Colour vision is aligned with natural scene statistics at 4-months of age

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Research Highlights

1. We find infants' hue sensitivity is aligned with the distribution of colours in the natural world, as it is in adults

2. At just 4-months, infants' visual system is tailored to extract and represent the statistical regularities of the natural world

3. This points to the fundamental drive for the human brain to attempt to optimally encode by representing statistical regularities even at a young age.

Abstract

Visual perception in adult humans is thought to be optimised to represent the statistical regularities of natural scenes (e.g. Parraga et al., 2000; Simoncelli, 2003). In infancy and early childhood, visual input is required to drive visual development (Berardi et al., 2000; Blakemore & Cooper, 1970; Jandó et al., 2012; Knudsen, 2004), but whether or not scene statistics are extracted and represented colour is currently unknown. In adults, visual sensitivity to different hues shows an asymmetry, which relates to the statistical regularity of colour in the natural world (Bosten et al., 2015). We measured colour discrimination in infants to investigate whether or not the visual system can in very early life represent scene statistics. Our results reveal the earliest association between vision and natural scene statistics that has yet been found: even as young as four months of age, colour vision is aligned with the distributions of colours in natural scenes.

Introduction

Human perception is optimised in many ways to extract information from the environments that we find ourselves in. Process to calibrate perception to the contents of natural environments occur over different time scales, both over evolutionary history (Changizi et al., 2006; Osorio & Vorobyev, 1996; Regan et al., 2001), and within the lifetime of the individual (Schefrin & Werner, 1990). Some calibrative processes undoubtedly occur during infancy: for example, face (Kelly et al., 2007), speech (Kuhl et al., 2006) and music (Trehub & Hannon, 2006) perception are refined during infancy to show biases for the stimuli

encountered in infants' individual environments. In mature perceptual systems, there is tuning to the statistical regularities of visual scenes: visual channels are thought to be tuned to extract the regularities of spatial frequency (Hansen & Hess, 2006; Knill et al., 1990; Tadmor & Tolhurst, 1994), orientation (Hansen & Essock, 2004), and attributes of colour (Long et al., 2006) in natural scenes. Relatively little is known about the developmental trajectory of visual representations of the statistical regularities of natural scenes. Ellemberg et al., 2012 have found that representations of the spatial frequency structure of natural scenes are present in 10 year-olds but undeveloped in 6- and 8- year-olds. The only existing work on infants finds that at 9-10 months, but not 3-6 months, infants' looking preference and their Event Related Potential components (P100 and P400) appear to distinguish between natural textures and one type of synthetic manipulation of those textures (Balas & Conlin, 2014; Balas & Woods, 2014). One interpretation of this work is that infants tune to natural texture statistics by 9-months. However, the lack of a consistent effect of another type of natural texture manipulation (contrast polarity), and the potential role of other low-level visual differences independent of naturalness suggests that further work is needed to clarify the nature of these effects.

Colour vision is a good example of a perceptual system that is optimised at several different levels to extract information from natural scenes. Human colour vision relies on three classes of retinal receptors, long- (L), medium- (M) and short- (S) wavelength sensitive cones. The particular sensitivities of the human cones are thought to have evolved to optimally represent colour information relevant to the diets or skin colours of our primate ancestors (Changizi et al., 2006; Osorio & Vorobyev, 1996; Regan et al., 2001). Postreceptorally, colour is processed predominantly in two chromatically opponent channels, which themselves seem to be optimised to minimise the redundancy of information acquired about natural scenes (Ruderman et al., 1998). There has been recent interest in a third level of alignment with natural scene statistics: colour discrimination is poorest along a blue-yellow colour axis (Honjyo & Nonaka, 1970; Krauskopf & Karl, 1992; Pearce et al., 2014; Álvaro et al., 2017) which is intermediate between the colour axes along which the two chromatically opponent retinogeniculate colour mechanisms are tuned (the vertical and horizontal axes in Figure 1a). It is the blue-yellow axis that contains most variance in natural scenes (Bosten et al., 2015;

Webster & Mollon, 1997). See figure 1b & c for an example of the variation found in natural scenes.

