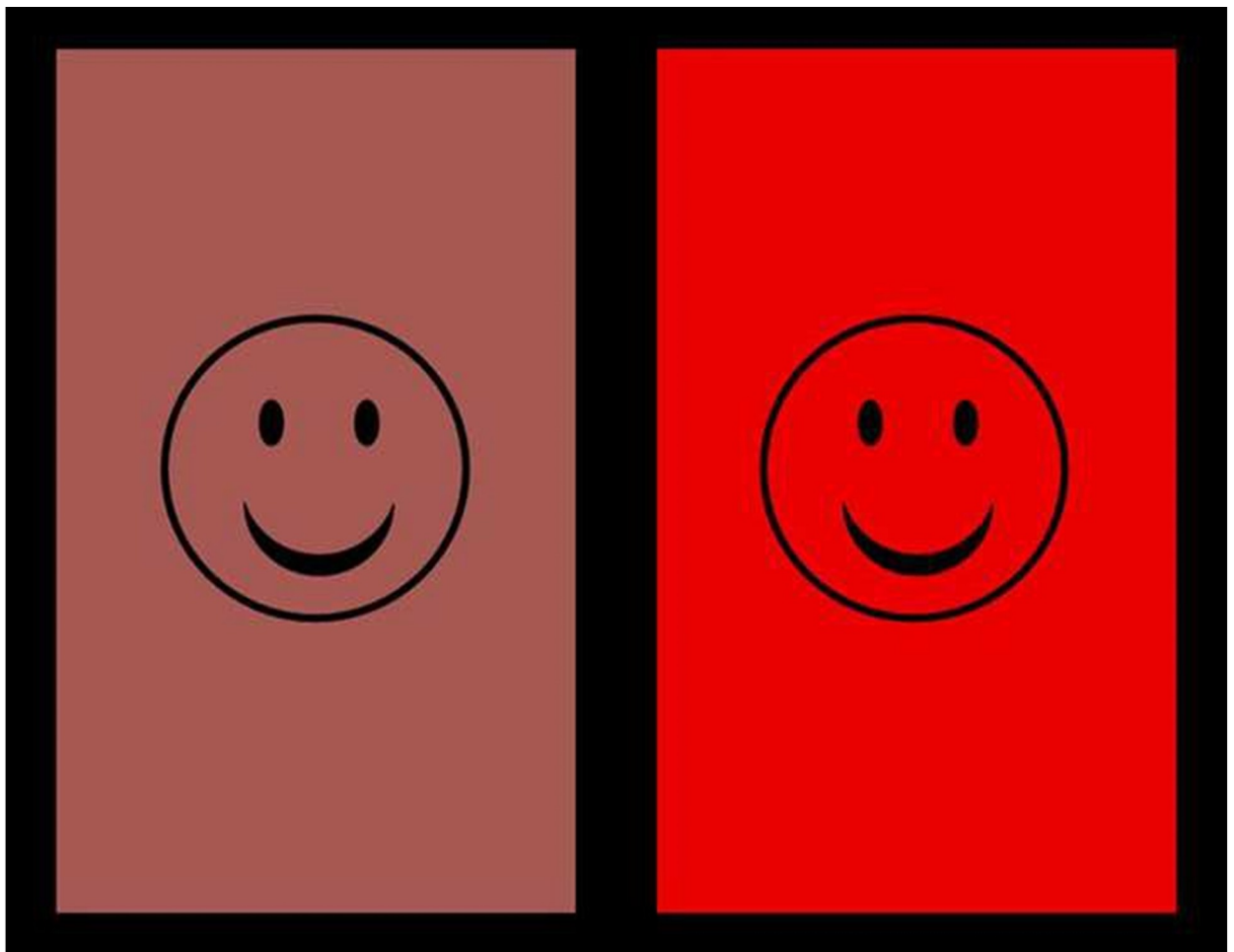


Fig 1. Stimulus exemplars from Experiment 1A.

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motivated (e.g., by attentional salience) to make eye movements towards chromatic stimuli with greater saturation than ones with lesser saturation [50].

Participants. Fifteen 6-month-old infants (M age = 24.5 w, SD = 1.2; 11 females) participated. Data from an additional 4 infants were not included due to inattentiveness during the procedure.

Stimuli and procedures. The more saturated and less saturated fields were presented simultaneously for trials that lasted 10 s each and alternated the left versus right location of the two saturated stimuli. We implemented an infant-controlled procedure, wherein each 10-s trial began when the infant was judged to be looking centrally at the stimulus screen (where the visual stimulus would appear). Intervals between trials therefore varied somewhat, averaging approximately 4 s.

Infants sat alone in an infant seat in a dimly lit room in front of the computer monitor at a viewing distance of 60 cm. An Applied Science Laboratories (ASL; Bedford, MA) Model 504 infant eye tracking system captured infants' fixations on each stimulus image. The system used infrared corneal reflection to record fixation coordinates on the stimulus plane continuously at 60 Hz. An ASL optical face tracker corrected angles on the eye camera relative to spontaneous movements of the head that exceed optical-tracking frame limits. GazeTracker (EyeResponse Technologies, Charlottesville, VA) software, running on a second microprocessor, synchronized eye movement recordings with stimulus presentations. The eye camera was located beneath the monitor in the same depth plane as the monitor screen and recorded infant looking.

Results and discussion. For each trial, infant visual fixations (dwell times) were plotted directly on the stimulus fields (off-display fixations were disregarded). Following conventional practices [51,52], the durations of individual infant fixations to different saturation levels (inclusive of field edges) were totaled, and preference scores were determined by dividing the total duration for the saturated fields only by the total of all fixations. Using a one-sample t -test, these preference scores were then compared to chance (0.50; with 15 participants and estimates from previous research, power was estimated at 0.75). As hypothesized, infants preferentially fixated the more saturated stimulus displays over the less saturated stimulus displays, $M = 0.61$, $SD = 0.16$, $t(14) = 2.70$, $p = .017$, $g = 1.41$ [53] (see Fig 2).

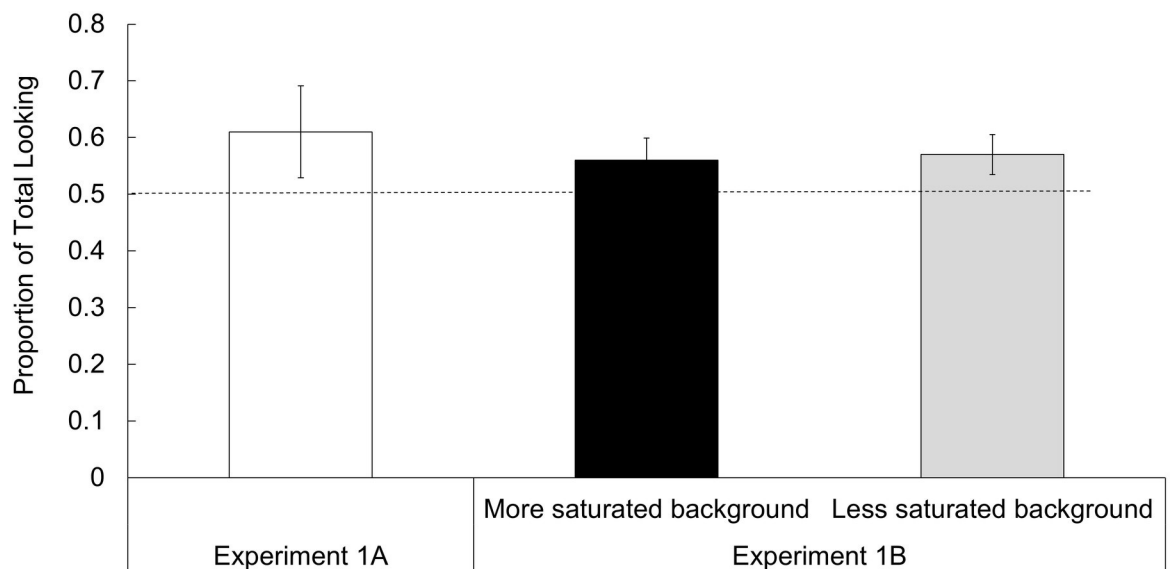


Fig 2. Mean (95% CI) proportions of total looking time directed to more saturated stimuli; the dashed line at 0.5 is chance.