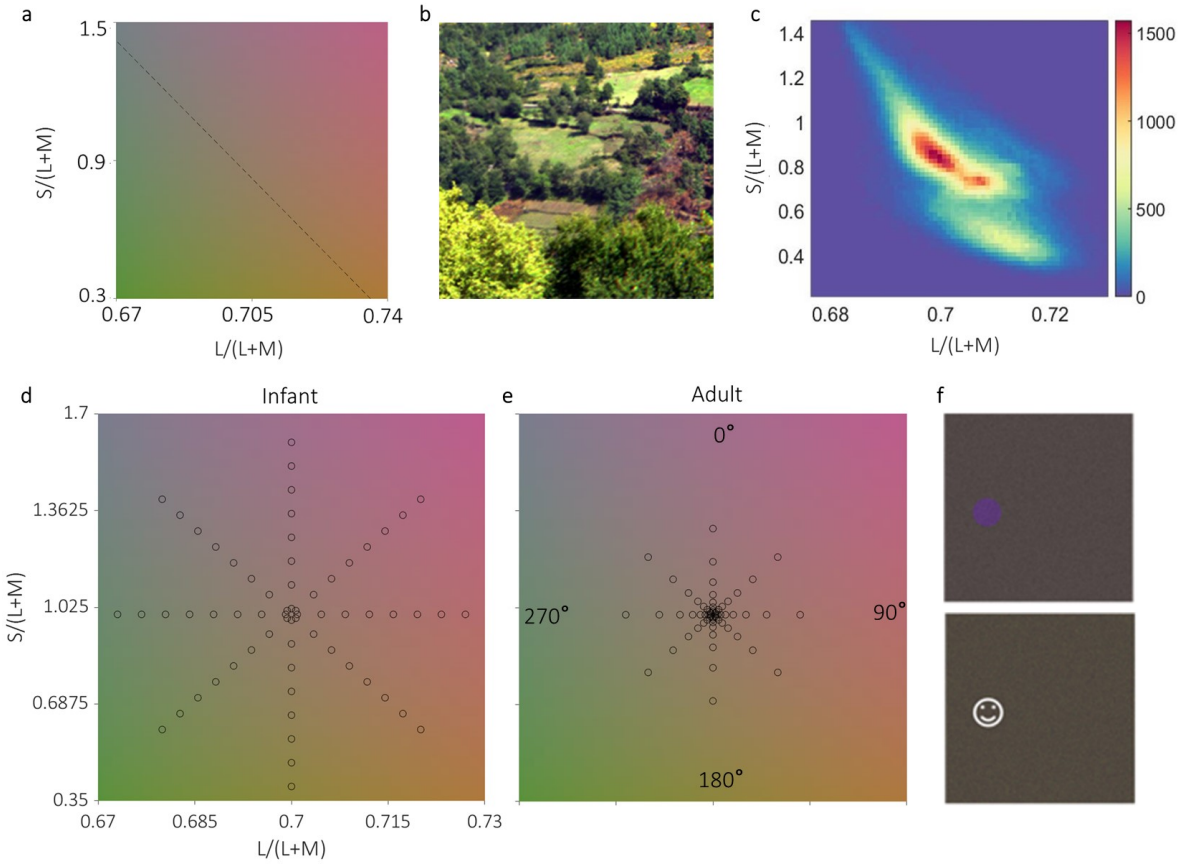

Figure 1 a) Our version of the MacLeod Boynton chromaticity diagram (Macleod & Boynton, 1979), using the Stockman, MacLeod and Johnson cone fundamentals (Stockman et al., 1993) representing the signals carried by the chromatically opponent retinogeniculate colour mechanisms, L/(L+M) and S/(L+M). The blue-yellow axis is intermediate to the cardinal axes, indicated by the dashed line. b) An example of a hyperspectrally imaged natural scene (Nascimento et al., 2002), and c) A histogram showing the distribution of chromaticities of the natural scene in (b) plotted in the MacLeod Boynton chromaticity diagram. The largest variance in chromaticities is along the negative diagonal. d) Infant and e) adult target chromaticities along the 8 individual axes presented in the MacLeod Boynton chromaticity diagram. The hue angles of the cardinal axes are indicated in (e). Towards the centre of the figure, colours are desaturated, increasing in saturation radially along the axes. f) An

example target (upper panel) displayed within 6.9° of the participant's current fixation point. If the target was subsequently fixated for a minimum of 160ms, it was replaced by a reward smiling face (lower), a sound was played, and a hit was recorded.

In the present study we investigated the development of representations of the distribution of colours in natural scenes by measuring colour discrimination in infants using a novel task (see methods). We chose infants aged 4-6 months, because it is thought that the S-cone reliant colour-opponent mechanism develops relatively late at 2-3 months (Bornstein, 1975; Brown & Teller, 1989; Knoblauch et al., 2001; Suttle et al., 2002), and it is only after this point that infants have trichromatic colour vision. For 60 infants and 19 adults we measured eye movements to chromatic targets varying across 8 levels of saturation in 8 hue directions (Figure 1(d) and (e)).

For each hue, when rate of detection is plotted against target saturation, a colour discrimination threshold can be defined at a certain performance criterion (alpha **K**) along the resulting psychometric function, which was fit using a local linear 'model-free' algorithm (Zychaluk & Foster, 2009) (Figure 2a). Through thresholds for each of the eight colours we fit colour discrimination ellipses, where the distance from the centre of the ellipse in each hue direction is the discrimination threshold in a version of the MacLeod-Boynton chromaticity diagram (Macleod & Boynton, 1979) based on the Stockman, MacLeod and Johnson cone fundamentals (Stockman et al., 1993). We chose the MacLeod-Boynton diagram as a colour metric because it represents along its cardinal axes activity in the two dominant post-receptoral retinogeniculate colour mechanisms (Webster & Mollon, 1991). If colour discrimination is limited by noise in either of these cardinal colour mechanisms, the resulting discrimination ellipse would be oriented either horizontally or vertically. An off-axis bias in colour discrimination, such as a blue-yellow bias, means that discrimination must be determined by noise in non-cardinal colour mechanisms(Bosten et al., 2015).

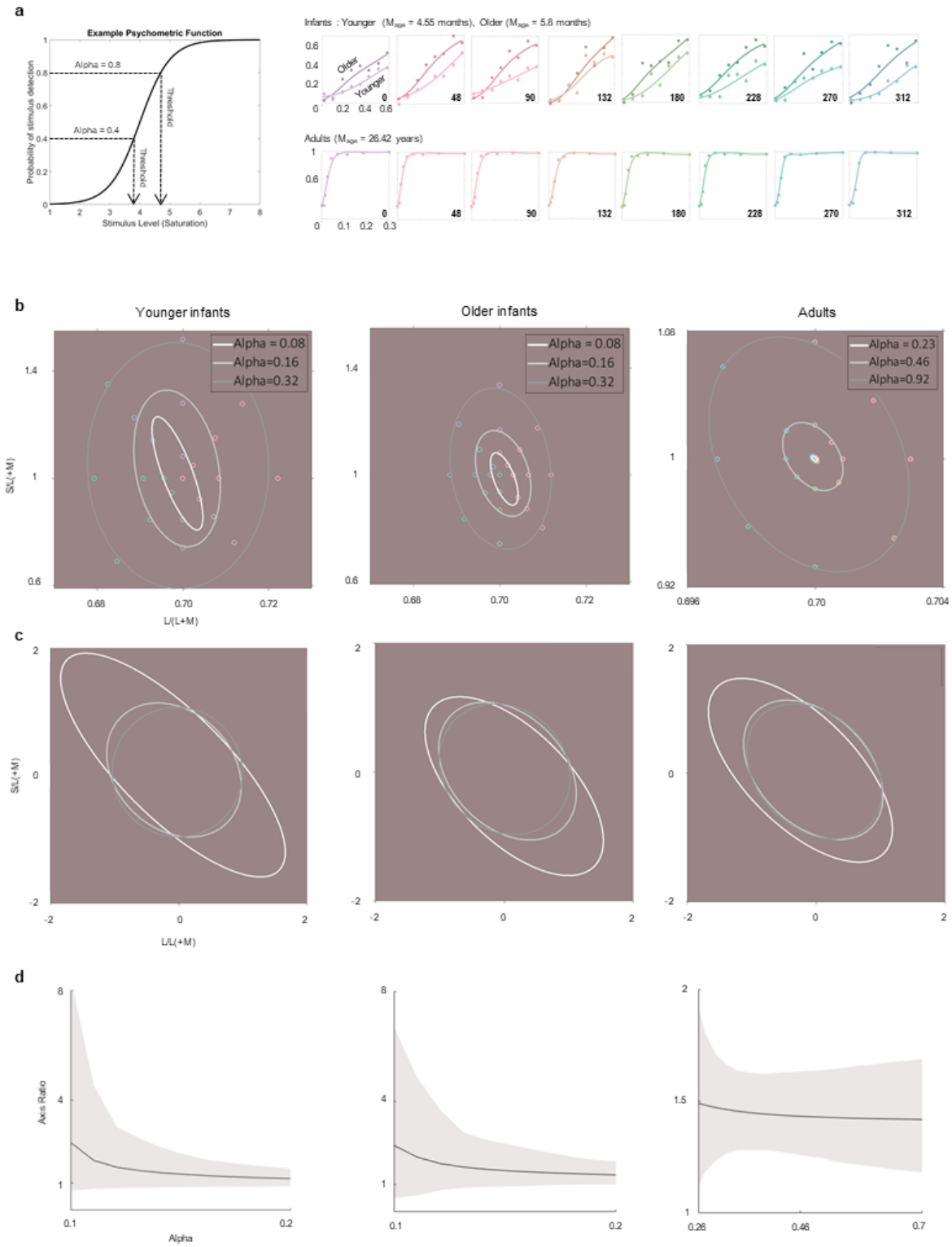

Figure 2. (a) Example psychometric function, and psychometric functions for infants and adults for the 8 colour axes tested, all showing the probability of target detection as a

function of stimulus intensity (saturation). The example psychometric function demonstrates how different alpha criteria result in different threshold measurements along the same psychometric function. For the infant and adult data, each individual graph shows group average psychometric functions for a specific hue axis, which is a radial line in the MacLeod Boynton chromaticity diagram (Figure 1 (d) and (e)), noted by the angle of the hue axis in the bottom left of each figure. (b) For each of a range of alphas, 8 colour discrimination thresholds were extracted (one for each hue), and then an ellipse was fit to each set of 8 thresholds plotted in the MacLeod-Boynton chromaticity diagram. Separate discrimination ellipses were plotted for the 3 groups: two infant groups (younger and older than the infant sample median age) and adults. The figures show ellipses for 3 example alphas. (c) In order to quantify the extent of the blue-yellow bias of each colour discrimination ellipse, an 'axis ratio' was calculated. This is the ratio of the length of the negative diagonal of the ellipse to the length of the positive diagonal, when the ellipse is plotted in a normalised version of the MacLeod Boynton chromaticity diagram, scaled to equate variances in the x and y directions. In both 3(b) and 3(c), ellipses fitted from thresholds extracted at lower alphas are shown lighter in colour, and those from higher alphas are shown darker in colour. (d) Axis ratios are plotted as a function of alpha with bootstrapped 95% confidence intervals for each of the 3 groups.