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Infants provided behavioral evidence of visually preferring the more saturated to the less saturated of otherwise equivalent (hue- and brightness- matched) chromatic stimuli. The results of Experiment 1A replicate Bornstein [2], who showed 20 4-month-olds six colors, three hues (two blues, greens, and reds with the same brightness) each at a low and high chromatic saturation singly for 15-s durations in different counterbalanced random orders. Infants in that study also looked more on average at the more saturated versions of hues than they looked at the less saturated versions of the same hues (see also [24]).

Experiment 1B. Experiment 1B assessed the influence of variation in foreground- background color saturation on infant spontaneous looking preferences. Because the relative saturation of background coloration can interact with infants' spontaneous visual preferences [26], additional examination of infant preference for a more over a less saturated version of the same hue and brightness was warranted. Pereverzeva and Teller presented infants with chromatic stimuli of varying saturation levels against both white and chromatic backgrounds. Infants looked longer at saturated stimuli in the white-background condition, and the researchers concluded that infant preference was due to maximal difference in purity. Additional investigation in Experiment 1B was also motivated by the related idea that the visual system may be sensitive to relative signals more than absolute stimulus attributes.

Participants. Twenty-five 6-month-old infants (M age = 25.8 w, SD = 2.4; 8 females) participated in Experiment 1B. (Data from an additional 6 infants were not included due to inattentiveness.) A larger number of infants was recruited in Experiment 1B than in Experiment 1A because an additional critical test of effects was needed.

Stimuli and procedures. Experiment 1B differed from Experiment 1A only in the background used in stimulus presentations. The same paired "red" color fields from Experiment 1A were presented in Experiment 1B, this time against "green" (instead of black) backgrounds, with two different saturation levels of "green" used (see Table 1). The more saturated and less saturated "green" background levels were counterbalanced with the left/right panel positions of the two "red" field saturation levels across trials. All other aspects of the task were identical to those of Experiment 1A.

Results and discussion. Infants again preferentially fixated the more saturated red fields of the stimulus displays over the less saturated versions across both saturation levels of the backgrounds (M = 0.56, SD = 0.10, $t(24)$ = 3.34, p = .003, g = 0.60, for stimuli with less saturated green backgrounds, and M = 0.57, SD = 0.09, $t(24)$ = 3.55, p = .002, g = 0.74, for stimuli with more saturated green backgrounds). No difference was observed between background saturation levels. Under the conditions examined here, the saturation level of background coloration did not affect infants' spontaneous preference for more saturated fields over less saturated ones. Thus, infant visual preference for relatively greater saturation is also robust to variation in chromatic background hue and saturation characteristics. Across both experiments, we used novel stimuli, controlled relevant stimulus characteristics, and presented stimuli only after infants were attending to the stimulus monitor. Thus, factors such as state and familiarity cannot account for the pattern of findings.

Experiment 2. Experiment 2 examined cortical activity in infants and adults to relatively less and more saturated chromatic stimuli of the same hue and brightness. Cortical responses to chromatic stimuli are robust, and electrical activity at the cortex in response to chromatic stimulation has become a sensitive and objective measure of neural development in infancy [54]. Experiment 2 used a task-based EEG paradigm in which EEG was measured to a specific set of stimuli with the aim to reveal real-time brain activity associated with looking at those stimuli.

Participants. Ten 6-month-old infants (M age = 26.7 w, SD = 1.1, 5 females) and ten adults (M age = 22.41 y, SD = 1.20, 7 females) participated. Data from an additional 16 infants were not included (8 due to fussiness or inattentiveness, 6 due to artifacts in the EEG data, and

2 due to equipment failure). This sample size is consistent with a predominance of infant visual attention studies [42].

Stimuli and procedures. Thirty trials of each of the two saturation levels were presented singly in random order for a total of 60 trials. On each trial, once infants were judged to be looking at the center of the stimulus monitor, a 300-ms baseline period preceded stimulus presentation; the stimulus appeared for 500 ms; then a variable duration 1800- to 2200-ms intertrial interval followed during which the presentation screen was black. The EGI 128-channel EEG system (Magstim EGI; Eugene, OR) was used to record cortical EEG. The international 10–10 system sites P3, Pz, P4, P7, Oz, and P8 were clustered and selected for analysis (Fig 3). EEG artifacts were detected and removed using the Automatic EEG Artifact Detection Based on Joint Use of Spatial and Temporal Features (ADJUST) [55,56] running in Matlab v8.0 (MathWorks; Chevy Chase, MD). Components corresponding to four classes of source artifact were removed: eye blink, vertical eye movement, horizontal eye movement, and generic discontinuity.

Results and discussion. Brain activity giving rise to the perceptual experience of color likely occurs at higher-level cortical areas upstream from the pre-cortical retina and lateral geniculate nucleus [57]. We therefore examined electroencephalographic cortical activity using event related spectral perturbation (ERSP), an index of changes in the spectral power of EEG frequency bands as a function of time following the onset of an experimental event [58–60]. The ESRP is a measure of mean amplitude changes in EEG frequency to an experimental

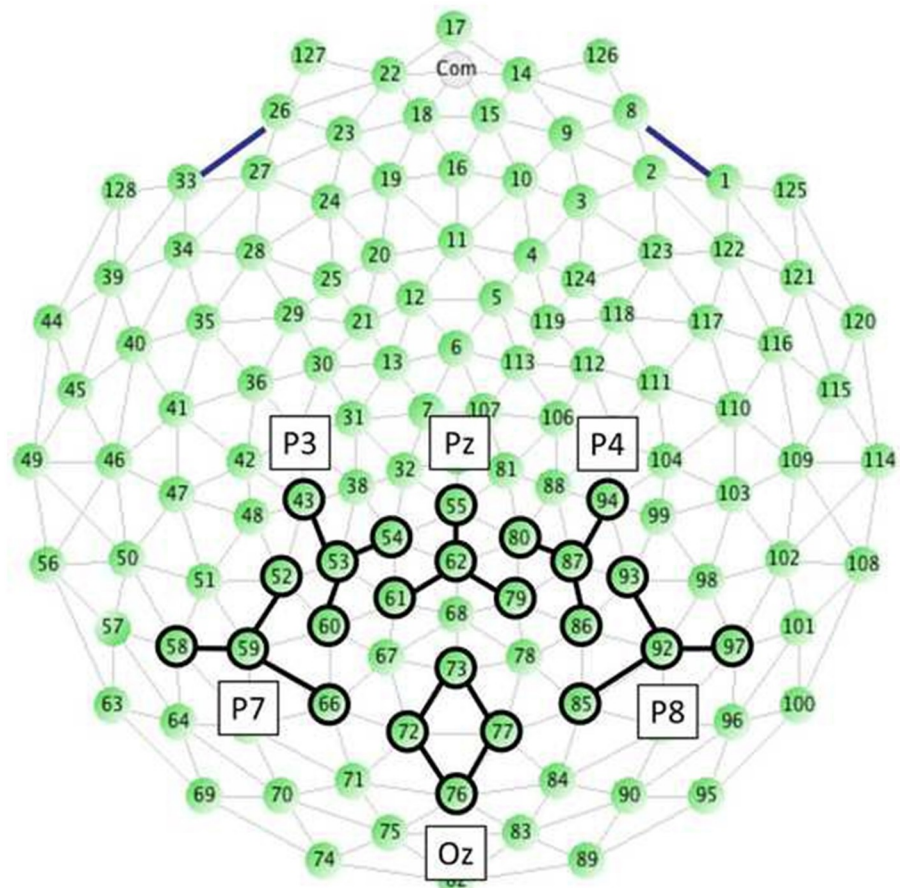


Fig 3. Recording site clusters used with infants.

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event across time [61], and ESRP is especially useful because it allows extraction of meaningful EEG signals from few trials [62]. Independent component analysis (ICA) is used to identify EEG rhythms to data from a single trial during a time period inclusive of the time window of components. It finds spatiotemporal patterns of consistent frequency content in participants' scalp topography. ERSP is calculated by segmenting the EEG signal into brief overlapping data windows, and a moving average of the amplitude spectra of the windows is calculated and divided by mean baseline spectra preceding the event. Spectral decomposition of signals from each channel proceeded with a Morlet wavelet transform [61]. A 100- ms window and wavelet cycles varying linearly from 2 to 9 were used to recover frequencies from 4 to 60 Hz over 57 equal-interval bins. The ERSP was used to examine time resolution of the spectral power evoked by stimuli assuming that attention increases with increased activation [59]. Among infants the relation between EEG response and attention depends on task demands and age but is well documented [63].

To identify predominant response timing, grand average time- frequency ERSP response maps were examined over trials, participants, stimulus saturations, and channels for each channel cluster. Infants' initial responses appeared around 80 ms in the beta and lower gamma bands (23–43 Hz) and waned by 210 ms. Adult responses appeared around 30 ms in a similar range of frequencies (13–53 Hz) and extending through 235 ms.

Beta waves are prominent during intense mental activity, focus, active thinking, and alert concentration; gamma waves are prominent during higher-order cognitive processing and are thought to reflect the binding of different populations of neurons into networks for the purpose of carrying out a certain cognitive or motor functions [64,65].

Fig 4 shows the topography of ERSP responses averaged over these selected time windows and frequency ranges by stimulus saturation level and age group. ERSP values were examined in a linear mixed models analysis including saturation level and recording site as repeated fixed effects, age group as a between-subjects fixed effect, 2- and 3-way fixed-effect interactions, and participants as a random effect (power to detect main effects based on previous research was estimated at 0.75). A significant effect of saturation level emerged, $F(1,21.63) = 6.60, p = .018, \omega_p^2 = 0.19$, with the greater ERSP in response to the more saturated ($M = .59, SD = .81$) than less saturated chromatic stimulus ($M = .15, SD = .79$; see Fig 5). No other effects were significant.

General discussion

Infants look longer at some features of their visual environment than at others, an observation that is historically well-grounded in the infancy studies literature [1,10,66–68]. Chromatic saturation is one such stimulus feature of the environment that draws infant attention. The reasons for such taxes have generated speculation. In these studies, infants and adults viewed otherwise equivalent stimuli of two contrasting levels of chromatic saturation, and their looking times and brain responses differed systematically between the two levels of chromatic saturation in both age groups.

In the first experiment, the preferential looking time behavior of 6- month-old infants was assessed. Infants displayed a preference for the more saturated over the less saturated chromatic stimulus as measured by the fraction of their looking time. The two stimuli were otherwise equivalent and presented against a neutral black background. Infants' preference was also maintained against green backgrounds of low and high colorimetric purity indicating that background contrast was not the differentiating factor that influenced infant looking (attention).

In the second experiment, cortical activity was measured in both infants and adults in response to the same more and less saturated chromatic stimuli used in the first experiment. Neural signals were analyzed at a series of electrode positions across the scalp in the frequency

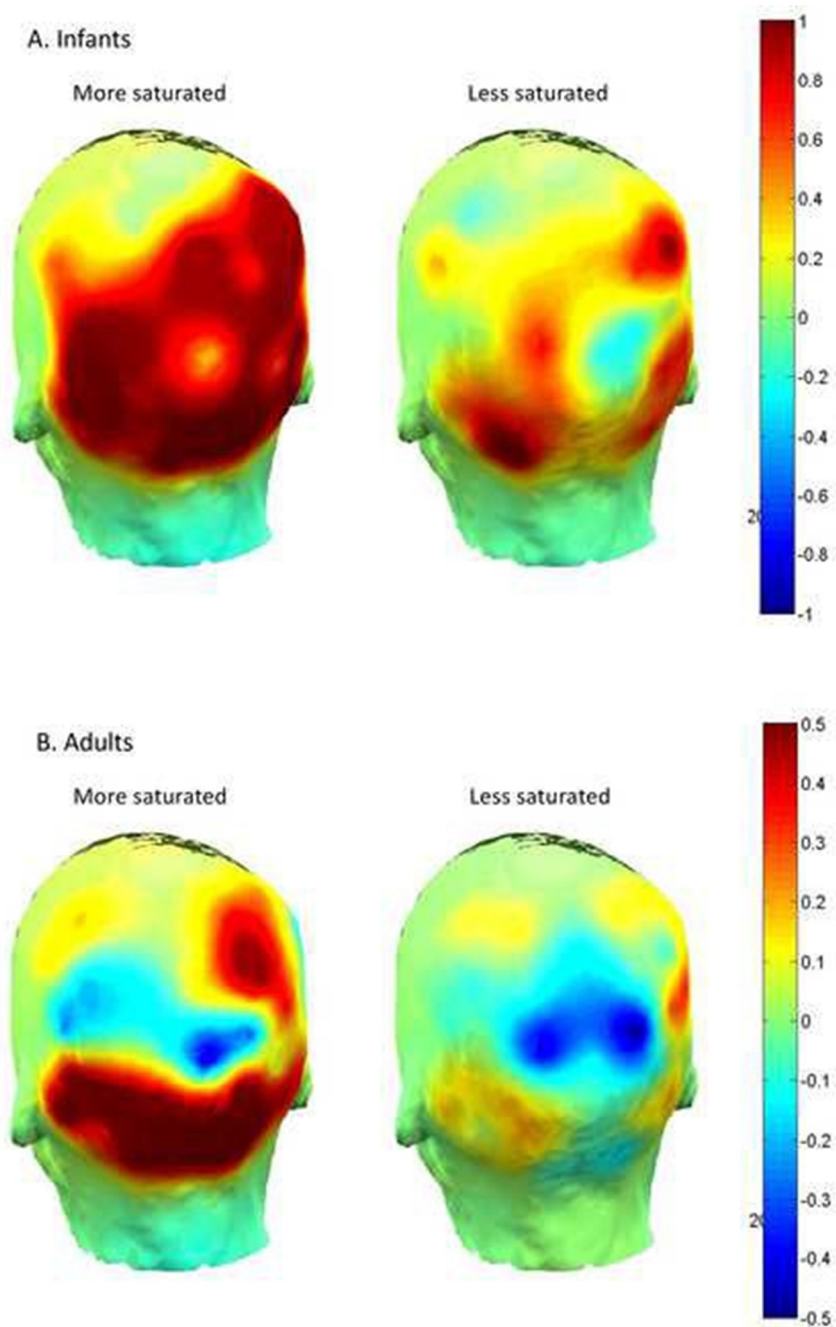


Fig 4. Topographic head maps of averaged ERSP responses across posterior sensors in A. Infants and B. adults.

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domain in a specified time window. The more saturated chromatic stimuli generated greater cortical activity than the less saturated stimuli in both infants and adults. Qualitatively, adult response differences appear to be more localized to posterior parietal locations than those of infants, although the location effect was not significant in the analysis.