Results

For our primary analysis we fit discrimination ellipses for three groups, two infant samples split above and below the median age (younger infants: N=30, M_{age}= 4.55 months, SD=0.27, and older infants: N=30, M_{age}= 5.82 months, SD=0.51), and adults. From the fitted ellipses we quantified the asymmetry in colour discrimination by taking an *axis ratio*. This is the ratio of the length of the ellipse along the negative diagonal to the length along the positive diagonal, in a normalised colour space in which the variances along the x and y axes are equated (Bosten et al., 2015). If the axis ratio is greater than 1, then colour discrimination is relatively poor in a blue-yellow colour direction, aligned with the axis of maximum variability of the colours in natural scenes.

For each of the three age groups and for each hue, we achieved very clear group psychometric functions (Figure 2a). One obvious difference between the groups is in the positions of asymptotes of the psychometric functions. For adults, performance quickly asymptotes close to 100% detection. For younger infants the asymptotes are at about 30-40% and for older infants they are at about 50-60%. This large difference means that any particular performance criterion (alpha) would fall on very different parts of the psychometric function for the different groups. This prompted us to extract thresholds at different alphas, and to fit different discrimination ellipses to each set of thresholds at different alphas (Jones et al., 2015; Trehub et al., 1980). Figure 2(d) shows the results of this analysis: for all three age groups, axis ratio is large at low alphas and then decreases as a function of alpha.

The large axis ratios show that for all three age groups colour discrimination is selectively poor in the blue-yellow colour direction, as would be expected if colour vision is aligned with the statistics of natural scenes. Figure 2(d) shows axis ratio as a function of threshold alpha. For infants, axis ratios are large at low alphas (1.89 for younger infants at alpha=0.08; 2.36 for older infants at alpha=0.08), but as alpha increases they tend towards 1. Adults show the same decrease in axis ratio with alpha as infants, but maintain an axis ratio larger than one at all alphas. We conducted similar analyses at the level of individual participants for all infants as one group and all adults as another group (for details see SI *Individual participant analysis*). Here, we found that there is a significant effect of alpha on axis ratio for both infants (using a Skillings-Mack test (Chatfield & Mander, 2009), a non-parametric Friedman type statistic which can be used when there are random data missing as is the case in the current study where the number and type of trials completed by each infant varies, T(18)=102.57, p=<.001) and adults (Skillings-Mack, T(18)=59.79, p=<0.001).

Discussion

The strong dependence of axis ratio on alpha that we observe for infants implies that the psychometric function describing performance as a function of saturation has both a higher mean and steeper slope for blue and yellow targets than for red and green targets. This does not fit the usual expectation, where the noise that limits detection tends to increase the mean (determined by signal:noise ratio) and *reduce* the slope(Arazi et al., 2017; Legge et al.,

1987). One possible explanation for the dependency of axis ratio on alpha is that non-visual processes contribute differentially to visual performance at different alphas. Specifically, it is generally assumed that the slope of the psychometric function is determined by visual signals and sensory noise, while attentional 'lapses' affect only its upper asymptote(Swanson & Birch, 1992; Wichmann & Hill, 2001). However, especially for infants, we propose that this is an unsafe assumption. Instead, there may be an interaction between visual and non-visual contributions to psychophysical decisions so that both the positively sloping region and the upper asymptote are influenced by non-visual factors such as attention and motivation. Importantly, the non-visual factors may have their greatest influence at high signal strengths. In the current study, an infant may be more motivated (e.g. by attentional salience) to make an eye movement towards a coloured stimulus with greater saturation than one with lower saturation. Thus, the lower reaches of the psychometric function at lower stimulus strengths may be more singularly determined by visual sensitivity than the upper reaches, where the presence or absence of attention and motivation may have a relatively greater influence on the probability of detection. This may explain why axis ratio is largest at low stimulus strengths, where visual sensitivity (tuned to natural scene statistics) is having its purest influence on detection performance.

Our results show that like adults, infants as young as 4 months of age show a bias in colour discrimination in a direction predicted from the distributions of colours in natural scenes. Though there is a significant improvement in colour discrimination with age (see SI *Development of Colour Sensitivity*), the discrimination ellipses show no evidence for development in the degree of bias (Figure 2b). Our results are compatible with two schemes: either the blue-yellow bias in colour discrimination is innate, perhaps calibrated to natural scene statistics neurogenetically, or it develops very early by calibration to the statistics of natural scenes, between the ages of 2-3 months (when trichromacy first develops) and 4 months (the age of the youngest infants in our sample).

Our finding that bias in colour discrimination is a function of threshold criterion (alpha) for all three age groups has important implications for psychophysics. The choice of alpha in psychophysical analysis is arbitrary, but there are conventions that are often applied. For example, alpha is often defined half way between the guess rate and the asymptote of the psychometric function (Watson & Pelli, 1983). Our finding implies that the choice of alpha

may have a substantial impact on the conclusions of psychophysical studies, and that actually a lower alpha than is typically chosen may better isolate the sensory processes (at least in infants) that psychophysicists are interested in.

The relationship between axis ratio and alpha that we have observed would not have been apparent had we not measured full psychometric functions. Typically, in infant studies, discrimination performance is measured using a variant of the 'preferential looking' technique, where gaze durations in the presence and absence of stimulus targets are compared statistically. This often results in one number to decide whether a given target is above or below threshold (seen versus not seen). Discrimination thresholds measured using preferential looking for infants of different ages (Knoblauch et al., 2001) but owing to the time-consuming nature of preferential looking, are available for only a limited number of colour axes (see SI *Development of Colour Sensitivity*). Our method of using eye movements (see also (Jones et al., 2014)) is more efficient, allowing measurement of performance at a greater number of points and full psychometric functions, as is good practice for psychophysics in adults. Our efficient measure enables infants' colour discrimination ellipses to be revealed for the first time.

Our results provide the first evidence that post-receptoral vision is aligned to natural scene statistics in early infancy. A major finding in colour vision science is that the L-, M- and S-cones are optimally spectrally positioned to extract colour information from the natural world. If the alignment that we see in infants is achieved by neurogenetic calibration, then there must be genetic optimisation post-receptorally as well. If the aligning process is ontogenetic, then the infant brain must be able to extract and calibrate to statistical information within a matter of months. This revises previous research that has demonstrated statistical optimisation of perception only later in infancy for social or linguistic stimuli. To distinguish these theoretically important accounts, future research will need to apply our methods to genetically similar infants living in radically different visual environments.

Methods

Participants

Sixty four infants (age range= 4.01-6.80 months, mean age= 5.18 months, SD= 0.76 months) took part in the experiment. Four infants were excluded from the study due to fussiness preventing them from proceeding past the initial calibration phase. All participants were born at 40 +/- 2 weeks, met a minimum birth weight of 2500g, had no known visual deficits, and no history of epilepsy, and reported no family history of colour vision deficiency.