What accounts for the variation in infant attention to different levels of chromatic saturation? Explanations that include learning experience and reinforcement history are feasible as

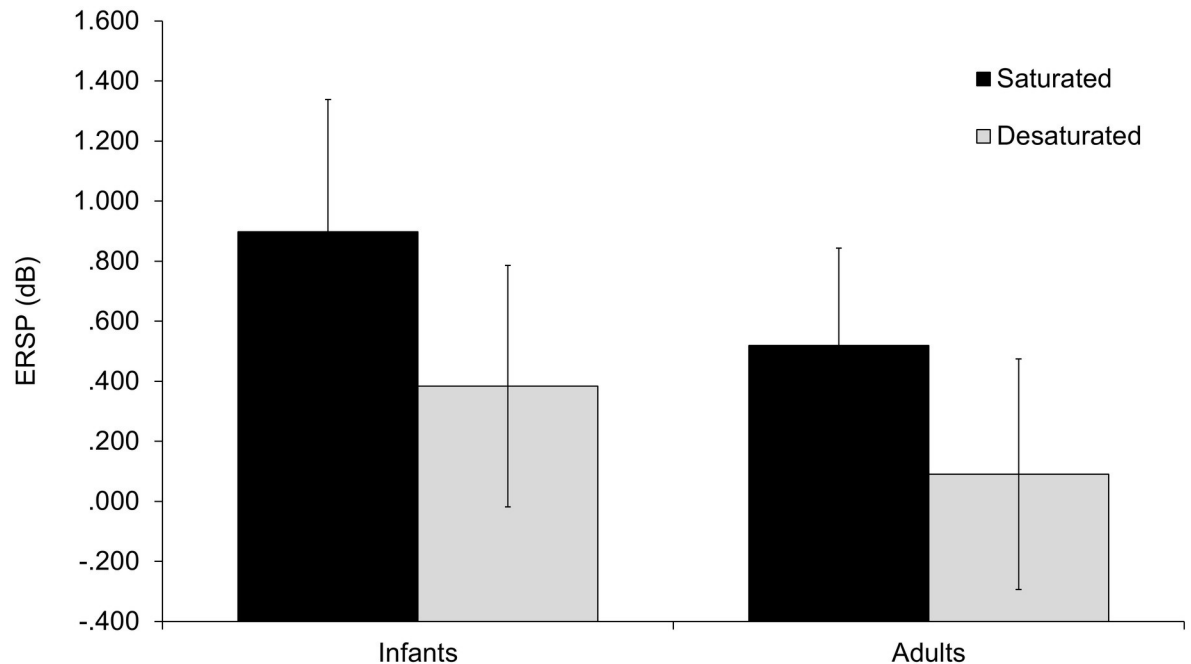


Fig 5. Mean (95% CI) spectral perturbations of responses to stimuli by age group and saturation level.

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social interactions and experiences influence the development of sustained attention [69,70]. However, young infants in the present experiments likely enjoyed little if any learning experience and no reinforcement history with respect to chromatic saturation. Taken together, data from the present experiments rather support the hypotheses that how much visual attention infants pay to a visual stimulus reflects in a regular way how much neural activity in the visual system that stimulus excites [2]. Specifically, the two hypotheses advanced here were both supported. Other EEG and fNIRS studies reinforce the conclusion that infant preferential looking is correlated with responses of neural ensembles that encode given stimulus types and attention networks [71–74].

These experiments reveal infants' relative visual preferences for more over less saturated versions of otherwise equivalent chromatic stimuli. These data also speak to two related issues in infancy and developmental science. First, these preference and neural data indicate that infants as young as 6 months of age discriminate levels of saturation of matched brightnesses within the same hue. Only one previous study has reported that infants discriminate chromatic saturation. There, 4-month-olds discriminated chromatic stimuli of moderate excitation purity (30 to 50%) from chromatic stimuli of lower purity (5–11%) [2]. Second, the replication documented here contributes to counteracting developmental science's replicability problem [75,76].

As with all brain-behavior experiments, explanations of behavioral events in terms of neural events are accompanied by important limitations. For example, interpretations of attention often appeal to two key assumptions: One is that single-neuron or aggregate-neuronal data accurately reflect central nervous system information processing, and the other is that central nervous system activity relates to manifest behavior [7]. Both assumptions raise questions and problems. Whether and how activity of single neurons in the visual system relate to gross electrical activity at the cortex are not well worked out. VEPs might reflect numbers of active neurons or a novel ensemble of overall neuronal activity; these are two among many possibilities. Population coding could also involve different patterns of neural activity, which might not

translate into increased total neural activity over the population [77–80]. Moreover, single neurons, larger groups of neurons, or neural patterns of activity may be stimulated by different segments of a stimulus range. The connection between the intensity of a stimulus and the focus of visual attention may not be determinate (even when the amplitude of a VEP correlates with stimulus intensity) [81], and many variables such as expectancy and affect drive the shape of the VEP. All these aspects aside, attention as a psychological variable notoriously challenges definition [82,83]. Moreover, some nervous activity is uncorrelated with the magnitude of stimulation [84], and VEP amplitude is only a statistical summary of synchronous neural activity [13,85,86].

Relatedly, this study is concerned with visual preference, but visual preference and visual attention are not necessarily congruent. That is, attention is a likely antecedent of preference in the sense that an observer must attend to a stimulus before any expression of preference, but whether preference is a valid measure of attention is less clear as it is possible to look at something and not “attend” to it in any deeper information processing sense. In short, visual preference is a proxy of attention but does not conclusively measure it. Nonetheless, infants with little or no experience exhibit reliable visual preferences, and some brain processes related to attention *must* subserve them.

To begin this article, we reflected that even newborns and certainly young infants spontaneously attend differently to different sources of stimulation in their environment, an activity that has been observed since the beginnings of developmental science [87], and we asked the question, *Why?* The cascade model which we invoked to account for this observation relates the visual attention-getting power of a stimulus to the level of excitation of stimulus-sensitive neural tissue along the visual pathway in the brain. The present findings do not speak to the deep localization of surface cortical activity, but discriminative ESRP responses aligned with our second hypothesis were clearly measurable at the cortical scalp surface. This taxic mechanism and its utility and functions have potential significance for the early development of sensation, perception, and cognition. For example, these findings document sensory discrimination of saturation by the infant visual system, and they advance understanding of the perceptual organization of infant behavior if only because the early development of object identification and recognition depends wholly on the preverbal infant’s encoding and retention of physical properties of objects, including their color [16,19,35,88–91]. Infants look longer at typically than at atypically colored objects, suggesting early object color knowledge [90]. Color also enters into infant cognition and memory, as infants represent color in visual short-term memory [92], color enhances children’s performance on memory tasks [93], and color is related to recall accuracy in problem solving [94]. Focused attention in infancy predicts standardized cognitive assessments at 2, 3, and 4 to 5 years of age [95], executive functioning at 3 [96] and 5 [97] years of age, as well as experimental tasks and cognitive and meta-cognitive abilities during childhood and adolescence [62]. Attention skills have a foundational role in infants’ information acquisition and learning [98]. Chromatic saturation may also exert a compelling influence on shaping the aesthetics of color preferences. The human visual system discriminates millions of colors [99], but humans appear to express reliable preferences for some colors over others. Color preference is often thought to reflect fluctuating fad, fancy, and framework. However, two key aspects of color preferences have been found to be relatively robust. One is that relatively more saturated colors are preferred over relatively less saturated colors of a fixed dominant wavelength independent of brightness variation, data collection method, developmental age, cultural diversity, and diachronic evaluation [31,32,100–103]. The second (and related) relatively robust color preference is for short (“blue”) and long (“red”) spectral wavelengths relative to mid- spectral (“green” and “yellow”) wavelengths. For example, mean looking times for infants (in paired-comparison and single-stimulus presentation conditions alike) and pleasantness ratings for adults plotted as a function of wavelength parallel one another