Nineteen adult participants were recruited by experimenters (13 female, mean age= 26.42 years). Participants had normal colour vision as assessed by the Ishihara pseudoisochromatic plates (38 plate edition, (Ishihara, 1936)) and the Lanthony tritan album (Lanthony, 1987).

Stimuli and apparatus

Target stimuli were coloured circles that subtended a visual angle of 6.9° on a surround metameric with equal energy white that subtended a visual angle of 41°. The chromatic difference between target and surround was isoluminant for the standard observer (Stockman et al., 1993). In order to prevent individual participants detecting targets via residual luminance differences with the surround, low-pass luminance noise was added over the whole display. The mean luminance of both target and surround was 28 cdm^{-2}, and luminance noise was linearly distributed to range between ±10% of the mean luminance. The chromaticities of the target stimuli varied in saturation along 8 axes within a version the MacLeod-Boynton (1979) chromaticity diagram (Macleod & Boynton, 1979) based on the Stockman, MacLeod and Johnson (1993) cone fundamentals (Stockman et al., 1993). The centre of our stimulus space was a point metameric with equal energy white (the background chromaticity), and there were 8 points per axis (64 points in total) increasing in saturation away from the centre. Four of the axes were the cardinal directions in the MacLeod-Boynton chromaticity diagram; two axes were in the blue-yellow direction (the cerulean line defined from 476 to 576 nm(Mollon, 2006)), and two axes were a reflection of this line through the vertical axis of the MacLeod-Boynton chromaticity diagram.

For adults, stimuli were spaced logarithmically along these axes, to focus the collection of data closest to where adult threshold levels were expected to be. For infants stimuli were sampled in equal steps along each axis (see main text Figure 1). Due to infants' higher

discrimination thresholds (Knoblauch et al., 2001) stimuli were sampled from a wider range of chromaticities than adults.

Stimuli were presented on a Diamond Pro 2070SB CRT Monitor (Mitsubishi, Tokyo, Japan) via a PC-driven ViSaGe MKII Stimulus Generator (Cambridge Research Systems Ltd, Rochester, UK). Eye-movement data was recorded via an Eyelink 1000 system (SR Research, Ontario, Canada), and the experimental programme was run in MATLAB (R2016a, The MathWorks Inc., Natick, MA). The system was gamma-corrected using a LS-100 luminance meter (Konica-Minolta, Tokyo, Japan), and the colour calibration achieved using a spectrascan PR655 spectroradiometer (Photo Research Inc., Chatsworth, CA).

Procedure

Infant participants were seated in a car seat mounted in a chair 60cm from the screen, and watched a cartoon on screen during camera set up, and then completed a 9-point spatial calibration. If necessary (e.g. if a participant moved a lot), participant eye movements were recalibrated during testing.

Before each trial, participants were presented with a blank screen of luminance noise for 250ms. Targets appeared within 6.9° of the participants' current fixation point on the display. If participants fixated the target (or a 1° area around the target) for 160ms, this was recorded as a successful fixation (a 'hit'), the target was replaced with an image of a smiley face, and a short musical tune was played. If the target was not fixated within 2250ms, no auditory or visual reward was played, and a miss was recorded (see figure *Methods.1*).

Figure Methods. 1) Example trial procedure. Participants were presented with a blank screen of luminance noise for 250ms before a target was presented. If fixated for a minimum of 160ms, the target was replaced by a smiley face, and a was noise presented, and a hit was recorded for the trial. After another blank display of luminance noise, the next target was displayed and was not fixated within 2250ms, no reward was presented, and the next trial started.

If participants' gaze left the screen, a looming black and white spiral accompanied by a loud noise was played to refocus infants' visual attention to the screen. Once the participant was centrally fixated, the experimenter pressed a key to allow trials to start again.

For adult participants, trials were presented as 10 blocks of 64 trials (total 640 trials), the testing duration was approximately 30 minutes. During each block of trials, each chromaticity was presented once, in a random order, resulting in each chromaticity being presented 10 times to each participant. Participants were told that their task was to continually search for and look at targets on the screen.

In order to encourage maximum engagement with the task for infants, informed by pilot testing (N=4), 3/10 trials presented a maximally saturated stimulus. Stimuli were presented in blocks of 64, and testing was continued until the infant became disengaged with the task.

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Supplementary Information is available for this paper.

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