along the spectrum and converge to show that babies visually prefer and adults rate as more pleasing more naturally saturated colors at the visible spectral extremes—short (blue) and long (red) wavelengths [24,25,28,30,31,35,68,104–106]. Although not all research conforms, and not all cultures have been tested [107], much research since at least 1897 [108] has attested to systematic and reliable adult color preferences across many cultures for blue hues over yellow-green hues [109]. Critically, the infant maxima and minima in preferences are robust to presentation mode (e.g., computer monitor displays as here; Munsell chips in [2,105]; and monochromatic lights in [100]), and these spontaneous preference variations remain after stimuli are equated for brightness [31] and hold across infant gender [30,100]. Together, these consistencies strongly suggest some shared sensory and neurological bases of color preference. One possibility is that these preferences have a similar sensory component in fundamental neural dimensions that underlie early color encoding [110]. Another is that chromatic saturation is implicated in both. Discrimination of saturation may not perfectly predict perceived saturation [111,112], and arguments have been marshalled that purity alone does not account for color preferences [30], but the natural coding of saturation by the nervous system offers a possible basis for both regularities observed in color preferences. Stimuli matched in colorimetric purity still vary in saturation [113–115]. The saturation- discrimination function shows that the blue and red (short- and long- wavelength) ends of the visible spectrum appear naturally as more saturated than green and yellow (middle-wave) portion of the visible spectrum, which is psychologically closer to white. Infant looking times and adult hue pleasantness ratings both parallel the saturation-discrimination function. Evolutionary psychology argues that certain visual stimuli are preferred and that those stimuli possess features which the human visual system likely processes in an optimal fashion. It may be as well that such preferences are to some extent innate or early maturing. Indeed, the color vision of infants as young as 4 months of age aligns with the distribution of colors in natural scenes to which they are exposed [50]. Gibson [116] characterized some infant visual behavior as "captive"—a formulation of behavior that invokes an ecological interpretation. Indeed, many animals exhibit innate taxes to specific stimuli that suggest that specific stimulus-behavior reactions likely serve some vital functions early in life. The spectral transmittance of the oil droplet which covers the laughing-gull chick's eye corresponds to the spectral reflectance of the red spot on the adult laughing-gull's mandible. Behavioral color preferences of the laughing-gull's chick, as manifest in their pecking, follow the same spectral function [117]. Thus, sustenance is assured. Compatible with the present study, Saito [118] proposed a general three-layered structure of color preference based "feelings of 'pleasantness'" with preferred feelings rooted in brain (amygdalar and hypothalamic) sensitivity forming the nucleus or the innermost first layer, and preferences based on other (individual and environmental) factors composing the surrounding second and third layers. He further speculated that "The closer the preference is to the center of this structure, the more stable it is, and the more it is a preference that is common to all people" (p. 6). As Saito (p. 4) admonished, if such a regular "tendency toward certain [preferences is found], . . . then . . . studies should be carried out to investigate whether the cause of such common tendencies in human response is related to an innate cognition style," as we have done here.

Conclusions

Attention initiates a cascade for perception, cognition, memory, and action, and specific relations between specific features of the visual environment and their specific processing along the visual system may underlie specific aspects of visual behavior. Here we showed that infants (and adults) selectively look at chromatic stimuli in consonance with the relative saturation of those stimuli and infants' looking behavior (and adults' hedonic preference) is likely mediated by central nervous system activity which that saturation excites.

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References

1. Arterberry ME, Bornstein MH. Development in infancy (6e). New York, NY: Routledge; 2024. Available from: <https://www.routledge.com/Development-in-Infancy/Arterberry-Bornstein/p/book/9781032374390>.
2. Bornstein MH. Visual behavior of the young human infant: Relationships between chromatic and spatial perception and the activity of underlying brain mechanisms. *J Exp Child Psychol.* 1978; 26:174–192. [https://doi.org/10.1016/0022-0965\(78\)90118-2](https://doi.org/10.1016/0022-0965(78)90118-2) PMID: 670880
3. Haith MM. Rules that babies look by: The organization of newborn visual activity. New York: Psychology Press; 1980.
4. Gross CG. Genealogy of the “Grandmother Cell.” *The Neuroscientist.* 2002; 8:512–518. <https://doi.org/10.1177/107385802237175> PMID: 12374433
5. Hubel DH, Wiesel TN. Receptive fields, binocular interaction and functional architecture in the cat’s visual cortex. *J Physiol.* 1962; 160:106–154. <https://doi.org/10.1113/jphysiol.1962.sp006837> PMID: 14449617
6. Hubel DH. Evolution of ideas on the primary visual cortex, 1955–1978: A biased historical account. Nobel lecture, 8 December 1981.
7. Regan D. Evoked potentials in psychology, sensory physiology, and clinical medicine. Wiley-Interscience; 1972.
8. Wang X, Lu T, Snider R, Liang L. Sustained firing in auditory cortex evoked by preferred stimuli. *Nature.* 2005; 435:341–346. <https://doi.org/10.1038/nature03565> PMID: 15902257
9. Berlyne DE. The influence of the albedo and complexity of stimuli on visual fixation in the human infant. *Br J Psychol.* 1958; 49:315–318. <https://doi.org/10.1111/j.2044-8295.1958.tb00669.x> PMID: 13596573
10. Kessen W, Salapatek P, Haith M. The visual response of the human newborn to linear contour. *J Exp Child Psychol.* 1972; 13:9–20. [https://doi.org/10.1016/0022-0965\(72\)90003-3](https://doi.org/10.1016/0022-0965(72)90003-3) PMID: 5059962

11. Karmel BZ, Hoffman RF, Fegy MJ. Processing of contour information by human infants evidenced by pattern-dependent evoked potentials. *Child Dev.* 1974; 45:39–48. <https://doi.org/10.2307/1127747> PMID: 4820284
12. Wilcox T, Haslup JA, Boas DA. Dissociation of processing of featural and spatiotemporal information in the infant cortex. *Neuroimage.* 2010; 53(4):1256–1263. <https://doi.org/10.1016/j.neuroimage.2010.06.064> PMID: 20603218
13. Karmel BZ, Maisel EB. A neuronal activity model for infant visual attention. In: Cohen LB, Salapatek P, editors. *Infant perception: From sensation to cognition.* Academic Press; 1975.
14. Elliot AJ, Fairchild MD, Franklin A, editors. *Handbook of color psychology.* Cambridge University Press; 2015.
15. Wyszecki G, Stiles WS. *Color science: Concepts and methods, quantitative data and formulae.* Wiley; 1982.
16. Elliot AJ, Maier MA. Color psychology: Effects of perceiving color on psychological functioning in humans. *Annu Rev Psychol.* 2014; 66:95–120. <https://doi.org/10.1146/annurev-psych-010213-115035> PMID: 23808916
17. Gegenfurtner KR, Rieger J. Sensory and cognitive contributions of color to the recognition of natural scenes. *Curr Biol.* 2000; 10(13):805–808. [https://doi.org/10.1016/S0960-9822\(00\)00563-7](https://doi.org/10.1016/S0960-9822(00)00563-7) PMID: 10898985
18. Catherwood D. Exploring the seminal phase in infant memory for color and shape. *Infant Behav Dev.* 1994; 17:235–43.
19. Kaldy Z, Blaser E. How to compare apples and oranges: Infants' object identification tested with equally salient shape, luminance, and color changes. *Infancy.* 2009; 14(2):222–243. <https://doi.org/10.1080/15250000802707088> PMID: 20161281
20. Osorio D, Vorobyev M. Colour vision as an adaptation to frugivory in primates. *Proc R Soc B.* 1996; 263(1370):593–99. <https://doi.org/10.1098/rspb.1996.0089> PMID: 8677259
21. Zeaman D, Hanley P. Stimulus preferences as structural features. In: Tighe TG, Shepp BE, editors. *Perception, Cognition and Development: Interactional Analyses.* Lawrence Erlbaum Associates; 1983. p. 103–238.
22. Adams RJ, Courage ML. Human newborn color vision: measurement with chromatic stimuli varying in excitation purity. *J Exp Psychol.* 1998; 68:22–34. <https://doi.org/10.1006/jecp.1997.2407> PMID: 9473313
23. Teller DY, Peeples DR, Sekel M. Discrimination of chromatic from white light by two-month-old human infants. *Vision Res.* 1978; 18:41–8. [https://doi.org/10.1016/0042-6989\(78\)90075-5](https://doi.org/10.1016/0042-6989(78)90075-5) PMID: 307296
24. Franklin A, Pitchford N, Hart L, Davies IRL, Clausse S, Jennings S. Salience of primary and secondary colours in infancy. *Br J Dev Psychol.* 2008; 26:471–483.
25. Brown AM, Lindsey DT. Infant color vision and color preferences: A tribute to Davida Teller. *Vis Neurosci.* 2013; 30:243–250. <https://doi.org/10.1017/S0952523813000114> PMID: 23879986
26. Pereverzeva M, Teller DY. Infant color vision: influence of surround chromaticity on spontaneous looking preferences. *Vis Neurosci.* 2004; 21(3):389–95. <https://doi.org/10.1017/S0952523804213086> PMID: 15518219
27. Zemach IK, Teller DY. Infants' spontaneous hue preferences are not due solely to variations in perceived saturation. *J Vis.* 2004; 4:323. <https://doi.org/10.1167/4.8.323>
28. Adams RJ. An evaluation of color preference in early infancy. *Infant Behav Dev.* 1987; 10:143–150. [https://doi.org/10.1016/0163-6383\(87\)90029-4](https://doi.org/10.1016/0163-6383(87)90029-4)
29. Yang J, Kanazawa S, Yamaguchi MK. Perception of Munker–White illusion in 4–8-month-old infants. *Infant Behav Dev.* 2010; 33:589–95. <https://doi.org/10.1016/j.infbeh.2010.07.010> PMID: 20797793
30. Zemach I, Chang S, Teller DY. Infant color vision: Prediction of infants' spontaneous color preferences. *Vision Res.* 2007; 47(10):1368–1381. <https://doi.org/10.1016/j.visres.2006.09.024> PMID: 17118421
31. Teller DY, Civan A, Bronson-Castain K. Infants' spontaneous color preferences are not due to adult-like brightness variations. *Vis Neurosci.* 2004; 21(3):397–401. <https://doi.org/10.1017/S0952523804213360> PMID: 15518220
32. De Valois RL, Marrocco RT. Single cell analysis of saturation discrimination in the macaque. *Vis Res.* 1973; 13:701–711. [https://doi.org/10.1016/0042-6989\(73\)90033-3](https://doi.org/10.1016/0042-6989(73)90033-3) PMID: 4632656
33. Bartels A, Zeki S. The architecture of the colour centre in the human visual brain: new results and a review. *Eur J Neurosci.* 2000; 12:172–193. <https://doi.org/10.1046/j.1460-9568.2000.00905.x> PMID: 10651872

34. Lodge A, Armington JC, Barnet AB, Shanks BL, Newcomb CN. Newborn Infants' Electroretinograms and Evoked Electroencephalographic Responses to Orange and White Light. *Child Dev.* 1969; 40:267–293. <https://doi.org/10.1111/j.1467-8624.1969.tb06045.x> PMID: 5787706
35. Bornstein MH. Hue is an absolute code for young children. *Nature.* 1975; 256:309–310. <https://doi.org/10.1038/256309a0> PMID: 1143329
36. Brown AM, Teller DY. Chromatic opponency in 3-month-old human infants. *Vis Res.* 1989; 29(1):37–45. [https://doi.org/10.1016/0042-6989\(89\)90172-7](https://doi.org/10.1016/0042-6989(89)90172-7) PMID: 2773335
37. Knoblauch K, Vital-Durand F, Barbur JL. Variation of chromatic sensitivity across the life span. *Vis Res.* 2001; 41(1):23–36. [https://doi.org/10.1016/s0042-6989\(00\)00205-4](https://doi.org/10.1016/s0042-6989(00)00205-4) PMID: 11163613
38. Maule J, Skelton AE, Franklin A. The Development of Color Perception and Cognition. *Annu Rev Psychol.* 2023; 74:87–111. <https://doi.org/10.1146/annurev-psych-032720-040512> PMID: 35973406
39. Suttle CM, Banks MS, Graf EW. FPL and sweep VEP to tritan stimuli in young human infants. *Vis Res.* 2002; 42(26):2879–2891. [https://doi.org/10.1016/s0042-6989\(02\)00333-4](https://doi.org/10.1016/s0042-6989(02)00333-4) PMID: 12450512
40. Mundy P, Jarrold W. Infant joint attention, neural networks and social cognition. *Neural Networks.* 2010; 23(8–9):985–997. <https://doi.org/10.1016/j.neunet.2010.08.009> PMID: 20884172
41. Slaughter V, Suddendorf T. Participant loss due to “fussiness” in infant visual paradigms: A review of the last 20 years. *Infant Behav Dev.* 2007; 30(3):505–14. <https://doi.org/10.1016/j.infbeh.2006.12.006> PMID: 17683758
42. Oakes LM. Sample size, statistical power, and false conclusions in infant looking-time research. *Infancy.* 2017; 22:436–469. <https://doi.org/10.1111/infa.12186> PMID: 28966558
43. Stets M, Stahl D, Reid VM. A Meta-Analysis Investigating Factors Underlying Attrition Rates in Infant ERP Studies. *Dev Neuropsychol.* 2012; 37(3):226–252. <https://doi.org/10.1080/87565641.2012.654867> PMID: 22545660
44. Crognale MA. Development, maturation, and aging of chromatic visual pathways: VEP results. *J Vis.* 2002; 2(6):2–2. <https://doi.org/10.1167/2.6.2> PMID: 12678643
45. Rogers M, Franklin A, Knoblauch K. A novel method to investigate how dimensions interact to inform perceptual salience in infancy. *Infancy.* 2018; 23(6):833–856.
46. Bieber ML, Volbrecht VJ, Werner JS. Spectral efficiency measured by heterochromatic flicker photometry is similar in human infants and adults. *Vis Res.* 1995; 35:1385–1392. [https://doi.org/10.1016/0042-6989\(95\)98718-o](https://doi.org/10.1016/0042-6989(95)98718-o) PMID: 7645267
47. Rabin J, Switkes E, Crognale M, Schneck ME, Adams AJ. Visual evoked potentials in three-dimensional color space: Correlates of spatio-chromatic processing. *Vis Res.* 1994; 34:2657–2671. [https://doi.org/10.1016/0042-6989\(94\)90222-4](https://doi.org/10.1016/0042-6989(94)90222-4) PMID: 7975303
48. Porciatti V, Sartucci F. Normative data for onset VEPs to red-green and blue-yellow chromatic contrast. *Clin Neurophysiol.* 1999; 110:772–781. [https://doi.org/10.1016/s1388-2457\(99\)00007-3](https://doi.org/10.1016/s1388-2457(99)00007-3) PMID: 10378751
49. Ruff HA. The function of shifting fixations in the visual perception of infants. *Child Dev.* 1975;857–865. PMID: 1201665
50. Skelton AE, Franklin A, Bosten JM. Colour vision is aligned with natural scene statistics at 4 months of age. *Dev Sci.* 2022;e13402.
51. Bornstein MH, Mash C, Arterberry ME. Perception of object-context relations: Eye-movement analyses in infants and adults. *Developmental Psychology.* 2011; 47:364–375. <https://doi.org/10.1037/a0021059> PMID: 21244146
52. Bornstein MH, Mash C, Arterberry ME. Young infants' eye movements over "natural" scenes and "experimental" scenes. *Infant Behavior and Development.* 2011; 34:206–210. <https://doi.org/10.1016/j.infbeh.2010.12.010> PMID: 21195480
53. Cohen J. *Statistical power analysis for the behavioral sciences.* 2nd ed. Hillsdale, NJ: Psychology Press; 1988.
54. Crognale MA, Switkes E, Rabin J, Schneck ME, Haegerstrom-Portnoy G, Adams AJ. Application of the spatiochromatic visual evoked potential to detection of congenital and acquired color-vision deficiencies. *Journal of the Optical Society of America A.* 1993; 10:1818–1825. <https://doi.org/10.1364/josaa.10.001818> PMID: 8350164
55. Mognon A, Jovicich J, Bruzzone L, Buiatti M. ADJUST: An Automatic EEG artifact Detector based on the Joint Use of Spatial and Temporal features. *Psychophysiology.* 2011; 48:229–240. <https://doi.org/10.1111/j.1469-8986.2010.01061.x> PMID: 20636297
56. Urigüen JA, Garcia-Zapirain B. EEG artifact removal—state-of-the-art and guidelines. *Journal of Neural Engineering.* 2015; 12(3):031001. <https://doi.org/10.1088/1741-2560/12/3/031001> PMID: 25834104

57. Conway BR. Color signals through dorsal and ventral visual pathways. *Visual Neuroscience*. 2014; 31:197–209. <https://doi.org/10.1017/S0952523813000382> PMID: 24103417
58. Makeig S, Debener S, Onton J, Delorme A. Mining event-related brain dynamics. *Trends in Cognitive Sciences*. 2004; 8(5):204–210. <https://doi.org/10.1016/j.tics.2004.03.008> PMID: 15120678
59. Makeig S. Auditory event-related dynamics of the EEG spectrum and effects of exposure to tones. *Electroencephalography and Clinical Neurophysiology*. 1993; 86:283–293. [https://doi.org/10.1016/0013-4694\(93\)90110-h](https://doi.org/10.1016/0013-4694(93)90110-h) PMID: 7682932
60. Jurgiel J, Miyakoshi M, Dillon A, Piacentini J, Makeig S, Loo SK. Inhibitory control in children with tic disorder: aberrant fronto-parietal network activity and connectivity. *Brain Communications*. 2021; 3(2):fcab067. <https://doi.org/10.1093/braincomms/fcab067> PMID: 33977267
61. Delorme A, Makeig S. EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*. 2004; 134:9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009> PMID: 15102499
62. Bell MA, Cuevas K. Using EEG to study cognitive development: Issues and practices. *Journal of Cognition and Development*. 2012; 13(3):281–294. <https://doi.org/10.1080/15248372.2012.691143> PMID: 23144592
63. Xie W, Mallin BM, Richards JE. Development of infant sustained attention and its relation to EEG oscillations: an EEG and cortical source analysis study. *Developmental Science*. 2017; 21:e12562. <https://doi.org/10.1111/desc.12562> PMID: 28382759
64. Kisley MA, Cornwell ZM. Gamma and beta neural activity evoked during a sensory gating paradigm: effects of auditory, somatosensory and cross-modal stimulation. *Clinical Neurophysiology*. 2006; 117(11):2549–2563. <https://doi.org/10.1016/j.clinph.2006.08.003> PMID: 17008125
65. Niedermeyer E, da Silva FL. *Electroencephalography: Basic Principles, Clinical Applications, and Related Fields*. Lippincott Williams & Wilkins; 2004.
66. Arterberry ME, Kellman PJ. *Development of perception in infancy: The cradle of knowledge revisited*. New York, NY: Oxford University Press; 2016.
67. Fagan JF. Infant color perception. *Science*. 1974; 183:973–975. <https://doi.org/10.1126/science.183.4128.973> PMID: 4810849
68. Franklin A, Bevis L, Ling Y, Hurlbert A. Biological components of colour preference in infancy. *Developmental Science*. 2010; 13(2):346–354. <https://doi.org/10.1111/j.1467-7687.2009.00884.x> PMID: 20136931
69. Niedzwiecka A, Ramotowska S, Tomalski P. Mutual gaze during early mother-infant interactions promotes attention control development. *Child Development*. 2018; 89:2230. <https://doi.org/10.1111/cdev.12830> PMID: 28510324
70. Yu C, Smith LB. The social origins of sustained attention in one-year-old human infants. *Current Biology*. 2016; 26(9):1235–1240. <https://doi.org/10.1016/j.cub.2016.03.026> PMID: 27133869
71. Buiatti M, Di Giorgio E, Piazza M, et al. Cortical route for facelike pattern processing in human newborns. *Proceedings of the National Academy of Sciences*. 2019; 116(10):4625–4630. <https://doi.org/10.1073/pnas.1812419116> PMID: 30755519
72. Clifford A, Franklin A, Davies IRL, Holmes A. Electrophysiological markers of categorical perception of color in 7-month old infants. *Brain and Cognition*. 2009; 71(2):165–172. <https://doi.org/10.1016/j.bandc.2009.05.002> PMID: 19501444
73. Yang J, Kanazawa S, Yamaguchi MK, Kuriki I. Cortical response to categorical color perception in infants investigated by near-infrared spectroscopy. *Proceedings of the National Academy of Sciences*. 2016; 113(9):2370–2375. <https://doi.org/10.1073/pnas.1512044113> PMID: 26858441
74. Reynolds GD. Infant visual attention and object recognition. *Behavioural Brain Research*. 2015; 285:34–43. <https://doi.org/10.1016/j.bbr.2015.01.015> PMID: 25596333
75. Duncan GJ, Engel M, Claessens A, Dowsett CJ. Replication and robustness in developmental research. *Developmental Psychology*. 2014; 50(11):2417–2425. <https://doi.org/10.1037/a0037996> PMID: 25243330
76. Peterson RA, Merunka DW. Convenience samples of college students and research reproducibility. *J Business Res*. 2014; 67:1035–1041.
77. Deco G, Rolls ET. A Neurodynamical cortical model of visual attention and invariant object recognition. *Vision Res*. 2004; 44:621–642. <https://doi.org/10.1016/j.visres.2003.09.037> PMID: 14693189
78. Ecker A, Berens P, Tolias A, Bethge M. The effect of noise correlations in populations of diversely tuned neurons. *Nat Preced [Internet]*. 2011 [cited 2024 Apr 8]. Available from: <https://doi.org/10.1038/npre.2011.6170.1> <https://doi.org/10.1523/JNEUROSCI.2539-11.2011> PMID: 21976512

79. Singer W. Distributed processing and temporal codes in neuronal networks. *Cogn Neurodyn*. 2009; 3:189–196. <https://doi.org/10.1007/s11571-009-9087-z> PMID: 19562517
80. Zhang Y, Meyers EM, Bichot NP, Serre T, Poggio TA, Desimone R. Object decoding with attention in inferior temporal cortex. *Proc Natl Acad Sci*. 2011; 108:8850–8855. <https://doi.org/10.1073/pnas.1100999108> PMID: 21555594
81. Schiller PH, Chorover SL. Metacontrast: Its relation to evoked potentials. *Science*. 1966; 153:1398–1400. <https://doi.org/10.1126/science.153.3742.1398> PMID: 5917773
82. Posner MI, Neill CM. Illuminating the neural circuits underlying orienting of attention. *Vision*. 2019; 3. <https://doi.org/10.3390/vision3010004> PMID: 31735805
83. Naatanen R. *Attention and brain function*. New York: Psychology Press; 2018.
84. Uttal WR. Evoked brain potentials: Signs or codes? *Perspect Biol Med*. 1967; 10:627–639. <https://doi.org/10.1353/pbm.1967.0010> PMID: 6034905
85. Stevens SS. Neural events and the psychophysical law. *Science*. 1970; 170:1043–1050. <https://doi.org/10.1126/science.170.3962.1043> PMID: 5475633
86. Uttal WR. Do compound evoked potentials reflect psychological codes? *Psychol Bull*. 1965; 64:377–392. <https://doi.org/10.1037/h0022682> PMID: 5323021
87. Baldwin JM. *Mental development in the child and the race*. MacMillan; 1895.
88. Jameson K. Culture and cognition: What is universal about the representation of color experience? *J Cogn Culture*. 2005; 5:293–347. <https://doi.org/10.1163/156853705774648527>
89. Joh AS, Spivey LA. Colorful success: Preschoolers' use of perceptual color cues to solve a spatial reasoning problem. *J Exp Child Psychol*. 2012; 113:523–534. <https://doi.org/10.1016/j.jecp.2012.06.012> PMID: 22878085
90. Kimura A, Wada Y, Yang J, Otsuka Y, Dan I, et al. Infants' recognition of objects using canonical color. *J Exp Child Psychol*. 2010; 105(3):256–63. <https://doi.org/10.1016/j.jecp.2009.11.002> PMID: 20015514
91. Wurm LH, Legge GE, Isenberg LM, Luebker A. Color improves object recognition in normal and low vision. *J Exp Psychol: Hum Percept Perform*. 1993; 19:899–911. doi: <https://doi.org/10.1017/S0952523808080826>. <https://doi.org/10.1037//0096-1523.19.4.899> PMID: 8409865
92. Oakes LM, Ross-Sheehy S, Luck SJ. Rapid development of feature binding in visual short-term memory. *Psychol Sci*. 2006; 17:781–7. <https://doi.org/10.1111/j.1467-9280.2006.01782.x> PMID: 16984295
93. Daehler M, Bukatko D, Benson K, Myers N. The effects of size and color cues on the delayed response of very young children. *Bull Psychonomic Soc*. 1976; 7:65–8.
94. Odom RD. Effects of perceptual salience on the recall of relevant and incidental dimensional values: a developmental study. *J Exp Psychol*. 1972; 92:285–91. <https://doi.org/10.1037/h0032092> PMID: 5058949
95. Lawson KR, Ruff HA. Early focused attention predicts outcome for children born prematurely. *J Dev Behav Pediatr*. 2004; 25(6):399–406. <https://doi.org/10.1097/00004703-200412000-00003> PMID: 15613988
96. Johansson M, Marciszko C, Brocki K, Bohlin G. Individual differences in early executive functions: A longitudinal study from 12 to 36 months. *Infant Child Dev*. 2016; 25:533–549.
97. Brandes-Aitken A, Braren S, Swingler M, Voegtline K, Blair C. Sustained attention in infancy: A foundation for the development of multiple aspects of self-regulation for children in poverty. *J Exp Child Psychol*. 2019; 184:192–209. <https://doi.org/10.1016/j.jecp.2019.04.006> PMID: 31039447
98. Abelkop BS, Frick JE. Cross-task stability in infant attention: New perspectives using the still-face procedure. *Infancy*. 2003; 4(4):567–588.
99. Linhares JM, Nascimento SMC, Foster DH, Amano K. Chromatic diversity of natural scenes. *Perception*. 2004; 33(1):65.
100. Bornstein MH. Qualities of color vision in infancy. *J Exp Child Psychol*. 1975; 19(3):401–419. [https://doi.org/10.1016/0022-0965\(75\)90070-3](https://doi.org/10.1016/0022-0965(75)90070-3) PMID: 1176886
101. Carrigoz N, Yener C, Guvenc D. Effects of hue, saturation, and brightness: Part 2: Attention. *Color Res Appl*. 2004; 29:20–28.
102. Fushikida W, Schloss K, Yokosawa K, Palmer S. Cross-cultural differences in color preference: Japan vs. the USA. *J Vision*. 2009; 9:336. <https://doi.org/10.1167/9.8.336>
103. Garth TR, Porter EP. The color preferences of 1032 young children. *Am J Psychol*. 1934; 46:448–451.
104. Hurlbert A, Ling Y. *Colour design* (2nd ed.). Elsevier; 2017.
105. Skelton AE, Franklin A. Infants look longer at colours that adults like when colours are highly saturated. *Psychon Bull Rev*. 2020; 27(1):78–85. <https://doi.org/10.3758/s13423-019-01688-5> PMID: 31848908

106. Taylor C, Schloss K, Palmer SE, Franklin A. Color preferences in infants and adults are different. *Psychon Bull Rev.* 2013; 20(5):916–922. <https://doi.org/10.3758/s13423-013-0411-6> PMID: 23435629
107. Taylor C, Clifford A, Franklin A. Color preferences are not universal. *J Exp Psychol: Gen.* 2013; 142(4):1015–1027. <https://doi.org/10.1037/a0030273> PMID: 23148465
108. Jastrow J. Popular esthetics of colour. *Pop Sci Monthly.* 1897; 50:361–368.
109. Taylor C, Franklin A. The relationship between color-object associations and color preference: further investigation of ecological valence theory. *Psychon Bull Rev.* 2012; 19(2):190–197. <https://doi.org/10.3758/s13423-012-0222-1> PMID: 22302645
110. Hurlbert A, Ling Y. Biological components of sex differences in color preference. *Curr Biol.* 2007; 17:R623–R625. <https://doi.org/10.1016/j.cub.2007.06.022> PMID: 17714645
111. Witzel C, Franklin A. Do focal colors look particularly “colorful”? *J Opt Soc Am A.* 2014; 31:A365–A374. <https://doi.org/10.1364/JOSAA.31.00A365> PMID: 24695195
112. Witzel C, Maule J, Franklin A. Red, yellow, green, and blue are not particularly colorful. *J Vision.* 2019; 19:1–26. <https://doi.org/10.1167/19.14.27> PMID: 31887224
113. Indow T. Scaling of saturation and hue in the nonspectral region. *Percept Psychophys.* 1978; 24:11–20. <https://doi.org/10.3758/bf03202969> PMID: 693236
114. Indow T, Stevens SS. Scaling of saturation and hue. *Percept Psychophys.* 1966; 1:253–271.
115. Kraft JM, Werner JS. Aging and the saturation of colors. 2. Scaling of color appearance. *J Opt Soc Am A.* 1999; 16(2):231–235. <https://doi.org/10.1364/josaa.16.000231> PMID: 9949719
116. Gibson EJ. *Principles of perceptual learning and development.* Appleton-Century-Crofts. 1969.
117. Hailman JP. Spectral Reflectance of Gull’s Bill: Physiological and evolutionary implications for animal communication. *Science.* 1968 Oct 4; 162(3849):139–40. <https://doi.org/10.1126/science.162.3849.139> PMID: 5675183
118. Saito M. Comparative (cross-cultural) color preference and its structure. *Encyclopedia of Color Science and Technology.* 2015:1–7.